

# The Miocene flora of Alum Bluff, Liberty County, Florida

TERRY A. LOTT<sup>1\*</sup>, STEVEN R. MANCHESTER<sup>1</sup> and SARAH L. CORBETT<sup>2</sup>

<sup>1</sup>Florida Museum of Natural History, University of Florida, Gainesville, Florida, 32611-7800, U.S.A.;  
e-mail: lott@flmnh.ufl.edu, steven@flmnh.ufl.edu

<sup>2</sup>Georgia Military College, 4201 North Forrest Street, Valdosta, Georgia, 31605, U.S.A.; e-mail: scorbett@gmc.edu

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**ABSTRACT.** The plant fossils of Alum Bluff, northwestern Florida, provide a unique insight into the rarely preserved Miocene flora of the eastern United States. A century has passed since the introductory treatment on the fossil leaf flora of Alum Bluff. More specimens have accumulated over the past two decades, allowing for an updated evaluation of the megafossil flora following a recent study of the palynoflora. The strata consisting of poorly consolidated sand and siltstones with intervening clay layers, here recognized as the Fort Preston Formation of the Alum Bluff Group, are considered to be of Barstovian age (16.3–13.6 Ma), based on co-occurring mammalian remains. Here we recognize 36 kinds of leaves and 10 kinds of fruits and seeds, giving a minimum estimate of at least one fungus, one fern, one gymnosperm, 38 angiosperms and 7 unknowns. We also report one new species and two new combinations. These taxa augment those already reported based on pollen from the same strata, allowing us to portray the vegetation as elm-hickory-cabbage palm forest occurring near the coastline in a deltaic, pro-deltaic, or intertidal shore face environment. The results of a climate analysis of the Alum Bluff flora, using leaf margin and leaf area, give estimates of 19.0°C mean annual temperature and 116.0 cm mean annual precipitation.

**KEYWORDS:** Alum Bluff, Miocene, seed, leaf, cuticle, Fort Preston Formation

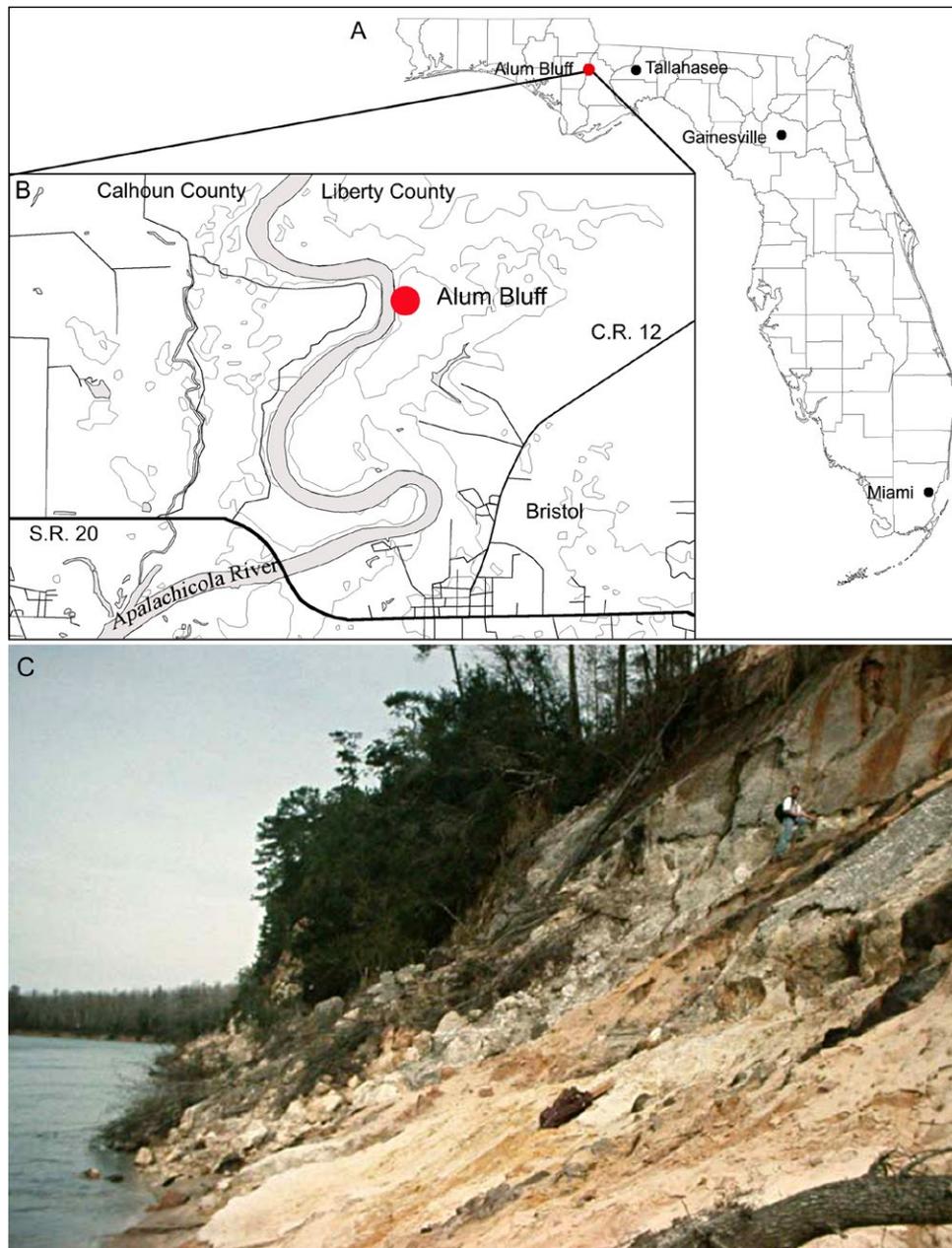
## INTRODUCTION

Ten to fifteen million years ago, broad-leaved deciduous forests were widespread in the Northern Hemisphere, but relatively little is known of the Miocene vegetation in eastern North America, because sediments of this age are rarely available (Graham 1999). Among eight Miocene plant megafossil sites in eastern North America, six are middle Miocene to late Miocene (Tab. 1). This stands in stark contrast with the numerous Miocene sites found elsewhere in the Northern Hemisphere, including western North America, Europe and Asia. The following Gulf and Atlantic coastal plain sites contain both megafossil and microfossil plants: the early Miocene of the Catahoula sandstone, Louisiana, Mississippi (Wrenn et al. 2003, Dockery & Thompson 2016), and the Brandon lignite, Vermont (Tiffney 1976, 1977, 1994,

Traverse 1955); the middle Miocene of the Hattiesburg Fm., Mississippi (Ufnar 2007, Dockery & Thompson 2016, Stults et al. 2016), and the Calvert Fm., Virginia/Maryland/Delaware (Berry 1916b, 1936a, Andrews 1988, Groot 1992); and the late Miocene of the Gray Fossil Site, Tennessee (Liu & Jacques 2010, Zobba et al. 2011), Brandywine flora (McCartan et al. 1990), Bridgeton Fm. (Hollick 1892, 1896, 1897) and Pennsauken of New Jersey (Berry 1940, Grellier & Rachele 1983) (Tab. 1). There are also some middle to late Miocene palynological sites in eastern North America (Tab. 1).

In addition to these, the middle Miocene of the Fort Preston Fm. (formerly Alum Bluff Fm.) in the Panhandle of northwestern Florida has yielded both megafossils and pollen (Berry 1916c, Corbett 2004, Jarzen et al. 2010). Alum Bluff (30.4595°N, –84.9859°W, WGS84) is a topographic high point ca 52.6 m in elevation,

\* Corresponding author



**Fig. 1.** Location of Alum Bluff fossil site. **A.** State of Florida, United States of America. **B.** Alum Bluff along the Apalachicola River, Liberty County, Florida. **C.** Alum Bluff outcrop

incised by the Apalachicola River. It is ca 7640 m upriver (north) of the Apalachicola bridge of State Road 20, town of Bristol, Liberty County, Florida (Fig. 1). The cutbank on the east side of the river exposes an excellent stratigraphic succession of marginal marine strata ca 25.7 m thick. The site is within the Apalachicola Bluffs and Ravines geomorphic province (Bryan & Means 2014).

Plant macrofossils have been noted from Alum Bluff since the late 1880s, starting with paleontological surveys by Langdon (1889) and Burns (1889), followed by various geological surveys (Dall & Stanley-Brown 1894, Sellards & Gunter 1909, Puri & Vernon 1964). The first

systematic treatment of plant macrofossils, by Berry (1916c), described 12 plant species and one fungal species. More recently a thesis by Corbett (2004) recognized 16 megafossil plant species and 30 pollen types; this was followed by a more detailed palynological treatment by Jarzen et al. (2010) recognizing 40 taxa of fungi, spores and pollen. Before Corbett (2004), the megafossil flora had not been examined in detail for nearly a century (Berry 1916c). The latter considered the Alum Bluff fossil flora to represent a flora with both tropical and temperate elements, while Corbett (2004) and Jarzen et al. (2010) inferred a subtropical to warm-temperate climate. The discovery of *Paliurus*

**Table 1.** Floristic comparison of Alum Bluff and other Miocene macrofossil and palynological floras of eastern North America

Order/Family	Genus	Species % and (number of specimens)	Local Habitat	Early Miocene		Middle Miocene					Late Miocene					Reference		
				Catahoula (LA, MS)	Brandon lignite (VT)	Hattiesburg (MS)	Alum Bluff (FL)	Ohoopsee (GA)	Calvert (VA, MD, DE)	Cohansey (NJ)	Martha's Vineyard (MA)	Gray (TN)	Brandywine (MD)	Bryn Mawr (MD)	St. Mary (MD)		Bridgeton (NJ)	Pensauken (NJ)
Melanconiaceae	<i>Pestalozzites</i>	<1% (3)		Spot			Spot										2, 3	
Salviniaceae	<i>Azolla</i>		water			L ( <i>Salvinia</i> )	P										20	
Schizaeaceae	<i>Lygodium</i>		non-native				P										1, 11, 20	
Pteridiaceae	<i>Ceratopteris</i>		absent				P										1, 20	
Pteridiaceae	<i>Pityrogramma</i>		absent				P										1, 20	
Pteridiaceae	<i>Pteris</i>		shaded slopes				P										11, 20	
Pteridiaceae	cf. <i>Adiantum</i>	<1% (1)	floodplain				L										This report	
Polypodiaceae			widespread				P										20	
Ephedraceae	<i>Ephedra</i>		absent: edaphic aridity				P										1, 20	
Pinaceae	<i>Pinus</i>		widespread	P	P		P	P	S,C,P	P		P	P	C, P		S,P	4-6, 7, 10, 12a, 13, 20, 22, 22a, 23, 25, 27, 32, 34, 35	
Pinaceae	conifer cone axis	<1% (1)					C										This report	
Podocarpaceae/Pinaceae	<i>Podocarpus/Cathaya</i>		non-native				P										1, 20	
Taxodiaceae	<i>Sequoia/Metasequoia/Cryptomeria</i>		absent				P										1, 20	
Taxodiaceae	<i>Taxodium</i>		water	P		L	P	P	L	P			L,F,S,P				4, 20, 22, 25, 27, 34	
Lauraceae	<i>Laurophyllum &amp; Daphnogene</i>	2% (9)	widespread		W	L	L								L,P	P	3, 9, 13, 17, 28a, 31	
Liliaceae			widespread	P			P	P			P						10, 20, 27, 34	
Areaceae	<i>Sabalites</i>	37% (160)	Sabal: floodplain, slope, sandhill (juvenile)	L			L								L?		2, 3, 8, 11, 17, 19, 26	
Areaceae	<i>Palmaecites</i>	<1% (1)	unknown	P		L	L,P	P			P						10, 20, 27, 28a, 34	
Cyperaceae	<i>Scirpus</i>	<1% (1)	wet				F										8, 11	
Cyperaceae	<i>Carex</i>	<1% (3)	floodplain, bluff			F ( <i>Cyperus</i> )	F				P?						8, 9, 10, 11, 28a	
Poaceae			widespread	P	P		P	P		P							20, 25, 27, 32, 34	
Platanaceae	cf. <i>Platanus</i>	<1% (2)	Platanus: floodplain	L		L	L	P	L				L,F				4, 9a, 11, 12a, 22, 27, 28a	
Hamamelidaceae	<i>Liquidambar</i>		uplands		P		P				P					L	10, 11, 17, 20, 22, 32	
Vitaceae	Morphotype AB1	3% (13)	widespread		S,P		L	P				S	L,S		L?	S	6, 12b, 17, 22, 27, 29, 31, 32	
Euphorbiaceae	<i>Alchornea</i>		absent				P										1, 20	
Malpighiaceae			absent				P										11, 20	
Salicaceae	<i>Salix</i>	2.5% (11)	wet	P, L?		L	L	P	L,P	P		P	L,P	P			2-4, 9, 13, 22, 23, 27, 28a, 33, 34	
Fabaceae	<i>Leguminosites</i>	3.9% (17)	widespread	L?		L	L		L			P	L			L,F	2-4, 16, 18, 22, 28a, 32, 35	
Rhamnaceae	<i>Paliurus</i>	2.5% (11)	Paliurus: absent	L	P ( <i>Rhamnus</i> )		L,F		L							S	1-4, 6, 32	
Ulmaceae	<i>Ulmus/ AB 36</i>	25.5% (110)	floodplain, bluff	P	P	L	L,P	P	L,P	P	P	P	L,P	P	P	L,P	2-4, 9, 10, 11, 13, 19, 20, 22, 23, 25, 27, 32, 33, 35	
Fagaceae	Morphotype AB5	<1% (2)	widespread	L	F,W,P	L	L,P	P	L,F,P	P	P	F,L,P	L,F,P	P	P	L,P	F,P	3, 4, 6, 7, 9, 9a, 10, 17, 19, 20-25, 27, 28a, 31, 32, 35
Juglandaceae	<i>Carya</i>	16.4% (71)	widespread	P	F,W,P	F	L,F,P	P	P	P	P	F,P	L,F,P	P	P	L,P	P	9, 10, 12a, 20, 22-24, 27, 28a, 31, 32, 34, 35
Juglandaceae	<i>Engelhardia</i> group		absent				P		P	P							14, 20, 25, 32	
Myricaceae	<i>Myrica</i>		swamp, sandhill	P	F,P		P	P	P								11, 14, 20, 27, 32, 34	
Onagraceae	nr. <i>Ludwigia</i>		widespread				P			P							11, 20, 25	
Oleaceae	Morphotype AB16	<1% (1)	widespread				L					P					35	
Adoxaceae	<i>Sambucus</i>	<1% (1)	floodplain, bluff			L	L						F?				9, 11, 22, 28a	
Loranthaceae			parasitic				P										20	
Theaceae	<i>Gordonia</i>		ravine botton, swamp		F,W,P		P		P	P							11, 14, 20, 25	
Aquifoliaceae	<i>Ilex</i>		widespread	P	S,P		P	P	L,P	P			L,S,F,P			L	4, 10, 11, 14, 17, 20, 22, 25, 27, 31, 32, 34	
Asteraceae			widespread	P			P						S,P				20, 22, 34	
Incertae sedis																		
Magnoliales	Morphotype AB54, AB11	1.4% (6)	widespread	L	S		L	P					P			L	2, 3, 17, 22, 27, 30, 31, 32	
?Ranunculaceae	Morphotype AB48	<1% (1)	bluff				S					P					8, 9, 11, 34	
ca. Chrysobalanaceae	Morphotype AB7	<1% (2)	circular leaf: absent	L?			L										11	
Rosales	Morphotype AB21, AB20	<1% (3)	widespread		S,P		L,P	P	L,S,P	P		P	P, F	P		L,P	5, 10, 13, 14, 17, 20, 22, 23, 25, 27, 31, 32, 33, 35	
?Moraceae	Morphotype AB29	<1% (3)	Artocarpus: absent	F	P	L	L		L							L,P	1-4, 13, 17, 28a, 32	
Asterids	Morphotype AB59	<1% (2)	wet		P		L, P	P	P	P			L,P	P		L,P	P	13, 14, 17, 20, 22, 23, 27, 32
Climate			mild/cool temperate	tropical	subtropical to warm temperate		warm temperate	warm temperate?	warm temperate	mild temperate	subtropical to warm temperate	warm to cool temperate	cool temperate	mild temperate	warm temperate	warm temperate	mild temperate	10, 20, 22, 23, 27, 28, 29, 31, 34
Total		432																

C = Cone, F = Fruit, L = Leaf, P = Pollen, S = Seed, W = Wood.

Atlas 2016 (1), Berry 1916a (3), b (4), c (2), 1936a (5), 1940 (6), 1941 (7), Clewell 1983 (8), 1985 (9), Dockery & Thompson 2016 (9a), Frederiksen 1984 (10), FSU Herbarium (11), Godfrey 1988 (12a), Gong et al. 2010 (12b), Grellier & Rachele 1983 (13), Groot 1992 (14), Herendeen & Dilcher 1991 (16), Hollick 1892 (17), 1896 (18), 1897 (19), Jarzen et al. 2010 (20), Liu 2011 (21), McCartan et al. 1990 (22), Miller 1978 (22a), Pazzaglia et al. 1997 (23), Per. obs. (24), Rachele 1976 (25), Read & Hickey 1972 (26), Rich et al. 2002 (27), Shunk et al. 2006 (28), Stults et al. 2016 (28a), Tiffney 1976 (29), 1977 (30), 1994 (31), Traverse 1955 & 1994 (32), Wallace & Wang 2004 (33), Wrenn et al. 2003 (34), Zobia et al. 2011 (35)

(Rhamnaceae), which is now restricted to Eurasia, indicates that some elements of the flora are no longer native to North America (Manchester 1999, Burge & Manchester 2008). Here we provide an overview of the Alum Bluff megafossil flora based on fossil leaves, fruits and seeds recovered in the past few decades.

Today this area consists of floodplain, bluff and sandhill communities. Taxa specific to the floodplain include *Azolla*, *Taxodium*, *Scirpus*, *Platanus*, *Salix* and *Gordonia*. The extant bluff flora is a continuation of the southern Appalachian flora and includes *Pteris* and *Liquidambar* (Clewell 1983) (Tab. 1).

### GEOLOGY

Alum Bluff received its name from the efflorescence of ferrous sulphate (Langdon 1889). Geologically, the name has been applied as Alum Bluff beds (Dall & Harris 1892), Alum Bluff Fm. (Matson & Clapp 1909) and Alum Bluff Group (Gardner 1926) (*sensu* Cooke & Mossom 1929). The exposed section at Alum Bluff consists of four or five lithologic units; in ascending order they are the lower Miocene Chipola Fm., the

middle Miocene Fort Preston Fm., the Pliocene Jackson Bluff and Citronella fms., and overlying surficial clastics (Berry 1916c,d, Schmidt 1986, Johnson 1989, Bryant et al. 1992, Otvos 1998, 2004, Means 2002, Stults et al. 2010, Dockery & Thompson 2016) (Fig. 2). The Chipola Fm. is rich in marine invertebrates, including as many as 1100 molluscan species (Huddlestun 1984, Schmidt 1983, 1986, Vokes 1989), and has been dated at 18.3–18.9 Ma based on biostratigraphy and isotopic data (Bryant et al. 1992) (Fig. 2).

The plant-bearing strata were included in the original description of the Alum Bluff Fm. (Matson & Clapp 1909) but the nomenclatural status of these beds was altered when the underlying shell-rich beds were reassigned to the Chipola Fm. The Chipola Fm. and overlying beds were upgraded to group status, that is, the Alum Bluff Group (Gardner 1926, Cooke & Mossom 1929, Braunstein et al. 1988), but the more cumbersome term “Alum Bluff Group undifferentiated” has been applied to the strata that overlie the Chipola Fm. This unit has also been informally called the Fort Preston sands (Puri & Vernon 1964) and alternatively been assigned to the Hawthorne Fm., which has its type area 264 km to the east-southeast (Dall

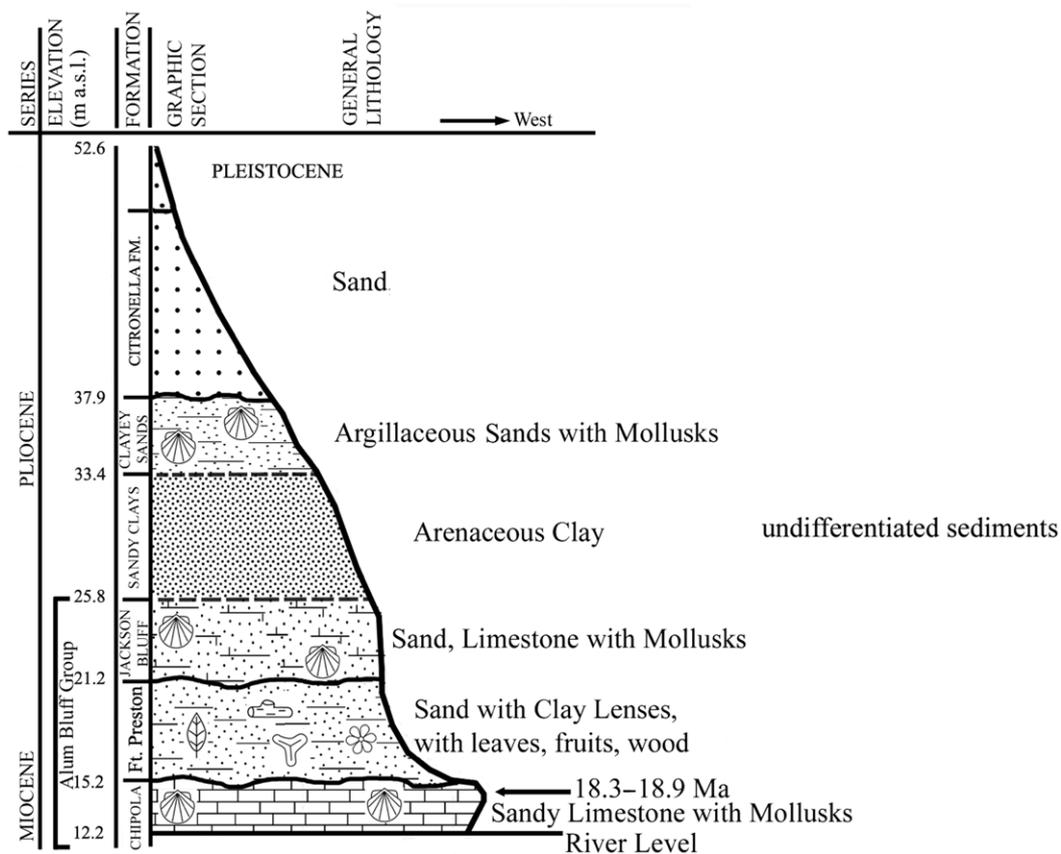


Fig. 2. Stratigraphic section of Alum Bluff. Modified from Schmidt (1986), Johnson (1989), Bryant et al. (1992), Means (2002), Portell et al. (2006)

& Harris 1892, Vaughan & Cooke 1914, Cooke & Mossom 1929, Schmidt 1984). We adopt the name “Fort Preston Formation”, according to the North American Commission on Stratigraphic Nomenclature (2005), for this well-established lithostratigraphic unit. This formation consists of non-marine clastic sediments found at the type locality at Alum Bluff near the former military installation of Fort Preston, which was ca 1.6 km northwest of State Road 20 and County Road 12 in Bristol on the east side of the Apalachicola River (Drew 1856). This horizon is composed of very light orange, gray to yellow and white clayey sands, with sandy limestone containing occasional mammalian fossils as well as leaf remains. This horizon has also been recognized in nearby cores at 30°27′29.3″N, 84°58′49.4″W (NAP 1983, Alum Bluff Core #1) and at 30°28′12″N, 84°59′05″W (WGS 1984, Alum Bluff Core #2) (Johnson 1986, FGS 2018). The Alum Bluff Group, consisting of the Chipola Fm. and the unconformably overlying Fort Preston Fm. is considered to be a deltaic, prodeltaic, or intertidal shore face (Huddleston 1984, Schmidt 1986, Johnson 1989, Bryant et al. 1992) with a high-energy riverine depositional environment (Jarzen et al. 2010).

The mammalian fossils from the Fort Preston Fm. at the same level as the fossil plant beds include a small anchitherine horse, a rhinocerotid, *Prosynthetocras texanus* and “*Merychippus gunteri*”. These vertebrate taxa indicate a late early or early middle Miocene age (late Hemingfordian or early Barstovian) (Bryant et al. 1992, Richard Hulbert pers. comm. 2016).

## MATERIAL AND METHODS

### MATERIAL

The collection site is on property of the Nature Conservancy of Florida known as the Apalachicola Bluffs and Ravine Preserve. Over 450 plant macrofossils (impressions and compressions) from Alum Bluff were examined for this investigation, which are housed in the Paleobotany Division at the Florida Museum of Natural History (UF). The original specimens of Berry (1916c) were examined at the U.S. National Museum of Natural History (USNM). Comparative Miocene material from other Miocene sites including the Catahoula Fm., Bridgeton Fm. and Gray fossil site were examined at USNM, the Yale Peabody Museum of Natural History (YPM), Florida Museum of Natural History (UF), East Tennessee State University (ESTU) and the East Tennessee State University and General Shale Brick Natural History Museum Fossil Collections (ETMNH).

Paleobotanical collections from Alum Bluff were made during multiple visits in the 1990s through 2018 with the help of Florida Museum of Natural History staff, Florida Paleontological Society members, and various paleobotanical/geological classes led by David Dilcher, Steven Manchester, and Roger Portell from the University of Florida, and Guy Harley Means from the Florida Geological Survey.

### METHODS

Macrofossil photographs were obtained with a Canon Rebel XSi digital camera fitted with Nikon 55 mm and Canon MP-E 65 mm lenses under transmitted and reflected light, employing Canon EOS Utility software. Stacked images were processed using Helicon Focus, with subtle contrast adjustments made with Adobe Photoshop. Epidermal anatomy was analyzed using digital images from light and epifluorescence (wavelength 546 nm) microscopy of in situ cuticle, and prepared cuticle slides. Photomicrographs of fossil cuticle were made with a Canon Rebel T3i digital camera mounted on a Zeiss Axiophot transmitted light microscope, employing Canon EOS Utility software. X-ray data were obtained by micro-CT scanning at the College of Engineering Nanoscale Research Facility (NRF), University of Florida, with a GE Phoenix V|tome|x240 CT Scanner, using a tungsten reflection target and 0.1 mm copper filter, with voltage of 100 kV and current of 50  $\mu$ A, with 844 images of a single specimen for 5  $\mu$ m voxel size. Fossil cuticle was pried from the matrix and separated from the remaining matrix by immersion in 49% hydrofluoric acid for 12–16 hours or soaked in Sparkleen detergent for ca 30 minutes. Cuticle fragments were soaked in Jefferey’s solution (50% nitric acid/50% of 10% chromic acid) to remove the mesophyll. The cuticle then went through a dehydration series of 50%, 95% and 100% ethanol, staining with 1% Safranin-O in 100% ethanol, then a series of 100% ethanol, 10%EtoH/ 90%HemoDe (or Citrisolv) and finally 100% HemoDe (or Citrisolv). The cuticle was then mounted in a drop of synthetic resin or Canada Balsam in HemoDe (or Citrisolv) on a microscope slide, placed on a slide warmer with a lead weight over the cover slip, and later sealed with nail polish. Highly fragmented cuticle was prepared by the collodion peel method. Two layers of collodion (Pyroxylin 40 g), ether (750 ml) and alcohol (250 ml) were applied to the cuticle, air-dried and then removed just before curling. The peel was placed in Sparkleen detergent, using a paintbrush to remove debris. The peel was flushed with distilled water, macerated in Jeffrey’s solution until the cuticle was light orange/brown, further flushed with distilled water and stained with 1% Safranin-O, then flushed with 50% ethanol until excess stain was removed. The cuticle was mounted on a microscope slide in glycerin jelly with a cover slip and a weight overnight, then sealed with nail polish. Specimens are housed in the Paleobotany/Palynology Collection at the Florida Museum of Natural History, University of Florida, Gainesville, Florida. Terminology for leaf descriptions follows Hickey (1973, 1979), Dilcher (1974) and Ellis et al. (2009), and classification follows Soltis et al. (2018) (Tab. 2). We reject the use of the character “primary vein pinnate” in reference to

leaves or leaflets with one major vein. Such leaves or leaflets should be characterized as “primary vein single”. Properly identified modern leaves from herbaria were used for subsequent fossil/modern comparisons when deemed necessary (Appendix 1), with data labels standardized. All fossil specimen numbers are given in Appendix 2. The number of extant species and the modern-day distribution of plant families are from Mabberley (1997) unless otherwise noted, and cited in Table 1. Laminar size, symmetry and leaf classes follow Raunkiaer (1934), Webb (1959) and Ellis et al. (2009). Where appropriate, incomplete leaf measurements have been extrapolated to those of complete leaves by length and width estimation. Leaf fragment measurements are based on apical, basal and/or marginal leaf sections that show distinct characters, and are not extrapolated to those of complete leaves due to insufficiency of material. Unless otherwise noted, leaf area is calculated as length  $\times$  width  $\times$  2/3 (Cain & Castro 1959) and is based on complete or estimated leaf size. Climate inferences for Alum Bluff are based on comparisons with living relatives and on analyses of leaf physiognomy. Leaf physiognomy analyses include leaf margin (Wolfe 1979, Wing & Greenwood 1993, Wilf 1997, Kowalski & Dilcher 2003, Miller et al. 2006, Peppe et al. 2011) for mean annual temperature (MAT), and leaf area (Wilf et al. 1998, Gregory-Wodzicki 2000, Jacobs 2002, Peppe et al. 2011) for mean annual precipitation (MAP), which together comprise a quantitative measure of climate.

## SYSTEMATICS

Order: Polypodiales Link 1833

Family: Pteridaceae Kirchn. 1831

Genus: cf. *Adiantum*

### Morphotype AB46

Pl. 1, figs 1, 2

**Description.** Leaf complete, possibly flabellate, crenate, microphyll. Length 2.6 cm, width 2.6 cm, l/w ratio 1, leaf area 450.66 mm<sup>2</sup> (n=1). Apex obtuse; base concave, margin with shallow rounded lobes, crenations slightly enrolled at margin. Petiole length 5 mm, width 1 mm. Venation closely spaced, bifurcating twice before reaching margin, lacking cross veins. Cuticle lacking.

**Material examined.** UF 18049-48377

**Discussion.** Patchy preservation prevents following the venation from the petiole to lobe apices. The general leaf shape, size, lobing (Pl. 1, fig. 1), dichotomous venation (Pl. 1, fig. 2) and crenations of Morphotype AB46 are

similar to those of extant *Ginkgo biloba* L. However, the recurved nature of the crenations and the lobing near the base are not normally found in modern *Ginkgo*. Cuticle is not preserved on this specimen, so we are unable to determine whether the epidermal anatomy is that of a fern and not *Ginkgo*. The enrolled margins of some lobes of the leaves resemble the structure of fertile *Adiantum*, but sori and sporangia are not preserved in this specimen. We compared Morphotype AB46 with Pteridaceae such as *Adiantum tenerum* Sw., and Schizaeaceae such as *Lygodium japonicum* (Thunb.) Sw., but they are readily distinguished. In *A. tenerum* the leaves are quite small and the lobes are minutely toothed, but the lobes in fertile leaves are recurved, similar to our fossil. In *L. japonicum* each lobe has a midvein, similar to fossil *L. kaulfussi* Heer (Manchester & Zavada 1987). Overall, the fossil is similar to extant *Adiantum* in size (upper limit), dichotomous venation and enrolled leaf margins, and the lack of cuticle is unusual for fossil *Ginkgo*. *Adiantum capillus-veneris* L. can be found on limestone ledges along the Apalachicola River (FSU Herbarium 2018) (Tab. 1).

*Ginkgo adiantoides* (Unger) Heer from the Miocene of the western United States has similar shape and venation but lacks the marginal lobing of Morphotype AB46 (Chaney & Axelrod 1959). *Adiantum* does not appear at other Miocene sites of the eastern United States. This may be a new species of fossil *Adiantum*, but fertile material would be required for confirmation.

Gymnospermae

Order: Pinales Lindley 1836

Family: Pinaceae Lindley 1836

Conifer cone axis

### Morphotype AB30

Pl. 1, figs 3, 4

**Description.** Woody cone scale with stalk. Scale length 1.7 cm, width 1.1 cm, stalk 5 mm (n=1). Scale convex, margins entire, apex rounded and incurved, base cuneate. Surface with longitudinal wrinkles out from stalk.

**Material examined.** UF 18049-48376, 48376'

**Table 2.** List of megafossil taxa from Alum Bluff, with families in phylogenetic sequence according to Soltis et al. (2018), giving percentages of total number of specimens

ASCOMYCOTA	Ulmaceae (25.5%)
MELANCONIALES	<i>Ulmus prestonia</i> sp. nov. (leaf)
Melanconiaceae	<i>Ulmus</i> sp. 1 (leaf)
<i>Pestalozzites sabalana</i> Berry (fungus) (<1%)	<i>Ulmus</i> sp. 2 (fruit)
Polypodiales	Morphotype AB36 (leaf)
Pteridaceae	FAGALES
cf. <i>Adiantum</i> (leaf) (<1%)	Fagaceae
GYMNOSPERMAE	Morphotype AB5 (leaf) (<1%)
PINALES	Juglandaceae (16.4%)
Pinaceae	<i>Carya</i> cf. <i>serraefolia</i> (Goepf) Kräusel (leaflet)
Conifer cone axis (<1%)	<i>Carya</i> sp. (nut)
ANGIOSPERMAE	LAMIALES
MAGNOLIIDS	Oleaceae
LAURALES	Morphotype AB16 (leaf) (<1%)
Lauraceae (2%)	DIPSACALES
cf. <i>Laurophyllum pseudovillense</i> Kvaček (leaf)	Adoxaceae
cf. <i>Laurophyllum pseudoprinceps</i> Weyland et Kilpper (leaf)	<i>Sambucus</i> sp. (leaf) (<1%)
<i>Daphnogene</i> sp. 1 (leaf)	Incertae Sedis (each type is <1% unless noted)
<i>Daphnogene</i> sp. 2 (leaf)	Lauraceae/Cannabaceae
COMMELINIDS	Morphotype AB54 (leaf)
ARECALES	MAGNOLIALES
Arecaceae	cf. Magnoliaceae/Annonaceae
<i>Sabalites apalachicolensis</i> Berry (leaf/infructescence) (37%)	Morphotype AB11 (leaf) (1.2%)
<i>Palmacites</i> (leaf) (<1%)	EUDICOTS
POALES	RANUNCULALES
Cyperaceae (<1%)	?Ranunculaceae
<i>Scirpus</i> L. (fruit)	Morphotype AB48 (seed)
<i>Carex</i> sp. 1 (fruit)	ROSIDS
<i>Carex</i> sp. 2 (fruit)	VITALES
EUDICOTS	?Vitaceae
PROTEALES	Morphotype AB6 (leaf)
Platanaceae	FABIDS
cf. <i>Platanus</i> (leaf) (<1%)	MALPIGHIALES
ROSIDS	cf. Chrysobalanaceae
VITALES	Morphotype AB7 (leaf)
Vitaceae	FABALES
Morphotype AB1 (leaf) (3%)	?Fabaceae
FABIDS	Morphotype AB19 (leaflet?)
MALPIGHIALES	Rosales
Salicaceae (2.5%)	Morphotype AB21 (leaf)
cf. <i>Salix varians</i> Goepf. (leaf)	Morphotype AB20 (leaf)
<i>Salix</i> sp. 1 (leaf)	?Moraceae
FABALES	Morphotype AB29 (leaf)
Fabaceae (3.9%)	ASTERIDS
<i>Leguminosites apalachicolensis</i> (Berry) n. comb. (leaflet)	Morphotype AB59 (leaf)
<i>Leguminosites sellardsii</i> (Berry) n. comb. (leaflet)	Unknown
<i>Leguminosites</i> sp. 1 (leaflet)	Morphotype AB12 (leaf)
<i>Leguminosites</i> sp. 2 (leaflet)	Morphotype AB64 (leaf)
ROSALES	Morphotype AB28 (fruit)
Rhamnaceae (2.5%)	Morphotype AB53 (seed?)
<i>Paliurus</i> sp. (leaf)	Morphotype AB63 (leaf)
<i>Paliurus favonii</i> Unger (fruit)	Morphotype AB56 (leaf)
	Morphotype AB65 (leaf)

Discussion. Morphotype AB30 is tentatively identified as a conifer scale with attachment for a centralized cone axis (Pl. 1, figs 3, 4) but we lack shoot and leaf characters and the

branching system to distinguish among extant Pinaceae genera. Differences in cone scales are helpful to distinguish among extant genera. *Pinus* cone scales have a raised protuberance

(umbo) and usually a spine on the apophysis (exposed surface of the scale). *Picea*, *Cathya*, *Cedrus* and *Pseudolarix* have small subtending bract scales, with cone scale shape flabellate for *Cedrus* and deltoid-triangular for *Pseudolarix*. *Abies* have small to large subtending bract scales, sometimes exserted, and the cone scale shape is usually cyathiform. *Nothotsuga* have large included subtending bract scales, while *Pseudotsuga* and *Keteleeria* have large, sometimes exserted, subtending bract scales. *Tsuga* have small bract scales, the cone scales have more or less auriculate bases, and the scales can be reflexed (Farjon 1990). In *Picea*, the scales near the top of the cone are more convex than those at the mid to basal axis, and the intraspecific variability of cone scale size and shape in *Picea* is considerable (LePage 2001). Morphotype AB30 characters are similar to those of modern *Picea* sp. except that there is no evidence of a bract scale, perhaps due to taphonomic processes or to the rudimentary nature of the bract scale in this particular species. Among the modern species that we compared, similarities were found with *Picea mariana* (Mill.) Britton, Sterns & Poggenb. except that the scales are too small and the apex is denticulate, and with *Picea glauca* (Moench) Voss except that the apex is not incurved.

*Picea* is not known in the Miocene of the eastern United States, but *Pinus* pollen is widespread at all early to late Miocene sites except Bridgeton. *Pinus* seeds are found at Calvert and Pensauken, and *Pinus* cones at Calvert, Martha's Vineyard and St. Mary (Tab. 1).

#### Angiospermae

#### Magnoliids

#### Order: Laurales

Juss. ex Bercht. & J.Presl 1820

Family: Lauraceae Juss. 1789

Genus: *Laurophyllum* Goeppert  
emended Hill 1986

#### cf. *Laurophyllum pseudovillense* Kvaček

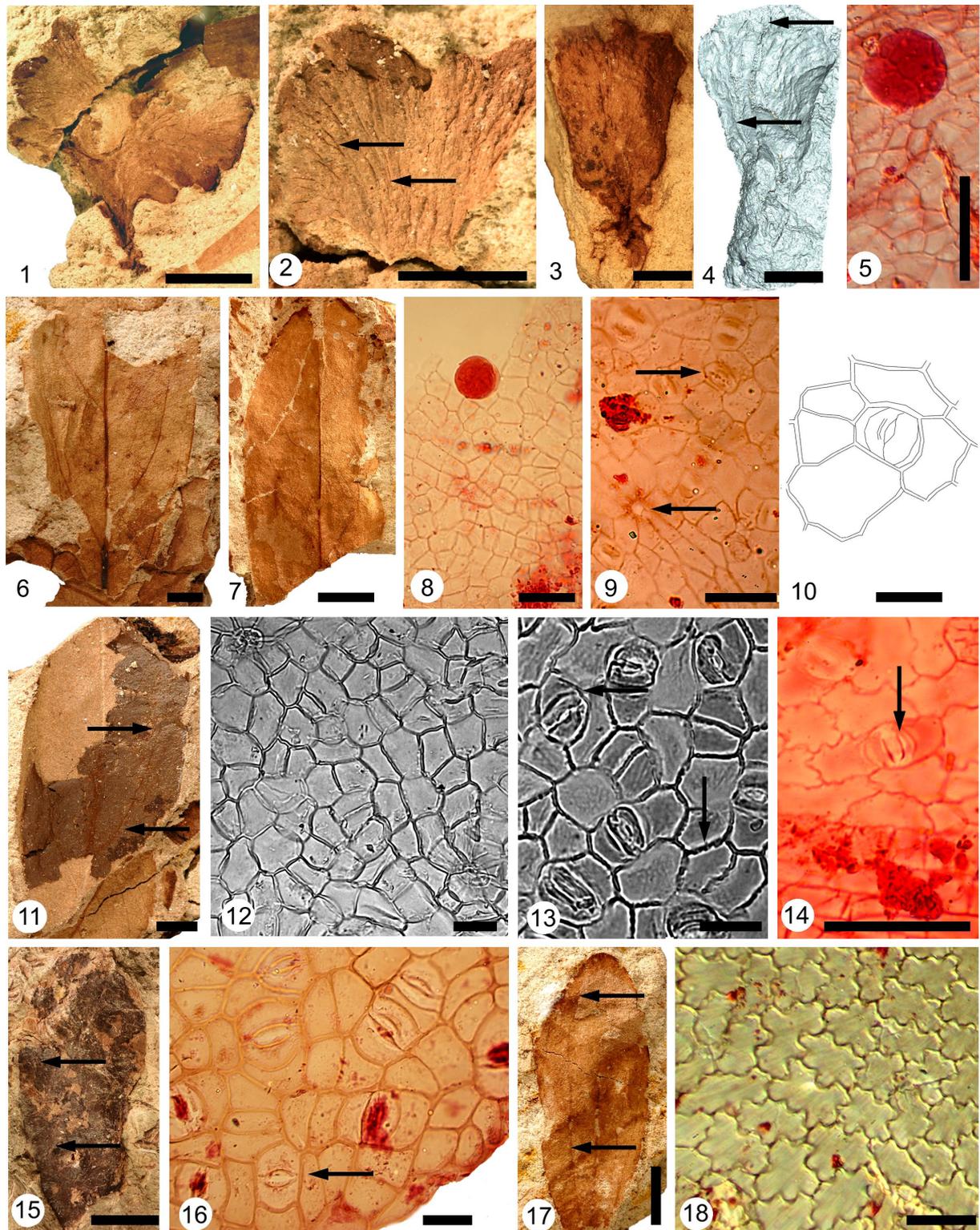
Pl. 1, figs 5–10

**Description.** Leaves incomplete or fragments, elliptic, unlobed, microphyll, with firm

light brown cuticle, darker on midvein. Length 5.0–7.0 cm, width 2.0–3.0 cm, l/w ratio 1.8–3, leaf area 799.2–1258.7 (avg. 1045) mm<sup>2</sup> (n=5). Apex missing; base acute with cuneate flanks, margin entire. Petiole 3.5–8 mm. Primary venation single, straight, weak to moderate. Secondary venation brochidodromous, at intervals of 5–21 mm, spacing irregular, angle of divergence 23–40° basal, 24–42° midsection, 40° apical. Secondaries arching smoothly or undulate, becoming less pronounced upward, loop length decreasing upward. Secondary attachment slightly decurrent to excurrent. A few intersecondary veins in lower portion of leaf, extending ca 1/2 the distance to margin, proximal course parallel to subadjacent secondaries, distal course intersecting intercostal tertiaries. A few percurrent tertiaries preserved. Adaxial epidermal cells random, elongate to isodiametric, 4–6-sided, anticlinal cell walls straight to arcuate, no ornamentation, 14.2–28.3 × 8.2–19.7 μm. Spherical mesophyll secretory bodies 22.3–44.3 μm. Abaxial epidermal cells random, elongate to isodiametric, 4–6-sided, anticlinal cell walls straight to arcuate, 14.8–38.5 × 8.9–23.4 μm. Stomata brachyparacytic, with squared subsidiary cells. Guard cells 8.8–21.4 × 2.6–8.3 μm, with inner thickened rim. Subsidiary cells 6.0–22.6 × 6.6–20.0 μm, sometimes barely exceeding guard cells. Isolated trichome bases.

**Material examined.** UF 18049-43523, 61113, 61114b, 68894, 68913, USNM 38284 (Holotype, Berry 1916c, Pl. 9, fig. 3.).

**Discussion.** Species determinations for fossil leaf fragments of this type are based on cuticle characters as compared with those of more complete leaf samples. Among the micro-morphological characters of cf. *Laurophyllum pseudovillense*, the presence of spherical secretory bodies with solidified oil content (Pl. 1, figs 5, 8) is distinctive. The secretory bodies are probably from the mesophyll because they are not connected to the epidermis. Spherical secretory bodies lightly embedded in the mesophyll are found mainly in extant lauralean families such as Monimiaceae (*Hedycarya arborea* J.R. Forst. & G. Forst.) and Siparunaceae (*Glossocalyx longicuspis* Benth.), and are characteristic in Lauraceae as oil cells (Metcalf & Chalk 1950). The relatively large size (>60 μm) of these bodies eliminates Monimiaceae and Siparunaceae from consideration. Entire margins,



**Plate 1.** 1, 2. cf. *Adiantum*, 1 – lobed lamina with cuneate base, 2 – venation dividing twice (arrows) in lobe, UF18049-48377; 3, 4. Conifer scale, 3 – scale, UF18049-48376; 4 – surface rendering from CT scan data of specimen in adaxial view showing longitudinal wrinkles (arrows), UF18049-48376; 5–10. cf. *Laurophyllum pseudovillense* Kvaček, 5, 8 – adaxial cells with spherical bodies, UF18049-61114b, UF18049-68894, respectively, 6, 7 – leaves with brochidodromous venation, UF18049-43523, UF18049-61113, respectively, 9 – brachyparacytic stomata with inner ledges (top arrow), and isolated trichome base (bottom arrow), 10 – brachyparacytic stomata, UF18049-61114b; 11–14. cf. *Laurophyllum pseudoprinceps* Weyland et Kilpper, 11 – brochidodromous vein (top arrow at junction of sub- and superadjacent secondaries), 12 – adaxial epidermis with multicellular trichome bases, 13 – abaxial cells with knobby projections (bottom arrow), brachyparacytic stomata and stomatal ledges (top arrow), UF18049-61196, 14 – brachyparacytic stomata, stomatal ledge (arrow) and sinuate anticlinal cell walls, UF18049-68916; 15, 16. *Daphnogene* sp. 1, 15 – leaf with acrodromous secondary vein (arrows), 16 – abaxial cells with brachyparacytic stomata and stomatal ledge (arrow), UF18049-56767; 17, 18. *Daphnogene* sp. 2, 17 – leaf with acrodromous venation to apex (arrows), UF18049-43575, 18 – adaxial, sinuate anticlinal cell walls, UF18049-69001. Scale bars: 1, 7, 15, 17 = 10 mm; 2–4, 11 = 5 mm; 10, 12, 13, 16 = 20 µm; 8, 9 = 40 µm; 5, 14, 18 = 50 µm

brochidodromous venation (Pl. 1, figs 6, 7) and epidermal characters such as secretory bodies and guard cell size, inner rim thickenings and straight anticlinal cell walls (Pl. 1, figs 5, 8–10) are similar to characters of Lauraceae such as *Litsea* sp.

The assignment of a fossil leaf taxon to any one Lauraceae genus is very difficult due to morphological and anatomical similarities with extant species in different genera such as *Ocotea* Aubl., *Nectandra* Rol. ex Rottb., *Beilschmiedia* Nees, *Litsea* Lam. and *Cryptocarya* R.Br. (Kvaček 1971, Worobiec 2003). Thus, the morphogenus name *Laurophyllum* Goeppert is used for lauraceous leaves with pinnate venation (Kvaček 1971).

Well-preserved leaves of Lauraceae are found in Cenozoic floras across the globe and are widely accepted as indicators of warm and wet conditions (Carpenter et al. 2007). Our leaves are similar to those of *Laurophyllum* sp. 1 from the Miocene of Iceland (Denk et al. 2005) in shape, size and the presence of mesophyll secretory bodies. The leaf shape, venation, adaxial cell wall shape, paracytic stomata, abaxial trichome bases (Pl. 1, fig. 9) and mesophyll bodies of our leaves are similar to those of *Laurophyllum pseudovillense* Kvaček of Knobloch & Kvaček (1976, see Plate IV, fig. 12, Plate XII, fig. 7, Plate XXV, figs. 3, 4) but the lower cuticle is very faint in Knobloch & Kvaček (1976) and no trichomes were noted on the adaxial surface of our leaves. Similar-size secretory glands have also been noted in *Laurophyllum pseudovillense* Kvaček from the Miocene of Austria (Kovar-Eder & Hably 2006). Berry (1916c) described *Nectandra apalachicolensis* Berry (USNM 38284) from Alum Bluff but the fragmentary nature of the holotype precludes verification. Elsewhere in the Miocene of the eastern United States, lauraceous leaves are found in Hattiesburg and Bridgeton, Lauraceae pollen in Bridgeton and Pennsauken, and *Persea* wood in the Brandon lignite (Hollick 1892, Grellier & Rachele 1983, Tiffney 1994, Stults et al. 2016) (Tab. 1).

cf. *Laurophyllum pseudoprinceps*

Weyland et Kilpper

Pl. 1, figs 11–14

**Description.** Leaves incomplete or fragmentary, elliptic, with firm dark brown cuticle, microphyll. Length 4.5 cm, width 2.0 cm, l/w ratio

2.3, leaf area 599.4 mm<sup>2</sup> (n=1). Apex and base missing, margin entire. Primary venation single, curved, weak. Secondary venation weakly brochidodromous, intervals of 13 mm, angle of divergence 25–30°, looping length decreasing upward. Adaxial epidermal cells random, elongate to isodiametric, 4–5-sided, anticlinal cell walls seldom beaded, mostly straight, some arcuate, 16.2–29.4 × 10.0–23.9 μm. Sporadic trichome bases. Abaxial epidermal cells random, elongate to isodiametric, slightly domed, 4–6-sided, anticlinal cell walls distinctly beading, straight to sinuate, 16.5–31.0 × 13.5–23.2 μm. Sporadic trichome bases. Stomata brachyparacytic, not sunken, with unequal to nearly equal-sized subsidiary cells. Guard cells stain mostly in inner ledges, cells 14.3–20.1 × 5.1–7.4 μm. Subsidiary cells evidently winged (butterfly-shaped) to sometimes barely exceeding guard cell width, rounded to square ends, with anticlinal cell wall beading, cells 10.2–27.4 × 6.6–19.0 μm.

**Material examined.** UF 18049-61196, 68916.

**Discussion.** Elliptical leaves with brochidodromous venation (Pl. 1, fig. 11) are found in numerous angiosperm families, but the presence of trichome bases, anticlinal cell walls with knobby projections (Christophel & Rowett 1996) and brachyparacytic stomata with stomatal ledges (Pl. 1, figs 12–14) (Bandulska 1926, Dilcher 1963, Hill 1986) is fairly distinctive for Lauraceae. Within extant Lauraceae, bead-like thickening of the anticlinal cell walls is found in *Litsea*, *Beilschmiedia*, *Endiandra* and *Cryptocarya*, although sometimes they are associated with papillae (Kvaček 1971). Unfortunately, the lack of well-preserved secondaries in the middle and upper portion of the lamina makes it difficult to determine precisely the secondary vein framework, which would be useful for resolving its relationships to particular extant genera of Lauraceae.

These leaves differ from the aforementioned cf. *Laurophyllum pseudovillense* in the presence of butterfly-shaped stomata and straight to sinuate abaxial anticlinal walls with distinct beading. Instead, these fossils are similar to *Laurophyllum pseudoprinceps* Weyland et Kilpper from the Tertiary of Bohemia in guard cell size, unequal size development of subsidiary cells, the butterfly-shaped stomatal apparatus (Pl. 1, figs 13, 14), abaxial anticlinal cell walls straight (Pl. 1, fig. 13) to sinuate (Pl. 1,

fig. 14) and beading (Pl. 1, fig. 13) (Knobloch & Kvaček 1976), and sporadic trichome bases (Pl. 1, fig. 12) (Kvaček 1971). The differences of our fossil from *L. pseudoprinceps* of Kvaček (1971) are that the adaxial anticlinal cells are seldom beaded, secondary preservation is poor, and no stomata were found to be amphibrachy-paracytic (Kvaček 1988). Our fossils are different from *L. pseudoprinceps* of Austria, whose secondaries are distinctly brochidodromous and the anticlinal walls for both adaxial and abaxial cells are sinuate (Kovar-Eder & Hably 2006). Elsewhere in the Miocene of the eastern United States, *Laurus* leaves (YPM 147071) are found in Bridgeton (Hollick 1892) (Tab. 1), possibly with basal acrodromous and upper eucamptodromous venation.

Genus: *Daphnogene* Unger 1845

***Daphnogene* sp. 1**

Pl. 1, figs 15, 16

1916c *Cinnamomum scheuchzeri* Heer. Berry, pg. 51, Pl. 10, fig. 4.

**Description.** Leaves incomplete, elliptic, unlobed, with firm dark brown cuticle, microphyll. Length 5.0 cm, width 2.0 cm, l/w ratio 2.5, leaf area 666 mm<sup>2</sup> (n=1). Apex obtuse, base missing. Margin entire, thick. Primary venation single, straight, weak. Secondary venation eucamptodromous, basal pair extending more than 1/2 of leaf length and becoming less pronounced on approaching the margin, angle of divergence 21–35°. Brochidodromous secondary veins preserved above basal pair of eucamptodromous veins. Interconnecting veins at acute angle to midvein, exmedial tertiary veins at right angles to secondary acrodromous veins. Adaxial cuticle lacking. Abaxial epidermal cells random, elongate to isodiametric, 4–5-sided, anticlinal wall mostly straight, some arcuate, 27.1–91.8 × 21.1–43.1 μm. Stomata mostly brachyparacytic to paracytic, a few are anomocytic. Guard cells 25.1–35.6 × 8.3–12.6 μm. Subsidiary cells 1–3, equal to unequal size, 41.0–54.9 × 15.0–21.0 μm. Possible resinous substances in mesophyll.

**Material examined.** UF 18049-56767, USNM 38285 (Plesiotype, Berry 1916c, Pl. 10, fig. 4).

**Discussion.** The basal eucamptodromous venation of *Daphnogene* sp. 1 can also be found

in numerous extant angiosperm families such as Lauraceae, Menispermaceae, Ranunculaceae, Coriariaceae, Rhamnaceae, Urticaceae, Ulmaceae, Ericaceae, Melastomataceae, Myrtaceae, Oleaceae, Loganiaceae, Compositae and Caprifoliaceae. Characters that differentiate *Daphnogene* sp. 1 from the aforementioned families include eucamptodromous venation extending to the leaf tip in Rhamnaceae (*Ziziphus*, *Lasiodiscus*), Melastomataceae, Urticaceae (*Pouzolzia*) and Cannabaceae (*Celtis*); agrophic venation, sinuate anticlinal cell walls in Menispermaceae (*Cocculus*) and Ranunculaceae (*Clematis*); number of subsidiary cells in Menispermaceae (*Cocculus*); narrow stomata in Coriariaceae (*Coriaria*); the presence of trichomes in Myrtaceae (*Myrtus*) and Oleaceae (*Jasminum*); sunken stomata in Loganiaceae (*Strychnos*); thickened cell walls in Caprifoliaceae (*Viburnum*); and conspicuous secondary veins and serrate margins in Compositae (*Eupatorium mikanioides* Chapm.) (see supplemental material for in-depth discussion). Overall, characters of *Daphnogene* sp. 1, such as elliptic shape with entire margins, acrodromous veins extending more than half of leaf length and becoming less pronounced (Pl. 1, fig. 15), upper part of leaf with brochidodromous veins, persistent cuticle, anticlinal cell walls mostly straight, some arcuate, and brachyparacytic stomata with an inner ledge (Pl. 1, fig. 16) fit well with Lauraceae. The one difficulty is the lack of secretory glands in the fossil leaf. Such glands are diagnostic for Lauraceae but may not appear in cuticle preparations such as extant *Cinnamomum camphora* (L.) J. Presl., *Laurus officinale* Nees and *Litsea glaucescens* Kunth. *Daphnogene* sp. 1 is unique among Alum Bluff specimens in having numerous minute holes in the dark brown cuticle while lacking holes in the light brown cuticle. Under epifluorescence there are fluorescent amorphous substances surrounding the guard cells in the light brown cuticle, which may represent products of the breakdown of the stomatal complex under taphonomic processes.

The fossil genus *Daphnogene* Ung. (syn. *Cinnamomophyllum* Kr. & Wld.) is used to accommodate leaves with features conforming to Lauraceae but which cannot be assigned to a particular extant genus (Kvaček 1971). *Daphnogene* leaves have acrodromous basal secondary veins, whereas *Laurophyllum*

accommodates leaves with normal pinnate venation. *Daphnogene* sp. 1 resembles *Daphnogene lanceolata* Unger (syn. *Cinnamomophyllum scheuchzeri* (Heer) Kräusel & Weyland) in leaf shape, acrodromous venation with similar angle of divergence, tertiary veins at right angle to acrodromous veins, abaxial anticlinal cell walls straight, and paracytic stomata. The differences are the lack of trichome bases and defined mesophyll bodies in *Daphnogene* sp. 1 (Mai & Walther 1978). The aforementioned characters of *Daphnogene* sp. 1 are also similar to those of the trichome-absent variety *Daphnogene polymorpha* (A. Braun) Ettingshausen of Kovar-Eder & Hably (2006, see plate 4, fig. 1) and of Knobloch & Kvaček (1976), and are common in early to middle Miocene floras of Europe. Again, the difference is the lack of defined mesophyll bodies in *Daphnogene* sp. 1. The lack of defined mesophyll bodies in *Daphnogene* sp. 1 may be similar to the lack of secretory glands in cuticle preps of certain extant lauraceous genera. Within the Miocene of the eastern United States, an incomplete leaf of *Cinnamomum scheuchzeri* Heer (= *Cinnamomophyllum scheuchzeri* (Heer) Kräusel & Weyland) (USNM 38285) was described from Alum Bluff (Berry 1916c), which is similar to our fossil in having acrodromous secondary venation and well-formed areoles. Along with these characters, the leaf described by Berry (1916c) does show tertiary veins at right angles to the midvein, similar to *C. camphora*. Elsewhere in the Miocene of the eastern United States, two unidentified acrodromous-veined leaves are noted from Bridgeton (YPM Collection, pers. obs.).

### *Daphnogene* sp. 2

Pl. 1, figs 17, 18; Pl. 2, figs 1–3

**Description.** Leaves incomplete, elliptic to ovate, symmetrical, unlobed, microphyll. Length 5.4–8.5 cm, width 2.0–2.7 cm, l/w ratio 2.7–3.1, leaf area 719.3–1528.5 (avg. 1123.9) mm<sup>2</sup> (n=2). Apex obtuse; base missing. Margin entire. Primary venation acrodromous, 3, weak, extending to leaf apex. Number of basal veins 3. Few preserved interior secondaries, at 30–60° angle from midvein or exmedial acrodromous veins. Higher-order veins not preserved. Leaf surface with minute polygonal pattern. Trichomes lacking. Adaxial cells random, rectangular, anticlinal cell walls sinuate,

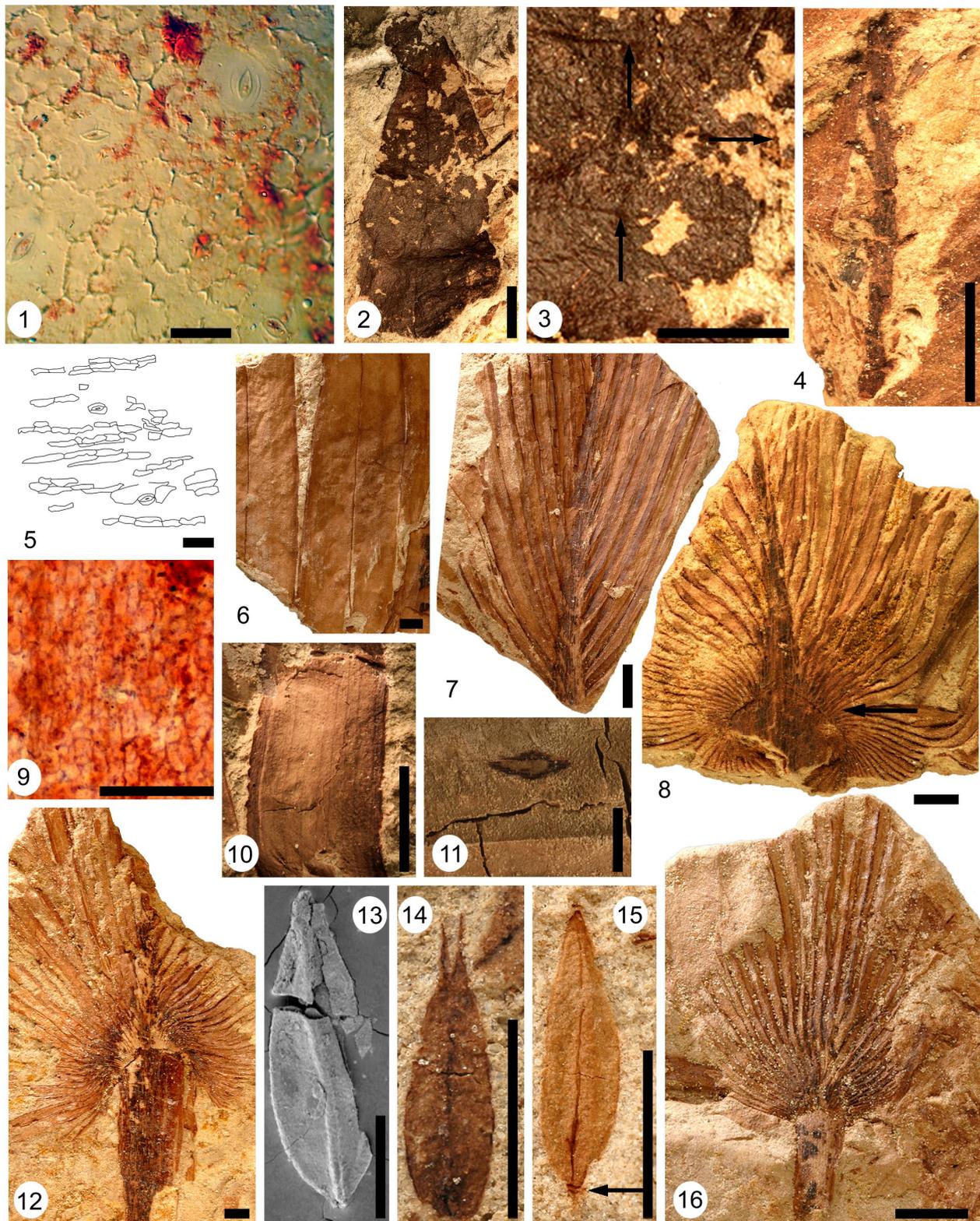
38.6–57.3 × 24.9–36.1 μm. Abaxial cells random, rectangular, anticlinal cell walls arcuate to mostly sinuate, 27.5–48.2 × 15.0–29.5 μm. Stomata random, paracytic, 18.6–24.2 × 17.9–23.6 μm, with stomatal ledge, subsidiary cell walls thin.

**Material examined.** UF 18049-43575, 69001.

**Discussion.** Shared characters of *Daphnogene* sp. 2 and extant angiosperm families such as Dioscoreaceae, Stemonaceae, Alstroemeriaceae, Petermanniaceae, Trilliaceae, Ripogonaceae, Smilacaceae, Rhamnaceae, Melastomataceae, Lauraceae, Adoxaceae and Ericaceae include an ovate to elliptic leaf with entire margins, and acrodromous venation to the leaf apex. However, the diagnostic feature of paracytic stomata rules out most of these families

Characters that differentiate *Daphnogene* sp. 2 from all of the aforementioned families except Lauraceae include nonsinuate anticlinal cell walls in Dioscoreaceae, stomata aligned transverse to the leaf axis in Stemonaceae (*Croomia*, *Stemona*, *Stichoneuron*) and Philesiaceae (*Philesia*), stomata aligned parallel to the leaf axis in Alstroemeriaceae (*Behnia*), Petermanniaceae (*Petermannia*) and Trilliaceae, stomatal ledges lacking in Ripogonaceae (*Ripogonum*) and Smilacaceae, anomocytic stomata in Rhamnaceae, complex trichomes in Melastomataceae (*Tetrazygia*, *Graffenrieda*, *Leandra scabra*), serrate margins near the apex in Adoxaceae (*Viburnum*), and two acrodromous secondary veins in Ericaceae (*Thibaudia*) (see supplemental material for in-depth discussion).

Overall, characters of *Daphnogene* sp. 2 such as three acrodromous veins extending to the leaf tip (Pl. 1, fig. 17), interior veins (Pl. 2, fig. 3), sinuate anticlinal cell walls (Pl. 1, fig. 18; Pl. 2 fig. 1), paracytic stomata with a stomatal ledge, and thin subsidiary cell walls (Pl. 2, fig. 1) are found in Lauraceae such as *Cinnanomum* Schaeff. and *Cryptocarya* R. Br. The stomatal size in our fossil is similar to that in *Cinnanomum* and *Cryptocarya* but the epidermal cells in the latter taxa are smaller than in *Daphnogene* sp. 2 (Christophel & Rowett 1996). Specimen 43575 is provisionally placed in *Daphnogene* sp. 2 due to similarity of venation with 69001 but the lack of cuticle makes its identification equivocal.



**Plate 2.** 1–3. *Daphnogene* sp. 2, 1 – abaxial, cell wall of guard cells and subsidiaries barely discernible, 2 – leaf with acrodromous veins, 3 – enlargement of 2 with interior secondary vein (right arrow) extending between midvein (upper arrow) and acrodromous vein (bottom arrow), UF18049-69001; 4–12. *Sabalites apalachicolensis* Berry, 4 – infructescence fragment found among *S. apalachicolensis* leaves, UF18049-61083b, 5 – line drawing of stomata and anticlinal cell walls from faint cuticle preparation, UF18049-43549, 6 – leaf segments with prominent midvein, UF18049-53778, 7 – costapalmate leaf that does not divide to insertion point, UF18049-29137, 8 – outline of hastula at apex of petiole (arrow), UF18049-29143, 9 – cells of adaxial epidermis in rows, UF18049-53803, 10 – leaf segment with longitudinal secondary veins, UF18049-48368, 11 – *S. apalachicolensis* leaf with *Petalozzites sabalana* Berry, UF18049-68863, 12 – costapalmate leaf with unarmed petiole, UF18049-29135; 13. *Scirpus* sp., 3-angled seed with prominent ridge, UF18049-43597; 14. *Carex* sp. 1, veinless perigynium with acuminate teeth, UF18049-43511; 15. *Carex* sp. 2, veinless perigynium with possible stipitate structure (arrow), UF18049-43538; 16. *Palmacites*, palmate leaf lacking costa, UF18049-29139; Scale bars: 1, 5 = 20  $\mu$ m; 2, 4, 6–8, 10, 12, 16 = 10 mm; 3, 11, 14, 15 = 5 mm; 9 = 40  $\mu$ m; 13 = 1 mm

Order: Arecales Bromhead 1840

Family: Arecaceae Bercht. & J.Presl 1820

Genus: *Sabalites* Saporta  
(emended Read & Hickey) 1972

***Sabalites apalachicolensis* Berry 1916**

Pl. 2, figs 4–12

1916c *Sabalites apalachicolensis* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 46, Pl. 8, figs 1–5, Pl. 9, fig. 9.

**Description.** Leaf blade plicate, palmately veined, prominently costapalmate with relatively short costa. Lamina up to 62 cm long (n=9). Rays incomplete, linear, single-folded, with prominent midrib, straight to curved and fused at base, free near upper length, 2–4.1 cm wide. Secondaries numerous, longitudinal, parallel, no transverse veinlets evident. Costa (n=23) bordered with crowded pinnae at leaf base, curved to sinuate towards petiole, ca 10–23 strands per 2 cm. Small symmetrical obtuse hastula present near apex of petiole (n=6) on abaxial surface. Petiole up to 80 cm long and 2.3 cm wide, with straight unarmed edges, striated and lacking transverse veinlets, with lanceolate acumen, abaxial side 7–9.5 cm, adaxial side ca 4.5 cm. Leaf fragments strap-like, with parallel straight-sided margins, with distinct midrib. Inflorescence fragments, 2.7–3.5 mm long, 1 mm wide axis, with spiral, spicate, rounded buds (n=2). Stomata and epidermal cells not well preserved. Abaxial epidermal cells loosely aligned, elongate, some with tapering ends, anticlinal cell wall straight and 4–5-sided, 5.8–21.1 × 2.7–5.6 μm (n=10). Stomata 12–12.2 × 7.7–8.6 μm (n=2).

**Material examined.** UF 18049-29135, 29137, 29143, 43549, 48368, 53778, 53803, 61083b, 68863, USNM 38281b, 38276, 175739a,b, 175738, 175740 (Lectotype: USNM 38277, Berry 1916c, pl. 8, fig. 2 [designated in Read & Hickey 1972, pg. 136]).

**Discussion.** Costapalmate palm leaves with unarmed petioles, and blades not divided to the insertion point in *Sabalites apalachicolensis* can also be found in extant genera of *Bismarckia* Hildebrandt & H. Wendl., *Livistona* R. Brown and *Sabal* Adanson (Dransfield et al. 2008, Zhou et al. 2013). In *Bismarckia* the hastula is large and distinctly lopsided, and in *Livistona* the petiole can be armed to unarmed,

interfold areas are sometimes with filaments (secondary veins), transverse veinlets are obscure to conspicuous, and the costa is relatively short (Dransfield et al. 2008). A short costa (3.5 cm) was figured in Berry (1916c, see Pl. 8, fig. 5) for *S. apalachicolensis*, suggesting that there may be two different *Sabalites* species, related to *Sabal* and *Livistona*. *Sabalites apalachicolensis* characters such as a costapalmate leaf, unarmed striated petiole that lacks transverse veinlets (Pl. 2, fig. 12), hastula (Pl. 2, fig. 8), lanceolate acumen, rays with prominent midvein (Pl. 2, fig. 6) and longitudinal secondary veins (Pl. 2, fig. 10), and leaf blades that are not divided to the insertion point (Pl. 2, figs 7, 8, 12) show similarity to extant *Sabal* Adanson except for an obtuse hastula apex on the abaxial side of the fossil leaf. An inflorescence fragment (Pl. 2, fig. 4) with spiral, spicate arrangement of putative pedicels is similar to that of *Sabal palmetto*. Small oval fruits (UF 18049-43539, 43571a, 48382, 70190), one with a granular interior, were occasionally found next to leaves of *S. apalachicolensis*, and are somewhat similar to those of *S. palmetto*, but the preservation is poor. Few stomata are preserved (Pl. 2, fig. 5), and the adaxial epidermal cells are elongate and 4-sided (Pl. 2, fig. 9), whereas in extant *Sabal palmetto* the cells in this position are elongate to equilateral and 5–6-sided. These differences support the placement of this fossil in the fossil genus *Sabalites* rather than in extant *Sabal*. Modern *Sabal* includes tree-sized palms found in scrub, savanna, hammock and swamps from the southeastern United States to South America (Mabberley 1997, Wunderlin 1998) in tropical to warm-temperate regions (USDA 2016). Adjacent to Alum Bluff, *Sabal* is found in floodplains and on slopes, with only juveniles on the sandhills (Clewley 1985, FSU Herbarium 2016) (Tab. 1).

The morphological characters of *Sabalites apalachicolensis* fit well with fossil palms and specifically *Sabalites* (Lesquereux 1878a, Read & Hickey 1972, Daghlian 1978), but distinct stomatal characters are lacking for comparison with Eocene fossil *Sabal* in the Claiborne Group (Daghlian 1978), which contains six subsidiary cells, of which the polar cells overlap the guard cells. For most representatives of fossil *Sabal* the leaves have deeply dissected leaf segments (Kvaček & Herman 2004). The abaxial cell arrangement, size and shape of

*S. apalachicolensis* are similar to the corresponding characters in *Sabalites robustus* Jin et Zhou from the Eocene of Hainan Island, China (Zhou et al. 2013). *Sabalites grayanus* Lesquereux (Eocene) and *S. vicksburgensis* Berry (Eocene) have a long, narrow acumen and conspicuously veined rays, with transverse veinlets evident in *S. vicksburgensis* (Berry 1916a, Daghlian 1978), whereas *S. apalachicolensis* lacks transverse veinlets (Pl. 2, fig. 10). Within the Miocene of the eastern United States, fragments of *Sabal*-like rays were noted by Dall and Stanley-Brown (1894) and Foerste (1894), but the first systematic treatment was published by Berry (1916c) as *Sabalites apalachicolensis* Berry. Elsewhere in the Miocene of the eastern United States, leaves of *Sabalites* are found in Catahoula (Berry 1916a), while *Amesoneuron bridgetonensis* (A. Hollick) Read and Hickey (YPM 14702', 147002, 147004) has been described from Bridgeton (Hollick 1892, 1897, Read & Hickey 1972) (Tab. 1).

Genus: *Palmacites* Brongniart 1828

***Palmacites* sp.**

Pl. 2, fig. 16

**Description.** Leaf blade plicate, palmate, lacking costa. Petiole incomplete, slightly rounded, 7 mm wide, margin smooth; remnant of hastula. Rays with single-folded segments and prominent midrib. Numerous secondary veins, longitudinal, parallel, no transverse veinlets. Rays straight to curved at base. No cuticle preserved.

**Material examined.** UF 18049-29139.

**Discussion.** *Palmacites* sp. differs from *Sabalites apalachicolensis* Berry by the lack of a costa. Characters of *Palmacites* sp. such as a palmate leaf with a hastula, an unarmed petiole and the lack of a costa (Pl. 2, fig. 16) can be found in numerous extant palm species (Dransfield et al. 2008). One would need characters of apical separation and transverse veinlets for a more refined species determination (Dransfield et al. 2008), plus a complete petiole in reference to the question of entire or toothed margins. Some teeth can be sloughed off, while minute teeth may be difficult to identify. An example would be *Serenoa*, which have petioles with teeth (Dransfield et al. 2008), but the upper portions of some petioles can have smooth margins or very minute teeth.

The fossil genus *Palmacites* is used for fossil palmate palm leaves that lack a costa or an extension of the petiole into the blade (Read & Hickey 1972). Within the Miocene of the eastern United States, palmate Arecaceae leaves (with spines on petiole) have been collected in Hattiesburg (Stults et al. 2016), while palm pollen has been noted in the Catahoula sandstone (Wrenn et al. 2003), Alum Bluff (Jarzen et al. 2010), Ohoopce (Rich et al. 2002) and Martha's Vineyard (Frederiksen 1984) (Tab. 1).

Order: Poales Small 1903

Family: Cyperaceae Juss. 1789

Genus: *Scirpus* L. 1753

***Scirpus* sp.**

Pl. 2, fig. 13

**Description.** Achene ovate, flat, 3-angled, with prominent ridge along full length, length 3 mm, width 1.29 mm. Apex acute, base cuneate. Not subtended by hyaline scales.

**Material examined.** UF 18049-43597.

**Discussion.** The aforementioned characters of *Scirpus* sp. can be found in extant *Scirpus* achenes for the size range of 0.8–4.5 mm long by 0.8–3.5 mm wide (Koyama 1958). *Scirpus* has 200 species, found predominantly in cold regions, with only a few species such as *Scirpus cyperinus* (L.) Kunth and *S. lineatus* Michx. reaching subtropical regions (Britton & Brown 1913, Wunderlin 1998, Institute for Systematic Botany 2016, USDA 2016). *Scirpus* are found in wet areas adjacent to Alum Bluff (Clewell 1983, FSU Herbarium 2016) (Tab. 1).

*Scirpus* fruits described from the Miocene of Central Europe are questionable (Kirchheimer 1957), with some found to be Cyclanthaceae (Smith et al. 2008). Within the Miocene of the eastern United States, Corbett (2004) was the first to note this fruit type at Alum Bluff.

Genus: *Carex* L.

***Carex* sp. 1**

Pl. 2, fig. 14

**Description.** Ovate veinless perigynium, 3-angled, length 7 mm, width 2 mm. Apex

acuminate with 1 mm teeth; base truncate and slightly cordate, surface with one suture.

Material examined. UF 18049-43511.

**Discussion.** The aforementioned characters of *Carex* sp. 1 are somewhat similar to the veinless perigynium of extant *Carex* having a combination of features from sections Paludosae and Stellulatae, for size (2.5–8 mm × 1.2–3.5 mm), ovate shape, acuminate apex with 2 teeth, cordate base, and one surface suture (Pl. 2, fig. 14) (Mastrogioseppe 1993, Ball & Reznicek 2002). This suture may also be the ridge of an underlying 3-angled achene. *Carex* have ca 1000 species found predominantly in cold regions, with only a few species such as *Carex lupuliformis* Sartw. ex. Dewey reaching subtropical regions (Britton & Brown 1913, Wunderlin 1998). *Carex* are found adjacent to Alum Bluff on floodplains and bluffs (Clewell 1983, 1985, FSU Herbarium 2016) (Tab. 1).

Early *Carex* fruits described from the Miocene of Central Europe lack any proof for placement within this genus (Kirchheimer 1957). Within the Miocene of the eastern United States, questionable Cyperaceae pollen is found in Martha's Vineyard (Frederiksen 1984), while *Cyperus* fruits are found in Hattiesburg (Stults et al. 2016) (Tab. 1).

### ***Carex* sp. 2**

Pl. 2, fig. 15

**Description.** Elliptic veinless perigynium, 3-angled, length 3–9 mm, width 2 mm. Apex acute, teeth missing; base cuneate with transverse indentations, surface with suture.

Material examined. UF 18049-43538.

**Discussion.** This specimen is different from *Carex* sp. 1 in that it lacks apical teeth and the base is cuneate with transverse indentations. The aforementioned characters are somewhat similar to the veinless perigynium of extant *Carex* having a combination of features of sections Infatae and Nardinae, for size (4–10 mm × ca 2 mm), elliptic shape, acute apex lacking teeth, cuneate base, and one surface suture (Pl. 2, fig. 15) (Ball & Reznicek 2002).

*Carex paucifloroides* Wieliczkievicz from the Miocene of Germany (Mai 2004) is similar to our fossil in shape, size and base, although in *C. paucifloroides* the apex is apiculate.

Order: Proteales  
Juss. ex Bercht. & J. Presl 1820

Family: Platanaceae T. Lestib 1826

Genus: cf. *Platanus*

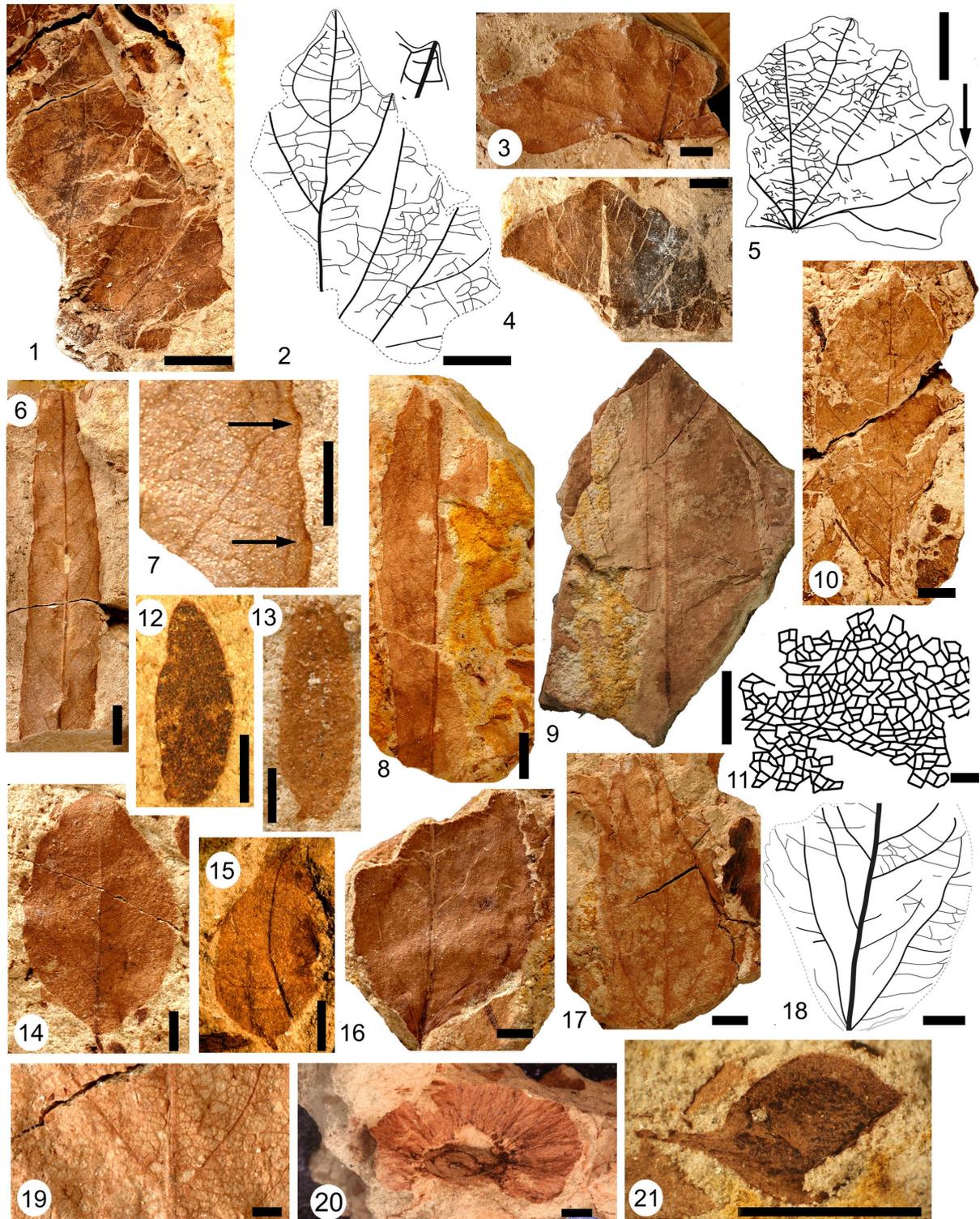
### **Morphotype AB17**

Pl. 3, figs 1, 2

**Description.** Leaves incomplete or fragmented, broadly ovate, lobed, sinus shallow and running ca 1/3 the distance to midrib. Length 16 cm, width 11.2 cm, l/w ratio 1.4, leaf area 11934.7 mm<sup>2</sup> (n=1). Apex acute, shape acuminate; base missing. Margin serrate. Basal and apical side of tooth convex to straight, tooth apex acute to sharply acute. Principal vein attenuate towards but slightly wider at tooth apex, with higher-order lateral vein terminating at tooth margin. Primary venation palmate, one lateral primary running straight to slightly curved to lateral lobe apex. Secondary venation craspedodromous to possibly eucamptodromous, spacing irregular, attachment excurrent. Two major secondary veins diverging at 35–42° in mid to upper portion of lamina, curving slightly upward towards margin and into tooth. Agrophic veins present. One pair of eucamptodromous minor secondary veins at leaf apex, diverging at 56–65°, running sharply curved upwards, then parallel to margin. Intercoastal tertiary venation not well preserved for overall pattern. Epimedial tertiaries possibly opposite percurrent, with distal course basiflex. Cuticle not preserved.

Material examined. UF 18049-53308.

**Discussion.** The fragmentary nature of the leaves precludes a precise determination, but the general leaf shape, palmate venation (Pl. 3, figs 1, 2) and tooth venation (Pl. 3, fig. 2 insert) of Morphotype AB17 suggest affinity with extant *Platanus* L. (Platanaceae) (Hickey & Wolfe 1975, Schwarzwald 1986), although *Hedera* L. (Araliaceae) also bears a resemblance. For generic determination, abaxial cuticular characters such as papillose epidermal cells, candelabra trichomes on the veins (which usually break, leaving trichome bases), and capitate glands (Meyer & Meola 1978) would be needed. Platanaceae, with one genus *Platanus* (7 species), are trees occurring



**Plate 3.** 1, 2. cf. *Platanus* sp., 1, 2 – palmately veined leaf, 2 – venation diagram of fig. 1, with one lateral primary running to lateral lobe fragment. Insert, composite line drawing with close-up of tooth venation. UF18049-53308; 3–5. Morphotype AB1, leaves widely ovate, crenate margins, 3, 5 – cordate base, basal actinodromous venation, UF18049-43520a, UF18049-53164a, respectively, 5 – agrophic venation (arrow), UF18049-53164a, 4 – obtuse apex, UF18049-43522; 6–8. cf. *Salix varians* Goepp., 6, 8 – linear serrate margin leaves with semicraspedodromous secondaries, UF18049-43567, 43547, respectively, 7 – enlargement of fig. 6 showing glandular teeth depressed against margin (arrows); 9. *Salix* sp. 1, wide leaf with compressed glandular teeth, UF18049-69542; 10, 11. *Leguminosites apalachicolensis*, 10 – leaflet, 11 – line drawing of adaxial cells from epifluorescence, UF18049-43527; 12, 13. *Leguminosites sellardsii*, narrowly elliptic leaflets with highly asymmetrical base, UF18049-43534, UF18049-53760, respectively; 14. *Leguminosites* sp. 1, elliptic, brochidodromous leaflet, UF18049-43512; 15. *Leguminosites* sp. 2, ovate, basal brochidodromous leaflet with obtuse base, UF18049-43533; 16–19. *Paliurus* sp., 16, 17 – leaves with simple agrophic venation and toothed margins, UF18049-43514, UF18049-43557, respectively, 18 – line drawing, UF18049-43543, 19 – percurrent tertiaries and reticulate quaternary veins, UF18049-43557; 20. *Paliurus favonii* Unger, disk-winged drupe, UF18049-26117; 21. *Ulmus* sp. (fruit), UF18049-71312. Scale bars: 1, 2 = 35 mm; 3, 6, 14–16, 18, 21 = 5 mm; 4, 5, 8, 10, 17 = 10 mm; 7, 12, 13, 19, 20 = 2 mm; 9 = 20 mm; 11 = 50  $\mu$ m

in the Northern Hemisphere, and *Platanus occidentalis* L. occurs in the floodplains adjacent to Alum Bluff (Godfrey 1988, FSU Herbarium 2016) (Tab. 1). This leaf looks similar in morphology to that of *Platanus leucophylla* (Unger) Knobloch of Austria, which is common in the late Miocene (Kovar-Eder & Hably 2006, see Pl. 2, fig. 3). Elsewhere in the Miocene of the eastern United States, *Platanus* leaves have been identified from Catahoula (Dockery & Thompson 2016), Hattiesburg (Stults et al. 2016), Calvert (Berry 1916b) and Brandywine (McCartan et al. 1990), fruits from Brandywine (McCartan et al. 1990), and pollen from Ochoopee (Rich et al. 2002) (Tab. 1).

### Rosids

#### Order: Vitales

Juss. ex Bercht. & J. Presl 1820

Family: Vitaceae Juss. 1789

#### Morphotype AB1

Pl. 3, figs 3–5

**Description.** Leaves incomplete or fragmented, very widely ovate, symmetrical, microphyll to notophyll. Length 4.2–8.5 cm, width 4.4–7.6 cm, l/w ratio 1.1–1.2, leaf area 1399–4302.4 (avg. 2482.8) mm<sup>2</sup> (n=3). Apex obtuse with rounded flanks; base shallow cordate. Margin of broad rounded teeth. Teeth 1–1.5 per cm, spacing regular, sinuses rounded. Primary venation basal actinodromous, 5 basal veins present, entering teeth. Midvein straight, weak, and terminates at apex. Lateral primary veins progressively decrease in thickness towards margin, angle of divergence 40–80°. One pair of upper pinnate secondaries visible, angle of divergence 30°. Secondaries craspedodromous. Agrophic venation, at least 2–3 exmedial curving secondaries departing from lateral primaries, angle of divergence 30–60°. Tertiaries mixed opposite/alternate percurrent. Cuticle fragmentary, adaxial cells pentagonal, random, straight-sided, 12.3–37.0 × 10.6–20.3 µm. Numerous glands present, 19.8 µm (avg.). Trichomes absent.

**Material examined.** UF 18049-43520a, 43522, 53164a.

**Discussion.** For Morphotype AB1, the characters of ovate lamina with cordate base,

rounded crenate teeth, basal actinodromous venation with five primary basal veins, and agrophic venation (Pl. 3, figs 3–5) are found in extant families of Malvaceae, Menispermaceae, Moraceae and Vitaceae. In Malvaceae (e.g. *Abutilon*, *Pavonia*) the teeth are smaller and the apex is acute to acuminate (Kearney 1958, Fryxell 1999, Shu Q 2007). The adaxial surface contains stomata, stellate and/or glandular trichomes in *Abutilon* (Shaheen et al. 2009), and stellate and/or glandular trichomes in *Pavonia* (Fryxell 1999). The broad teeth in our specimens match those of *Hibiscus rosasinensis* L. but the base and apex in the latter do not match our specimens. The venation is similar to Menispermaceae except that the margins are predominately entire (except in *Sinomenium acutum* (Thunb.) Rehder & E.H. Wilson which have a few teeth), and *Cissampelos hirta* Klotzsch and *Pericampylus glaucus* (Lamk.) Merr. which can have shallowly crenate margins (Forman 1988, De Wit 2008). In Moraceae (e.g. *Ficus palmeri* S. Watson, *F. religiosa* L.) the secondaries are brochidodromous. In Vitaceae, (e.g. *Vitis aestivalis* Michx.) the leaf shape, teeth and venation match but the base is deeply cordate, not widely cordate as in our specimens. The presence of numerous glands, the absence of trichomes and the polygonal cells with straight to arched walls of *V. aestivalis* (Ren et al. 2003) are similar to the morphology of specimen UF 18049-43522.

Within the Miocene of the Northern Hemisphere occur *Vitis teutonica* A. Braun and *V. subintegra* Sap. of Europe, *V. alia* Hollick and *V. washingtonensis* (Knowlton) Brown of the western United States (Hollick 1927, Brown 1936). Kirchheimer (1939) suggests that the western United States species are either poorly preserved or lack sufficient characters to prove affinity with *Vitis*. Elsewhere in the Miocene of the eastern United States, Vitaceae leaves are found at Brandywine (McCartan et al. 1990) and possibly Bridgeton, where *Viburnum bridgetonense* Hollick (YPM 74684, 74680, 74650, 147094) has numerous leaf forms under this name (Hollick 1892), leaving open the systematics of this species as *Vitis* or *Viburnum*. Vitaceae seeds occur at Brandon (Tiffney 1976, 1994), the Gray Fossil Site (Gong et al. 2010), Brandywine (McCartan et al. 1990) and Pensauken (Berry 1940), and pollen at Brandon (Traverse 1955, 1994) and Ochoopee (Rich et al. 2002) (Tab. 1).

## Fabids

Order: Malpighiales

Juss. ex Bercht. &amp; J.Presl 1820

Family: Salicaceae Mirb. 1815

Genus: *Salix* L. 1753cf. *Salix varians* Goepp. 1855

Pl. 3, figs 6–8

**Description.** Leaves incomplete or fragmented, narrowly elliptic, symmetrical, unlobed, microphyll. Length 7.0–11 cm, width 1.5–2.6 cm, l/w ratio 3.2–4.7, leaf area 699.3–1904.8 (avg. 1268.3) mm<sup>2</sup> (n=5). Extreme apex missing but tending acute, straight flanks; base missing. Margin serrate to rarely entire towards leaf base. Teeth inconspicuous, spacing regular, one tooth order, 2–3 teeth per cm, compressed against margin, basal side longer than apical side, basal side convex, apical side straight, tooth sinus rounded. Tooth apex possibly glandular. Primary venation single, straight, stout. Secondary venation semicraspedodromous, at least 10 pairs, at intervals of 5–10 mm, spacing irregular, angle of divergence 30–44°. Secondary attachment slightly decurrent, secondary course straight and slightly to gently curving up and out towards margin, then arching back to subadjacent secondaries. 1–2 intersecondaries per intercostal, proximal course mostly parallel to secondary vein and running more than 1/2 the distance to margin, distal course merging into percurrent tertiary vein. Tertiary veins mixed percurrent. Exmedial tertiaries branching from secondaries near leaf margin and extending into teeth. Quaternary and higher-order venation not well preserved, areoles poorly developed. Trichomes and cuticle not preserved.

**Material examined.** UF 18049-43547, 43567.

**Discussion.** This species is distinguished by the narrowly elliptic lamina, serrate to entire leaf margin (Sargent 1933) with semicraspedodromous secondaries (Pl. 3, figs 6, 8), secondary vein attachment slightly decurrent, intersecondaries running more than half the distance to the margin, and glandular teeth (Pl. 3, fig. 7). These features are shared with

extant genera of *Salix* L. and *Casearia* Jacq. (Salicaceae). *Casearia corymbosa* Kunth differs slightly by having numerous intersecondaries which terminate at an adjacent secondary vein. Overall, this fossil fits well with extant *Salix* and is consistent with Group 1 (subgenera *Salix* and *Vetrix*) of Buechler (2014). Leaf shape in extant *Salix* can vary from circular to obovate, ovate, lanceolate and narrowly elliptic (Buechler 2014). Salicaceae has 435 species, with *Salix* (400 sp.) found predominantly in cold regions, with only one species (*Salix caroliniana* Michx.) extending to subtropical regions (Britton & Brown 1913, Wunderlin 1998), and near Alum Bluff they are found in wet areas (Clewell 1985) (Tab. 1).

Buechler (2014) noted that Miocene leaves reveal no systematic differences in venation pattern between modern and fossil *Salix* of the same general morphotypes (e.g. Group 1), and no examples of leaves with intramarginal veins have been found. Miocene *Salix* leaves are found throughout the Northern Hemisphere (Tidwell 1998, Collinson 1992); many of those species are generally similar to our fossils, such as *S. venosiusula* Smith of Idaho, *S. varians* Goepp. of Switzerland, *S. k-suzukii* Tanai of Japan, and *S. miosinica* Hu & Chaney of China (Heer 1856, Hu & Chaney 1940, Smith 1941, Uemura 1988). The leaf size, apex, shape, venation, angle of divergence and teeth characters of our fossils seem closer to the morphology of *S. varians* (including syn. *S. lavateri* Heer) of Mai & Walther (1978) and Knobloch & Kvaček (1976). One problem is the lack of a base in our fossils, preventing us from confirming whether the basal secondaries extend a quarter of the leaf length as in *S. varians* (Mai & Walther 1978). *Salix varians* is common in Europe and East Asia in the Miocene and Oligocene (Heer 1856, Mai & Walther 1978, Collinson 1992, Worobiec et al. 2008). At Alum Bluff, Dall & Stanley-Brown (1894) first noted leaves resembling willows. Elsewhere in the Miocene of eastern North America, *Salix* leaves have been reported from Hattiesburg (Stults et al. 2016), Catahoula (Berry 1916a, questionable), Calvert (Berry 1916b) and Brandywine (McCartan et al. 1990). *Salix* pollen has been found in the Catahoula (Wrenn et al. 2003), Ohoopsee (Rich et al. 2002), Calvert and Cohansey (Greller & Rachele 1983), Gray (Wallace & Wang 2004), Brandywine (McCartan et al. 1990) and Bryn Mawr (Pazzaglia et al. 1997) sites (Tab. 1).

***Salix* sp. 1**

Pl. 3, fig. 9

**Description.** Leaves incomplete, elliptic, microphyll to notophyll. Length 8.0–10 cm, width 3.0–5.4 cm, l/w ratio 1.9–2.7, leaf area 1498.5–3596.4 (avg. 2597.4) mm<sup>2</sup> (n=2). Apex and base missing. Margin serrate. Teeth spacing regular, one tooth order, 4–5 teeth per cm, compressed against margin, basal side longer than apical side, basal side convex, apical side straight, tooth sinus angular. Tooth apex rounded and glandular. Primary venation single, straight, moderate. Secondary venation semicraspedodromous, at least 10 pairs, at intervals of 10–20 mm, spacing irregular, angle of divergence 50–65°. Secondary vein attachment excurrent, course gently curving up and out towards margin, then arching back to superadjacent secondaries in a series of lessening vein width. 1–2 intersecondaries per intercostal area, proximal course mostly parallel to secondary vein and running more than 1/2 the distance to margin, distal course merging into percurrent tertiary vein. Tertiary veins mixed percurrent. Exmedial tertiaries branching from secondaries near leaf margin and extending into apical side of teeth. Quaternary venation reticulate. Cuticle not preserved.

**Material examined.** UF 18049-69542.

**Discussion.** The lamina of *Salix* sp. 1 is much wider than that of cf. *Salix varians*. The size and venation of *Salix* sp. 1 (Pl. 3, fig. 9) are close to those of extant *S. appendiculata* Villars (Buechler 2014) and *S. floridana* Chapm. but those species have rounded sinuses, unlike the fossil. The shape, size and direction of the teeth resemble *Prunus serotina* Ehrh. but *P. serotina* has alternate percurrent tertiaries and the exmedial tertiaries near the margin are reticulate.

*Salix* sp. 1 somewhat resembles *Salix hesperia* (Knowlton) Condit. from the Miocene of the western United States, due to its larger size, serrate margin and numerous intersecondary veins (Chaney & Axelrod 1959). This species also closely resembles *S. hausruckensis* Kovar-Eder from the Miocene of Austria (Kovar-Eder & Wójcicki 2001) in venation (especially the intersecondary veins), size, teeth shape, and finer venation running into the apical portion of the teeth, but more Alum Bluff specimens

with a preserved base and cuticle are needed for confirmation.

Order: Fabales Bromhead 1838

Family: Fabaceae Lindl. 1836

Genus: *Leguminosites* Bowerbank 1840

***Leguminosites apalachicolensis***

(Berry) n. comb.

Pl. 3, figs 10, 11

1916c *Pisonia apalachicolensis* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 49, pl. 10, fig. 1.

**Description.** Leaflets complete or fragmented, elliptic, slightly asymmetrical, unlobed, microphyll. Length 4.5–7.0 cm, width 2.6–4.0 cm, l/w ratio 1.7–2.0, leaf area 779.2–1864.8 (avg. 1305.2) mm<sup>2</sup> (n=4). Apex acute breviacuminate; base convex to cuneate. Margin entire. Petiolule wider than midvein, 2 mm long, 1 mm wide. Primary venation single, straight, weak. Secondary venation basally eucamptodromous, others brochidodromous. At least 9 pairs of secondary veins at intervals of 4–34 mm, spacing irregular, angle of divergence 45–53° basal, 40–42° midsection, 38–43° apical. Secondary attachment excurrent, secondary course predominantly straight, towards apex curving upwards and out to margin. Intersecondary veins at least one per intercostal, proximal course parallel to secondary vein and running 1/2 the distance to margin, distal course joining percurrent tertiary vein. Tertiary venation mostly alternate percurrent. Cuticle poorly preserved, characters from epifluorescence. Adaxial cuticle lack trichomes. Epidermal cell shape 4–6-sided, anticlinal cell walls straight, 15–37.7 × 12.2–26.4 μm.

**Material examined.** UF 18049-43527, USNM 38280 (Holotype, Berry 1916c, Pl. 10, fig. 1).

**Discussion.** We reject the designation of *Pisonia apalachicolensis* by Berry (1916c), due to poor preservation of the original specimen's venation. Higher-order venation is important for a *Pisonia* designation; for example, *Pisonia aculeata* L. and *P. rotundata* Griseb. have intersecondary veins that extend to the outer secondary loops and sometimes branch admedially. *Leguminosites apalachicolensis* is somewhat similar to Morphotype AB11 (which we

attribute to Magnoliaceae/Annonaceae) but in AB11 the base is obtuse to cordate, the secondaries are gently curving, and the angle of divergence is broader. Numerous extant angiosperm families such as Magnoliaceae, Fagaceae and Leguminosae share characters of *L. apalachicolensis* such as an elliptic leaf with an entire margin, short acuminate apex, cuneate base, at least nine pairs of proximal eucamptodromous to distal brochidodromous secondaries that are mostly straight (Pl. 3, fig. 10), at least one intersecondary per intercostal, and percurrent tertiaries. In Magnoliaceae (e.g. *Michelia* sp.) there are numerous intersecondary veins, and in *Magnolia fordiana* (Oliv.) Hu there are simple trichomes on the adaxial surface. For Fagaceae (e.g. *Castanopsis acuminatissima* (Blume) A. DC.) the base shape is concave and the acuminate apex is twice larger than in *L. apalachicolensis*, and for *C. tonkinensis* Seemen the intersecondaries are obscure and the tertiaries are mixed percurrent to reticulate (Yu & Chen 1991). In the Leguminosae, *Ormosia* Jacks seems very close to *L. apalachicolensis* in size, shape and venation. The distance apart and divergence of the secondary veins (Yu & Chen 1991) and glabrate adaxial surface in *Ormosia panamensis* Benth. (Rudd 1965) are similar to *L. apalachicolensis*. The adaxial cells of *Ormosia calavensis* Azaola ex Blanco are similar in size to those of *L. apalachicolensis* but in *O. calavensis* the anticlinal walls are 4–5-sided and are predominately sinuate, some straight-sided and knobby. Polygonal cells with straight-sided anticlinal walls occur in a few *Ormosia* species (Herendeen 1992, Luo & Zhang 2004). Better-preserved cuticle is needed for *L. apalachicolensis* (Pl. 3, fig. 11), especially for the abaxial surface, since inflated trichomes are found in most extant *Ormosia* species (Herendeen 1992) while some have only regular simple trichomes (Luo & Zhang 2004, Duarte et al. 2012). This cuticle is different from other cuticle from Alum Bluff in that it lack glands or trichomes, the cells are straight or arched, and there are size differences such as are found in Morphotype AB7.

***Leguminosites sellardsii* (Berry) n. comb.**

Pl. 3, figs 12, 13

1916c *Caesalpinia sellardsii* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 49, pl. 9, fig. 1, 2.

**Description.** Leaflets complete, narrowly elliptic or elliptic, medial asymmetrical,

leptophyll to nanophyll. Length 0.5–1.5 cm, width 0.2–0.5 cm, l/w ratio 2–4.1, leaf area 6.7–50 (avg. 17.3) mm<sup>2</sup> (n=10). Apex obtuse or acute, with rounded flanks; base obtuse, lobed on one side, convex on other, highly asymmetrical. Margin entire. Petiolule 0.3–0.5 mm long. Primary venation single, straight. Secondaries brochidodromous.

**Material examined.** UF 18049-43534, 53760, USNM 38281 (Holotype, Berry 1916c, Pl. 9, fig. 1, 1a)

**Discussion.** *Caesalpinia sellardsii* Berry (USNM 38281) is unique at Alum Bluff due to its small size and asymmetrical base (Berry 1916c; Pl. 3, figs 12, 13); it is similar to a few caesalpinoid and numerous mimosoid genera (Herendeen 1992, see Figs 318, 319). We found additional specimens that appear to be conspecific with Berry's specimen. Although it may represent Leguminosae, there are not enough characters to confirm the identification to *Caesalpinia*. Elsewhere, in the Miocene of the eastern United States, caesalpinoid fruits have been described from the Bridgeton Fm. as *Mezoneuron bridgetonense* Hollick (YPM 147068), although anatomical characters are needed for generic determination (Hollick 1896, Herendeen & Dilcher 1991).

***Leguminosites* sp. 1**

Pl. 3, fig. 14

**Description.** Leaflet complete, elliptic, symmetrical, unlobed, microphyll. Length 3.0 cm, width 2.0 cm, l/w ratio 1.5, leaf area 399.6 mm<sup>2</sup> (n=1). Apex obtuse, with rounded flanks; base acute, with rounded to straight flanks and slightly asymmetrical. Margin entire. Petiolule 2.0 mm long, 1 mm thick. Primary venation single, straight, weak. Secondary venation brochidodromous, at least three pairs, angle of divergence 43–52°. Secondary course straight to near margin, then looping upwards to superadjacent secondary. One pair of minor basal secondaries. Intersecondaries 1–2 per intercostal, extending ca 1/2 the distance to margin, proximal course parallel to secondaries, distal course splits, joining sub- and superadjacent secondaries. At least 3–4 distinct epimedial tertiaries per intercostal, angle of divergence 44–60°. Tertiary venation not well preserved.

Material examined. UF 18049-43512.

**Discussion.** The affinity of *Leguminosites* sp. 1 is uncertain because there is only one specimen. The general shape, apex and base, venation (Pl. 3, fig. 14) and distinct epimedial tertiaries can be found in extant genera of Fabaceae (e.g. *Abarema*, *Swartzia*). In *Abarema glauca* (Urb.) Barneby & J.W. Grimes the number of secondary vein pairs, their course and angle of divergence are very similar. Leaf morphology in *Swartzia* is diverse and would need cuticular characters for precise determination of species (Herendeen 1992). Thus, we have assigned morphotype status to this fossil specimen until better-preserved specimens are discovered. Fabaceae has 16 400 species and is cosmopolitan and widespread (Tab. 1).

Our specimen is similar to *Leguminosites* sp. 1 of the Miocene of Greece in shape, size, apex and base, and secondary venation, but there is no mention of intersecondary veins (Mantzouka et al. 2015). Elsewhere in the Miocene of the eastern United States, fabaceous leaflets are found at Hattiesburg (Stults et al. 2016) and Catahoula as *Pithecolobium oligocaenum* Berry but the leaflets are diamond-shaped (Berry 1916a). At Calvert, leaves of *Cassia toraformis* Berry seem relatively close to the Alum Bluff specimen in shape and venation, but they are half the size of the Alum Bluff specimen (Berry 1916c). *Gleditsia* and *Sophora* leaves are reported from Brandywine (McCartan et al. 1990), and *Leguminosites phaseolites* Heer leaves (YPM74645, 74644) from Bridgeton. Pollen is found at Gray (Zobba et al. 2011) and questionably from Brandon (Traverse 1955, 1994) (Tab. 1).

### ***Leguminosites* sp. 2**

Pl. 3, fig. 15

**Description.** Leaflet complete, curved, ovate, symmetrical, unlobed, nanophyll. Length 2 cm, width 1.3 cm, l/w ratio 1.5, leaf area 173.2 mm<sup>2</sup> (n=1). Apex acute, with straight flanks; base obtuse, with rounded flanks, asymmetrical. Margin entire. Petiolule 1.7 mm long. Primary venation single, curved. Secondary venation at base brochidodromous.

Material examined. UF 18049-43533.

**Discussion.** *Leguminosites* sp. 2 differs from *Leguminosites* sp. 1 of Alum Bluff in its curved,

ovate shape, and is similar to fossil *Sophora* species of Herendeen (1992, see Fig. 179) except for the curved shape of our specimen (Pl. 3, fig. 15).

Rosales

Family: Rhamnaceae Juss. 1789

Tribe: Paliureae Reiss. ex Endl.

Genus: *Paliurus* Mill. 1754

### ***Paliurus* sp.**

Pl. 3, figs 16–19

**Description.** Leaves incomplete or fragments, ovate to elliptic, unlobed, symmetrical, microphyll to mesophyll. Length 5.0–12.5 cm, width 2.6–7.0 cm, l/w ratio 1.7–2.3, leaf area 865.8–5594.4 (avg. 3210.3) mm<sup>2</sup> (n=5). Petiole slender, 5 mm long. Apex acuminate; base obtuse, with rounded flanks. Margin crenate/serrate. Tooth spacing irregular, one order of teeth, 4–6 teeth per cm, basal side convex, apical side flexuous to straight, sinus shape angular. Principal vein of tooth terminates at tooth apex (glands not observed). Primary venation single, straight to slightly sinuate, moderate. Secondaries craspedodromous with one pair of simple agrophic veins. Basal major secondary angle of divergence 25–55°, curving upwards ca 1/2 of leaf length, gradually thinning and running close to margin. 3–4 major secondaries diverging 28–60° from midvein at mid-portion of lamina, curving upward and becoming parallel to lateral secondaries. Major secondary spacing irregular, 22–27 mm apart, attachment excurrent. Two minor secondaries below basal secondaries, angle of divergence 40–45°. Minor secondary veins craspedodromous, diverging exmedially from lateral secondaries, at least 10 pairs, running straight to curving upward, sometimes branching before reaching margin. Minor secondary angle of divergence predominately acute (avg. 62° at mid-portion of lateral primary), with occasional obtuse angle. Intersecondaries 2–3, proximal course usually parallel to subadjacent secondaries, extending ca 1/2 the distance to margin, distal course merging with intercostal tertiaries. Tertiary veins mixed percurrent, angle in respect to

midvein obtuse. Epimedial tertiaries present, proximal course mostly acute to midvein, distal course parallel to intercostal tertiaries. Quaternary veins reticulate. Cuticle not preserved.

Material examined. UF 18049-43514, 43543, 43557.

**Discussion.** Characters of this leaf type, including simple agrophic venation, toothed margins (Pl. 3, figs 16–18), branching of secondaries from the midvein at or below the middle of the lamina (Pl. 3, fig. 18), and percurrent tertiary veins (Pl. 3, fig. 19) are found in extant genera of Rhamnaceae, specifically *Paliurus orientalis* (Franch.) Hemsl. (Schirarend & Olabi 1994), *Ziziphus obtusifolia* (Hook. ex Torr. & A. Gray) A. Gray, *Frangula sphaerosperma* (Sw) Kartesz & Gandhi (syn. *Ceanothus pubescens* Ruiz & Pav.) and *Colubrina asiatica* (L.) Brongn. These characters are also found in extant Salicaceae, such as some leaves of *Populus monticola* Brandegee, but the lower third of the leaves is entire or with minute teeth. Anatomical characters would be needed for verification of Salicaceae, such as paracytic stomata with lateral thickened margins of the stomatal pore, and trichomes on the veins of the adaxial surface (Mai & Walther 1978). In Rhamnaceae (e.g. *Paliurus*/*Ziziphus*/*Ceanothus* group) the stomata are anomocytic, and distinguishing between these three genera based on anatomical characters is very difficult (Knobloch & Kvaček 1976). Leaf architectural features of *Paliurus* Mill. and *Ziziphus* Mill. overlap, which bears out the relationship of *Paliurus* nested within *Ziziphus* (Islam & Simmons 2006), or *Paliurus* and *Ziziphus* placed within the tribe Paliureae (Schirarend & Olabi 1994, Richardson et al. 2000). On the basis of leaves alone it would be very difficult to distinguish *Paliurus*, *Ziziphus* and some species of *Ceanothus* (Johnston 1963, Bůžek 1971). We place the Alum Buff leaves tentatively in *Paliurus* based on the presence of the distinctive co-occurring winged fruit (Manchester 1999, Burge & Manchester 2008). Leaves of *Paliurus hemsleyanus* Rehder ex Schirarend & Olabi of eastern China are similar in shape, size, apex, base and margin, plus the adaxial and abaxial surfaces are glabrous (Shu M 2007). Shrubs and trees of *Paliurus* (5 species) occur in Asia and Southern Europe in a wide range

of habitats (Schirarend & Olabi 1994) but are no longer native to North America (Tab. 1).

The general shape, size, toothed margin, acrodromous and agrophic venation of *Populus zaddachii* Heer from the Oligocene of Germany (Mai & Walther 1978) and *Paliurus tiliaefolius* Unger from the Miocene of the North-Bohemian Basin (Bůžek 1971) are strikingly similar to our leaves. Leaves of *P. tiliaefolius* described by Knobloch & Kvaček (1976) are rounder than our fossil leaves. *Paliurus protonipponicus* K. Suzuki from the middle-late Miocene of Central Honshu, Japan, are also strikingly similar to our leaves, except that in *P. protonipponicus* the quaternary veins are percurrent, rather than reticulate (Ozaki 1991). Fossil *Paliurus* leaves are abundant in the Tertiary of the Northern Hemisphere (Hu & Chaney 1940, Knobloch & Kvaček 1976, Ozaki 1991, Meyer & Manchester 1997, Burge & Manchester 2008, Li et al. 2014). Elsewhere in the Miocene of the eastern United States, rhamnaceous fossils include leaves of *Paliurus catahoulensis* Berry from Catahoula (similar in shape and venation but the margins are entire) (Berry 1916a), and *Berchemia priscaformis* Berry from Calvert (Berry 1916b) (Tab. 1).

### *Paliurus favonii* Unger

Pl. 3, fig. 20

**Description.** Fruit an indehiscent disk-winged drupe; endocarp diameter 4 mm, wing diameter 16.5 mm; receptacle with evidence of rim. Wing 4.8 mm wide, oriented perpendicular to main axis of fruit, with fine, radiating, dichotomizing and anastomosing venation.

Material examined. UF 18049-26117.

**Discussion.** The general form and wing venation of fossil *Paliurus* fruit (Pl. 3, fig. 20) are similar to extant *Cyclocarya* Ljinsk. However, the presence of a receptacular rim in *Paliurus*, which is absent in *Cyclocarya*, supports the identification of this fossil (Manchester 1999, Burge & Manchester 2008). Fossil fruits of *Paliurus* described from North America fall within the range of variation known for *P. favonii* from Europe and Asia (Corbett 2004, Burge & Manchester 2008).

*Paliurus* fruits are known from Miocene deposits of western North America, Europe, Asia and Kazakhstan (Manchester 1999, Burge

& Manchester 2008). Elsewhere in the eastern United States, rhamnaceous seeds have been noted from Pensauken (Berry 1940), and pollen from Brandon (Traverse 1955, 1994) (Tab. 1).

Family: Ulmaceae Mirb. 1815

Genus: *Ulmus* L. 1753

***Ulmus prestonia* sp. nov.** (leaf)

Pl. 4, figs 1–4

1916c *Ulmus floridana* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 47, pl. 9, figs 5–7.

**Holotype.** One of the syntypes of Berry's *U. floridana* (non *U. floridana* Chapm.), USNM 38278b, is here designated holotype. Specimens USNM 38278a and c, treated previously among the syntypes of Berry 1916c, are here designated as paratypes. These are stored at the Department of Paleobiology, National Museum of Natural History, Washington, DC.

**Additional significant specimens.** UF18049-43510, 43513, 56769, deposited in the Division of Paleobotany, Florida Museum of Natural History, Gainesville, Florida.

**Etymology.** This species is named for the historic army post of Fort Preston, near Alum Bluff, Florida.

**Diagnosis.** Lamina elliptic-ovate, apex acute; base acute-obtuse, slightly asymmetrical to symmetrical. Petiole short. Margin simple serrate to occasionally doubly serrate with minute subsidiary teeth. Primary venation single, straight, moderate to stout. Secondary venation craspedodromous. Minor secondaries branching near margin. Intersecondaries few, tertiaries mostly reticulate with occasional percurrent veins. Exmedial tertiaries usually terminating at sinuses. Quaternary venation polygonal reticulate.

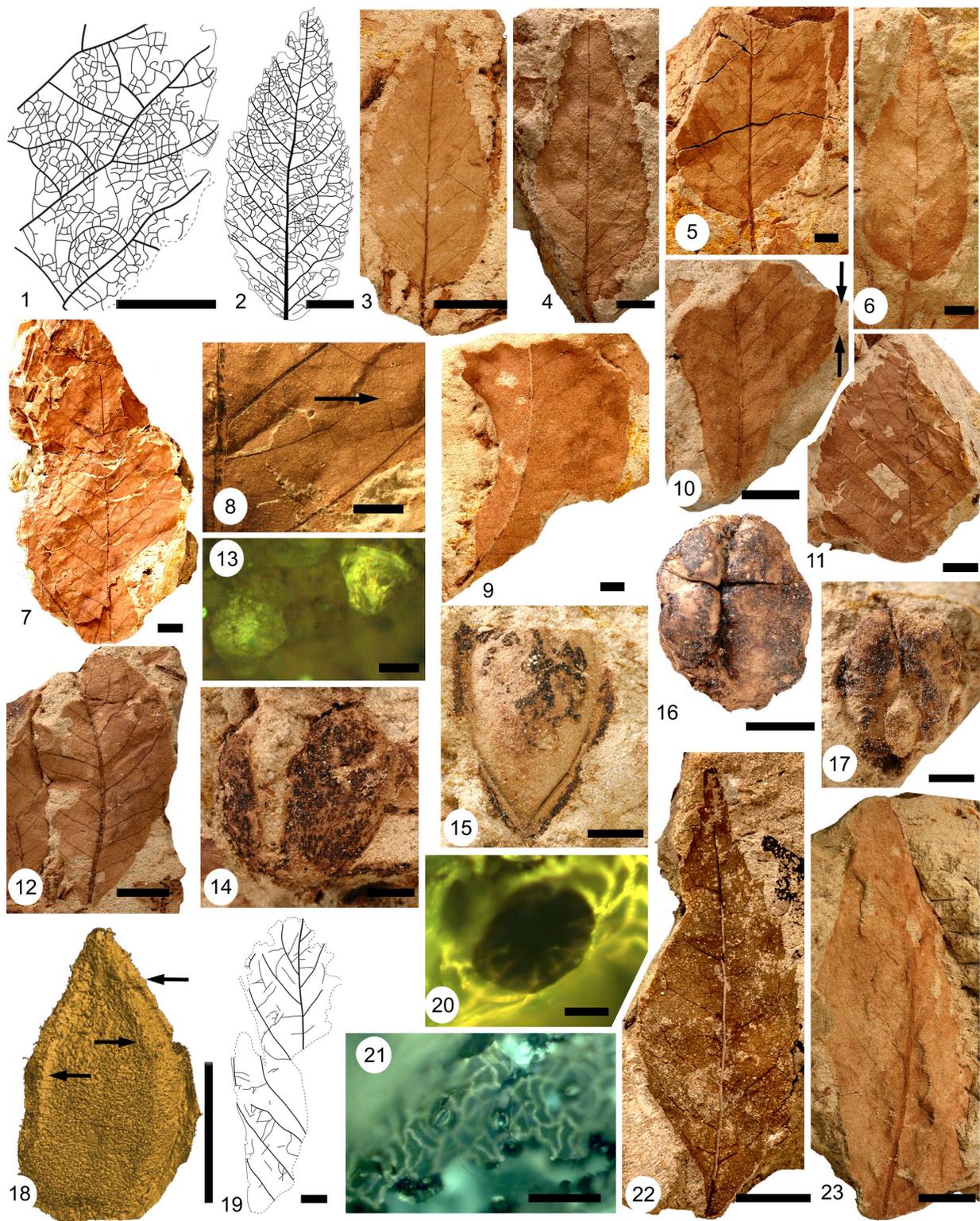
**Description.** Leaves complete to incomplete, elliptic to ovate, unlobed, symmetrical, nanophyll to microphyll. Length 1.4–6.3 cm, width 0.9–3.4 cm, l/w ratio 1.7–3.8, leaf area 83.9–1426.6 (avg. 482.3) mm<sup>2</sup> (n=54). Apex acute, with straight flanks; base acute or obtuse, with rounded, convex, cuneate to subcordate flanks, slightly asymmetrical to symmetrical. Margin serrate to occasionally compound serrate with one minute subsidiary tooth. Tooth spacing irregular, 3–10 teeth per cm, asymmetrical to

symmetrical, shallow triangular. Tooth basal side convex to straight, apical side straight, flexuous to concave, sinus shape angular. Principle vein central to tooth and terminates at tooth apex, 2 pairs of tertiary accessory veins present, upper pair crossing principal vein at acute to obtuse angle, lower pair crossing at right angles. Tooth apex lacks features. Petiole 2–9 mm, mostly wider than basal portion of midvein. Primary venation single, straight, moderate to stout, with evident striations. Secondary venation craspedodromous, up to 10 pairs, at intervals of 1.5–10 mm, spacing irregular, angle of divergence 20–65°, mostly 20–35° near apex. Secondary veins originating from midvein slightly decurrent to excurrent; secondary vein course straight or curving upward to margin; all major secondaries terminating in a tooth. Minor secondaries craspedodromous, branching 2–4 per leaf at or less than 1/2 the distance from margin. Intersecondary veins none or one per leaf, rarely 2, extending at or less than 1/2 the distance from margin, proximal course parallel to secondary, distal course intersects tertiary. Tertiary venation reticulate, less often alternate percurrent, vein angle obtuse relative to midvein. Epimedial tertiaries present. Straight exmedial tertiaries from secondaries that terminate at sinus, or looped tertiaries that merge with sinus and then join adjacent secondary vein, or exmedial quaternaries from tertiaries terminate at sinus. Quaternary venation irregular polygonal reticulate. Areolation well developed. Cuticle not preserved.

**Material examined.** UF 18049-43510, 43513, 43555a, 56769, USNM 109206b, 38278a–c.

**Discussion.** We reject the previous assignment to *Ulmus floridana* by Berry (1916c) because *U. floridana* Chapman (1860) is an extant species (syn. of *Ulmus americana* L.) that takes priority, and the leaf characters of this fossil are dissimilar to *U. americana*. Also, Berry's description of an acuminate apex and doubly compound teeth do not match his illustrations of an acute apex and only occasional doubly compound teeth.

The *Ulmus prestonia* characters of major and prominent minor craspedodromous venation, and serrate leaf margin with one to occasionally 2 orders of teeth (Pl. 4, figs 1–4) are found in Ulmaceae (e.g. *Ulmus* L., *Zelkova* Spach,



**Plate 4.** 1–4. *Ulmus prestonia*, leaves with serrate margins and slightly asymmetrical to symmetrical base, 1, 2 – line drawings, UF18049-43555a, UF18049-56769, respectively; 3, 4 – UF18049-43510, UF18049-43513, respectively; 5, 6. *Ulmus* sp. 1, serrate margin leaves with highly asymmetrical base, UF18049-43531, UF18049-29132, respectively; 7, 8. Morphotype AB36, 7 – serrate margin leaf with craspedodromous major and minor secondary veins, 8 – intersecondary vein terminating at percurrent tertiary (arrow), UF18049-43556; 9, 10. Morphotype AB5, 9 – curved shape with incurved lamina and coriaceous texture, UF18049-43573, 10 – distal serrations (arrows), UF18049-61184; 11–13. *Carya* cf. *serraefolia* (Goepf.) Kräusel, 11, 12 – craspedo- to semicraspedodromous leaves, UF18049-43504a, UF18049-43588a, respectively, 13 – embedded glands, UF18049-53703; 14–18. *Carya* sp., 14 – dehiscent husk, UF18049-43528a, 15 – nut valve, UF18049-43528b, 16, 17 – locule cast, UF18049-43526, UF18049-43500, respectively, 18 – surface rendering from CT scan data of 4-valved nut, with three ridges showing (arrows), UF18049-53716a; 19–21. Morphotype AB16, 19 – camptodromous venation, 20 – gland, 21 – brachyparacytic stomata with sinuate to sinuolate anticlinal cell walls, UF18049-53309; 22. *Sambucus* sp., asymmetrical leaf with serrate margin and acuminate apex, UF18049-43521; 23. Morphotype AB54, ovate leaf with acuminate apex, UF18049-69528. Scale bars: 1, 4–6, 9, 14–17 = 5 mm; 2, 3, 7, 10–12, 18, 22 = 10 mm; 8 = 2 mm; 13 = 50  $\mu$ m; 19 = 15 mm; 20 = 20  $\mu$ m; 21 = 40  $\mu$ m; 23 = 20 mm

*Planera* Giseke) and Betulaceae (e.g. *Ostrya* Scop). In *Ostrya virginiana* (Mill.) K. Koch the tooth apices are usually longer and much narrower than in *Ulmus*. Within Ulmaceae the number of intersecondaries distinguishes *Planera* from *Ulmus* (Burnham 1986). *Planera aquatica* Walt. ex J.F. Gmel. can have more than five intersecondaries per leaf, and the secondaries readily branch 2–6 per leaf side. Leaf venation in *Ulmus* and *Zelkova* is very similar but there is a difference in the tertiary venation pattern and secondary branching (Tanai & Wolfe 1977, Burnham 1986, Wang et al. 2001). In *Zelkova schneideriana* Hand.-Mazz. and *Z. sinica* C.K. Schnied. the tertiary veins are conspicuously alternate percurrent and secondary branching occurs at three fourths the distance from the margin. Our specimens show a serrate margin, tertiary veins reticulate and sometimes alternate percurrent, and secondary branching at up to half the distance from the margin in the mid-portion of the lamina (Pl. 4, figs 1, 2), characters also found in extant *Ulmus*. Species very similar to *Ulmus prestonia* are *Ulmus pumila* L. and *U. crassifolia* Nutt., except that they predominantly have compound teeth and the exmedial tertiaries branch near the margin and terminate at the sinuses, whereas the fossil has predominantly simple teeth and the exmedial tertiaries may join the sinus or loop to the sinus and then join the superadjacent secondary. In North America, *Ulmus* has 18 species ranging from north temperate regions (Radford et al. 1968) to the fringe of subtropical regions in Mexico (Britton & Brown 1913, Wunderlin 1998). Adjacent to Alum Bluff, today *Ulmus alata* Michx. and *U. americana* are found in floodplain and bluff habitats, while *U. rubra* is restricted to the bluff (Clewell 1985, FSU Herbarium 2016) (Tab. 1).

Berry (1916c) noted that his fossil species from Alum Bluff is similar to *U. longifolia* Unger (*U. pyramidalis* Goepfert) of Europe, but the latter seems to have more secondaries (Bůžek 1971). Unfortunately the preservation of the Alum Bluff specimens is not good enough for the marginal ultimate venation to be identified. Leaves similar to our specimens include the smaller form of *Ulmus speciosa* Newberry from the Miocene of western North America, although subsidiary teeth are more common in that taxon (Newberry 1898, Tanai & Wolfe 1977, Burnham 1986), and the slightly asymmetrical leaves of *Ulmus*

*protoparvifolia* Hu and Chaney from the Miocene of China (Hu & Chaney 1940). Elsewhere in the Miocene of the eastern United States, *Ulmus* leaves are reported from Hattiesburg (Berry 1916a), Calvert (Berry 1916b), Brandywine (McCartan et al. 1990) and Bridgeton (YPM 147057, Hollick 1897). *Ulmus* pollen is found from several Miocene sites, but not Hattiesburg and Pensauken (Traverse 1955, 1994, Grellier & Rachele 1983, Frederiksen 1984, McCartan et al. 1990, Pazzaglia et al. 1997, Rich et al. 2002, Wallace & Wang 2004, Jarzen et al. 2010, Zobba et al. 2011) (Tab. 1).

### *Ulmus* sp. 1 (leaf)

Pl. 4, figs. 5, 6

**Description.** Leaves incomplete to complete, ovate, unlobed, symmetrical, microphyll. Length 4.1–8.0 cm, width 1.7–3.4 cm, l/w ratio 1.8–2.4, leaf area 464.2–1811.5 (avg. 1122.1) mm<sup>2</sup> (n=3). Apex acute, with straight flanks; base acute or obtuse, with cuneate to convex flanks, highly asymmetrical, one side with rounded base. Petiole 0.7–1.0 cm, width same as basal portion of midvein. Margin serrate to sometimes compound serrate with one large subsidiary tooth, 3–4 teeth per cm, basal shape straight to convex, apical shape straight, sinus shape angular. Principle vein central to tooth and terminating at tooth apex. Primary venation single, straight, moderate, with striations. Secondary venation craspedodromous, up to 7 pairs, at intervals of 3–10 mm, spacing irregular, angle of divergence 52–60° basal, 37–44° mid and apical portion of lamina. Secondary attachment excurrent, secondary course straight or curving slightly upward to margin. All major secondaries terminate in a tooth. Minor secondaries craspedodromous, branching ca 2 per leaf at or less than 1/2 the distance from margin. Intersecondary veins 0–1 per leaf, proximal course parallel to secondary, distal course merging with percurrent tertiary vein. Tertiary venation inconspicuously percurrent and reticulate. Epimedial tertiaries mostly perpendicular or acute to midvein. Curved exmedial tertiaries from secondaries that terminate at sinus, or tertiary from percurrent tertiary that terminate at sinus. Quaternary venation and cuticle not preserved.

**Material examined.** UF 18049-29132, 43531.

**Discussion.** *Ulmus* sp. 1 is distinguished from *Ulmus prestonia* by the former's highly asymmetrical base and relatively large subsidiary teeth. In *Ulmus* sp. 1 the highly asymmetrical base, inconspicuous percurrent tertiaries, and exmedial tertiaries terminating at the sinuses (Pl. 4, figs 5, 6) are similar to those of *U. americana* L., *U. glabra* Hudson and *U. procera* Salisbury, except that the teeth in these extant species are mostly to strictly doubly compound with 1–3 subsidiary teeth. There are over 40 specimens (Appendix 2) in the collection that appear to represent *Ulmus*, but due to incomplete preservation it is difficult to determine whether they conform to one or multiple species.

*Ulmus paucidentata* H.V. Smith from the Miocene of the western United States is similar to our specimens, except that its subsidiary teeth are small (Tanai & Wolfe 1977).

#### ***Ulmus* sp. 2 (fruit)**

Pl. 3, fig. 21

**Description.** Fruit stipitate, with well-developed wing surrounding the elliptical body but without free stigmatic arms. Fruit body (minus stipe) length 8 mm, width 4 mm, elliptical central body length 6 mm, width 3 mm, stipe length 3 mm. Wing with prominent marginal vein and laterally deflected axial vein extending from stipe to fruit body.

**Material examined.** UF 18049-71312.

**Discussion.** A stipitate winged fruit with a marginal vein and an axial vein extending from the stipe to the fruit body are characteristic of the genus *Ulmus* (Manchester 1989). The fossil is similar to *Ulmus pseudo-fulva* from the Eocene of western North America but our fossil lacks a persistent calyx (Manchester 1989). At present, no fruits of *Ulmus* have been described from the Miocene of the eastern United States.

#### **Morphotype AB36 (leaf)**

Pl. 4, figs 7, 8

**Description.** Leaf incomplete, ovate, unlobed, mesophyll. Length 13.5 cm, width 6.1 cm, l/w ratio 2.2, leaf area 5484.5 mm<sup>2</sup> (n=1). Apex acute, with straight flanks; base missing. Margin serrate. Tooth spacing irregular, 1–2 orders of teeth, 3–5 teeth per cm, basal shape convex, straight to flexuous, apical shape straight to concave, sinus shape angular. Principle vein

central to tooth and terminating at tooth apex, tooth apex lacking features. Primary venation single, straight, weak, with evident striations. Secondary venation craspedodromous, 12 pairs at intervals of 5–18 mm, spacing irregular, angle of divergence 42–70°, decreasing apically. Secondary attachment mostly excurrent, some slightly decurrent, secondary course straight to curved slightly upward to margin, all major secondaries terminate in a tooth. Minor secondaries craspedodromous, dividing at 1/2 the distance from margin. Intersecondaries at least 5, length at or less than 1/2 the distance from margin, proximal course parallel to secondary, distal course perpendicular to subadjacent major secondary or terminating at percurrent tertiary. Tertiaries predominantly alternate percurrent. Epimedial tertiaries present. Straight exmedial tertiaries from secondaries that terminate at sinus. Cuticle not preserved.

**Material examined.** UF 18049-43556.

**Discussion.** Based on a single leaf it is difficult to determine where Morphotype AB36 falls between extant *Ulmus* and *Planera*. The distal course of the intersecondaries and the predominantly alternate percurrent tertiaries (Pl. 4, figs 7, 8) are similar to those of *Planera aquatic* Walt. ex J.F. Gmel. and *Ulmus palmetta*, while its size is similar to that of *U. palmetta*. The number and thickness of *U. palmetta* intersecondaries come closer to those of any other *Ulmus* species than to *Planera*, but *Planera* intersecondaries are still more pronounced.

*Ulmus speciosa* Newberry from the Miocene of the western United States is similar in size and shape but has 1–4 subsidiary teeth and lacks intersecondaries, unlike Morphotype AB36 (Chaney & Axelrod 1959). Within the Miocene of the eastern United States, *Planera* leaves have been noted from Calvert (Berry 1916b), and pollen from Cohansey (Rachele 1976) (Tab. 1).

Order: Fagales Engl. 1892

Family: Fagaceae Dumort 1829

Gen. et sp. indet.

#### **Morphotype AB5**

Pl. 4, figs 9, 10

**Description.** Leaves incomplete, obovate, asymmetrical, unlobed, microphyll. Length

6.2–6.4 cm, width 3.4–4.0 cm, l/w ratio 1.6–1.9, leaf area 1449.2–1651.7 (avg. 1150.5) mm<sup>2</sup> (n=2). Apex missing; base acute with cuneate flanks. Margin entire proximally, sometimes serrate distally. Petiole 5 mm long. Tooth basal side concave, apical side convex, tooth apex simple, tooth sinus angular. Primary venation single, curved, weak to moderate. Secondary venation brochidodromous to craspedodromous, at least 8 pairs, at intervals of 3.5–7 mm, spacing decreasing slightly basally, irregular, angle of divergence rather consistent, averaging 51°. Secondary attachment excurrent, secondary course straight up and out towards margin. Higher-order venation and cuticle not preserved.

Material examined. UF 18049-43573, 61184.

**Discussion.** The incurved lamina and curved shape, suggesting a coriaceous texture, along with asymmetry, straight secondaries, obovate shape and short petiole of UF 18049-43573 (Pl. 4, fig. 9) suggest an affinity with Fagaceae. The obovate shape, asymmetry, parallel craspedodromous secondaries and distal serrations of UF 18049-61184 (Pl. 4, fig. 10) also suggest an affinity with Fagaceae (e.g. some species of *Quercus* L.). This morphology can be found in four subgenera of *Quercus*: *Cyclobalanopsis*, *Lepidobalanus* (= *Quercus*), *Protobalanus* and *Erythrobalanus* (Jones 1986). Unfortunately, the specimens lack cuticle, which precludes the use of trichome type and stomatal shape, important characters for confirming a *Quercus* affiliation. Better-preserved specimens may help to determine whether these two different morphotypes should be distinguished within Fagaceae. Fagaceae has 1050 species, is cosmopolitan, and is locally widespread for *Quercus* (Clewell 1985) (Tab. 1).

The obovate leaf shape, distal serrations and straight secondary veins of Morphotype AB5 are superficially similar to *Quercus deperdita* (Ung.) Iljinskaja from the Miocene of Swoszowice, Poland (Iljinskaja 1964). Elsewhere in the Miocene of eastern North America, *Quercus* leaves are found at Hattiesburg (Stults et al. 2016, both lobed and entire), Calvert (Berry 1916b, 1941, lobed), Gray (pers. obs., lobed), Brandywine (McCartan et al. 1990) and Bridgeton with entire-margined *Quercus klipstenii* Etts. and *Quercus imbricaria* Michx. (YPM 147078) (Hollick 1897). *Quercus* fruits are

found at Brandon (Tiffney 1994, plus wood), Calvert (Berry 1916b), Gray (Liu 2011), Brandywine (McCartan et al. 1990), and Pensauken (Berry 1940). *Quercus* pollen is relatively common at Alum Bluff and at all Miocene sites in the eastern United States except for Hattiesburg and Catahoula (Traverse 1955, 1994, Rachele 1976, Frederiksen 1984, Pazzaglia et al. 1997, Rich et al. 2002, Jarzen et al. 2010, Zobaa et al. 2011) (Tab. 1).

Family: Juglandaceae DC. ex Perleb 1818

Genus: *Carya* Nutt. 1818

*Carya* cf. *serraefolia* (Goepp.) Kräusel

Pl. 4, figs 11–13

**Description.** Leaflets incomplete or fragmented, elliptic or obovate, unlobed, asymmetrical, microphyll to notophyll. Length 4.5–11 cm, width 2–6 cm (n=27), l/w ratio 1.5–3.0, leaflet area 200.1–2953.4 (avg. 1576.8) mm<sup>2</sup>. Apex acute, with straight flanks; base acute, with cuneate to rounded flanks, symmetrical to asymmetrical. Margin serrate in upper 2/3 of leaf. Tooth spacing irregular, 1–2 orders of teeth, 3–5 teeth per cm, basal side convex, straight to flexuous, apical side concave, straight to flexuous, sinus angle acute. Prominent vein central to tooth but sharply curved towards apex, one pair of opposite accessory veins at base of tooth, extending out to margin. Tooth apex lacks features. Primary venation single, straight or curved, weak to stout. Secondary venation craspedodromous to semicraspedodromous, up to 12 pairs, at intervals of 2–10.0 mm, spacing irregular, angle of divergence 58–90° basally, 48–74° mid-lamina, 42–68° apically. Secondaries running straight to near margin, then arching abruptly upwards, near apex secondaries arching upward to margin. A few secondaries dividing near midvein into 2 major branches. Secondaries have 1–3 successive exmedial branched minor secondaries at or more than 1/2 the distance from midvein, each branch entering a successive tooth. Occasionally one intersecondary per intercostal, extending up to 1/2 the distance to leaf margin, proximal course parallel to secondaries, distal course basiflex. Tertiary veins mostly opposite percurrent, rarely alternate percurrent, straight, rarely sinuous, parallel to each other. Tertiary angle obtuse and decreasing exmedially. Quaternary

veins not well preserved. Marginal ultimate venation looped. Glands ca 0.1 mm diameter, embedded in cuticle.

Material examined. UF 18049-43504a, 43588a, 53703.

**Discussion.** The asymmetrical base, craspedodromous to semicraspedodromous secondary veins having successive exmedial branches that enter the teeth (Pl. 4, figs 11, 12), and opposite percurrent tertiary veins of *Carya* cf. *serraefolia* are consistent with characters of extant juglandaceous leaflets, particularly *Carya* Nutt. (Sargent 1933), *Pterocarya* Kunth and *Cyclocarya* Iljinsk. In *Cyclocarya paliurus* (Batalin) Iljinsk. the opposite percurrent tertiaries run in a sinuous pattern and the teeth are simple. The assignment to *Carya* is supported by its predominantly craspedodromous secondaries, the secondaries having 1–3 exmedial branches that successively enter the teeth, and tertiaries that are percurrent, straight and parallel to each other, as in extant *C. glabra* (Mill.) Sweet. The spherical dots embedded in the cuticle (Pl. 4, fig. 13) are interpreted as glands, sometimes called “resin dots” (Hardin 1992), that are also characteristic of *Carya*. Fasciculate trichomes and peltate scales are common in *Carya* but can be sloughed off on mature leaves such as *Carya glabra* (Mill.) Sweet (Hardin & Stone 1984). The lack of this trichome type and scales on *Carya* cf. *serraefolia* may be due to this process. The size of the fossil leaflet is within the range of *Carya floridana* Sarg. Hence we hypothesize that these leaflets represent *Carya*, which has 17 species, extending from eastern North America to Central America as well as Eastern Asia (Radford et al. 1968), preferring higher latitudes but which can extend to the fringe of subtropical regions (Britton & Brown 1913, Wunderlin 1998). Adjacent to Alum Bluff, *Carya* (5 species) is widespread (Godfrey 1988, Clewell 1985) (Tab. 1).

Within the Neogene, fossil leaflets and pollen of *Carya* are widespread, with occurrences in, for example, the Miocene of Clarkia, Idaho, USA (Smiley & Rember 1985), Shandong Province, China (Hu & Chaney 1940), Bohemia, Czech Republic (*C. serraefolia* (Goepf.) Kräusel; Knobloch 1961, Bůžek 1971, Teodoridis 2003) and central Honshu, Japan (Ozaki 1991). Characters shared with *Carya* cf. *serraefolia* (Goepf.) Kräusel include serration type,

asymmetrical leaf base and cuneate shape, and predominately craspedodromous secondaries that sometimes divide into two major branches near the midvein, secondaries giving off three successive exmedial minor veins at three fourths the distance to the margin and entering the teeth, and occasionally one intersecondary per intercostal, extending up to half the distance to the leaf margin (Kräusel 1921, Worobiec 2003). Elsewhere in the Miocene of the eastern United States, *Carya* leaflets are found at Brandywine (McCartan et al. 1990) and Bridgeton (YPM 147072), and *Carya* pollen at all the Miocene sites except for Hattiesburg (Traverse 1955, 1994, Rachele 1976, Frederiksen 1984, Pazzaglia et al. 1997, Rich et al. 2002, Wrenn et al. 2003, Jarzen et al. 2010, Zobaa et al. 2011) (Tab. 1).

### ***Carya* sp.**

Pl. 4, figs 14–18

**Description.** Fruit ovate, dehiscent, 4-valved, with 4 longitudinal ridges, surface smooth. Apex acute; base unknown, 1.6–2.9 × 1.2–1.9 cm (n=4). Nut ovoid, 4-valved, unilocular, single-seeded, surface smooth, apex and base rounded; length 1.8–2.7 cm, equatorial width 1.1–2.2 cm wide (n=8). Nut valves 1.7–2.6 cm long, 1.0–1.8 cm wide (n=8). Locule cast (mold) ovoid to globose, 1.5–2.5 cm long, 1.0–1.8 cm wide, 0.4–1.1 cm thick (n=15), 4-lobed. Primary septum ca 0.75 mm, secondary septum ca 0.5 mm.

Material examined. UF 18049-43500, 43526, 43528a,b, 53716a.

**Discussion.** The fruit with a dehiscent husk (Pl. 4, fig. 14), nut valves (Pl. 4, fig. 15) and the general outline of the locular casts (Pl. 4, figs 16, 17) of Alum Bluff *Carya* sp. are also found in extant *Carya* (Sargent 1933, Stone 1997). The general shape, acute apex and four longitudinal ridges of the Alum Bluff *Carya* sp. nuts (Pl. 4, fig. 18) are similar to those of extant *Carya illinoensis* (Wangenh.) K. Koch but *C. illinoensis* is twice the size of our fossils.

Within the Neogene, fossil fruits of *Carya* are widespread, such as in the Miocene of western North America, Europe and Asia (Hu & Chaney 1940, Gregor 1978, Smiley & Rember 1985, Manchester 1987, Van der Burgh 1987). Elsewhere in the Miocene of the eastern United States, *Carya* fruits are found

at Hattiesburg (Stults et al. 2016), Brandon (Tiffney 1994), Gray (Per. obs.) and Brandywine (McCartan et al. 1990) (Tab. 1).

Order: Lamiales

Family: Oleaceae

Gen. et sp. indet.

### Morphotype AB16

Pl. 4, figs 19–21

**Description.** Leaf incomplete, elliptic, mesophyll. Length 16.0 cm, width 6.4 cm, l/w ratio 2.5, leaf area 6819.8 mm<sup>2</sup> (n=1). Apex and base missing. Margin poorly preserved, with entire margin visible at middle to lower portion on one side. Upper portion of primary venation single, straight, weak. Secondary venation eucamptodromous, upper venation possibly brochidodromous, angle of divergence 36–40°. One intersecondary vein extending more than 1/2 of leaf width, possibly merging into tertiary vein. Tertiary venation not well preserved, some percurrent. Areoles tetragonal, predominantly closed. Abaxial epidermal cells random, oblong, 3–4-sided, anticlinal cell walls sinuate to sinuolate, sometimes straight, 26.5–51.4 × 7.1–20.5 µm. Stomata brachyparacytic, guard cells 10.5–14.1 × 2.1–3.8 µm, subsidiary cells 13.9–22.4 × 3.3–8.1 µm. Glands sessile, 41.8–66.0 µm diameter (epifluorescence).

**Material examined.** UF 18049-53309.

**Discussion.** The cuticle description of Morphotype AB16 is based on light microscopy and epifluorescence. The general shape, size, margin, camptodromous venation, intersecondary veins (Pl. 4, fig. 19) and glands (Pl. 4, fig. 20) of Morphotype AB16 can be found in numerous extant families such as Myristicaceae (*Osteophloeum platyspermum* (Spruce ex A. DC.) Warb.; Smith 1937), Oleaceae (*Osmanthus americanus* (L.) A. Gray; Hardin 1992) and entire-margin Lamiaceae (e.g. *Aegiphila*; Moldenke 1934). In *Aegiphila lhotskiana* Cham. the stomata are anomocytic (Bieras & Sajo 2009). In *O. platyspermum* the anticlinal cell walls are straight to round and the stomata are barely visible, anomocytic, and not on the same plane as the epidermal cells. The sinuate to sinuolate anticlinal cell walls and

brachyparacytic stomata of Morphotype AB16 (Pl. 4, fig. 21) are close to those of Oleaceae. In numerous *Osmanthus* species the abaxial anticlinal cell walls are sinuolate to sinuate; the stomata are usually anomocytic to rarely cyclocytic but have been noted as brachyparacytic, while the glands have radial striations (Xu et al. 2007, Chang et al. 2008). Oleaceae has 900 species and is subcosmopolitan. *Osmanthus* has 1–2 species in the southern United States.

Within the Miocene of the eastern United States, pollen of Oleaceae is found at Gray (Zobba et al. 2011) (Tab. 1).

Order: Dipsacales

Juss. ex Bercht. & J. Presl 1820

Family: Adoxaceae E. Mey. 1839

Genus: Sambucus L.

### *Sambucus* sp.

Pl. 4, fig. 22

**Description.** Leaflet complete, ovate, unlobed, symmetrical, microphyll. Length 6.2 cm, width 2.2 cm, l/w ratio 2.8, leaf area 909.8 mm<sup>2</sup> (n=1). Apex acuminate, with straight flanks; base acute, with straight and concave flanks, highly asymmetrical. Margin serrate. Tooth spacing irregular, one order of teeth, 4 teeth per cm, proximal and distal shape of teeth straight, sinus angle angular. One tertiary vein exmedial of secondary vein loop entering each tooth medially and terminating at tooth apex. Exmedial veins from secondary loop entering sinuses. Tooth apex sharply acute. Primary venation single, curved, moderate. Secondary venation semicraspedodromous, at least 7 pairs, at intervals of 3.5–4.0 mm basally, 9.0 mm at midsection of lamina, and 2.5–5.0 mm apically, angle of divergence 52–57° at basal and midsection, 65–70° at apical section. Secondary course gently arching outward and upward to near margin, then arching admedially to superadjacent secondary, with exmedial branching sending tertiary vein to teeth. Intersecondaries 1–2 per intercostal, short to long, with long intersecondaries traversing ca 1/2 the distance to margin. Tertiary and quaternary veins regular polygonal reticulate. Few percurrent tertiaries present. Cuticle not preserved.

Material examined. UF 18049-43521.

**Discussion.** The basal veins being closer to one margin than the other suggest asymmetry of the leaflet rather than a simple leaf. Characters of an elliptic leaflet with an asymmetrical leaf base, acuminate apex, one order of serrate teeth (Pl. 4, fig. 22), secondary veins semicraspedodromous, 1–2 short and long intersecondaries, exmedial veins from secondary loops entering both teeth and sinuses, tertiary veins reticulate and a few percurrent tertiaries are similar to characters of extant Sapindaceae (e.g. *Koelreuteria elegans* (Seem.) A.C. Sm.) and Adoxaceae (e.g. *Sambucus canadensis* L.). The difference is that leaflets of *K. elegans* have one entire side toothed and the opposite side with teeth only near the apex, and the teeth apices in *K. elegans* are sometimes hooked towards the apex. The only difference from *S. canadensis* is that the angle of divergence is 35–40° throughout the leaflet. *Sambucus* has 20 species and can tolerate cold to subtropical climates, as in *Sambucus nigra* L. (Institute for Systematic Botany 2016, USDA 2016). Adjacent to Alum Bluff, *Sambucus nigra* L. is found on the floodplains (Clewell 1985, FSU Herbarium 2016) (Tab. 1).

In *Sambucus* sp. of Alum Bluff there is a superficial similarity to *Rhus lesquereuxi* Knowlton and Cockerell from the Eocene Florissant Beds of Colorado, except for the craspedodromous venation as opposed to semicraspedodromous venation in *Sambucus* sp. (MacGinite 1953). Within the Miocene of the eastern United States, *Sambucus* leaves are common at Hattiesburg (Stults et al. 2016), and possibly fruit at Brandywine (McCartan et al. 1990) (Tab. 1).

Incertae Sedis

Lauraceae/Cannabaceae

#### Morphotype AB54

Pl. 4, fig. 23

**Description.** Leaves incomplete, ovate, notophyll. Length 10.5–14.0 cm, width 4.0–4.5 cm, l/w ratio 2.6–3.1, leaf area 2797.2–4195.8 (avg. 3496.5) mm<sup>2</sup> (n=2). Apex acuminate, angle acute; base missing. Margin entire. Primary venation single, curved, stout. Secondary

venation eucamptodromous, alternate, spacing 10–12 mm, excurrent to midvein, running straight then curving upwards and thinning towards margin. Secondary angle of divergence 40–48° midsection, 30–35° apically. Few percurrent tertiaries preserved.

Material examined. UF 18049-69528.

**Discussion.** Morphotype AB54 seems to be a unique leaf type within the Alum Bluff flora. Numerous angiosperm species have acuminate apices and entire margins, such as *Diospyros virginiana* L., *Cinnamomum camphora*, *Licaria triandra* (Sw.) Kosterm., *Nectandra* sp., *Wisteria sinensis* (Sims) Sweet (Godfrey 1988), *Trichilia* sp., *Sapindus saponaria* L. and *Aphananthe monoica* (Hemsl.) J.-F. Leroy. There are very few characters for Morphotype AB54, but the acuminate apex, general leaf shape, angle of divergence of the secondaries, the secondaries curving upward and thinning towards the margins, and percurrent tertiaries (Pl. 4, fig. 23) are close to features of Lauraceae and Cannabaceae (*A. monoica*).

Order: Magnoliales

Juss. ex Bercht. & J. Presl 1820

cf. Magnoliaceae/Annonaceae

#### Morphotype AB11

Pl. 5, fig. 1

**Description.** Leaves incomplete to fragmentary, elliptic, symmetrical, unlobed, microphyll to notophyll. Length 7.5–10.5 cm, width 4.0–5.0 cm, l/w ratio 1.9–2.1, leaf area 1998–3496.5 (avg. 2747.3) mm<sup>2</sup> (n=4). Leaf surface clearly evident, with well-defined primary and secondary veins. Apices missing; base obtuse with rounded to slightly cordate flanks, margin entire. Primary venation single, straight, stout. Secondary venation basally eucamptodromous, otherwise brochidodromous. At least 9 pairs of secondary veins, at intervals of 3.5–10 mm, spacing irregular, angle of divergence decreasing apically: 60–84° basal, 54–74° middle and 48–53° apical portion of lamina. Secondary attachment excurrent to slightly flared, course gently curving upward and out towards margin. 0–2 intersecondary veins per intercostal, traversing from 3/4 to 1/4 distance to margin, proximal course parallel to

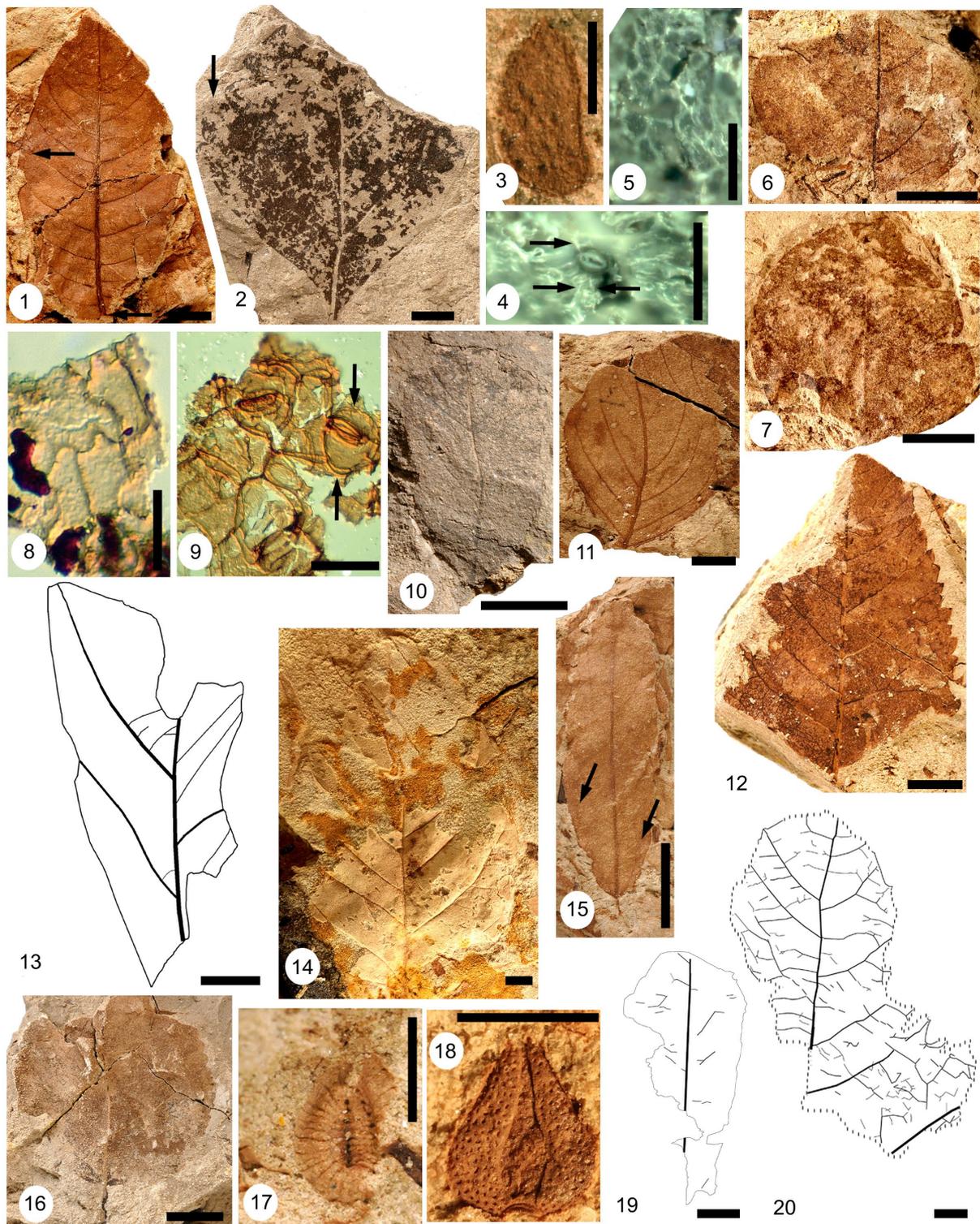
secondaries, distal course merging with a few weak percurrent tertiaries or looping down to subadjacent secondaries. Tertiary veins percurrent, quaternary veins reticulate. Cuticle not preserved.

Material examined. UF 18049-43551.

**Discussion.** The Morphotype AB11 characters of an entire leaf margin, brochidodromous venation (Pl. 5, fig. 1), intersecondaries that extend from 3/4 to 1/4 distance to margin and then join an intercostal tertiary or the secondary vein are found in extant Magnoliales (Hickey & Wolfe 1975), Laurales, Theaceae and many other angiosperm taxa. In Magnoliales we have six families, of which Annonaceae and Magnoliaceae come close to matching our fossils. Since our fossils lack cuticle, identification to species would be futile since trichome types are very important in discerning genera of Annonaceae and Magnoliaceae (Baranova 1972, Baranova et al. 2000, Roth 1981). For Annonaceae such as *Rollinia exsucca* (DC.) A. DC. the secondary angle of divergence, one series of exmedial loops, and intersecondaries that merge into percurrent tertiaries or loop to subadjacent secondaries match Morphotype AB11 (Klucking 1986). For Magnoliaceae such as *Magnolia posana* (Pittier) Dandy and *Magnolia liliifera* (L.) Baill. all the aforementioned characters match Morphotype AB11, but these extant species have tertiaries that are mostly reticulate, and cuneate leaf bases. Morphotype AB11 has a few weak percurrent tertiaries. For Degeneriaceae such as *Degeneria vitiensis* L.W. Bailey & A.C. Sm. the angle of divergence is too steep and the tertiaries are reticulate. For Eupomataceae such as *Eupomatia laurina* R. Br. the angle of divergence is too steep. For Himantandraceae such as *Galbulimima belgraveana* (F. Muell.) Sprague there are 1–3 intersecondaries per intercostal, and they sometimes extend to the brochidodromous loop. For Myristicaceae the angle of divergence is too steep and there are zero to few intersecondary veins. For Lauraceae such as *Beilschmiedia recurva* B. Hyland the angle of divergence, intersecondaries and weakly percurrent tertiaries match Morphotype AB11 but there are two series of exmedial loops in *B. recurva* (Christophel & Rowett 1996). For Theaceae such as *Cleyera pachyphylla* Chun

ex H.T. Chang the apical portion of the leaf is denticulate (Yu & Chen 1991). Magnoliaceae has 220 species regionally distributed from eastern North America to Central America (Stevens 2001), and Annonaceae has ca 2440 species regionally distributed from the northern United States to the tropics (Klucking 1986). Adjacent to Alum Bluff, both families are widespread.

The vast majority of Miocene fossil records for Magnoliaceae and Annonaceae are based on leaf venation, a character of limited diagnostic value. One can point to the convergent evolution of leaf venation traits in other families such as Lauraceae (Ferguson 1971). Putative fossil *Magnolia* leaves are abundant throughout the Northern Hemisphere (Lesquereux 1878b, Berry 1938, Uemura 1988), among which Morphotype AB11 is most similar to *M. miocenica* Hu & Chaney from the Miocene of China, although the apex differs (Hu & Chaney 1940). *Magnolia* leaves with higher identification certainty due to the inclusion of cuticular characters include *M. latahensis* (Berry) Brown from the Miocene of Idaho (Baranova & Figlar 2000), *Magnolia* sp. from the Miocene of Iceland (Grimsson et al. 2007) and *M. kristinae* Knobloch and Kvaček from the Miocene of Bohemia (Knobloch & Kvaček 1976); of those, Morphotype AB11 most resembles the last two species. Fossil Annonaceae leaves are found in the West Indies, Central and South America (Berry 1918, 1923, Hollick 1928); among them, Morphotype AB11 resembles *Anona guppyi* Berry from the Miocene of Columbia and Venezuela except for the cuneate base (Berry 1922, 1936b). Within the Miocene of the eastern United States, *Magnolia* leaves have been noted at Bridgeton (Hollick 1892) but the secondary veins are straight and the secondary angle of divergence is steeper than in Morphotype AB11. *Magnolia* seeds are reported from Brandon (Tiffney 1977, 1994), pollen from Ohoopsee (Rich et al. 2002) and Magnoliaceae pollen from Brandywine (McCartan et al. 1990). Annonaceae leaves are noted from Catahoula as *Anona texana* Berry (Berry 1916a), and *Asimina triloba* (L.) Don (YPM 74675) from Bridgeton (Hollick 1892) (Tab. 1). In *A. triloba* the secondary angle of divergence is steeper and the exmedial looping is much broader than in Morphotype AB11.



**Plate 5.** 1. Morphotype AB11, elliptic leaf with slightly cordate base (lower arrow) and brochidodromous venation (upper arrow), UF18049-43551; 2, 4, 5. Morphotype AB6, 2 – ovate leaf with wide tooth (arrow), 4 – anomocytic stomata with at least three anticlinal cell walls perpendicular to oblique to guard cell (arrows), 5 – adaxial rectangular cells, UF18049-43553; 3. Morphotype AB48, oval seed with thickened margin, UF18049-69389; 6–9. Morphotype AB7, 6, 7 – orbicular shape leaves with entire margins and brochidodromous venation, UF18049-43501, UF18049-43574, respectively. 8 – adaxial anticlinal cell walls straight and sinuate, 9 – paracytic stomata with symmetrical to asymmetrical subsidiary cells (arrows), UF18049-43574; 10. Morphotype AB19, USNM 38282; 11. Morphotype AB21, ovate leaf with curved eucamptodromous secondary venation, UF18049-56766; 12. Morphotype AB20, ovate leaf with serrate margin, UF18049-62093; 13. Morphotype AB29, line drawing, basal section of oblong leaf, USNM 38279c; 14. Morphotype AB59, ovate leaf with eucamptodromous secondary venation, UF18049-70099; 15. Morphotype AB12, elliptical leaf with brochidodromous venation, UF18049-43589; 16. Morphotype AB64, round leaf with crenate serrate teeth, UF18049-56765; 17. Morphotype AB28, endocarp with radially aligned ridges, UF18049-53157; 18. Morphotype AB53, shield-shaped structure with numerous pits, UF18049-62239; 19. Morphotype AB63, line drawing of degraded leaf, USNM 38287; 20. Morphotype AB56, line drawing of pinnately lobe leaf with small teeth, UF18049-70108; Scale bars: 1, 6, 7, 10, 13–16, 19 = 10 mm; 2, 11, 12 = 5 mm; 3 = 2 mm; 4, 5, 9 = 50  $\mu$ m; 8 = 25  $\mu$ m; 17 = 3 mm; 18 = 2.5 mm, 20 = 15 mm

## Eudicots

Order: Ranunculales Juss.  
ex Bercht. & J. Presl

?Ranunculaceae Juss. 1789

**Morphotype AB48**

Pl. 5, fig. 3

**Description.** Seed elliptic, 4 mm long, 2 mm wide (n=1). Apex asymmetrical, shortly acute proximally; base cuneate and finely striate. Margins thickened, proximal slightly sinuate, distal deeply convex. Surface with rounded indentations.

**Material examined.** UF 18049-69389.

**Discussion.** The surface of this specimen has numerous rounded indentations, which indicate possible protuberances on the opposite side. This small seed with thickened margins, a shortly acute asymmetrical apex, cuneate finely striated base, and possible protuberances is similar to *Ranunculus pusillus* Poir., *R. platensis* A. Spreng and *R. trilobus* Desf.

## Rosids

Order: Vitales Juss. ex. Bercht. J. Presl. 1820

?Vitaceae Juss. 1789

**Morphotype AB6**

Pl. 5, figs 2, 4, 5

**Description.** Leaf incomplete, ovate, symmetrical, unlobed, microphyll. Length 4.5 cm, width 3.7 cm, l/w ratio 1.2, lamina area 1108.9 mm<sup>2</sup> (n=1). Apex folded over; base cuneate with slightly concave flanks, slightly asymmetrical. Margin with a few wide teeth. Tooth proximally and distally convex, sinus narrowly acute. Petiole 5 mm long. Primary venation single, curved, weak. Secondary venation craspedodromous, at least 3 secondary veins, at intervals of 7–12 mm, angle of divergence 42–53°. Secondary attachment excurrent, course wide, looping up and outward. One secondary vein with one exmedial branching to tooth apex, just proximal to mid-tooth. Tertiary veins not well-preserved except for a few exmedial looping tertiary veins from

basal secondary veins, and a few percurrent epimedial tertiary veins. Marginal vein present. Adaxial cells rectangular with straight to slightly sinuate anticlinal walls. Abaxial cells random, triangular to rectangular, anticlinal cell walls 3–4-sided, straight, 11.4–29.5 × 10.3–24.2 μm, stomata anomocytic, 20.1 × 5.2 μm.

**Material examined.** UF 18049-43553.

**Discussion.** Morphotype AB6 differs from Morphotype AB1 in base shape, pinnate venation and adaxial cell characters. Morphotype AB6 characters such as shape, venation and tooth type (Pl. 5, fig. 2) are also seen in extant Caprifoliaceae such as *Viburnum dentatum* L. and in extant Rosaceae such as *Crataegus aestivalis* (Walt.) Torr. & A. Gray except for the numerous exmedial branching of the secondaries to the teeth and sinuses. Exmedial branching of the secondary vein extends to the tooth tip just proximal to mid-tooth, but for Morphotype AB6 no other venation is preserved, which is crucial for rosoid tooth type confirmation (Hickey & Wolfe 1975). The Morphotype AB6 characters of craspedodromous venation, exmedial branching from the secondary vein entering the tooth, marginal veins, slightly asymmetrical acute base with tissue extending down the petiole, wide convex teeth and narrowly acute sinus can be found in extant Vitaceae such as *Ampelopsis arborea* (L.) Koehne except for the apiculate teeth. Cuticle preparation yielded only adaxial rectangular cells (Pl. 5, fig. 5) with poorly preserved trichome bases and few stomata (Pl. 5, fig. 4). The Morphotype AB6 characters of an adaxial surface with rectangular cells and straight anticlinal cell walls, and anomocytic stomata with at least three anticlinal cell walls perpendicular to one guard cell are similar to those of *Parthenocissus* (Ren et al. 2003, see figs. 4, 17).

*Ampelopsis* sp. from the Oligocene Weißelster Basin of Germany has a similar shape, venation, adaxial and abaxial cell shape, anticlinal wall structure and anomocytic stomata, although there are striations on the cells and stomata (Mai & Walther 1978). *Ampelopsis populifolia* Hu and Chaney from the Miocene of China (Hu & Chaney 1940) and *Populus heliadum* Unger (considered close to *A. populifolia*) from the Miocene of the Czech Republic and Italy have cordate to truncate leaf bases (Unger 1850, Gaudin & Strozzini 1862).

## Fabids

## Order: Malpighiales

Juss. ex. Bercht. &amp; J. Presl 1820

Family: cf. Chrysobalanaceae R.Br. 1818

**Morphotype AB7**

Pl. 5, figs 6–9

**Description.** Leaves incomplete, circular, symmetrical, unlobed, microphyll. Length 3.5–4.0 cm, width 3.0–3.4 cm, l/w ratio 1.2, leaf area 699.3–905.8 (avg. 802.5) mm<sup>2</sup> (n=2). Apex obtuse with rounded flanks; base missing. Margin entire. Primary venation single, straight, weak. Secondary venation brochidodromous, at least 4 pairs, at intervals of 6–14 mm from base to midsection of lamina, reducing to 4 mm apically, angle of divergence 46–64° basal to midsection of lamina, reducing to 25° apically. Secondary attachment excurrent to decurrent basally, course gently looping up and outwards close to margin before looping back to superadjacent vein. Tertiary and higher-order veins not preserved. Adaxial cells random, straight to sinuate, 4-sided, 10.5–32.3 × 7.5–17.8 µm. Abaxial cells random, anticlinal cell walls straight to sinuate, 4-sided, 15.8–31.3 × 16.2–26.4 µm. Stomata paracytic, guard cells 26.4–39.4 × 5.0–9.7 µm, subsidiary cells symmetrical to asymmetrical that overlap the guard cells or even with ends of guard cells, 41.1–47.0 × 12.7–20.7 µm.

**Material examined.** UF 18049-43501, 43574.

**Discussion.** Although the apex is missing in UF18049-43501, all other macromorphology characters are similar to those of UF18049-43574. Morphotype AB7 is somewhat similar to *Leguminosites* sp. 1 but in sp. 1 the shape is elliptic, the secondaries are straight, and 1–2 intersecondaries and epimedial tertiaries are present. Morphotype AB7 characters such as circular shape, entire margin and brochidodromous venation (Pl. 5, figs 6, 7) are found in numerous extant families such as Rutaceae (*Zanthoxylum eliasii* D.M. Porter; Porter 1976), with leaf size close to that of *Z. pittieri* P. Wilson (Woodson et al. 1979), Burseraceae (*Bursera simaruba* (L.) Sarg.) and Chrysobalanaceae (*Chrysobalanus icaco* L.). In

Rutaceae, numerous pellucid secretory cavities occur in the mesophyll of *Zanthoxylum fagara* (L.) Sarg.; they are not found in Morphotype AB7. Also, the stomata of Morphotype AB7 are paracytic (Pl. 5, fig. 9), while in *Zanthoxylum martinicense* (Lam.) DC. they are cyclocytic. In *B. simaruba* the leaf base can be asymmetrical and short intersecondary veins are evident, and the stomata do not match those of Morphotype AB7. The *C. icaco* characters (Espinoza-Osornio et al. 2002) of guard, subsidiary and epidermal cell size, paracytic stomata, subsidiary cells symmetrical to asymmetrical, and abaxial epidermal cells rectangular with straight anticlinal cell walls are similar to features of Morphotype AB7 (Pl. 5, figs 8, 9). The difference is that in *C. icaco* the adaxial epidermal cells are only straight-sided and it is uncommon for the subsidiary cells to have a distinct overlap of the guard cells, while in Morphotype AB7 the adaxial anticlinal cell walls are sinuate and straight (Pl. 5, fig. 8). Chrysobalanaceae has 460–533 species (Mabberley 1997, Christenhusz & Byng 2016) in tropical to warm-temperate regions; adjacent to Alum Bluff, circular-shaped chrysobalanaceous leaves are absent (FSU Herbarium 2016) (Tab. 1).

The Morphotype AB7 characters of shape, size and venation are similar to those of *Fagara catahouleensis* Berry (Berry 1916a) of Catahoula but cuticular samples would be needed to verify whether the Catahoula leaves are really *Fagara* (syn. *Zanthoxylum*). Subsequent extant phylogenetic studies placed *Fagara* in *Zanthoxylum* (Waterman 1975). Specimen 18049-53805 may be another specimen similar to Morphotype AB7 but only the base is preserved, showing a decurrent secondary vein at the base.

## Fabales

**Morphotype AB19**

Pl. 5, fig. 10

1916c *Fagara apalachicolensis* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 50, pl. 9, fig. 2.

**Description.** Possible leaflet, complete, elliptical, unlobed, microphyll. Length 2.7 cm, width 1.7 cm, l/w ratio 1.6, leaf area 305.7 mm<sup>2</sup> (n=1). Apex missing; base shallow convex and asymmetrical. Margin entire, petiole 4 mm. Primary venation single, curved, weak. Secondary

venation of 3 pairs, brochidodromous, straight to curved, spacing ca 7 mm, angle of divergence 40–50°. Tertiary venation of polygonal mesh preserved only near apex. Cuticle not preserved.

**Material examined.** USNM 38282 (Holotype, Berry 1916c, Pl. 9, fig. 2).

**Discussion.** Morphotype AB19 is somewhat similar to *Leguminosites* sp. 1, except sp. 1 has intersecondary veins and a complete apex. Leaf shape and venation (Pl. 5, fig. 10) in Morphotype AB19 are common in dicotyledons and are almost impossible to identify without anatomical characters. Berry (1916c) described *Fagara apalachicolensis* as in the family Rutaceae but also noted that it could be confused with entire-margined *Quercus* sp.

## Rosales

### Morphotype AB21

Pl. 5, fig. 11

1916c *Rhamnus apalachicolensis* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 50–51, pl. 9, fig. 8.

**Description.** Leaves incomplete, ovate, unlobed, symmetrical, microphyll. Length 3.5–7.3 cm, width 2.0–4.0 cm, l/w ratio 1.8, leaf area 466.2–1944.7 (avg. 1205.5) mm<sup>2</sup> (n=2). Apex missing; base acute with slightly convex flanks, margin entire. Primary venation single, curved, stout, thickened near base, thinning upwards but still thicker than upper secondaries. Secondary venation eucamptodromous, at least 4 pairs, parallel, excurrent basally, bent near midvein at mid to apical region of leaf, angle of divergence at base of leaf 45–50°, then angle decreasing to less than 40° towards upper portion of leaf. Secondary course at base of leaf straight, then strongly arched distad near margin, course at middle and upper portion of leaf arching upward, then strongly arched distad near margin. Tertiary venation and cuticle not preserved.

**Material examined.** UF 18049-56766, USNM 38283 (Holotype, Berry 1916c, Pl. 9, fig. 8).

**Discussion.** Morphotype AB21 seems to be a unique leaf type in the Alum Bluff flora. The Morphotype AB21 characters of ovate leaf with entire margins and uniformly curved eucamptodromous secondary venation (Pl. 5, fig. 11) are found in extant Rhamnaceae (*Berchemia*

Neck ex DC., *Karwinskia* Zucc.) and Cornaceae (*Cornus*). In Rhamnaceae the angle of divergence increases towards the lamina base, and prominent closely spaced percurrent tertiary veins are perpendicular to the midvein (Correa et al. 2010). In *Cornus* the widely spaced percurrent tertiary veins are perpendicular to the midvein, and in many species the width of the midvein and secondaries in the upper half of the leaf are not the same (Meyer & Manchester 1997). The lack of preserved tertiary venation in Morphotype AB21 makes it impossible to distinguish between Rhamnaceae and Cornaceae, and from the form genus *Cornophyllum* (Newberry 1895). Also, the lack of well-preserved cuticle makes precise determination difficult, since T-shaped hairs are diagnostic for many Cornaceae species (Eyde 1988, Manchester et al. 2009).

Fossil leaves of *Cornus* and Rhamnaceae are difficult to differentiate, and numerous fossil *Cornus* leaves are of uncertain placement (Kirchheimer 1938). A few may be *Cornus* or *Berchemia*; examples include *Cornus rhamnifolia* Weber, *C. sanguinea* L. and *Berchemia multinervis* (A. Braun) Heer, all from the Miocene of Europe (Kirchheimer 1938). The morphological characters of Morphotype AB21 are superficially similar to those of *Cornus ovalis* Lesqx. from the Miocene of the western United States (Brown 1936) and *C. miowalteri* Hu and Chaney from the Miocene of China (Hu & Chaney 1940). *Cornus ovalis* has been noted as being similar to *Viburnum* sp. or *Nyssa knowltoni* Berry (*N. hesperia* Berry) (Kirchheimer 1938). *Rhamnus apalachicolensis* Berry (USNM 38283) described by Berry (1916c) has curving secondaries that are subparallel to the margins, plus intersecondary and percurrent tertiary veins, similar to *Cornus amomum* Miller. Elsewhere in the Miocene of the eastern United States, *Cornus* fruits are found at Brandywine (McCartan et al. 1990), Cornaceae pollen at Ohooppee (Rich et al. 2002) and Martha's Vineyard (Frederiksen 1984), and *Berchemia* pollen at Calvert (Greller & Rachele 1983) (Tab. 1).

### Morphotype AB20

Pl. 5, fig. 12

**Description.** Leaf incomplete, ovate, unlobed, microphyll. Length 4.5 cm, width 2.4 cm, l/w ratio 1.9, leaf area 719.3 mm<sup>2</sup> (n=1).

Apex missing; base obtuse with straight flanks. Margin serrate. Teeth of 2 orders, acute, spacing irregular, basal side convex and long, sometimes sinuate near tooth apex, apical side straight, convex or sinuate, apex sometimes apiculate, sinus angular. Petiole fragmented. Primary venation single, straight, moderate. Secondary venation craspedodromous, at least 6 pairs, at intervals of 4–8 mm, spacing irregular, angle of divergence 50–75°. Secondary course slightly arching, dividing into 2 prominent veins each entering a tooth, plus one exmedial vein entering a tooth. Intercostal tertiary veins reticulate. Cuticle not preserved.

Material examined. UF 18049-62093.

Discussion. Morphotype AB20 characters such as toothed margin with two tooth sizes, teeth with convex sides, craspedodromous venation (Pl. 5, fig. 12) and secondaries giving off 1–2 exmedial veins that enter the teeth are found in extant Betulaceae and Rosaceae. The teeth and on rare occasions the base of *Betula alleghaniensis* Britt. look similar to those of Morphotype AB20. Within Betulaceae it is often difficult to determine genera based on the macromorphology of a fragmentary leaf (Worobiec & Szykiewicz 2007); well-preserved areole veinlets that branch more than twice would be needed to distinguish *Betula* from *Carpinus* and *Ostrya* (Wolfe 1966, Uemura 1988). In Rosaceae (e.g. *Rosa palustris* Marsh.) some secondaries do divide into two prominent veins each entering a tooth, but there are prominent short intersecondary veins.

Morphotype AB20 is similar to Type LXX of Ferguson (1971) from the Miocene of Germany, except for the double serration in Type LXX. Within the Miocene of the eastern United States, Betulaceae pollen has been identified from Alum Bluff (Corbett 2004, Jarzen et al. 2010), Ohoopie (Rich et al. 2002), Calvert (Groot 1992), Martha's Vineyard (Frederiksen 1984) and Gray (Zobaa et al. 2011), and Betulaceae and Rosaceae pollen from Cohansey (Greller & Rachele 1983), Brandywine (McCartan et al. 1990) and Bryn (Pazzaglia et al. 1997). A Betulaceae leaf was noted from the Catahoula Fm. of Mississippi (Dockery & Thompson 2016). Rosaceae seeds are at Brandon (Tiffney 1994), possibly at Calvert (Berry 1936a), leaves possibly at Bridgeton (Hollick 1892), and pollen at Brandon (Traverse 1955, 1994) and Bridgeton (Greller & Rachele 1983) (Tab. 1).

?Moraceae

### Morphotype AB29

Pl. 5, fig. 13

1916c *Artocarpus lessigiana floridana* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 48 pl. 10, figs. 5–7.

Description. Leaf fragments, oblong, pinately lobed, notophyll. At least 9.4 cm long by 6 cm wide, leaf area 3761.9 mm<sup>2</sup>. Apex and base missing, margin entire. Primary venation single, sinuate to straight, weak. Secondary venation angle of divergence 35–62°. Major secondaries possibly one to each lobe, minor secondaries to margin, some to sinus with sinal bracing. Intercostal tertiaries alternate percurrent.

Material examined. USNM 38279a–c.

Discussion. Morphotype AB29 seems to be a unique leaf type within the Alum Bluff flora in terms of size and lobing, and was initially described as *Artocarpus lessigiana floridana* (Berry 1916c). In this study the venation description is supplemented by Berry's (1916c) diagram, since the surviving original specimens (USNM 38279a–c) have very few discernable veins (Pl. 5, fig. 13), and no other specimen of this type has been found since Berry's publication. Thus, we question the validity of *Artocarpus* at Alum Bluff. Extant genera with lobed leaves and sinal bracing include *Artocarpus altilis* (Parkinson ex F.A. Zorn) Fosberg, *Acer* sp. (Wolfe & Tanai 1987) and *Quercus austrina* Small. Sinal bracing is an important character for confirmation, for in *Artocarpus* this bracing is closely adjacent to the sinus, while in *Acer* sp. and *Q. austrina* there are tertiary and quaternary veins between the fork and sinus. Elsewhere in the Miocene of the eastern United States, Moraceae leaves are at Hattiesburg (Stults et al. 2016), possibly at Calvert (Berry 1916b) and Bridgeton (Hollick 1892), and pollen at Brandon (Traverse 1955, 1994) and Bridgeton (Greller & Rachele 1983) (Tab. 1).

Asterids

### Morphotype AB59

Pl. 5, fig. 14

1916c *Diospyros brachysepala* Alex. Braun; Berry, Profess. Pap. U.S. Geol. Surv., 98-E, pg. 52 pl. 10, figs. 3.

**Description.** Leaf incomplete, possibly ovate, symmetrical, unlobed, mesophyll. Length 14.5 cm, width 9.0 cm (n=1), leaf to width ratio 1.6, leaf area 8704.4 mm<sup>2</sup>. Apex and base missing. Margin entire. Primary venation single, straight, weak. Secondary venation eucamptodromous, at least 7 pairs, 3 mm apart basally, then 12–24 mm apart, angle of divergence basally 75°, then 45–60°, basal veins decurrent, excurrent otherwise, course gently curving to margin. A few percurrent tertiary veins preserved near margin. Cuticle not preserved.

**Material examined.** UF 18049-70099, ?USNM 38288 (Plesiotype, Berry 1916c, Pl. 10, fig. 3).

**Discussion.** Morphotype AB59 seems to be a unique leaf type in the Alum Bluff flora in terms of leaf size. Entire-margined *Nyssa*-like leaves can be found in numerous extant families such as Annonaceae, Moraceae, Juglandaceae, Fagaceae, Magnoliaceae, Lauraceae, Sapindaceae, Apocynaceae, Cornaceae and Ebenaceae (Kirchheimer 1938, Eyde & Barghoorn 1963). The Morphotype AB59 characters of eucamptodromous secondary venation being alternate at the lamina midsection, and opposite percurrent tertiaries (Pl. 5, fig. 14) can be found in Cornaceae (e.g. *Nyssa ogeche* Bartram ex Marshall), including the decrease in angle of divergence apically, and in Ebenaceae (e.g. *Diospyros virginiana* L.). The one difference that may be applicable is that the basal secondaries are decurrent in *Nyssa* and excurrent in *Disopyros* (Yu & Chen 1991). Cuticular characters would be needed to improve the systematic placement of Morphotype AB59. For example, spatulate glands characterize *Nyssa* (Kvaček & Bůžek 1972) but not *Cornus* and *Davidia*.

We reject the designation *Diospyros brachysepala* Alex by Berry (1916c), due to poor preservation of the original specimen. The preservation of Morphotype AB59 is poor, but it is an ovate leaf with eucamptodromous secondary veins that are decurrent (basally) and excurrent, and percurrent tertiaries near the margin are similar to *Nyssa haidingeri* (Ett.) Kvaček & Bůžek from the Miocene of Europe (Kvaček & Bůžek 1972) and *N. hesperia* Berry from the Miocene of the western United States (Chaney & Axelrod 1959). *Diospyros brachysepala* A. Braun and *D. lotoides* Ung. from

the Miocene of Europe do not match our fossil (Ettinghausen 1868). Within the Miocene of the eastern United States, *Nyssa* pollen is found at Brandon, Alum Bluff, Ohoopee, Calvert, Cohansey, Brandywine, Bryn Mawr, Bridgeton and Pensauken (Greller & Rachele 1983, Groot 1992, McCartan et al. 1990, Pazzaglia et al. 1997, Rich et al. 2002, Jarzen et al. 2010). *Nyssa* leaves have been reported at Brandywine (McCartan et al. 1990), and *N. uniflora* Wangenheim at Bridgeton (Hollick 1892, Kirchheimer 1938).

Unknown

### Morphotype AB12

Pl. 5, fig. 15

**Description.** Leaf complete, elliptic, symmetrical, unlobed, microphyll. Length 4.0 cm, width 2.1 cm, l/w ratio 1.9, leaf area 559.4 mm<sup>2</sup> (n=1). Apex missing; base acute. Margin entire. Petiole ca 0.3 cm. Primary venation single, straight, stout. Secondary venation brochidodromous, at least 3 pairs, extending ca 1/3 of leaf length in shallow loops, angle of divergence 20–25°. Tertiary venation and cuticle not preserved.

**Material examined.** UF 18049-43589.

**Discussion.** Morphotype AB12 possesses characters of size, shape, brochidodromous venation and angle of divergence (Pl. 5, fig. 15) similar to those of cf. *Laurophyllum pseudoprinceps* of this study, cellular details such as beading of anticlinal cell walls would be needed for confirmation. Also, these characters can be found in numerous angiosperm families.

### Morphotype AB64

Pl. 5, fig. 16

**Description.** Leaf incomplete, circular, symmetrical, unlobed, microphyll. Length 4.2 cm, width 3.5 cm, l/w ratio 1.2, leaf area 979.0 mm<sup>2</sup> (n=1). Apex missing; base obtuse. Margin crenate to serrate, lower margin of disorganized smaller rounded to acute teeth, upper margin of larger crenate teeth. Petiole 6 mm. Primary venation single, curved, weak. Secondary venation craspedodromous, opposite, straight, excurrent, spacing irregular, 5–7 mm, angle of divergence 55–65°. Secondaries with 2

exmedial branchings of weaker secondaries entering successive teeth. Tertiaries reticulate. Cuticle not preserved.

Material examined. UF 18049-56765.

Discussion. Morphotype AB64 is somewhat similar to Morphotype AB20, except in AB20 the secondaries divide into two prominent branches and the width of AB20 is slightly less than that of AB64.

### Morphotype AB28

Pl. 5, fig. 17

Description. Fruit fragmented, possibly 4-winged, 5.3 mm long, 3.0 mm wide. Major veins parallel, ca 15, transverse over central locular region and fanning outward. Two rows of ventral spines or wing veins, 9 preserved in one row.

Material examined. UF 18049-53157.

Discussion. Micro-CT shows the ventral side with two rows of spines or wing veins. The size, number of putative wings, and the presence of prominent parallel veins over the locular region and fanning outward are similar to features of Polygalaceae (*Monnina philippiana* Chodat) and Polygonaceae (*Calligonum leuocladum* (Schrenk) Bunge) (Manchester & O'Leary 2010). Unfortunately the fragmentation of this singular specimen precludes determination even to family level.

### Morphotype AB53

Pl. 5, fig. 18

Description. Triangular ovate seed, 2.75 mm long, 2.5 mm wide. Apex acute; base rounded and abbreviated cordate. Surface with numerous minute indentations surrounding ovate central depression.

Material examined. UF 18049-62239.

Discussion. Morphotype AB53 is similar in shape, size and surface indentations to the pronotum of the beetle *Papusus andrewsi* Okeefe, but the pronotum lacks an abbreviated cordate base and ovate central depression (Okeefe 2003). Morphotype AB53 (Pl. 5, fig. 18) resembles Aristolochiaceae in its shape, size, cordate base and verrucose surface (Gongalez & Poncy 1999, Phuphathanaphong 2006).

### Morphotype AB63

Pl. 5, fig. 19

1916c *Sapotacites spatulatus* Berry; Profess. Pap. U.S. Geol. Surv., 98-E, pg. 52, pl. 10, fig. 2.

Description. Leaf incomplete, obovate, symmetrical, unlobed, microphyll. Length 6.4 cm, width 2.9 cm, l/w ratio 2.2, leaf area 1241.9 mm<sup>2</sup> (n=1). Apex obtuse; base fragmented but tending cuneate. Margin entire. Primary venation single, straight, weak. Secondaries obscure, but one pair with angle of divergence 26–38°. Cuticle not preserved.

Material examined. USNM 38287 (Holotype, Berry 1916c, Pl. 10, fig. 2).

Discussion. Morphotype AB63 is highly degraded and the secondary venation is obscure. Berry (1916c) placed this specimen (Pl. 5, fig. 19) in the form genus *Sapotacites* for undeterminable specimens in the family Sapotaceae, with USNM 38287 near *Mimusops* L. and *Sideroxylon* (*Bumelia*). The obovate species of *Mimusops* (e.g. *Mimusops balata* (Aubl.) C.F. Gaertn., *M. coriacea* (A. DC.) Miq.) have the secondary angle of divergence nearly at right angles to the midvein, and the secondary looping is very close to the margin, while USNM 38287 has steep-angled secondaries, but secondaries near the margin are obscure. Most species in *Sideroxylon* have elliptic leaves. The general shape and angle of divergence do seem to be close to those of *Sapotacites bilinicus* Ettingshausen (Hably et al. 2001) from the Eocene of Europe. The lack of distinct venation makes it very difficult to determine the family.

### Morphotype AB56

Pl. 5, fig. 20

Description. Leaf incomplete, lobed, ovate, mesophyll. Length 12.0 cm, width 11.0 cm, l/w ratio 1.1, leaf area 8791.2 mm<sup>2</sup> (n=1). Apex and base missing. Margin serrate. Teeth small, thin, sinus angular. Primary venation unknown. Secondary venation eucamptodromous and craspedodromous. One major vein entering fragmented lobe. At least 6 pairs of secondary veins in central lobe, spacing 10–20 mm, angle of divergence 42–60°, decreasing upward. Interior veins angled, one forked near sinus with one exmedial tertiary to sinus and merging into marginal vein. Tertiary veins mixed percurrent. Epimedial

tertiaries at nearly 90° to midvein. Exmedial tertiary vein enters minor tooth. Cuticle not preserved.

Material examined. UF 18049-70108.

Discussion. The possibly lobed leaf with craspedodromous secondaries, an exmedial tertiary vein entering a minor tooth, and a marginal vein suggest *Acer* sp., but the fragmentary nature of Morphotype AB56 precludes a precise determination. Morphotype AB56 is somewhat similar to *Menispermites latahensis* Berry from the Miocene of Washington, except that in *M. latahensis* the venation at the sinuses is not forked as in Morphotype AB56 (Berry 1931).

### Morphotype AB65

1916c *Bumelia apalachicolensis* Berry, Profess. Pap. U.S. Geol. Surv., 98-E pg. 51, pl. 9, fig. 4.

Description. Leaf complete, obovate, unlobed, microphyll. Length 3.7 cm, width 1.9 cm, l/w ratio 1.9, leaf area 465.7 mm<sup>2</sup> (n=1). Apex obtuse; base concave. Margin entire. Petiole 4 mm. Primary venation single, curved, stout. Secondary venation obscure near margin, 10–12 pairs, straight, subparallel, spacing 1.8–3.2 mm, angle of divergence 38–42°. Secondaries sometimes branch at or less than 3/4 the distance from margin. Cuticle fragments preserved.

Material examined. USNM 38286a,b (part [Holotype, Berry 1916c, Pl. 9, fig. 4], counterpart).

Discussion. Berry (1916c) placed this specimen as an intermediate between extant *Bumelia tenax* (L.) Willdenow (syn. of *Sideroxylon tenax* L.) and *B. lanuginosa* Persoon (syn. of *Sideroxylon lanuginosum* Michx.). We question the previous assignment to *Bumelia apalachicolensis* by Berry (1916c) because the preservation of the original specimen is too poor for generic assignment, which would require characters such as the strength of secondary venation near the margin. Also, prominent intersecondary and reticulate tertiary veins, important characters in *S. tenax* and *S. lanuginosum*, are lacking or not preserved. The one character that is relevant to *S. tenax* and *S. lanuginosum* is branching of the secondaries at or less than 3/4 the distance from the margin.

## DISCUSSION

### FLORISTIC COMPOSITION

In this study we recognized 46 morphologically distinct species or morphotypes; 26 of them are assigned to genera or species, 9 are placed at or near family level, 5 show similarities to multiple families, and 7 are of unknown affiliation (Tab. 2). This assemblage is predominantly angiospermous, with one conifer fragment, and fossil fungal damage. The fungal damage found on *Sabalites apalachicolensis* Berry was identified as *Pestalozzites sabalana* Berry (Berry 1916c) (Pl. 2, fig. 11), similar to extant *Pestalozzia* sp. on extant palm leaves (Edgerton 1912) and *Pestalotiopsis* sp. known to occur on at least 39 extant palm species including *Sabal palmetto* (Walter) Lodd. ex Schult. & Schult.f. (Elliott et al. 2004). Table 2 lists the taxonomically determined leaf/fruit/seed taxa, organized according to the phylogenetic sequence of Soltis et al. (2018). We examined over 450 specimens representing *Sabalites* (37%), *Ulmus* (25.5 %) and *Carya* (16.4%), with Fabaceae (3.9%), Lauraceae (2%), Vitaceae (3%), Salicaceae (2.5%), Rhamnaceae (2.5%) and Magnoliaceae/Annonaceae (1.2%); and all other taxa were represented by three or fewer specimens accounting for less than 1% of the total (Tab. 2). Overall, palm (*Sabalites*), elm (*Ulmus*) and hickory (*Carya*) dominate the fossil assemblage. Their actual abundance in the original vegetation probably was different, due to taphonomic bias. For example, larger leaves are more difficult to collect as complete specimens in friable sediment than small ones are, and deciduous leaves are likely over-represented as compared to evergreens.

### CLIMATIC INTERPRETATIONS

We base our inferences about the climate of Alum Bluff on comparisons with living relatives and on leaf physiognomy. The taxa identified with the most confidence, including *Sabal*, *Ulmus* and *Carya*, are helpful as climate indicators. Many of these taxa range from warm to cool-temperate conditions (e.g. *Scirpus*, *Carex*, *Salix*, *Carya*, *Ulmus*) but *Sabal* stands out because even the most frost-tolerant palm species (*Trachycarpus fortunei* (Hook.) H. Wendl.) are physiologically limited to warmer climates, generally being confined to

habitats with minimum temperature warmer than  $-10^{\circ}\text{C}$  ( $14^{\circ}\text{F}$ ) (Wing & Greenwood 1993).

Among the megafossil remains, we recognized 34 species/morphotypes of dicotyledonous foliage. Of these, 18 or 53% are entire-margined, while the others are serrate-margined. Using the regressions provided by Wolfe (1979), Wing & Greenwood (1993), Wilf (1997), Kowalski & Dilcher (2003), Miller et al. (2006) and Peppe et al. (2011) for mean annual temperature (MAT), we get an estimate range of  $16.2\text{--}22.9^{\circ}\text{C}$  ( $61.2\text{--}73.2^{\circ}\text{F}$ ) with an average of  $19.0^{\circ}\text{C}$  ( $66.2^{\circ}\text{F}$ ). Mean annual temperature for Marianna Municipal Airport, Florida (50.2 km from Alum Bluff) for the period 1981–2010 is  $19.7^{\circ}\text{C}$  ( $67.4^{\circ}\text{F}$ ) (NOAA 2018). Using the leaf area formulas of Wilf et al. (1998), Gregory-Wodzicki (2000), Jacobs (2002) and Peppe et al. (2011), we get mean annual precipitation (MAP) of  $99.5\text{--}134.3$  (avg.  $116.0$ ) cm, which is close to the average of Gainesville, Florida, in 2010 ( $110.31$  cm) (NOAA 2018).

The climate of the eastern United States during the Miocene underwent numerous changes. During the early Miocene (ca 20 Myr.), Central America was separated from North America by the narrow Culebra Strait, and from South America by the Atrato Seaway (Kirby et al. 2008, Montes et al. 2012). At this time, rising global temperatures and sea levels promoted poleward migration of equatorial megathermal vegetation (Feng et al. 2013). During the beginning of the middle Miocene (15 Myr.), the Culebra Strait closed and the Atrato Seaway was greatly restricted (Montes et al. 2012), allowing exchange of fauna and flora (Cody et al. 2010). This coincided with the Miocene Climatic Optimum (MMCO, 17–14.5 Ma), when deep oceans were warmer and temperatures at mid to high latitudes were higher than at present (Meller et al. 2015). Also, increased siliciclastic sediment from the north was filling the Florida Platform, and sea level rose to its maximum (Scott 1997). Rainfall was moderately low for middle-latitude temperate regions, except for moisture from low-pressure systems in the Gulf of Mexico (Graham 2011). The landscape hosted temperate forests extending from the eastern United States to Mexico, bordered by shrubland/chaparral-woodland-savanna and Neotropical lowlands of Mexico, and lower-elevation grassy woodlands of the North American midcontinental region (Graham 2011). The deciduous forests of the

eastern United States had a number of East Asian exotics (Wen 1999) such as *Paliurus*, with vertebrate fossils also showing faunistic affinities with East Asia (Shunk et al. 2006). The macro- and microfossil data indicate that the climate in the eastern United States during the Miocene varied from tropical to warm temperate in the early Miocene, subtropical to mild temperate in the middle Miocene, and warm to cool temperate in the late Miocene (Tab. 1). The Miocene sites ranged from the Catahoula Fm. in Louisiana to the Brandon lignite in Vermont. Macrofossils shared between Alum Bluff and other Miocene sites in the eastern United States include *Sabal*, *Salix*, *Paliurus*, *Ulmus* and *Carya* (Tab. 1)

The Alum Bluff fossil flora was considered by Berry to represent “an endemic tropical flora gradually becoming invaded by members of a temperate flora as a result of changing climate condition.” (Berry 1916c, p. 44). He also envisioned three components of source vegetation: semi-swamp palmetto-brake, sandy strand, and low hammock. This hypothesis was also based on the underlying Chipola Fm., which represented a near-shore shallow marine environment under tropical conditions (Vaughan 1910, Randazzo & Jones 1997). We have not been able to confirm truly tropical elements such as the *Artocarpus* that Berry identified. Based on pollen from the same sediments as the macrofossils considered here, Corbett (2004) and Jarzen et al. (2010) inferred that the Alum Bluff flora included both subtropical and warm-temperate elements, set in a floodplain with elements of upland forest flanking a river. Our study corroborates the interpretation of a warm-temperate climate with winter temperatures sufficiently warm to allow the survival of marginally subtropical plants such as *Sabalites*. In this study we found that the pollen and leaf taxa of Alum Bluff include plants that can tolerate a wide range of climatic conditions from cold to subtropical, such as *Sambucus*, *Carya* and *Ulmus*. Some species of *Scirpus*, *Carex* and *Salix* reach into subtropical regions (Britton & Brown 1913, Wunderlin 1998, Institute for Systematic Botany 2016, USDA 2016). Subtropical to warm-temperate elements include *Azolla*, *Ceratopteris*, *Taxodium*, *Gordonia*, *Sabal*, *Abutilon*, *Alchornea*, representatives of Moraceae and Chrysobalanaceae, and cool-temperate elements such as *Adiantum*. The presence of *Ephedra* pollen

suggests a xeric habitat within the Alum Bluff region. Low-lying areas in the region may have supported *Azolla*, *Ceratopteris*, *Taxodium*, *Gordonia*, *Sabal*, *Scirpus*, *Carex*, *Salix*, *Carya*, *Ulmus*, *Platanus* and *Sambucus*. Higher-elevation areas may have supported *Pinus*, *Carex*, *Carya* and *Ulmus*. Fossil taxa that are presently absent from the modern flora include *Paliurus* and *Artocarpus*(?) (Tab. 1).

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#### REFERENCES

- ANDREWS G.W. 1988. A revised marine diatom zonation for Miocene strata of the Southeastern United States. Profess. Pap. U.S. Geol. Surv., 1481: 1–29.
- BALL P.W. & REZNICEK A.A. 2002. *Carex* Linnaeus: 254–572. In: Flora of North America Editorial Committee (eds.) 1993+, Flora of North America North of Mexico. 19+ vols. New York, New York, USA. Volume 23.
- BANDULSKA H. 1926. On the cuticles of some fossil and recent Lauraceae. Bot. J. Linn. Soc., 47: 383–425.
- BARANOVA M.A. 1972. Systematic anatomy of the leaf epidermis in the Magnoliaceae and some related families. Taxon, 2: 447–469.
- BARANOVA M.A. & FIGLAR R.B. 2000. Leaf cuticular features of (fossil) Miocene *Magnolia latahensis* show affinity to extant *Magnolia grandiflora*. 58–64. In: Y.-H. Liu et al. (eds.), Proceedings of the International Symposium on the Family Magnoliaceae. Science Press, Beijing, China.
- BARANOVA M.A., JEFFREY J., OI-GEN W. & JING-PING L. 2000. Leaf epidermis features of Magnoliaceae and their systematic significance, with special reference to the genera *Parakmeria*, *Manglietiastrum* and *Woonyoungia*: 143–149. In: Y.-H. Liu et al. (eds.), Proceedings of the International Symposium on the Family Magnoliaceae. Science Press, Beijing, China.
- BERRY E.W. 1916a. The flora of the Catahoula Sandstone. Profess. Pap. U.S. Geol. Surv., 98–M: 227–251.
- BERRY E.W. 1916b. The physical conditions indicated by the flora of the Calvert Formation. Profess. Pap. U.S. Geol. Surv., 98–F: 61–73.
- BERRY E.W. 1916c. The physical conditions and age indicated by the flora of the Alum Bluff Formation. Profess. Pap. U.S. Geol. Surv., 98–E: 41–59.
- BERRY E.W. 1916d. The flora of the Citronelle Formation. Profess. Pap. U.S. Geol. Surv., 98–L: 193–208.
- BERRY E.W. 1918. The fossil higher plants from the Canal Zone. 15–44. In: Contributions to the Geology and Paleontology of the Canal Zone, Panama, and Geologically Related Areas in Central America and the West Indies. U.S. Natl. Mus. Bulletin, 103.
- BERRY E.W. 1922. Tertiary fossil plants of Venezuela. Proc. U.S. Natl. Mus., 59: 553–580.
- BERRY E.W. 1923. Miocene plants from southern Mexico. Proc. U.S. Natl. Mus., 62: 1–27.
- BERRY E.W. 1931. A Miocene flora from Grand Coulee, Washington. Profess. Pap. U.S. Geol. Surv., 170C: 31–42.
- BERRY E.W. 1936a. Pine and cherry from the Calvert Miocene. Torreyia, 36: 124–127.
- BERRY E.W. 1936b. Miocene plants from Colombia, South America. Bull. Torr. Bot. Club, 63: 53–66.
- BERRY E.W. 1938. Additional Miocene plants from Grand Coulee, Washington. Bull. Torr. Bot. Soc., 65: 89–98.
- BERRY E.W. 1940. Additions to the Pleistocene flora of New Jersey. Torreyia, 10(12): 261–267.
- BERRY E.W. 1941. *Pinus* and *Quercus* in the Chesapeake Miocene. J. Wash. Acad. Sci., 31: 506–508.
- BIERAS A.G. & SAJO M.G. 2009. Leaf structure of the cerrado (Brazilian savanna) woody plants. Trees, 23: 451–471.
- BRAUNSTEIN J., HUDDLESTUN P. & BIEL R. 1988. Gulf Coast region correlation of stratigraphic units of North America: American Association of Petroleum Geologists, Correlation Chart. Tulsa, Oklahoma.
- BRITTON N.L. & BROWN A. 1913. An illustrated flora of the Northern United States and Canada. Dover Publications, Inc., New York, New York.
- BROWN R.W. 1936. Additions to some fossil floras of the western United States. Profess. Pap. U.S. Geol. Surv., 186: 163–207.

- BRYAN J.R. & MEANS G.H. 2014. Geology and paleontology of the Florida panhandle: 3–38. In: Portell R.W., Hulbert R.C. Jr. & Robins C.M. (eds.), 10<sup>th</sup> North American Paleontological Convention Field Guide 2014, Florida Museum of Natural History, Gainesville, Florida.
- BRYANT J.D., MACFADDEN B.J. & MUELLER P.A. 1992. Improved chronologic resolution of the Hawthorn and the Alum Bluff Groups in northern Florida: Implications for Miocene chronostratigraphy. *Bull. Geol. Soc. Amer.*, 104: 208–218.
- BUECHLER W.K. 2014. Variability of venation patterns in extant genus *Salix*: Implications for fossil taxonomy. *PaleoBios*, 30(9): 89–104.
- BURGE D.O. & MANCHESTER S.R. 2008. Fruit morphology, fossil history, and biogeography of *Paliurus* (Rhamnaceae). *Int. J. Pl. Sci.*, 169: 1066–1085.
- BURNHAM R.J. 1986. Foliar morphology analysis of the Ulmoideae (Ulmaceae) from the Early Tertiary of Western North America. *Palaeontographica*, B, 201: 135–167.
- BURNS F. 1889. Field notes, RU 73 Box 6 folder, Dec. 21<sup>st</sup>, 1889. <https://siarchives.si.edu>.
- BŮŽEK C. 1971. Tertiary flora from the northern part of the Petipsy area (North-Bohemian Basin). *Rozpr. Ústředního Ústavu Geol.*, 36: 1–118.
- CAIN S.A. & CASTRO G.M.O. 1959. *Manual of Vegetation Analysis*. Harper and Brothers, Publishers, New York, New York.
- CARPENTER R.J., JORDAN G.J. & HILL R.S. 2007. A toothed Lauraceae leaf from the Early Eocene of Tasmania, Australia. *Int. J. Pl. Sci.*, 168: 1191–1198.
- CHANEY R.W. & AXELROD D.I. 1959. Miocene floras of the Columbia Plateau. Part II. Systematic considerations. *Carnegie Inst. Wash. Publ.*, 617: 135–229.
- CHANG S.H., DENG C.L., GAO W.J. & LU L.D. 2008. Study on leaf micro-morphological characteristics of *Osmanthus* (Oleaceae). *Acta Bot. Boreali-Occidentalia Sin.*, 28: 278–288.
- CHAPMAN A.W. 1860. *Flora of the Southern United States: containing an abridged description of the flowering plants and ferns of Tennessee, North and South Carolina, Georgia, Alabama, Mississippi, and Florida: arranged according to the natural system*. Ivison, Blakeman, Taylor, New York, New York.
- CHRISTENHUSZ M.J.M. & BYNG J.W. 2016. The number of known plant species in the world and its annual increase. *Phytotaxa*, 261(3): 201–217.
- CHRISTOPHEL D.C. & ROWETT A.I. 1996. Leaf and cuticle atlas of Australian leafy Lauraceae. *Flora of Australia Supplementary Series*, 6: 1–217.
- CLEWELL A.F. 1983. Vegetational overview of the Apalachicola River area: 1–84. In: Southeastern Geological Society (eds.), *Cenozoic Geology of the Apalachicola River Area Northwest Florida*. Southeastern Geological Society Guidebook 25, Tallahassee, Florida.
- CLEWELL A.F. 1985. *Guide to the Vascular Plants of the Florida Panhandle*. University Presses of Florida, Tallahassee, Florida.
- CODY S., RICHARDSON J.E., RULL V., ELLIS C. & PENNINGTON T. 2010. The Great American Biotic Interchange revisited. *Ecography*, 33: 326–332.
- COLLINSON M.E. 1992. The early fossil history of Salicaceae: a brief review. *Proc. R. Soc. Edinb. Sect. B (Biol. Sci.)*, 98: 155–167.
- COOKE C.W. & MOSSOM S. 1929. *Geology of Florida*. *Fl. Geol. Surv. 20<sup>th</sup> Ann. Rep.*, 1–227.
- CORBETT S.L. 2004. *The Middle Miocene Alum Bluff Flora, Liberty County, Florida*. MS thesis, University of Florida, Gainesville, Florida.
- CORREA E., JARAMILLO C.A., MANCHESTER S.R. & GUTIERREZ M. 2010. A fruit and leaves of Rhamnaceae affinities from the Late Cretaceous (Maastriichtian) of Colombia. *Amer. J. Bot.*, 97: 71–79.
- DAGHLIAN C.P. 1978. Coryphoid palms from the lower and middle Eocene of Southeastern North America. *Palaeontographica*, B, 166: 44–82.
- DALL W.H. & HARRIS G.D. 1892. The Neocene of North America. *U.S. Geol. Surv. Bull.*, 84: 15–268.
- DALL W.H. & STANLEY-BROWN J. 1894. Cenozoic geology along the Apalachicola River. *Bull. Geol. Soc. Amer.*, 5: 147–170.
- DENK T., GRIMSSON F. & KVAČEK Z. 2005. The Miocene floras of Iceland and their significance for late Cainozoic North Atlantic biogeography. *Bot. J. Linn. Soc.*, 149: 369–417.
- DE WIT H. 2008. *An ethnobotanical and chemotaxonomic study of South African Menispermaceae*. The University of Johannesburg. Available from: <http://hdl.handle.net/10210/233>.
- DILCHER D.L. 1963. Cuticular analysis of Eocene leaves of *Ocotea obtusifolia*. *Amer. J. Bot.*, 50: 1–8.
- DILCHER D.L. 1974. Approaches to the identification of angiosperm leaf remains. *Bot. Rev. (Lancaster)*, 40: 1–157.
- DOCKERY D.T. & THOMPSON D.E. 2016. *The Geology of Mississippi*. University Press of Mississippi, Jackson, MS.
- DRANSFIELD J., UHL N.W., ASMUSSEN C.B., BAKER W.J., HARLEY M.M. & LEWIS C.E. 2008. *Genera Palmarum. The Evolution and Classification of Palms*. Kew Publishing, Royal Botanic Gardens, Kew.
- DREW C. 1856. Map of the State of Florida showing the progress of the surveys; from the Annual Report of the Surveyor General for the year 1856. Jacksonville. Map. Retrieved from the Library of Congress, <https://www.loc.gov/item/198688455/>.
- DUARTE M.B., DRANKA E.R.K. & YANO M. 2012. Leaf microscopic characters of *Ormosia arborea* (Vell.) Harms, Fabaceae. *Latin Am. J. Pharm.*, 31: 526–530.

- EDGERTON C.W. 1912. The Melanconiales. Trans. Amer. Microscop. Soc., 31: 243–265.
- ELLIOTT M.L., BROCHAT T.K., UCHIDA J.Y. & SIMONE G.W. 2004. Compendium of ornamental palm diseases and disorders. The American Phytopathological Society, APS Press, St. Paul, Minnesota.
- ELLIS B., DALY D.C., HICKEY L.J., JOHNSON K.R., MITCHELL J.D., WILF P. & WING S.L. 2009. Manual of Leaf Architecture. Cornell University Press, Ithaca, New York.
- ESPINOSA-OSORNIO G., VARGAS-SIMÓN G. & ENGLEMAN M. 2002. Contribucion al estudio de la anatomia foliar del Icacó (*Chrysobalanus icaco* L.). Bioagro, 14(1): 29–36.
- ETTINGHAUSEN C.R. 1868. Die Fossile Flora der äletern Braunkohlenformation der Wetterau. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Classe, 57: 807–893.
- EYDE R.H. 1988. Comprehending *Cornus*: Puzzles and progress in the systematics of the Dogwoods. Bot. Rev., 54: 234–351.
- EYDE R.H. & BARGHOORN E.S. 1963. Morphological and Paleobotanical studies of the Nyssaceae, II The fossil record. J. Arnold Arbor., 44: 328–370.
- FARJON A. 1990. Pinaceae, drawings and descriptions of the genera. Koeltz Scientific Books, Königstein, Germany.
- FENG X., TANG B., KODRUL T.M. & JIN J. 2013. Winged fruits and associated leaves of *Shorea* (Dipterocarpaceae) from the Late Eocene of South China and their phytogeographic and paleoclimatic implications. Amer. J. Bot., 100: 574–581.
- FERGUSON D.K. 1971. The Miocene flora of Kreuzau, Western Germany. I. The leaf-remains. Verhandlungen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde Tweede Reeks, Dell 60(1): 1–297.
- FLORIDA GEOLOGICAL SURVEY (FGS). Accessed 2018. [http://fldeploc.dep.state.fl.us/geodb\\_query/WellIndexResults.asp](http://fldeploc.dep.state.fl.us/geodb_query/WellIndexResults.asp).
- FLORIDA STATE UNIVERSITY (FSU) HERBARIUM. Accessed 2016/2018. [herbarium.bio.fsu.edu](http://herbarium.bio.fsu.edu).
- FOERSTE A.F. 1894. Fossil palmettos at Alum Bluff, Florida. Bot. Gaz., 19: 37.
- FORMAN L.L. 1988. A synopsis of Thai Menispermaceae. Kew Bull., 43: 369–407.
- FREDERIKSEN N.O. 1984. Stratigraphic, paleoclimatic, and paleobiogeographic significance of Tertiary sporomorphs from Massachusetts. Profess. Pap. U.S. Geol. Surv., 1308: 1–25.
- FRYXELL P.A. 1999. *Pavonia* Cavanilles (Malvaceae). Fl. Neotrop. Monogr., 76: 1–284.
- GARDNER J. 1926. The Molluscan Fauna of the Alum Bluff Group of Florida. Profess. Pap. U.S. Geol. Surv., 142-A: 1–709.
- GAUDIN C.T. & STROZZI M.C. 1862. Contributions a la Flore Fossile Italienne. Zuerich, Switzerland.
- GODFREY R.K. 1988. Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia and Alabama. University of Georgia Press, Athens, Georgia.
- GONG F., KARSA I. & LIU Y.-S. (C.). 2010. *Vitis* seeds (Vitaceae) from the late Neogene Gray Fossil Site, Northeastern Tennessee, U.S.A. Rev. Palaeobot. Palynol., 162: 71–83.
- GONZALER F. & PONCY O. 1999. A new species of *Aristolochia* (Aristolochiaceae) from Thailand. Brittonia, 51: 452–456.
- GRAHAM A. 1999. Late Cretaceous and Cenozoic History of North American vegetation. Oxford University Press, New York, New York.
- GRAHAM A. 2011. A Natural History of the New World. The University of Chicago Press, Chicago, Illinois.
- GREGOR H.J. 1978. The Miocene fruit- and seed-floras of the Oberpfalz Brown Coal. I. Findings from the sandy interbeds. Palaeontographica B, 167: 8–103.
- GREGORY-WODZICKI K.M. 2000. Relationships between leaf morphology and climate, Bolivia; implications for estimating paleoclimate from fossil floras. Paleobiology, 26: 668–688.
- GRELLER A.M. & RACHELE L.D. 1983. Climatic limits of exotic genera in the Legler palynoflora, Miocene, New Jersey, U.S.A. Rev. Palaeobot. Palynol., 40: 149–163.
- GRÍMSSON F., DENK T. & SÍMONARSON L.A. 2007. Middle Miocene floras of Iceland – The early colonization of an island? Rev. Palaeobot. Palynol., 144: 181–219.
- GROOT J.J. 1992. Plant microfossils from the Calvert Formation of Delaware. Del. Geol. Surv. Rep. Invest., 50: 1–6.
- HABLY L., ERDEI B. & KVAČEK Z. 2001. 19<sup>th</sup> century's palaeobotanical types and originals of the Hungarian Natural History Museum. Hungarian Natural History Museum, Budapest.
- HARDIN J.W. 1992. Foliar morphology of common trees of North Carolina and adjacent states. Techn. Bull. North Carolina Agric. Res. Serv., 298: 1–135.
- HARDIN J.W. & STONE D.E. 1984. Atlas of foliar surface features in woody plants, VI. *Carya* (Juglandaceae) of North America. Brittonia, 36: 140–153.
- HEER O. 1856. Die tertiäre Flora der Schweiz, Volume 2. Winterthur.
- HERENDEEN P.S. 1992. The fossil history of the Leguminosae from the Eocene of Southeastern North America: 85–160. In: Herendeen P.S. & Dilcher D.L. (eds.), Advances in Legume Systematics: Part 4. The Fossil Record. The Royal Botanic Gardens, Kew.
- HERENDEEN P.S. & D.L. DILCHER. 1991. *Caesalpinia* subgenus *Mezoneuron* (Leguminosae, Caesalpinioideae) from the Tertiary of North America. Amer. J. Bot., 78: 1–12.
- HICKEY L.J. 1973. Classification of the architecture of dicotyledonous leaves. Amer. J. Bot., 60: 17–33.

- HICKEY L.J. 1979. A revised classification of the architecture of dicotyledonous leaves: 25–39. In: Metcalfe C.R. & Chalk L. (eds.), *Anatomy of the dicotyledons*, Vol I. (second edition), Clarendon Press, Oxford, England.
- HICKEY L.J. & WOLFE J.A. 1975. The bases of angiosperm phylogeny: vegetative morphology. *Ann. Missouri Bot. Gard.*, 62: 538–589.
- HILL R.S. 1986. Lauraceous leaves from the Eocene of Nerriga, New South Wales. *Alcheringa*, 10: 327–351.
- HOLLICK A. 1892. Palaeobotany of the Yellow Gravel at Bridgeton, N.J. *Bull. Torrey Bot. Club.*, 19: 330–333.
- HOLLICK A. 1896. New species of leguminous pods from the Yellow Gravel at Bridgeton, N.J. *Bull. Torrey Bot. Club.*, 23: 46–49.
- HOLLICK A. 1897. A new fossil monocotyledon from the Yellow Gravel at Bridgeton, N.J. *Bull. Torrey Bot. Club.*, 24: 329–331.
- HOLLICK A. 1927. The flora of the Saint Eugene Silts, Kootenay Valley, British Columbia. *Mem. New York Bot. Gard.*, 7: 389–427.
- HOLLICK A. 1928. Scientific Survey of Porto Rico and the Virgin Islands. Volume VII-Part 3. Paleobotany of Porto Rico. New York Academy of Sciences, New York, New York.
- HU H.H. & CHANEY R.W. 1940. A Miocene flora from Shantung Province, China. *Publ. Carnegie Inst. Wash.*, 507: 1–147.
- HUDDLESTUN P.F. 1984. The Neogene Stratigraphy of the Central Florida Panhandle. PhD, Florida State University, Tallahassee, Florida.
- ILJINSKAJA I.A. 1964. The Tortonian flora of Swoszowice and the Pliocene floras of Transcarpathia. *Int. Geol. Rev.*, 6: 716–723.
- INSTITUTE OF SYSTEMATIC BOTANY. 2016. Atlas of Florida plants. Available from [www.florida.plantatlas.usf.edu](http://www.florida.plantatlas.usf.edu). Accessed March 2018.
- ISLAM M.B. & SIMMONS M.P. 2006. A thorny dilemma: testing alternative intrageneric classifications within *Ziziphus* (Rhamnaceae). *Syst. Bot.*, 31: 826–842.
- JACOBS B.F. 2002. Estimation of low-latitude paleoclimates using fossil angiosperm leaves: examples from the Miocene Tugen Hills, Kenya. *Paleobiology*, 28: 399–421.
- JARZEN D.M., CORBETT S.L. & MANCHESTER S.R. 2010. Palynology and paleoecology of the Middle Miocene Alum Bluff flora, Liberty County, Florida, USA. *Palynology*, 34: 261–286.
- JOHNSTON M.C. 1963. The species of *Ziziphus* indigenous to United States and Mexico. *Amer. J. Bot.*, 50: 1020–1027.
- JOHNSON R.A. 1986. Shallow stratigraphic core tests on file at the Florida Geological Survey. *Fla. Geol. Surv. Inf. Cir.*, 103: 1–431.
- JOHNSON R.A. 1989. Geologic descriptions of selected exposures in Florida. Florida Geological Survey Special Publication, 30: 1–173.
- JONES J.H. 1986. Evolution of the Fagaceae: The implications of foliar features. *Ann. Missouri Bot. Gard.*, 73: 228–275.
- KEARNEY T.H. 1958. A tentative key to the South American species of *Abutilon*, Miller. *Leaf. W. Bot.*, 8: 210–224.
- KIRBY M.X., JONES D.S. & MACFADDEN B.J. 2008. Lower Miocene stratigraphy along the Panama Canal and its bearing on the Central American Peninsula. *PLoS ONE* 3: e2791, DOI: 10.1371/journal.pone.0002791.
- KIRCHHEIMER F. 1938. *Fossilium Catalogus II: Plantae. Pars 23: Umbelliflorae: Cornaceae*. W. Junk, Gravenhage (The Hague), The Netherlands.
- KIRCHHEIMER F. 1939. *Fossilium Catalogus II: Plantae. Pars 24: Rhamnales I: Vitaceae*. W. Junk, -Gravenhage (The Hague), The Netherlands.
- KIRCHHEIMER F. 1957. *Die Laubgewächse der Braunkohlenzeit*. Wilhelm Knapp Verlag, Halle (Saale), Germany.
- KLUCKING E.P. 1986. Leaf Venation Patterns, Volume 1, Annonaceae. J. Cramer, Berlin.
- KNOBLOCH E. 1961. Die oberoligozäne Flora des Pirskenberges bei Sluknov I Nord-Böhmen. *Sborn. Ústředního Ústavu Geol., Palaontol.*, 26: 241–315.
- KNOBLOCH E. & KVAČEK Z. 1976. Miozäne Blühtefloren vom Westrand der Böhmisches Masse. *Rozpravy Ústředního Ústavu Geologického*, 42: 1–131.
- KOVAR-EDER J. & HABLY L. 2006. The flora of Mataschen – a unique plant assemblage from the Late Miocene of Eastern Styria (Austria). *Acta Palaeobot.*, 46: 157–233.
- KOVAR-EDER J. & WÓJCICKI J.J. 2001. A Late Miocene (Pannonian) flora from Hinterschlagen, Hausruck lignite area, Upper Austria. *Acta Palaeobot.*, 41: 221–251.
- KOWALSKI E.A. & DILCHER D.L. 2003. Warmer paleotemperatures for terrestrial ecosystems. *Proc. Nat. Acad. Sci., USA*, 100: 167–170.
- KOYAMA T. 1958. Taxonomic study of the genera *Scirpus* Linné. *J. Fac. Sc., Univ. Tokyo*, III, 7: 271–366.
- KRÄUSEL R. 1921. Nachträge zur Tertiärflora Schlesiens. 3. Über einige Originale Göpperts und neuere Funde. *Jahrb. Preuss. Geol. Landesanst.*, 40: 363–433.
- KVAČEK J. & HERMAN A.B. 2004. Monocotyledons from the Early Campanian (Cretaceous) of Grünbach, Lower Austria. *Rev. Palaeobot. Palynol.*, 128: 323–353.
- KVAČEK Z. 1971. Fossil Lauraceae in the stratigraphy of the North-Bohemian Tertiary. *Sborn. Geologických věd, Paleontol.*, 13: 47–86.

- KVAČEK Z. 1988. The Lauraceae of the European Paleogene, based on leaf cuticles. *Cour. Forsch. Inst. Senckenberg*, 107: 345–354.
- KVAČEK Z & BŮŽEK C. 1972. *Nyssa*-leaves from the Tertiary of Central Europe. *Čas. Mineral. Geol., Roč.*, 17: 373–382.
- LANGDON D.W. JR. 1889. Some Florida Miocene. *Amer. J. Sci.* 3<sup>rd</sup> series, 38: 322–324.
- LEPAGE B.A. 2001. New species of *Picea* A. Dietrich (Pinaceae) from the middle Eocene of Axel Heiberg Island, Arctic Canada. *Bot. J. Linn. Soc.*, 135: 137–167.
- LESQUEREUX L. 1878a. Contributions to the fossil floras of the western Territories. The Tertiary flora. Rep. (Annual) U.S. Geol. Geogr. Surv. Territ., 7: 1–366.
- LESQUEREUX L. 1878b. Report of the fossil plants of the auriferous gravel deposits of the Sierra, Nevada. *Memoirs of the Museum of Comparative Zoology*, Vol. 6. John Wilson and Son, Cambridge.
- LI X, WANG H., LENG Q., XIAO L., GUO J. & HE W. 2014. *Paliurus* (Paliureae, Rhamnaceae) from the Miocene of East China and its macrofossil-based phylogenetic and phytogeographical history. *Acta Geol. Sin.*, 88: 1364–1377.
- LIU Y.-S. 2011. Why are the oak acorns from the Late Neogene Gray site so small? Mid Continental Palaeobotanical Colloquium, May 20–22, Raleigh, North Carolina.
- LIU Y.-S. & JACQUES F.M.B. 2010. *Sinomenium macrocarpum* sp. nov. (Menispermaceae) from the Miocene-Pliocene transition of Gray, northeastern Tennessee, USA. *Rev. Palaeobot. Palynol.*, 159: 112–122.
- LUO S.-X. & ZHANG D.-X. 2004. Leaf epidermal morphology of *Ormosia* Jacks. (Leguminosae) in China. *J. Trop. Subtrop. Bot.*, 12: 298–308.
- MABBERLEY D.J. 1997. *The Plant-Book, A portable dictionary of the higher plants*. Cambridge University Press, Cambridge.
- MACGINITE H.D. 1953. Fossil plants of the Florissant Beds, Colorado. *Carnegie Inst. Wash. Publ.*, 599.
- MAI H.D. 2004. The Miocene and Pliocene floras from Northeast-Brandenburg and Southwest-Mecklenburg. *Palaeontogr., B: Paläophytol.*, 269: 1–130.
- MAI H.D. & WALTHER H. 1978. Die floren der Haselbacher Serie im Weissen-See-Becken (Bezirk Leipzig, DDR). *Abh. Staatl. Mus. Mineral. Geol. Dresden*, 28: 1–200.
- MANCHESTER S.R. 1987. The fossil history of the Juglandaceae. *Monogr. Syst. Bot. Missouri Bot. Gard.*, 21: 1–137.
- MANCHESTER S.R. 1989. Systematics and fossil history of the Ulmaceae: 221–251. In: Crane P.R. & S. Blackmore (eds.), *Evolution, Systematics, and Fossil History of the Hamamelidae*. Clarendon Press, Oxford, UK.
- MANCHESTER S.R. 1999. Biogeographical relationships of North American Tertiary floras. *Ann. Missouri Bot. Gard.*, 86: 472–522.
- MANCHESTER S.R. & O'LEARY E.L. 2010. Phylogenetic distribution and identification of fin-winged fruits. *Bot. Rev.*, 76: 1–82.
- MANCHESTER S.R. & ZAVADA M.S. 1987. *Lygodium* foliage with intact sporophores from the Eocene of Wyoming. *Bot. Gaz.*, 148: 392–399.
- MANCHESTER S.R., XIANG Q.-Y., KODRUL T.M. & AKHMETIEV M.A. 2009. Leaves of *Cornus* (Cornaceae) from the Paleocene of North America and Asia confirmed by trichome characters. *Int. J. Plant. Sci.*, 170: 132–142.
- MANTZOUKA D, KVAČEK Z., TEODORIDIA V., UTESCHER T., TSAPARAS N. & KARAKITSIOS V. 2015. A new late Miocene (Tortonian) flora from Gavdos Island in southernmost Greece evaluated in the context of vegetation and climate in the Eastern Mediterranean. *N. Jb. Geol. Paläont. Abh.*, 275: 47–81.
- MASTROGIUSEPPE J. 1993. *Carex*: 1107–1138. In: Hickman J.C. (ed.), *The Jepson Manual, Higher Plants of California*. University of California Press, Berkeley, California.
- MATSON G.C. & CLAPP F.G. 1909. A preliminary report of the geology of Florida, with special reference to the stratigraphy: 25–173. In: Florida State Geological Survey, 2<sup>nd</sup> Annual Report, Tallahassee, Florida.
- MCCARTAN L., TIFFNEY B.H., WOLFE J.A., AGER T.A., WING S.L., SIRKIN L.A., WARD L.W. & BROOKS J. 1990. Late Tertiary flora assemblage from upland gravel deposits of the southern Maryland Coastal Plain. *Geology*, 18: 311–314.
- MEANS H. 2002. Introduction to the Geology of the Upper Apalachicola River Basin: 1–15. In: Southeastern Geological Society (eds.), *Geologic Exposures Along the Upper Apalachicola River*. Southeastern Geological Society Field Trip Guidebook 42. Tallahassee, Florida.
- MELLER B., ZETTER R., HASSLER A., BOUCHAL J.M., HOFMANN C.-C. & GRÍMSSON F. 2015. Middle Miocene macrofloral elements from the Lavanttal Basin, Austria, Part I. *Ginkgo adiantoides* (Unger) Heer. *Aust. J. Earth. Sci.*, 108: 185–198.
- METCALFE C.R. & CHALK L. 1950. *Anatomy of the Dicotyledons, Volume II*. Clarendon Press, Oxford.
- MEYER H.W. & MANCHESTER S.R. 1997. The Oligocene Bridge Creek flora of the John Day Formation, Oregon. *Univ. Calif. Publ. Geol. Sci.*, 141: 1–194.
- MEYER R.E. & MEOLA S.M. 1978. Morphological characteristics of leaves and stems of selected Texas woody plants. *U.S. Dep. Agric. Tech. Bull.*, 1564.
- MILLER C.N. JR. 1978. *Pinus burtii*, a new species of petrified cones from the Miocene of Martha's Vineyard. *Bull. Torrey Bot. Club.*, 105: 93–97.
- MILLER I.M., BRANDON M.T. & HICKEY L.J. 2006. Using leaf margin analysis to estimate

- Mid-Cretaceous (Albian) paleolatitude of the Baja BC Block. *Earth Planetary Sci. Lett.*, 245: 95–114.
- MOLDENKE H.N. 1934. Artificial key to the species and varieties of *Aegiphila*. *Brittonia*, 1(5/6): 263–280.
- MONTES C., CARDONA A., MCFADDEN R., MORÓN S.E., SILVA C.A., RESTREPO-MORENO S., RAMÍREZ D.A., HOYOS N., WILSON J., FARRIS D., BAYONA G.A., JARAMILLO C.A., VALENCIA V., BRYAN J. & FLORES J.A. 2012. Evidence for middle Eocene and younger land emergence in central Panama: Implications for Isthmus closure. *Bull. Geol. Soc. Amer.*, 124: 780–799.
- NEWBERRY J.S. 1895. The flora of the Amboy Clays. *U.S. Geol. Surv. Mong.*, 26: 1–260.
- NEWBERRY J.S. 1898. The later extinct floras of North America. *U.S. Geol. Surv. Mong.*, 35: 1–151
- NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION (NOAA). 2018. National Environmental Satellite, Data, and Information Service. [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov). Accessed 14 March 2018.
- NORTH AMERICAN COMMISSION ON STRATIGRAPHIC NOMENCLATURE. 2005. North American Stratigraphic Code. *AAPG Bulletin*, 89(11): 1547–1591.
- O'KEEFE S.T. 2003. Revision of the Nearctic genus *Papusus* Casey (Coleoptera, Scydmaenidae): 257–309. In: Cuccodoro G. & Leschen R.A.B. (eds.), *Systematics of Coleoptera: Papers Celebrating the Retirement of Ivan Löbl*, Vol. 17: Memoirs on Entomology International. Associated Publishers, Gainesville, Florida.
- OTVOS E.G. 1998. Citronelle Formation, Northeastern Gulf Coastal Plain: Pliocene stratigraphic framework and age issues. *Trans. GCAGS*, 48: 321–333.
- OTVOS E.G. 2004. Lithofacies and depositional environments of the Pliocene Citronelle Formation, Gulf of Mexico Coastal Plain. *Southeast. Geol.*, 43(1): 1–20.
- OZAKI K. 1991. Late Miocene and Pliocene floras in central Honshu, Japan. *Bull. Kanagawa Pref. Mus., Nat. Sci., Special Issue*. Kanagawa Prefectural Museum, Yokohama.
- PAZZAGALIA F.J., ROBINSON R.A.J. & TRAVERSE A. 1997. Palynology of the Bryn Mawr Formation (Miocene): insights on the age and genesis of Middle Atlantic margin fluvial deposits. *Sediment. Geol.*, 108: 19–44.
- PEPPE D.J., ROYER D.L., CARIGLINA B., OLIVER S.Y., NEWMAN S., LEIGHT E., ENIKOLOPOV G., FERNANDEZ-BURGOS M., HERRERA F., ADAMS J.M., CORREA E., CURRANO E.D., ERICKSON J.M., HINOJOSA L.F., HOGANSON J.W., IGLESIAS A., JARAMILLO C.A., JOHNSON K.R., JORDAN G.J., KRAFT N.J.B., LOVELOCK E.C., LUSK C.H., NIINEMETS Ü., PENUELAS J., RAPSON G., WING S.L. & WIRGHT I.J. 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New Phytologist*, 190: 724–739.
- PHUPHATHANAPHONG L. 2006. New taxa of *Aristolochia* (Aristolochiaceae) from Thailand. *Thai For. Bull.*, 34: 179–194.
- PORTELL R.W., POLITES G.L. & SCHMELZ G.W. 2006. Mollusca. Shoal River Formation (Middle Miocene). *Florida Fossil Invertebrates*, 9: 1–52.
- PORTER D.M. 1976. *Zanthoxylum* (Rutaceae) in North America North of Mexico. *Brittonia*, 28: 443–447.
- PURI H.S. & VERNON R.O. 1964. Summary of the geology of Florida and a guidebook to the classic exposures. *Fla. Geol. Surv. Special Pub.*, 5: 1–312.
- RACHELE L.D. 1976. Palynology of the Legler Lignite: A deposit in the Tertiary Cohansey Formation of New Jersey, U.S.A. *Rev. Palaeobot. Palynol.*, 22: 225–252.
- RADFORD A.E., AHLES H.E. & RITCHIE BELL C. 1968. *Manual of the Vascular Flora of the Carolinas*. The University of North Carolina Press, Chapel Hill, North Carolina.
- RANDAZZO A.F. & JONES D.S. 1997. *The Geology of Florida*. University Press of Florida, Gainesville, Florida.
- RAUNKIAER C. 1934. The use of leaf size in biological plant geography: 368–378. In: *The Life forms of Plants and Statistical Plant Geography*. Clarendon Press, Oxford.
- READ R.W. & HICKEY L.J. 1972. A revised classification of fossil palms and palm-like leaves. *Taxon*, 21: 129–137.
- REN H., PAN K.Y., CHEN V.Z.D. & WANG R.Q. 2003. Structural characters of leaf epidermis and their significance in Vitaceae. *Acta Phytotax. Sin.*, 4: 531–544.
- RICH F.J., PRIKLE F.L. & ARENBERG E. 2002. Palynology and paleoecology of strata associated with the Ochopee River dune field, Emanuel County, Georgia. *Palynology*, 26: 239–256.
- RICHARDSON J.E., FAY M.F., CRONK Q.C.B., BOWMAN D. & CHASE M.W. 2000. A phylogenetic analysis of Rhamnaceae using *RBCL* and *TRNL-F* plastid DNA sequences. *Amer. J. Bot.*, 87: 1309–1324.
- ROTH J.L. 1981. Epidermal studies in the Annonaceae and related families. PhD, Indiana University. Bloomington, Indiana.
- RUDD V.E. 1965. The American species of *Ormosia* (Leguminosae). *Contrib. U.S. Nat. Herb.*, 32: 279–384.
- SARGENT C.P. 1933. *Manual of the trees of North America*. The Riverside Press, Cambridge, Massachusetts.
- SCHIRAREND C. & OLABI M.N. 1994. Revision of the genus *Paliurus* Tourn. ex Mill. (Rhamnaceae). *Bot. Jahrb. Syst. Pflanzengesch. Pflanzengeogr.*, 116: 333–359.
- SCHMIDT W. 1983. Cenozoic geology of the Apalachicola River area Northwest Florida. *Southeastern Geological Society Guidebook*, 25: 1–95.

- SCHMIDT W. 1984. Neogene stratigraphy and geologic history of the Apalachicola embayment, Florida. Florida Geol. Surv. Bull., 58: 1–146.
- SCHMIDT W. 1986. Alum Bluff, Liberty County, Florida: 355–357. In: Neathery T.L. (ed.), Centennial Field Guide. Southeastern Section of the Geological Society of America, Vol. 6. Geological Society of America, Boulder, Colorado.
- SCHWARZWALDER R.N. 1986. Systematic and early evolution of the Platanaceae. PhD, Department of Biology, Indiana University, Bloomington, Indiana.
- SCOTT T.M. 1997. Miocene to Holocene History of Florida: 57–67. In: Randazzo A.F. & Jones D.S. (eds.), The Geology of Florida. University of Florida Press, Gainesville, Florida.
- SELLARDS E.H. & GUNTER H. 1909. The fullers earth deposits of Gadsden County. Fla. Geol. Surv. 2<sup>nd</sup> Ann. Rep., 299 pgs.
- SHAHEEN N, KHAN M.A., YASMIN G., AHMAD M.Q.H., ZAFAR M. & JABEEN A. 2009. Implications of foliar epidermal features in the taxonomy of *Abutilon* Mill. (Malvaceae). J. Med. Plants Res., 3: 1002–1008.
- SHU M.J.Z. 2007. *Paliurus* Miller. Flora of China, 12: 116–117. Accessed 20 July 2017, Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA.
- SHU Q.M. 2007. *Abutilon* Miller. Flora of China, 12: 275–279. Accessed August 2016, Missouri Botanical Garden, St. Louis, MO & Harvard University Herbaria, Cambridge, MA.
- SHUNK A.J., DRIESE S.G. & CLARK G.M. 2006. Latest Miocene to earliest Pliocene sedimentation and climate record derived from paleosinkhole fill deposits, Gray Fossil Site, northeastern Tennessee, U.S.A. Palaeogeogr. Palaeoclimatol. Palaeoecol., 231: 265–278.
- SMILEY C.J. & REMBER W.C. 1985. Composition of the Miocene Clarkia flora: 95–112. In: Smiley C.J. (ed.), Late Cenozoic History of the Pacific Northwest. Pacific Division of the American Association for the Advancement of Science, San Francisco, California.
- SMITH A.C. 1937. The American species of Myristicaceae. Brittonia, 2(5): 393–510.
- SMITH H.V. 1941. A Miocene flora from Thorn Creek, Idaho. Am. Midl. Nat., 25(3): 473–522.
- SMITH S.Y., COLLINSON M.E. & RUDALL P.J. 2008. Fossil *Cyclanthus* (Cyclanthaceae, Pandanales) from the Eocene of Germany and England. Am. J. Bot., 95(6): 688–699.
- SOLTIS D., SOLTIS P., ENDRESS P., CHASE M., MANCHESTER S., JUDD W., MAJURE L. & MAVRODIEV E. 2018. Phylogeny and Evolution of the Angiosperms. The University of Chicago Press, Chicago, Illinois.
- STEVENS P.F. 2001 onwards. Angiosperm Phylogeny Website. Version 12, July 2012. <http://www.mobot.org/MOBOT/research/APweb/>.
- STONE D.E. 1997. Juglandaceae: 416–428. In: Flora of North America Editorial Committee (eds.), Flora of North America, North of Mexico. Oxford University Press, New York, New York.
- STULTS D.Z, AXSMITH B.J. & LIU Y.-S. 2010. Evidence of white pine (*Pinus* subgenus *Strobus*) dominance from the Pliocene Northeastern Gulf of Mexico Coastal Plain. Palaeogeogr., Palaeoclimatol., Palaeoecol., 287: 95–100.
- STULTS D.Z, AXSMITH B.J., MCNAIR D. & ALFORD M. 2016. Preliminary investigations of a diverse Miocene megafauna from the Hattiesburg Formation, Mississippi. Botanical Society of America Conference, July 30–August 3, 2016, Savannah, Georgia, Abstract.
- TANAI T. & WOLFE J.A. 1977. Revisions of *Ulmus* and *Zelkova* in the middle and late Tertiary of Western North America. Profess. Pap. U.S. Geol. Surv., 1026: 1–14.
- TEODORIDIS V. 2003. Tertiary flora and vegetation of the locality Záhoví near Žatec (Most Basin, Czech Republic). Bull. Geos., 78: 261–276.
- TIDWELL W.D. 1998. Common fossil plant of Western North America. Smithsonian Institution Press, Washington D.C.
- TIFFNEY B.H. 1976. Fruits and seeds of the Brandon Lignite. I. Vitaceae. Rev. Palaeobot. Palynol., 22: 169–191.
- TIFFNEY B.H. 1977. Fruits and seeds of the Brandon Lignite: Magnoliaceae. Bot. J. Linn. Soc., 75: 299–323.
- TIFFNEY B.H. 1994. Re-evaluation of the age of the Brandon Lignite (Vermont, USA) based on plant megafossils. Rev. Palaeobot. Palynol., 82: 299–315.
- TRAVERSE A. 1955. Pollen analysis of the Brandon Lignite of Vermont. U.S. Bur. Mines Rep. Invest., 5151: 1–107.
- TRAVERSE A. 1994. Palynofloral geochronology of the Brandon Lignite of Vermont, USA. Rev. Palaeobot. Palynol., 82: 265–297.
- UEMURA K. 1988. Late Miocene floras in Northeast Honshu, Japan. National Science Museum, Tokyo.
- UFNAR D.F. 2007. Clay coatings from a modern soil chronosequence: A tool for estimating the relative age of well-drained paleosols. Goederma, 141: 181–200.
- UNGER F. 1850. Die Fossile Flora von Sotzka. Denkschr. Akad. Wiss. Wien, Germany.
- UNITED STATES DEPARTMENT OF AGRICULTURE (USDA): PLANTS DATABASE. 2016. [Plants.usda.gov/java/](https://plants.usda.gov/java/).
- VAN DER BURGH J. 1987. Miocene floras in the Lower Rhenish Basin and their ecological interpretation. Rev. Palaeobot. Palynol., 52: 299–366.
- VAUGHAN T.W. 1910. A contribution to the geological history of the Floridian Plateau. Carnegie Inst. Wash. Publ., 133: 103–185.

- VAUGHAN T.W. & COOKE C.W. 1914. Correlations of the Hawthorne Formation. Wash. Acad. Sci. Jour., 4: 250–253.
- VOKES E.H. 1989. An overview of the Chipola Formation, northwestern Florida. Tulane Stud. Geol. Paleont., 22: 13–24.
- WALLACE S.C. & WANG X. 2004. Two new carnivores from an unusual late Tertiary forest biota in Eastern North America. Nature, 431: 556–559.
- WANG Y.F., FERGUSON D.K., ZETTER Z., DENK T. & GARFI G. 2001. Leaf architecture and epidermal characters in *Zelkova*, Ulmaceae. Bot. J. Linn. Soc., 136: 255–265.
- WATERMAN P.G. 1975. New combinations in *Zanthoxylum* L. (1753). Taxon, 24: 361–366.
- WEBB L.J. 1959. A physiognomic classification of Australian rain forest. J. Ecol., 47: 551–570.
- WEN J. 1999. Evolution of Eastern Asia and Eastern North America disjunct distributions in flowering plants. Annual Rev. Ecol. Syst., 30: 421–455.
- WILF P. 1997. When are leaves good thermometers? A new case for leaf margin analysis. Paleobiology, 23: 373–390.
- WILF P., WING S.L., GREENWOOD D.R. & GREENWOOD C.L. 1998. Using fossil leaves as paleoprecipitation indicators: An Eocene example. Geology, 26: 203–206.
- WING S.L. & GREENWOOD D.R. 1993. Fossils and fossil climate: the case for equable continental interiors in the Eocene. Philos. Trans. R. Soc. Lond. B, 341: 243–252.
- WOLFE J.A. 1966. Tertiary plants from the Cook Inlet Region, Alaska. Profess. Pap. U.S. Geol. Surv., 398-B: 1–32.
- WOLFE J.A. 1979. Temperature parameters of humid to mesic forests of Eastern Asia and relation to forests of other regions in the Northern Hemisphere and Australasia. Profess. Pap. U.S. Geol. Surv., 1106: 1–37.
- WOLFE J.A. & TANAI T. 1987. Systematics, phylogeny, and distribution of *Acer* (maples) in the Cenozoic of Western North America. Jour. Fac. Sci., Hokkaido Univ. Ser. IV, 22: 1–246.
- WOODSON R.E., SCHERY R.W., PORTER D.M. & ELIAS T.S. 1979. Flora of Panama. Part VI. Family 89. Rutaceae. Ann. Missouri Bot. Gard., 66: 123–164.
- WOROBIEC G. 2003. New fossil flora from the Neogene deposits in the Belchatów lignite mine. Acta Palaeobot., Suppl., 3: 3–133.
- WOROBIEC G. & SZYNKIEWICZ A. 2007. Betulaceae leaves in Miocene deposits of the Belchatów Lignite Mine (Central Poland). Rev. Palaeobot. Palynol., 147: 28–59.
- WOROBIEC G., WOROBIEC E. & KASIŃSKI J. 2008. Plant assemblages of the drill cores from the Neogene Ruja lignite deposit near Legnica (Lower Silesia, Poland). Acta Palaeobot., 48(2): 191–275.
- WRENN J.H., ELSIK W.C. & MCCULLOH R.P. 2003. Palynologic age determination of the Catahoula Formation, Big Creek, Sicily Island, Louisiana. GCAGS/GCSSEPM Trans., 53: 865–875.
- WUNDERLIN R.P. 1998. Guide to the Vascular Plants of Florida. University Press of Florida, Gainesville, Florida.
- XU B.Q., XIA N.H., WANG S.P. & HAO G. 2007. Leaf epidermal morphology of *Osmanthus* (Oleaceae) from China. J. Wuhan Bot. Res., 25: 1–10.
- YU C.-H. & CHEN Z.-L. 1991. Leaf Architecture of the Woody Dicotyledons from Tropical and Subtropical China. Pregamon Press, Oxford, England.
- ZHOU W.J., LIU X.Y., XU Q.Q., HUANG K.Y. & JIN J.H. 2013. New coryphoid fossil palm leaves (Arecaceae: Coryphoideae) from the late Eocene Changchang Basin of Hainan Island, South China. Sci. China Earth Sci., 56: 1493–1501.
- ZOBBA M.K., ZAVADA M.S., WHITELAW M.J., SHUNK A.J. & OBOH-IKUENOBE F.E. 2011. Palynology and palynofacies analyses of the Gray Fossil Site, Eastern Tennessee: Their role in understanding the basin-fill history. Palaeogeogr. Palaeoclimatol. Palaeoecol., 308: 433–444.

## Supplementary Material

Genus: *Daphnogene* Unger 1845

### *Daphnogene* sp. 1

Pl. 1, figs 15, 16

Material examined. UF18049-56767

**Discussion.** The basal eucamptodromous venation of *Daphnogene* sp. 1 can also be found in numerous extant angiosperm families such as Lauraceae, Menispermaceae, Ranunculaceae, Coriariaceae, Rhamnaceae, Urticaceae, Ulmaceae, Ericaceae, Melastomataceae, Myrtaceae, Oleaceae, Loganiaceae, Compositae and Caprifoliaceae. In Lauraceae (e.g. *Cinnamomum camphora* (L.) J. Presl) the stomata are paracytic (Baruah & Nath 1997). In Menispermaceae (e.g. *Cocculus heterophyllus* Hemsl. et E.H. Wilson) the stomata have 4–8 subsidiary cells, while in *C. laurifolius* DC. the anticlinal cell walls are sinuate (Ferguson 1971, 1974). In Loganiaceae (e.g. *Strychnos spinosa* Lam.) the paracytic stomata are sunken, and in Ranunculaceae (e.g. *Clematis reticulata* Walt.) the venation is highly pronounced to the fourth order, the stomata are anomocytic and the anticlinal cell walls are highly sinuate. In Coriariaceae (*Coriaria*) the stomata are narrow (Ferguson 1971). In Rhamnaceae (e.g. *Ziziphus chloroxyylon* (L.) Oliv., *Z. inermis* Merr., *Lasiodiscus gillardinii* Staner) the eucamptodromous veins extend to the leaf tip and the stomata are anomocytic, paracytic to amphibrachyparacytic. In Urticaceae (e.g. *Pouzolzia zeylanica* (L.) Benn.) the eucamptodromous veins extend to the leaf tip, with hooked or conical trichomes (Gangadhara & Inamdar 1977). In Cannabaceae (e.g. entire-margined *Celtis*) the eucamptodromous veins are accompanied by agrophic veins. In Myrtaceae (e.g. *Myrtus*) there are trichomes and a second pair of weaker veins that are sinuate along the leaf margin (Ettinghausen 1886, Ferguson 1971). In Oleaceae (e.g. *Jasminum*) there are characteristic unicellular, glandular to peltate trichomes (Upadhyay et al. 1989). In Caprifoliaceae (e.g. *Viburnum*) the subsidiary cells are separated from the epidermal cells by a thickened cell wall (Ferguson 1971). In Compositae (e.g. *Eupatorium mikanioides* Chapm.) the secondary veins are conspicuous and the margin is serrate. Overall, *Daphnogene* sp. 1 characters such as elliptic shape with entire

margins, acrodromous veins extending more than 1/2 leaf length and then becoming less pronounced (Pl. 1, fig. 15), the upper part of the leaf with brochidodromous veins, persistent cuticle, anticlinal cell walls mostly straight, some arcuate, and brachyparacytic stomata with an inner ledge (Pl. 1, fig. 16) fit well with features of Lauraceae. The one difficulty is the lack of secretory glands in the fossil leaf. Such glands are diagnostic for Lauraceae but may not appear in cuticle preparations such as those of extant *Cinnamomum camphora*, *Laurus officinalis* and *Litsea glaucescens* Kunth.

*Daphnogene* sp. 1 is unique among Alum Bluff specimens in having numerous minute holes in its dark brown cuticle, while lacking holes in its light brown cuticle. Under epifluorescence there are fluorescent amorphous substances surrounding the guard cells in the light brown cuticle that may lead to the breakdown of the stomatal complex under the action of taphonomic processes.

### *Daphnogene* sp. 2

Pl. 1, figs 17, 18, Pl. 2, figs 1–3

Material examined. UF18049-43575, 69001

**Discussion.** Characters of *Daphnogene* sp. 2 shared with extant angiosperm families such as Dioscoreaceae, Stemonaceae, Alstroemeriaceae, Petermanniaceae, Trilliaceae, Ripogonaceae, Smilacaceae, Rhamnaceae, Melastomataceae, Lauraceae, Adoxaceae and Ericaceae include an ovate to elliptic leaf with entire margins, and acrodromous venation to the leaf apex. In Dioscoreaceae the leaf base is cordate, with non-sinuate anticlinal walls (Ding et al. 2011); *Dioscorea* has multicellular club-shaped trichomes (Ferguson 1971), *Trichopus* has crescent-shaped multicellular glands on short unicellular stalks (Ayensu 1966), and *Rajania ovata* Sw. has numerous resin cells on the abaxial surface, along with scattered single trichomes. In Stemonaceae (*Croomia*, *Stemona*, *Stichoneuron*) and Philesiaceae (*Philesia*) the stomata are aligned transverse to the leaf axis (Conran & Clifford 1985, Conover 1991, Conran et al. 2009, Ding et al. 2011). In *Croomia pauciflora* (Nutt.) Torr. the leaf base is cordate, and in *Lapageria* (Philesiaceae) the stomata are exclusively anomocytic (Conover 1991). In Alstroemeriaceae (*Behnia*),

Petermanniaceae (*Petermannia*) and Trilliaceae the stomata are aligned parallel to the leaf axis (Ding et al. 2011). Also, in Alstroemeriaceae (e.g. *Alstroemeria pulchella* L. f., *Bomarea acutifolia* (Link & Otto) Herb.) there are more than ten parallel major and minor acrodromous veins. In Ripogonaceae (*Ripogonum*) the stomata are paracytic to brachyparacytic and lack a stomatal ledge (Pole 2007, Conran et al. 2009, Ding et al. 2011). In Smilacaceae the vegetative and epidermal characters are similar in *Smilax* and *Heterosmilax* (Ferguson 1971), and the number of acrodromous veins can vary from three to seven (Ding et al. 2011). Sinuate anticlinal cell walls and paracytic stomata are found in *S. glaucochina* Warb. ex Diels, *S. hayatae* T. Koyama and *S. ocreata* A.DC., and stomata size in our fossil is similar to that of *S. ocreata* (Ding et al. 2011), but extant Smilacaceae lack a stomatal ridge. In Rhamnaceae, *Trevoa quinquerteria* Gillies & Hook. has trichomes, while the ovate leaves of *Ziziphus chloroxylon* and *Z. inermis* have interior secondaries at 68–80°, straight anticlinal cell walls and anomocytic stomata. In Melastomataceae, *Tetrazygia discolor* (L.) DC., *Graffenrieda jucunda* (DC.) Mart. and *Leandra scabra* DC. (Ettinghausen 1886) have acrodromous veins extending to the leaf tip, but the surfaces are covered with various and often complex trichomes. In Lauraceae the distinctive feature is the stomatal ledge, and the species with three acrodromous veins to the apex include *Cinnamomum corneri* Kosterm., *C. javanicum* Koorders., *C. wilsonii* Gamble and *Cryptocarya isonerua* Kosterm. (Klucking 1987). In Adoxaceae, *Viburnum davidii* Franch. has three deeply impressed acrodromous veins to the apex, and the margin has teeth near the apex (Dirr 2007). In Ericaceae, *Thibaudia costaricensis* Hoer. has three primary and two secondary acrodromous veins, the surface has a minute polygonal pattern and the stomata are paracytic, but the abaxial surface has scattered single trichomes and the subsidiary cells are distinct from the guard cells. Overall, characters of *Daphnogene* sp. 2 such as three acrodromous veins to the leaf tip (Pl. 1, fig. 17), interior veins (Pl. 2, fig. 3), sinuate anticlinal cell walls (Pl. 1, fig. 18, Pl. 2, fig. 1), paracytic stomata with a stomatal ledge, and thin subsidiary cell walls (Pl. 2, fig. 1) are found in Lauraceae (e.g. *Cinnanomum* Schaeff., *Cryptocarya* R. Br.). The stomatal size in our fossil is similar to that of *Cinnanomum* and *Cryptocarya* but their

epidermal cells are smaller than in *Daphnogene* sp. 2 (Christophel and Rowett 1996). Specimen 43575 is provisionally placed in *Daphnogene* sp. 2 due to the similarity of venation to 69001, but the lack of cuticle is troubling.

## REFERENCES

- AYENSU E.S. 1966. Taxonomic status of *Trichopus*: anatomical evidence. Bot. J. Linn. Soc., 59: 425–430.
- BARUAH A. & NATH S.C. 1997. Foliar epidermal characters in twelve species of *Cinnamomum* Schaeffer (Lauraceae) from Northeastern India. Phytomorphology, 47(2): 127–134.
- CHRISTOPHEL D.C. & ROWETT A.I. 1996. Leaf and cuticle atlas of Australian leafy Lauraceae. Flora of Australia Supplementary Series, 6: 1–217.
- CONOVER M.V. 1991. Epidermal patterns of the reticulate-veined Liliiflorae and their parallel-veined allies. Bot. J. Linn. Soc., 107(3): 295–312.
- CONRAN J.G., CARPENTER R.J. & JORDAN G.J. 2009. Early Eocene *Ripogonum* (Liliales: Ripogonaceae) leaf macrofossils from southern Australia. Aust. Syst. Bot., 22(3): 219–228.
- CONRAN J.G. & CLIFFORD H.T. 1985. The taxonomic affinities of the genus *Ripogonum*. Nord. J. Bot., 5: 215–219.
- DING S.T., SUN B.N., WU J.Y. & LI X.C. 2011. Miocene *Smilax* leaves and associated epiphyllous fungi from Zhejiang, East China and their paleoecological implications. Rev. Palaeobot. Palynol., 165(3–4): 209–223.
- DIRR M.A. 2007. *Viburnums*. Flowering Shrubs for Every Season. Timber Press, Portland, Oregon, U.S.A.: 1–262.
- ETTINGHAUSEN C.R. 1886. Die Blätter-Skelete der Dikofyledonen mit besonderer Rücksicht auf die Untersuchung und Bestimmung der fossilen Pflanzenreste. Wien.
- FERGUSON D.K. 1971. The Miocene flora of Kreuzau, Western Germany. I. The leaf-remains. Verhandlungen der Koninklijke Nederlandse Akademie van Wetenschappen, Afd. Natuurkunde Tweede Reeks, Dell 60(1): 1–297.
- FERGUSON D.K. 1974. The significance of the leaf epidermis for the taxonomy of *Cocculus* (Menispermaceae). Kew Bull., 29(3): 483–492.
- GANGADHARA M. & INAMDAR J.A. 1977. Trichomes and stomata, and their taxonomic significance in the Urticales. Plant Syst. Evol, 127: 121–137.
- KLUCKING E.P. 1987. Leaf Venation Patterns, Volume 2, Lauraceae. J. Cramer, Berlin.
- POLE M.S. 2007. Monocot macrofossils from the Miocene of southern New Zealand. Palaeontologia Electronica, 10(3.14A): 1–21.
- UPADHYAY N., TRIVEDI B.S. & VERMA C.L. 1989. Foliar epidermal studies in Indian *Jasminum*. Bull. Bot. Surv. India, 31(1–4): 136–148.

Appendix 1. Extant plant specimens examined

Genus	Species	Author	Collector	Collector #	Location	Collection date	Specimen #	Notes
<i>Abarema</i>	<i>glauca</i>	(Urb.) Barneby & J.W. Grimes	Brumbach	9413	United States: Florida	21 October 1978	FLAS 140695	
<i>Adiantum</i>	<i>tenerum</i>	Sw.	Ward	1745	United States: Florida	15 Dec. 1959	FLAS P5137	
<i>Alstroemeria</i>	<i>pulchella</i>	L.f.	Abbott	24710	United States: Florida	21 May 2008	FLAS 226866	
<i>Ampelopsis</i>	<i>arborea</i>	(L.) Koehne	Koch	55	United States: Florida	30 September 2006	FLAS 222874	
<i>Aphananthe</i>	<i>monoica</i>	(Hemsl.) J.-F. Leroy	Manchester		Tamaulipas, Mexico	Oct. 2003	UF 5675	
<i>Artocarpus</i>	<i>altalis</i>	(Parkinson ex F.A. Zorn) Fosberg	Thomas	MT606	Brazil: Bahia	16 September 1998	FLAS 201744	
<i>Artocarpus</i>	<i>altalis</i>	(Parkinson ex F.A. Zorn) Fosberg	Abbott	15549	Ecuador: Napo	14 November 1994	FLAS 190144	
<i>Betula</i>	<i>allegahaniensis</i>	Britt.	Dearn	54173	United States: Indiana	July 27, 1933	UF 4096	
<i>Bomarea</i>	<i>acutifolia</i>	(Link & Otto) Herb.	Smith, Beckner, Hall	2287	Costa Rica: Cartaga	10 April 1968	FLAS 107864	
<i>Bursera</i>	<i>sinaruba</i>	(L.) Sarg.	Brumbach	5820	United States: Florida	29 April 1967	FLAS 100800	
<i>Calligonum</i>	<i>leucocladum</i>	(Schrenk) Bunge	Nejli	212	Tadzhikistan		UF 2460	
<i>Carya</i>	<i>floridana</i>	Sarg.	Abbott	24801	United States: Florida	6 June 2008	FLAS 226873	
<i>Carya</i>	<i>glabra</i>	(Mill.) Sweet	Hinojosa et al.		United States: Florida	1997	UF 5243	
<i>Carya</i>	<i>illinoensis</i>	(Wangenh.) K. Koch	V. Call		United States: Florida		UF 1541	
<i>Casearia</i>	<i>corymbosa</i>	Kunth	Alcorn	757	Belize: Orange Walk	11.01.1989	FLAS 207332	
<i>Castanopsis</i>	<i>acuminatissima</i>	(Blume) A.D.C.	Brass	5216	British New Guinea	1933	UF 3069	MO 1261159
<i>Chrysobalanus</i>	<i>icaco</i>	L.	Abbott & Judd	7201	United States: Florida	13 July 1994	FLAS 188020	
<i>Chrysobalanus</i>	<i>icaco</i>	L.	Wright	1607	Cuba		UF 324	
<i>Cinnamomum</i>	<i>camphora</i>	(L.) J. Presl	Moore		Thailand: BKF	2006	UF 3838	
<i>Clematis</i>	<i>reticulata</i>	Walt.	Dilcher & Davanzo		United States: Florida	13 April 1995	UF 5581	
<i>Colubrina</i>	<i>asiatica</i>	(L.) Brongn.	Lott	DT 1796.04	United States: Florida	28 February 2003	UF 6264	
<i>Cornus</i>	<i>amomum</i>	Miller	Horn	1962	United States: South Carolina	17 June 1987	FLAS 172900	
<i>Crataegus</i>	<i>aestivalis</i>	(Walt.) Torr. & A. Gray	Abbott	13539	United States: Florida	9 May 2000	FLAS 207614	
<i>Croomia</i>	<i>pauciflora</i>	(Nutt.) Torr.	McDaniel	9252	United States: Alabama	June 13 1967	FLAS 102335	
<i>Cyclocarya</i>	<i>paliurus</i>	(Batalin) Iljinsk.	Shan		China: Kiangsi	6 July 1922	UF 1932	MO 903638
<i>Degeneria</i>	<i>vitiensis</i>	L.W. Bailey & A.C. Sm.	Degener	14537	Fiji: Viti Levu	4 Feb. 1941	UF 3278	MO 1257017
<i>Diospyros</i>	<i>virginiana</i>	L.	Abbott	20597	United States: Florida	6 Sep 2005	FLAS 234848	
<i>Diospyros</i>	<i>virginiana</i>	L.	Davis	294	United States: Florida	15 April 2002	FLAS 211368	
<i>Eupatorium</i>	<i>mikanioides</i>	Chapm.	Lott et al.	DT 1677.00	United States: Florida	5.ix.1993		
<i>Eupomatia</i>	<i>laurina</i>	R. Br.	Caley		Australia: Botany Bay	January 1804	UF 2119	MO 1618519
<i>Ficus</i>	<i>palmeri</i>	S. Watson	Johnson	3162	Mexico: Gulf of California	18 April 1921	UF 1800	
<i>Ficus</i>	<i>religiosa</i>	L.	Jarzen & Jarzen		United States: Florida	17 February 2001	UF 5441	
<i>Frangula</i>	<i>sphaerosperma</i>	(Sw) Kartesz & Gandhi			United States: Kansas		UF 2971	MO 979365
<i>Galbulimima</i>	<i>belgraveana</i>	(F. Muell.) Sprague	Carr	12711	Papua: Koitaki		UF 2777	NY s.n.
<i>Ginkgo</i>	<i>biloba</i>	L.	Lott	DT 1900.00	United States: Florida	17 August 2016	UF 6776	
<i>Glossocalyx</i>	<i>longicuspis</i>	Benth.	Zaukay		Cameroon: Lokundje	1911	UF 1671	F 760964
<i>Hedycarya</i>	<i>arborea</i>	J.R. Forst. & G. Forst.	Beecher		New Zealand: Auckland		UF 787	F 1448986

## Appendix 1. Continued

Genus	Species	Author	Collector	Collector #	Location	Collection date	Specimen #	Notes
<i>Hibiscus</i>	<i>rosa-sinensis</i>	L.	Lott	DT 1756.09	United States: Florida	6 October 1996		
<i>Koeleruteria</i>	<i>elegans</i>	(Seem.) A.C. Sm.	Levins		United States: Florida	29 October 1999	FLAS 200763	
<i>Lastodiscus</i>	<i>gillardinii</i>	Staner	Leonard	3780	Congo	10 April 1959	UF 2999	MO 2220762
<i>Laurus</i>	<i>officinale</i>	Nees			Italy: Naples	1893	UF 4	
<i>Licaria</i>	<i>triantandra</i>	(Sw.) Kosterm.	Goodfriend		Jamaica: St. Ann	2 June 1970	FLAS 145509	
<i>Litsea</i>	sp.				Borneo: Mt. Kinabalu	1932	UF 1	U I27928
<i>Litsea</i>	sp.				Borneo: Mt. Kinabalu	1932	UF 14	U I27784
<i>Litsea</i>	sp.				Borneo: Mt. Kinabalu	1932	UF 15	UD 28409
<i>Litsea</i>	<i>glaucescens</i>	Kunth			Mexico	1943	UF 12	UI 12800
<i>Lygodium</i>	<i>japonicum</i>	(Thunb.) Sw.	Scanlon, Matthews, Woods	176	United States: Florida	07.02.2000	FLAS 205088	
<i>Magnolia</i>	<i>fordiana</i>	(Oliv.) Hu	Levine	1345	China: Canton	10 August 1917	UF 3282	MO 825331
<i>Magnolia</i>	<i>liliiifera</i>	(L.) Baill.	Clemens	36936-2	Philippines: Lake Lanao	Nov. 1906	UF 1573	F 239252
<i>Magnolia</i>	<i>poasana</i>	(Pittier) Dandy	Jemendz M.	761	Costa Rica: Alajuela	22 June, 1963	UF 1559	F 1657452
<i>Michelia</i>	sp.		Fhung	20057	China: Hainan	April 1932	UF 1731	USNM 1665151
<i>Mimusops</i>	<i>balata</i>	(Aubl.) C.F. Gaertn.	Allen		United States: Florida	30 Jan. 1972	FLAS 112414	
<i>Mimusops</i>	<i>coriacea</i>	(A.DC.) Miq.	Cochran		United States: Florida	28 Feb. 2014	FLAS 241750	
<i>Nyssa</i>	<i>ogeche</i>	Bartram ex Marshall	Lott	DT 782.32	United States: Florida	12 Sept. 1987		
<i>Ormosia</i>	<i>calavensis</i>	Azaola ex Blanco	West & Arnold		United States: Florida	1953	UF 5445	FLAS 65526
<i>Osmanthus</i>	<i>americanus</i>	(L.) A. Gray	Weber	326	United States: Florida	3/11/1931	FLAS 19454	
<i>Osteophloeum</i>	<i>platyspermum</i>	(Spruce ex A. DC.) Warb.	Rodriguez	12261	Brazil: Acre	1971	UF 2065	MO 2180786
<i>Ostrya</i>	<i>virginiana</i>	(Mill.) K. Koch	Lott	DT 782.31	United States: Florida	3 October 1987		
<i>Picea</i>	<i>glauca</i>	(Moench) Voss	Lange	1627	United States: New York	14 September 2012	FLAS 241435	
<i>Picea</i>	<i>mariana</i>	(Mill.) Britton, Sterns & Poggenb.	Duncan, Duncan	30211	Canada: New Foundland	22 Sept. 1976	FLAS 134591	
<i>Pisonia</i>	<i>aculeata</i>	L.	Abbott	25073	United States: Florida	14 September 2008	FLAS 232346	
<i>Pisonia</i>	<i>rotundata</i>	Griseb.	Brumbach	9474	United States: Florida	2 April 1979	FLAS 139236	
<i>Planera</i>	<i>aquatica</i>	Walt. ex J.F. Gmel.	Call		United States: Florida	10 Jan. 1993	UF 5657	
<i>Planera</i>	<i>aquatica</i>	Walt. ex J.F. Gmel.	Lott	DT 794.14	United States: Florida	31 October 1987	UF 6259	
<i>Planera</i>	<i>aquatica</i>	Walt. ex J.F. Gmel.	Abbott	22610	United States: Florida	4 June 2007	FLAS 233803	
<i>Populus</i>	<i>monticola</i>	Brandegee	Lange	835	United States: Florida	July 5, 2011	FLAS 233344	
<i>Pouzolzia</i>	<i>zeylanica</i>	(L.) Benn.	Abbott	24172	United States: Florida	4 March 2008	FLAS 226889	
<i>Prunus</i>	<i>serotina</i>	Ehrh.	Dilcher & Davanzo		United States: Florida	13 April 19952	UF 5452	
<i>Quercus</i>	<i>austrina</i>	Small	Judd	3293	United States: Florida	19 April 1983	FLAS 150613	
<i>Rajania</i>	<i>ovata</i>	Sw.	Judd	4782	Haiti: De L'Quest	17 May 1984	FLAS 176752	
<i>Ranunculus</i>	<i>pusillus</i>	Poir.	Rogers	40690	United States: Tennessee	April 20, 1988	FLAS 118556	

## Appendix 1. Continued

Genus	Species	Author	Collector	Collector #	Location	Collection date	Specimen #	Notes
<i>Ranunculus</i>	<i>platensis</i>	A. Spreng	Allen	6428	United States: Louisiana	19 March 1975	FLAS 126322	
<i>Ranunculus</i>	<i>trilobus</i>	Desf.	Dale Thomas	104308	United States: Louisiana	3 May 1988	FLAS 168778	
<i>Rosa</i>	<i>palustris</i>	Marsh.	Hall	1148	United States: Florida	8 Dec. 1982	FLAS 148203	
<i>Sabal</i>	<i>palmetto</i>	(Walter) Lodd. ex Schultes & Schultes f.	Smith	2769	United States: Georgia	Feb. 1910	UF 668	
<i>Sabal</i>	<i>palmetto</i>	(Walter) Lodd. ex Schultes & Schultes f.	Lott	DT 1901.00	United States: Florida	5 August 2016	UF 2553	
<i>Salix</i>	<i>floridana</i>	Chapm.	Judd	2766	United States: Florida	4 Sept. 1980	FLAS 144201	
<i>Sambucus</i>	<i>canadensis</i>	L.	Lott	DT 781.14	United States: Florida	16 August 1987		
<i>Sapindus</i>	<i>saponaria</i>	L.	Davis	1232	United States: Florida	21 June 2005	FLAS 215667	
<i>Sideroxylon</i>	<i>lanuginosum</i>	Michx.	Herring	393	United States: Florida	August 31, 1991	FLAS 183377	
<i>Sideroxylon</i>	<i>tenax</i>	L.	Allison	12116	United States: Georgia	July 22, 1999	FLAS 216256	
<i>Strychnos</i>	<i>spinosa</i>	Lam.	Matthews Lott	DT 1480.06	United States: Florida	28 August 1992		
<i>Thibaudia</i>	<i>costaricensis</i>	Hoer.	Wilbur, Stone	10157	Costa Rica: Cartaga	23 March 1968	FLAS 105733	
<i>Trevoa</i>	<i>quinquenervia</i>	Gillies & Hook.	Zollner	9042	Chile	Oct. 5 1975	UF 3042	MO 2398537
<i>Trichilia</i>	sp.		Dilcher		Panama: Barro Colorado		UF 5808	
<i>Ulmus</i>	<i>alata</i>	Michx.	Rider	283	United States: Florida	7/26/00	FLAS 237321	
<i>Ulmus</i>	<i>americana</i>	L.	Corogin	TC558	United States: Florida	5 Aug. 2007	FLAS 228101	
<i>Ulmus</i>	<i>crassifolia</i>	Nutt.	Hubbard	685	United States: Florida	12 Mar 2007	FLAS 229774	
<i>Ulmus</i>	<i>palmetta</i>		Dilcher		Morris Arboretum	Nov. 5, 1974	UF 2352	
<i>Ulmus</i>	<i>procera</i>	Salisbury	Meyer et al.	15931	Washington D.C.	24 June 1977	FLAS 147281	
<i>Ulmus</i>	<i>pumila</i>	L.	Lange	1622	United States: New York	13 Sep 2012	FLAS 236560	
<i>Viburnum</i>	<i>dentatum</i>	L.	Farabee		United States: Florida	18 May 2008	FLAS 225654	
<i>Vitis</i>	<i>aestivalis</i>	Michx.	Skean	1997	United States: Florida	28 July 1986	FLAS 161658	
<i>Zanthoxylum</i>	<i>fagara</i>	(L.) Sarg.	Lott	DT 1836.63	Bahamas: Abaco	8 January 2006	UF 5787	
<i>Zanthoxylum</i>	<i>martinicense</i>	(Lam.) DC.			Puerto Rico	1885	UF 463	Munich Herbarium
<i>Zelkova</i>	<i>schneideriana</i>	Hand.-Mazz.	Manchester	s.n.	Austria: Zurich Bot. Garden	Aug. 30, 1987	UF 6263	
<i>Zelkova</i>	<i>sinica</i>	C.K. Schneid.	Wilson	2699	China: Western Hupeh	7/1907	UF 3336	F 477783
<i>Ziziphus</i>	<i>chloroxylon</i>	(L.) Oliv.	Adams	12312	Jamaica: St. Catherine Parish	3/3/1963	UF 2411	
<i>Ziziphus</i>	<i>inermis</i>	Merrill	Ramos	1960	Philippines: Zuzon	Nov. 1914	UF 2413	MO 836766
<i>Ziziphus</i>	<i>obtusifolia</i>	(Hook. ex Torr. & A. Gray) A. Gray	Palmer				UF 2415	

## Appendix 2. Alum Bluff fossil plant specimens examined

Taxon	Material examined (UF 18049)
Morphotype AB46	48377, 48377'
Morphotype AB30	48376, 48376'
cf. <i>Laurophyllum pseudovillense</i> Kvaček	43523, 43587, 61112, 61113, 61114b, 61195, 68906b, 68909, 68894, 68894', 68913, USNM 38284 (Holotype, Berry 1916c, Pl. IX, fig. 3.)
cf. <i>Laurophyllum pseudoprinceps</i> Weyland et Kilpper	61196, 68916
<i>Daphnogene</i> sp. 1	56767, USNM 38285 (Plesiotype, Berry 1916c, Pl. X, fig. 4)
<i>Daphnogene</i> sp. 2	43575, 69001
<i>Sabalites apalachicolensis</i> Berry 1916	29127a, b thru 29130, 29134–29138, 29140–29144, 29149, 43507, 43520b, 43548–43550, 43552, 43554, 43555b, 43576b, 43571b, 48365, 48368, 48368', 48369a,b,b', 48370, 48371, 48372, 48372', 48373a, 48374a, 48375, 48375', 48378, 48378', 48380a, b, 48383, 48383', 53156a, 53712b, 53762b, 53777–53783, 53800–53804, 55154a, 59497–59499, 60736, 60737, 60737', 60740, 60744b, 61026, 61055, 61057–61059a, b, 61060–61065b, 61066–61074, 61077–61083a,b, 61084a,b, 61085–61088, 61090, 61092–61103, 61182b, 62035g, 62230b, 62230b', 62237, 62245b, 68861, 68861', 68862–68864, 68865, 68889, 68889', 68890–68893, 68896–68899, 68900, 68900', 68901, 69441–69443, 69535, 69535', 69536a, 69543b, 69543b', 70087, 70092b, 70093, 70094a, 70095, 70097, 70097', 70098, 70100, 70101, 70106a, 70174, 70175, 70181a, 70200b, 70202a, 70207, 70208, 70209b, USNM 38281b, 38276, 175739a,b, 175738, 175740. (Lectotype: USNM 38277, Berry 1916c, pl. 8, fig. 2 [designated in Read & Hickey 1972, pg. 136])
<i>Palmacites</i> sp.	29139
<i>Scirpus</i> sp.	43597
<i>Carex</i> sp. 1	43511, 43511'
<i>Carex</i> sp. 2	43538, 43538', 68904b
Morphotype AB17	53308, 53308', 53310
Morphotype AB1	29133b, 29133b', 43520a, 43522, 43522', 43559, 43566, 43577, 43586a, 53164a, 53164a', 62252, 62252', 69536b, 70074a, 70075, 70178
cf. <i>Salix varians</i> Goepf.	43547, 43567, 43567', 48384, 53567, 61108–61110, 68905
<i>Salix</i> sp. 1	69542, 69544a, 70797
<i>Leguminosites apalachicolensis</i> (Berry) n. comb.	43527, 56744, 68867, 70106b, USNM 38280 (Holotype, Berry 1916c, Pl. X, fig. 1).
<i>Leguminosites sellardsii</i> (Berry) n. comb.	43534, 43534', 43578c, 53759–53761, 61065a, 61076, 61076', 70104, 70177, USNM 38281 (Holotype, Berry 1916c, Pl. IX, fig. 1, 1a)
<i>Leguminosites</i> sp. 1	43512, 43512'
<i>Leguminosites</i> sp. 2	43533
<i>Paliurus</i> sp.	43505, 43506, 43514, 43543, 43557, 43562, 62113, 70187
<i>Paliurus favonii</i> Unger	26117, 26117', 62410a, 62410a', 70079, 70079'
<i>Ulmus prestonia</i> sp. nov.	43504c, 43510, 43510', 43513, 43513', 43518, 43519, 43532, 43535, 43536, 43545, 43555a, 43560, 43561, 43563, 43563', 43572, 43572', 43579, 56769, 60742, 60747, 61056, 61056', 61111, 61187, 62001, 62003–62006, 62008–62012, 62021, 62022a, 62022a', 62023, 62025, 62025', 62027, 62030, 62032–62034, 62035d–f, 62230a, 62230a', 62231, 62232, 62236, 62236', 62238, 62242, 68868, 68903, 68910, 69540, 69540', 70069, 70071, 70078, 70080, 70082, 70083, 70085, USNM 109206b, 38278a–c
<i>Ulmus</i> sp. 1	29132, 43531, 62013b
<i>Ulmus</i> spp.	43515, 43565, 43578a,b, 51107, 56770, 60735, 60735', 60738, 60739, 60741, 60741', 60743, 60745, 60750, 61114a, 62002, 62002', 62013a, 62024, 62028, 62029, 62031, 62035b, 62233a,b,62233a'b', 62234, 62235b, 62240, 62241, 62241', 62243, 62243', 62244, 68866, 68914, 69531, 69533, 70073, 70074b, 70086, 70107, 70109, 70109', 70110, 70176, 70197
<i>Ulmus</i> sp. (fruit)	71312, 71312'
Morphotype AB36	43556
Morphotype AB5	43573, 61184
<i>Carya</i> cf. <i>serraefolia</i> (Goepf.) Kräusel	43502, 43504a,b, 43504a', 43542, 43544, 43588a,b, 43588a', 48386, 53156b, 53164b, 53154b', 53703–53705, 53716a, 53718, 53719, 53722–53724, 53724', 61104, 61182a, 61182a', 61183, 61183', 61185, 61186, 61192, 62035a,c, 68902, 68902', 68918a, 69525, 69527, 69543a, 69543a', 70081, 70541.
<i>Carya</i> sp.	20963, 43500, 43509, 43516a,b, 43524–43526, 43528a,b, 43529a,b, 43530, 43564a,b, 43568, 43569, 43576a, 43581, 43582, 43584, 53149, 53712a, 53713a, 53714, 53715, 53716a–d, 53721, 53725, 61075, 61181, 61188–61191, 61193, 68911, 68912
Morphotype AB16	53309

**Appendix 2.** Continued

Taxon	Material examined (UF 18049)
<i>Sambucus</i> sp.	43521
Morphotype AB54	69528, 69529
Morphotype AB11	29133a, 29133a', 43503, 43517, 43517', 43551, 43551'
Morphotype AB48	69389, 69389'
Morphotype AB6	43553, 43553'
Morphotype AB7	43501, 43574
Morphotype AB50	56768a
Morphotype AB19	USNM 38282 (Holotype, Berry 1916c, Pl. IX, fig. 2).
Morphotype AB21	56766, USNM 38283 (Holotype, Berry 1916c, Pl. IX, fig. 8)
Morphotype AB20	62093
Morphotype AB29	USNM 38279a–c
Morphotype AB59	70099, USNM 38288 (Plesiotype, Berry 1916c, Pl. X, fig. 3)
Morphotype AB12	43589, 43589'
Morphotype AB28	53157
Morphotype AB31	68904a
Morphotype AB53	62239
Morphotype AB56	70108
Morphotype AB57	69537
Morphotype AB61	62251a
Morphotype AB63	USNM 38287 (Holotype, Berry 1916c, Pl. X, fig. 2)
Morphotype AB64	56765
Morphotype AB65	USNM 38286a,b (part [Holotype, Berry 1961c, Pl. IX, fig. 4], counterpart)