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New plant fossil records and paleoclimate analyses of the late Pliocene Citronelle Formation flora, U.S. Gulf Coast

Debra Z. Stults and Brian Axsmith

ABSTRACT

The late Pliocene was an important time of relatively recent global warmth, and it heralded the end of Neogene Epoch. However, plant fossils from this time are uncommon in North America. This study provides detailed descriptions of 23 plant fossil taxa representing 14 woody angiosperm families from the late Pliocene (mid-Piacenzian) Citronelle Formation in coastal Alabama. This is the only significant late Pliocene megafossil plant assemblage in eastern North America, and one of the few from the entire Neogene of this region. Many are first records of their kind, and several are confidently identified to the species level. Overall, the floral composition is similar to that of the modern Gulf Coast. These findings, along with previous records, form the basis of quantitative paleoclimate estimates using leaf margin analysis (LMA), the Coexistence Approach (CoA), the Bioclimatic Analysis/Mutual Climate Range Technique (BA/MCRT), and the climate leaf multivariate program (CLAMP). The CLAMP analysis had the highest site-to-site disparity and provided anomalously low mean annual temperature (MAT) and mean annual precipitation (MAP) values. The LMA, CoA analysis, and BA/MCRT results are likely better proxies in this case, as the climate estimates obtained are closer to independent proxies and modern values. The BA/MCRT MAT results were most convincing at 18ºC. Nevertheless, higher MAT results were expected, as the mid-Piacenzian was a time of global warmth. Precipitation estimates below modern values obtained in all the relevant analyses are consistent with the presence of white pine in the Citronelle flora.

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INTRODUCTION

The original description of the late Pliocene (Piacenzian) Citronelle Formation flora of south Alabama by Berry (1916a) included 18 taxa from two localities. Little work was done subsequently, which is unfortunate, as the Citronelle Formation remains the only late Pliocene megafossil plant-producing unit in eastern North America, and one of the few from the entire Neogene. The paucity of Neogene fossil plant sites from the southeastern Coastal Plain is particularly troubling, as this area is now a significant locus of North American botanical diversity (Christensen, 2000). Recent work at Berry's original sites and several new localities has greatly increased the number of taxa to 54, and includes many first records of plants that still occur in the region (e.g., *Liquidambar styraciflua, Populus deltoides, Vitis rotundifolia*) as well as taxa now extirpated regionally or continent-wide (e.g., *Begonia* and *Pterocarya* sp.). Several of these taxonomic studies have been published individually, or as part of family level treatments (Stults and Axsmith 2009, 2011a, 2011b; Stults et al., 2002, 2010); however, many recently discovered taxa remained undescribed. A major objective of this study is to provide descriptions of many of these plant fossils.

Berry (1916a) originally proposed that the climate during deposition of the Citronelle Formation was like that of south Alabama today based mainly on the similarity of the fossil and extant floras, but no paleoclimate analyses using modern techniques has since been attempted. This is significant, as the Citronelle Formation flora existed during a climatic event previously called the mid-Pliocene warm interval (now late Pliocene due to subsequent boundary redefinitions). This contrasts with most of the Pliocene, which overall was characterized by gradual cooling and increased northern hemisphere glaciation. Well-documented responses to Pliocene cooling include the regional disappearance of tropical plant and animal taxa, decreases in plant diversity, increases in seasonally adapted taxa, and changes in patterns of competition (Bertini, 2010; Jimenez-Moreno et al., 2010; Karas et al., 2011). However, during the late Pliocene (~ 3.28 to 2.97 Ma) there was a sustained warm episode with mean global temperatures 2–3° higher than today, sea-level about 25 m higher, reduced Antarctic ice, and less pronounced seasonality (Dowsett and Cronin, 1990; Zachos et al., 2001; Haywood et al., 2005; Dwyer and Chandler, 2009; Knowles et al., 2009; Williams et al., 2009). Additionally, the atmospheric CO_2 concentration was probably similar to modern levels (approximately 350 ppm in 1988, increasing to 400 ppm by 2015) (Friedli et al., 1986; Neftel et al., 1994; Kurschner et al., 1996; Raymo et al., 1996; Seki et al., 2010; Stults et al., 2011b; Dlugokencky and Tans, NOAA/ESRL). This warm interval has attracted the attention of researchers as a geologically recent model for exploring the causes and possible consequences of current and future global climate change (Goddard Institute for Space Studies, 2005; Arctic Monitoring and Assessment Report, 2011).

Evidence is provided that the Citronelle Formation flora existed during the Pliocene warm interval and, therefore, provides a unique window into an eastern North American terrestrial flora during this intriguing time in Earth history. It is in this temporal and paleoecological context that the paleoclimate of the Citronelle Formation flora is estimated using several well-established techniques, including leaf margin analysis (LMA), the Climate Leaf Multivariate Program (CLAMP), and two variations of Nearest Living Relative (NLR) approaches – the Coexistence Approach (CoA) and the Bioclimatic Analysis/Mutual Climate Range Technique (BA/MCRT).

GEOLOGICAL SETTING

The Citronelle Formation is one of the most widespread sedimentary units of the Gulf of Mexico Coastal Plain, and was originally designated as Pliocene in age based primarily on the plant fossils (Berry, 1916a; Matson, 1916). The age was intensely disputed thereafter, with estimates ranging from Miocene to Pleistocene (Roy, 1939; Stringfield and LaMoreaux, 1957; Doering, 1958). Several lines of evidence have more recently been brought to bear on this problem, and the original Pliocene designation has been confirmed and refined. The Citronelle Formation is of Piacenzian age and was deposited sometime between 3.4–2.7 Ma (Otvos, 1997, 1998, 2004). Previous estimates of paleo-CO_2 based on the cuticular micromorphology of *Taxodium* fossils from the Citronelle Formation (Stults et al., 2011) indicate that deposition occurred before the rapid CO_2 drawdown that occurred between 3.2–2.8 Ma (Pagani et al., 2009; Seki et al., 2010). This would place the plant fossils closer to the older part of the age range estimate and, therefore, within the Pliocene warm interval.

The depositional setting of the Citronelle Formation is complex, and its study has been nearly as controversial as the age issue. Otvos (2004) provides compelling evidence that the depositional environment was mainly a braided river system, but noted that muddy units at several localities indicate some deep meandering river channels. *Ophiomorpha* burrows at some localities also indicate estuarine conditions. The plant fossils occur in relatively rare, unoxidized claystone lenses. The only other macrofossils found within the plant-bearing claystone are occasional mussel shells at the Perdido Park locality. Overall, fossils are exceedingly rare in the Citronelle Formation.

METHODS

Fossil Collection and Identification

Recent collecting at five sites in the Citronelle Formation of Alabama over the last several years by the authors has resulted in the recovery of over 1000 plant specimens (Figure 1). Two of the sites were part of the original study by Berry (1916a), which are still productive: Lambert Station, close to the type locality of the Citronelle Formation (31°1.73'N, 88° 12.23'W) just south of the town of Citronelle, and Red Bluff (30° 20.61' N, 87° 29.12'W) near the Alabama/Florida border on the western shore of Perdido Bay. Two more recently discovered sites are Scarborough School (30° 43.74'N, 88° 8.57'W), within the Mobile city limits, and Perdido Park (30° 24.05'N, 87° 26.97'W) about 7 km north of the Red Bluff site on Perdido Bay. The HMR site (30° 50'N, 88° 7'W), originally described by Otvos (2004), occurs north of the city of Saraland. Two of the sites, Scarborough School and Perdido Park, have been the most productive for leaf specimens and are the sources of most of the fossils described here. The clay layers at Lambert Station have been largely penetrated by the roots of modern plants making it impossible to recover many intact specimens. Nevertheless, several taxa described below are based upon rare specimens from this site. The Red Bluff site is now inundated with ground water seeps that have destroyed most of the broadleaf fossils; however, it still produces abundant fruit and seed material including some of the specimens described here. The HMR site has also produced mainly fruits and seeds that were described in an earlier paper (Stults and Axsmith, 2011b).

Most of the macrofossils described here were recovered by splitting clay containing the impression/compression fossils. Minimal preparation with fine needles was performed to fully expose the plant organs as needed. Cuticles are not often present, but in a few cases (e.g., specimens of *Carya aquatica*) some epidermal features were imaged under epifluorescence even though there was no obvious organic matter present. This phenomenon was previously documented with *Betula nigra* specimens from the Citronelle Formation (Stults and Axsmith, 2009). Residual epicuticular waxes may be responsible, but the cause of this phenomenon remains uncertain.

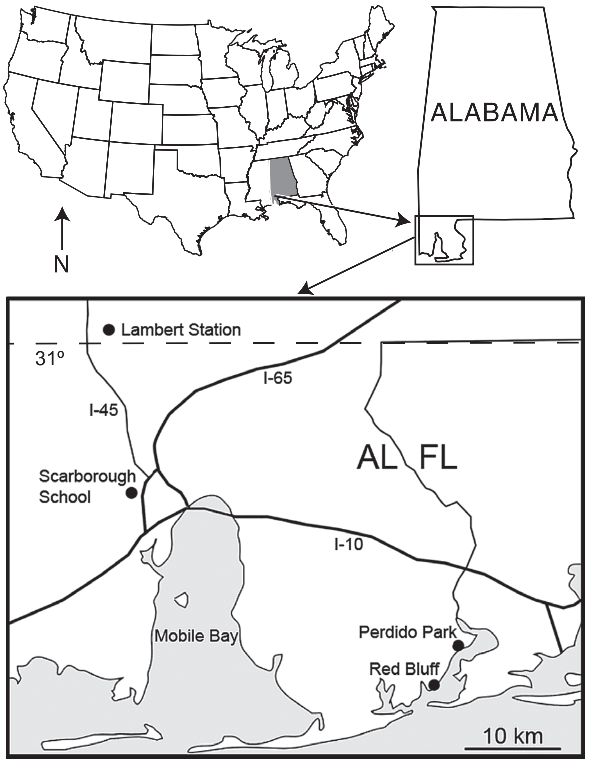

FIGURE 1. Index map of plant fossil localities of the Citronelle Formation.

The fossils were photographed with a Pentax K20 digital camera, and with a Nikon SMZ1500 dissecting microscope equipped with a Nikon DS-Ri1 digital camera. The images were processed and measurements obtained using Nikon Elements and Adobe Photoshop software. The identifications were made based on comparisons with literature sources, museum collections, living material, and herbarium specimens. Pollen samples were processed using routine palynological methods (Faegri and Iversen, 1989).

Paleoclimate Analyses

Coexistence Approach (CoA). The objective of the CoA technique is to reconstruct the paleoclimate based on the identification of climate intervals wherein all the taxa in a fossil flora could have coexisted based on their nearest living relative's (NLRs) tolerances (Mosbrugger and Utescher, 1997). This technique uses the entire climate

TABLE 1. Taxa used in Coexistence Approach analysis (CoA). C.Form= Citronelle Formation combined sites, H=HMR site, LS=Lamberts Station site, PP=Perdido Park site, RB=Red Bluff site, Sc=Scarborough site, Organs recognized per taxon: P=pollen, L=leaf, F=fruit, C=catkin.

Fossil taxa	C.Form	H	LS	PP	RB	Sc	Organ
Acer rubrum	X			X		X	L
Acer saccharinum	X					X	L
Acer sp.	X		X		X		PL
Alnus sp.	X	X	X	X	X		P
Betula nigra	X			X		X	LF
Betula sp.	X		X		X		PLF
Carpinus caroliniana	X			X		X	LFC
Carpinus sp.	X		X		X		LFC
Carya aquatica	X		X			X	L
Carya sp.	X	X	X	X	X	X	PLC
Castanea sp.	X			X		X	L
Chenopodiaceae	X	X					P
Clethra sp.	X			X			L
Cornus sp.	X				X		F
Crataegus sp.	X			X		X	L
Cyrilla racemiflora	X	X					F
Fagus sp.	X		X	X		X	P
Fraxinus sp.	X		X		X	X	PL
Gaylussacia sp.	X					X	L
Gordonia sp.	X			X			L
Ilex sp.	X	X		X			PL
Juglans sp.	X		X	X	X	X	P
Lindera sp.	X			X			L
Liquidambar styraciflua	X	X		X	X	X	PL
Liriodendron	X	X					PL
Liriodendron tulipifera	X					X	L
Magnolia sp.	X	X		X			PL
Myrica sp.	X	X	X		X	X	PL
Nyssa aquatica	X			X		X	LF
Nyssa sp.	X	X	X		X	X	PLF
Persea sp.	X			X			L
Pinus sp.	X	X	X	X	X	X	PL
Planera aquatica	X	X	X			X	LF
Platanus occidentalis	X					X	LF
Platanus sp.	X			X	X		PLF
Populus deltoides	X					X	L
Populus sp.	X		X		X		PL
Ptelea trifoliata	X			X			L
Pterocarya sp.	X					X	LF
Quercus falcata	X			X		X	L
Quercus nigra	X					X	L
Quercus virginiana	X			X	X	X	LF
Quercus sp.	X	X	X	X	X	X	PLFC

TABLE 1 (continued).

Fossil taxa	C.Form	H	LS	PP	RB	Sc	Organ
Rhus sp.	X	X			X		P
Rubus sp.	X		X				L
Salix sp.	X	X	X	X	X	X	PL
Sassafras sp.	X			X			L
Smilax sp.	X		X				L
Taxodium distichum	X	X	X	X	X	X	PLF
Trapa sp.	X			X	X	X	F
Ulmus sp.	X	X	X	X	X	X	PL
Vaccinium sp.	X					X	L
Vitis rotundifolia	X			X		X	LF
Vitis sp.	X	X			X		PLF

ranges of the NLRs, and excludes outlier taxa. In this study, the analysis was performed on five individual Citronelle Formation sites followed by a combined analysis. Most of the taxa used are based on macrofossils, whereas some at Red Bluff and HMR were identified from pollen (Table 1). The presence of several well-identified macrofossils (e.g., *Betula nigra, Carpinus caroliniana, Cyrilla racemiflora*, etc.) allowed for the inclusion of some species level NLR intervals (Stults et al., 2002; Stults and Axsmith, 2011b). Otherwise, genus-level intervals were mainly used and, in one instance, a family level interval based on pollen (i.e., Chenopodiaceae) was included.

The NLR climate intervals were obtained primarily from the PALAEOFLORA database; however, MAT data for *Betula nigra, Quercus nigra*, and *Q. virginiana* came from Thompson et al. (1999b). Some intervals were also obtained from Müller (1996). The coexistence intervals were calculated using the CLIMSTAT computer program (provided by T. Utescher, University of Bonn). Uncertainties are considered part of the interval measure, so no standard errors were calculated (Liang et al., 2003). Seven paleoclimate interval categories were estimated: mean annual temperature (MAT), cold month mean temperature (CMMT), warm month mean temperature (WMMT), mean annual precipitation (MAP), precipitation wettest month (PTWM), precipitation driest month (PDRM), and precipitation warmest month (PWMM).

Bioclimatic Analysis/Mutual Climate Range Technique (BA/MCRT). The BA/MCRT method of Kotthoff et al. (2014) was employed, which is similar to CoA except that 10th and 90th percentiles are assigned to the climate ranges. Most of the same taxa used in the CoA were utilized (Table 2) depending upon the availability of precise climate range information. Data from all sites was combined. The ranges and percentiles were obtained from Thompson et al. (1999a, 1999b, 2000) for MAT, MAP, January mean temperature (MT), July MT, January mean precipitation (MP), and July MP. The intervals for *Pterocarya* come from Fang et al. (2011), as this is now an Asian genus extirpated in North America.

Leaf Margin Analysis (LMA). This technique is based on the positive relationship between MAT and the proportion of native, woody angiosperm

TABLE 2. Taxa used in Bioclimatic Analysis/Mutual Climate Range Technique (BA/MCRT).

Acer rubrum
Acer saccharinum
Acer sp.
Alnus sp.
Betula nigra
Betula sp.
Carpinus caroliniana
Carya aquatica
Carya sp.
Castanea sp.
Clethra sp.
Cornus sp.
Crataegus sp.
Cyrilla racemiflora
Fagus sp.
Fraxinus sp.
Gordonia sp.
Ilex sp.
Liquidambar styraciflua
Liriodendron
Liriodendron tulipifera
Magnolia sp.
Myrica sp.
Nyssa aquatica
Nyssa sp.
Persea sp.
Planera aquatica
Platanus occidentalis
Platanus sp.
Populus deltoides
Populus sp.
Ptelea trifoliate
Pterocarya sp.
Quercus falcata
Quercus nigra
Quercus virginiana
Quercus sp.
Rhus sp.
Salix sp.
Sassafras sp.
Taxodium distichum
Ulmus sp.
Vaccinium sp.

TABLE 3. CLAMP scoring of Citronelle Formation sites.

Leaf character	Scarborough site %	Perdido Park site %	Combined Sites %
Lobed	14	21	17
No teeth	36	47	48
Regular teeth	49	30	35
Close teeth	14	7	10
Round teeth	14	16	13
Acute teeth	52	37	40
Compound teeth	13	5	8
Nanophyll	0	0	0
Leptophyll I	3	0	2
Leptophyll II	7	8	8
Microphyll I	19	19	22
Microphyll II	36	59	45
Microphyll III	28	14	21
Mesophyll I	3	0	2
Mesophyll II	3	0	2
Mesophyll III	0	0	0
Emarginate Apex	0	0	0
Round Apex	20	16	14
Acute Apex	62	74	69
Attenuate Apex	18	10	17
Cordate Base	39	18	25
Round Base	9	8	11
Acute Base	52	74	64
L:W <1:1	14	1	7
L:W 1-2:1	48	47	47
L:W 2-3:1	28	45	38
L:W 3-4:1	10	4	7
L:W >4:1	0	3	2
Obovate	24	26	25
Elliptic	45	49	42
Ovate	32	25	32
Completeness	88	85	88

leaf morphotypes with entire margins in a flora, as first documented in a seminal paper by Bailey and Sinnott (1916). The method is generally considered robust and has been widely employed in determining MAT for fossil assemblages based on linear regressions derived from extant floras (Wilf, 1997; Su et al., 2010). A combined analysis was performed using all of the leaf-producing sites that presented at least one unique morphotype (i.e., Lambert Station, Scarborough School, and Perdido Park, for a total of 47 morphotypes, 47% of which have entire margins). The MAT was calculated from these values using the Kowalski and Dilcher (2003) regression equation: LMAT = 36.3P + 2.223, applicable to possible MATs ranging from 4–23.3° (see table 5 in Kowalski and Dilcher, 2003). This equation was used because its calibration included a nearby wetland flora in Florida with many of the same taxa used in the present study. Such wetland corrected equations also eliminate some of the potential taphonomic biases inherent in MAT estimates (Burnham et al., 2001). In addition, this equation performed well in predicting the modern MAT of the local flora in a pilot study (Stults, 2003). The standard deviation was calculated following the procedure of Wilf (1997).

Climate Leaf Multivariate Program Analysis (CLAMP**).** The CLAMP method employs 31 features of native, woody dicot leaves to estimate 11 climate variables. Improvements and refined data sets have been incorporated into the most recent online version of CLAMP (http://clamp.ibcas.ac.cn/Clampset2.html) (Kovach and Spicer, 1995; Stranks and England, 1997; Spicer, 2000, 2007; Spicer et al., 2004, 2009; Peppe et al., 2011; Teodoridis et al., 2011) which was used in this study. Paleoclimate analysis with CLAMP requires at least 20 leaf morphotypes preserved with sufficient detail to allow scoring of characters. Citronelle Formation sites meeting this criterion are Scarborough School with 32 taxa/morphotypes, and Perdido Park with 37 taxa/morphotypes. Separate and combined analyses were performed. The combined analysis included 51 morphotypes, as some were common to both sites. Included in these analyses were morphotypes that have been taxonomically identified and a few that have not. All scoring was performed according to the CLAMP protocol (Wolfe, 1990, 1993; Spicer, 2000; Spicer et al., 2004, 2009) (Table 3). The CLAMP website includes modern calibration datasets, downloadable data score sheets, and the ability to run the analysis online via CANOCO 4.5. This analysis used CLAMP dataset Physg3brcAZ, which incorporates meteorological data calibrated for altitudinal differences, and excludes significantly cold climates. Although CLAMP currently estimates 11 climate variables, the analysis here focused on MAT, WMMT, CMMT, as they could be compared directly with the results of the other analyses. Precipitation values were also considered.

SYSTEMATIC DESCRIPTIONS

The climate analyses are based on the entire Citronelle Formation flora as it is now understood, but the descriptions below only include taxa that have not appeared in previous publications (Stults et al., 2002, 2011; Stults and Axsmith, 2009; 2011b). Additionally, there are a few taxa used in the climate analyses that are well-identified, but will be treated in detail in forthcoming papers as other implications of their occurrence are still under investigation (i.e., Fagaceae, *Pterocarya*). The numbers of specimens listed per taxon description refer to those that provided the clearest characters for identification, and do not necessarily reflect the total number present. Terminology follows the *Manual of Leaf Architecture* (Ellis et al., 2009).

All the figured specimens are curated in the Paleobotany and Palynology Collection of the Florida Museum of Natural History, University of Florida, Gainesville. Specimen numbers can be found in the figure captions. All of the of fossils are assigned to extant families and genera, and in some cases species. A "cf." designation indicates that the fossil likely represents the referenced extant species, but the specific identification is not certain. All of the described taxa are flowering plants (angiosperms) and are presented below alphabetically by family. The extant biogeographic ranges provided below are based primarily on the following sources: the Flora of North America online database (www.floranorthamerica.org), the Germplasm Resources Information Network (GRIN online database), *Trees, Shrubs, and Woody Vines of Northern Florida and Adjacent Georgia, and Alabama* (Godfrey, 1988), and USGS Professional Paper 1650 (Thompson et al., 1999).

Family AQUIFOLIACEAE von Berchtold and Presl, 1825

Genus *ILEX* Linnaeus, 1753

Ilex sp.

Figure 2.1

Description. One simple, petiolate leaf is attributed to *Ilex*. Petiole attachment is marginal. The blade is a notophyll (4 cm long, 1.8 cm wide), shape ovate, symmetrical with a L:W ratio 2:1. The margin is unlobed, serrate. The base is acute, straight, symmetrical. The apex is acute, straight, the terminal apex possibly retuse (as occurs in some extant *Ilex* species such as *I. decidua* and *I. coricea*). Primary vein framework pinnate. Two basal veins are present. The secondary vein framework is mixed craspedodromous and semicraspedodromous. Secondaries are irregularly spaced, excurrent, and arcuate. Tertiary, quaternary, and quinternary veins are more difficult to characterize probably because the leaf was coriaceous, however, they appear to be irregular reticulate. Teeth are small, of a single order, regularly spaced, 6–8 per cm. Sinuses are angular. Teeth are straight/convex proximally, straight distally, apices spinose.

Site Occurrence. Perdido Park.

Remarks. Of the 35 native species of *Ilex* in the United States, approximately 40% occur within the southeast. *Ilex* is first documented in the Late Cretaceous; however, the common ancestor of all modern *Ilex* species has been estimated as Miocene as the most basal lineages of the genus were extinct by that time (Manen et al., 2010). In North America, *Ilex* seeds have been described from the early Miocene Brandon Lignite of Vermont (Tiffney, 1977).

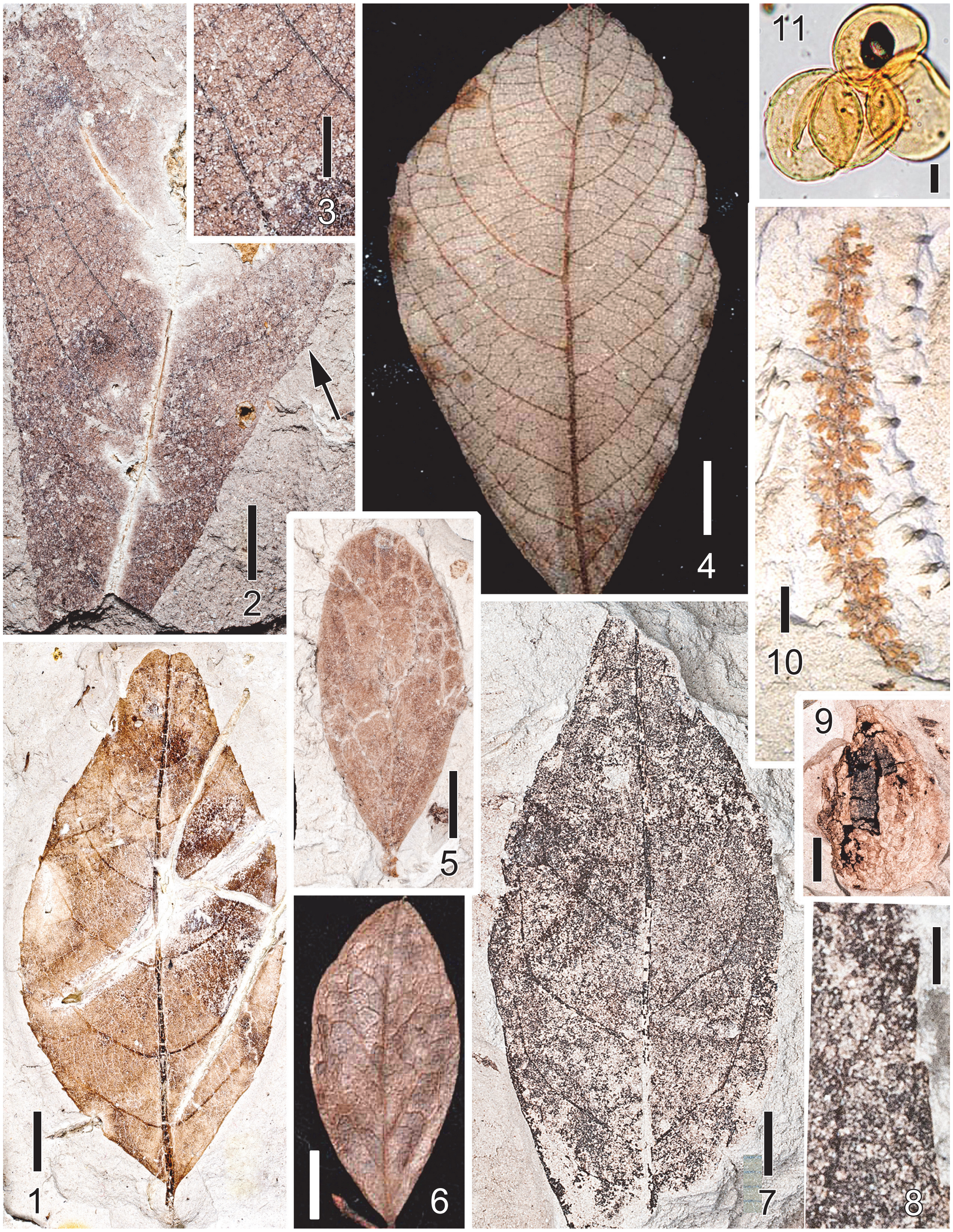

FIGURE 2. Representative Aquifoliaceae through Juglandaceae from the Citronelle Formation. **1.** *Ilex* sp. leaf (UF 19210–062063), scale bar equals 5 mm. **2.** *Clethra* cf. *alnifolia* (UF 19210–062064) partial leaf, arrow indicates mucronate tooth apex, scale bar equals 5 mm. **3**. Close-up of Figure 2.2 *Clethra* leaf, note mixed-percurrent tertiaries, scale bar equals 2.5 mm. **4.** Extant *Clethra alnifolia* leaf from USAM herbarium for comparison with Figure 2.2, scale bar equals 5 mm. **5.** *Gaylussacia* sp. leaf (UF 19315–062065), scale bar equals 5 mm. **6.** Extant *Gaylussacia* sp. from USAM herbarium for comparison with Figure 2.5, scale bar equals 5 mm. **7.** *Vaccinium* sp. leaf (UF 19315–062066), scale bar equals 5 mm. **8.** Close-up of *Vaccinium* leaf margin from Figure 2.7 showing teeth, scale bar equals 2.5 mm. **9.** *Carya* fruit (UF 19315 – 062068), scale bar equals 5 mm. **10.** *Carya* sp. catkin with in situ pollen (UF 19315 – 062067), scale bar equals 5 mm. **11.** *Carya* sp. pollen tetrad from specimen in Figure 2.10, scale bar equals 10 μm.

Family CLETHRACEAE Klotzsch, 1851
Genus *CLETHRA* Linnaeus, 1753
Clethra cf. *alnifolia* Linnaeus, 1753
Figure 2.2–2.3

Description. One partial leaf is identified as *Clethra* sp., measuring 4 cm long and 2.5 cm wide. The leaf is simple, petiolate, obovate. The margin is unlobed, serrate. The base is incomplete, but was probably acute. Primary venation is pinnate. Secondary venation is semicraspedodromous and excurrent. Secondaries emerge from the midrib at approximately 45°. Tertiary veins are mixed-percurrent (both alternate and opposite percurrent); some of the opposite percurrent veins are sinuous, but most are straight. Quaternary venation is predominantly regular reticulate, occasionally irregularly reticulate. Quinternary veins are regular, reticulate. Teeth are of a single order, small, irregularly spaced, the number increasing distally. Tooth sinuses are generally round, teeth straight/convex proximally, straight/concave distally. On some teeth all that is visible is a long, mucronate apex, a characteristic common to modern forms of *C. alnifolia*.

Site Occurrence. Perdido Park.

Remarks. *Clethra* today encompasses approximately 65 species, but only three occur in North America. *Clethra acuminata* occurs mostly in montane woodlands. *Clethra alnifolia* and *C. tomentosa* are found at lower elevations and in wetland areas. Of these two, *C. alnifolia* (Figure 2.4) has a wider distribution and is found mainly along the coastal plain from southern Maine to northern Florida and then westward to southeastern Texas. Fossil flowers within the core Ericales somewhat comparable to those of the Clethraceae have been found from Late Cretaceous deposits of Georgia, USA. (Schönenberger et al., 2012). Fruits and seeds of *Clethra* have been described from the middle Miocene of Europe (Friis, 1985).

Family ERICACEAE de Jussieu, 1789
Genus *GAYLUSSACIA* Kunth, 1819
Gaylussacia sp.
Figure 2.5

Description. One simple, 2.4 cm long, 1.0 cm wide, petiolate leaf displays characteristics of *Gaylussacia.* The petiole is very short (~1 mm long) with a significant expansion near the stem. The blade is obovate, symmetrical. Margin is unlobed and entire. Base is acute, cuneate. Apex is obtuse, rounded. Primary venation is pinnate. Secondary venation is brochidodromous and decurrent. Secondaries form long and irregularly spaced loops that depart the midvein at angles of 20–30°, the angles increasing to approximately 45° distally. Tertiary venation is reticulate.

Site occurrence. Scarborough School.

Remarks. Of the approximately 50 species of *Gaylussacia* worldwide*,* most of the North American species occur on the southeastern coastal plain, including *G. baccata, G. dumosa, G. frondosa* (Figure 2.6)*, G. mosieri, G. nana,* and *G. tomentosa*. The Citronelle Formation leaf described here is the first report of fossil *Gaylussacia* in North America. The unique, disjunct biogeographical pattern of *Gaylussacia* (it is present in eastern portions of North America and South America) is most commonly explained as a probable origination in South America with subsequent migration into North America during the Paleogene via the Caribbean islands. However, molecular approaches suggest that the genus originated in North America and subsequently expanded into South America (Floyd, 2002).

Genus *VACCINIUM* Linnaeus, 1753
Vaccinium sp.
Figure 2.7–2.8

Description*.* One mostly complete, simple, petiolate, elliptic, symmetrical leaf, 4 cm long, 1.7 cm wide (L:W ratio 2:1) is attributed to *Vaccinium*. Margin is unlobed, apically serrate. The base and apex are acute. Primary framework is pinnate. Secondary venation is brochidodromous. The secondary veins are regularly spaced, noticeably thickened, and form angles approximately 45° from the midrib. Veins of a gauge between secondary and tertiary thicknesses (but not intersecondaries) form loops off the secondary veins toward the basal end, a common feature in extant *Vaccinium* species. Tertiary veins are irregular, reticulate. Teeth on the apical portion of the leaf are few and small, sinuses angular, straight proximally and distally. The presence of these few, small apical teeth occur in several extant species of *Vaccinium* (such as some morphotypes of *V. corymbosum* and *V. tenellum*).

Site occurrence. Scarborough School.

Remarks. *Vaccinium* has 25 recognized species in North America, most of which occur in the west. However, five species occur in the warmer southeastern portion of the continent (*V. crassifolia, V. darrowii, V. hirsutum, V. myrsinites*, and *V. tenellum*). Fossil leaves of *Vaccinium* were listed as a possible component of the Miocene Clarkia flora of Idaho (Smiley and Rember, 1985) and have been identified from the Miocene Succor Creek flora of Oregon (Fields, 1996).

Family JUGLANDACEAE de Candolle and Perleb, 1818
Genus *CARYA* Nuttal, 1818
Carya sp.
Fruits and catkins
Figure 2.9–2.11

Description. Several *Carya* fruit specimens have been found, but are not very informative. However, one displays a pericarp approximately 2 mm thick (Figure 2.9), which is thicker than the pericarp of typical *C. aquatica,* a common leaflet type in the flora. A husk of another fruit that is at least 3 mm thick suggests the presence of a second species of *Carya* where the husk splits apart from the rest of the fruit, such as in extant *C. tomentosa* or *C. myristicaeformis. Carya* catkins with in situ pollen are also common at most sites (Figure 2.10–11). Although they cannot be identified to species, they underscore the prominence of *Carya* in the Citronelle flora.

Site occurrence. Scarborough School.

Remarks. Berry (1916a) assigned the *Carya* nuts (and leaflets) in the original collection from the Lambert Station site to a new species, *"Hicoria" pretexana*, indicating close affinity or ancestral status to the extant species *Carya texana*, but there is no clear justification for this specific assignment. *Carya* fruits from the late Miocene to earliest Pliocene of Tennessee were recently assigned to a new fossil species, *C. tenneseensis*, with possible affinities with the European fossil *C. ventricosa* (Huang et al., 2014). Unfortunately, the Citronelle Formation fruits provide few points of comparison with this and other fossil or extant *Carya* fruits due to preservational limitations beyond that presented above.

Leaflets (general description). All *Carya* leaflet specimens from the Citronelle Formation share the general characteristics of the genus. Leaf margins are generally toothed. Bases are often asymmetrical, although some are symmetrical. Primary venation is pinnate. Secondary veins are semicraspedodromous with angles increasing from apex to base. Tertiary veins are percurrent. Leaflet variability within the assemblage indicates that at least three species of *Carya* are represented, which are described separately below.

Carya cf. *aquatica* (Michaux, 1811) Nuttal, 1818
Figure 3.1 – 3.2, 3.5

Description. Approximately 18 leaflet specimens represent *Carya* cf. *aquatica*. Leaflets are oblong or elliptical, a few are ovate, and L:W ratios are mostly > 3:1. Many have an asymmetrical lamina, thus displaying the distinctive curvature common in this species. Sizes range from 3.2–8.5 cm long and 0.8–3.5 cm wide. Bases are cuneate and mostly asymmetrical. Apices are straight and acute. Secondary veins are numerous, often irregularly spaced, with increasing angles from 45º apically to 75º (or greater) basally. Tertiary veins are mostly opposite percurrent (straight or sinuous), although some are alternate percurrent. Margins are often entire, but sometimes with a few, small teeth that are usually straight distally and straight or convex proximally. Often, however, the margins appear erose rather than serrate. Peltate scales are often visible under epifluorescent light (Figure 3.2).

Site occurrence. Scarborough School.

Remarks. *Carya aquatica* today occurs in floodplain forests along a wide area of the southeastern coastal plain. It is remarkable that no fruits clearly assignable to this species have been recovered from the Citronelle Formation despite the abundance of leaflets with convincing features, which is one of the major reasons a "cf." designation was used here.

Carya cf. *tomentosa* Nuttal, 1818
Figure 3.3, 3.6

Description. Ten *Carya* specimens show features common to leaflets of extant *C. tomentosa.* Laminae are mostly obovate, although some are elliptical or ovate and L:W ratios are ~ 2:1. Leaflet size ranges from 5.3–9.9 cm long and 2.2–3.8 cm wide. Bases are mostly symmetrical, although a few are asymmetrical, and most are cuneate. Secondaries are regularly spaced with 45º angles apically and 60º angles basally. Tertiary veins are generally opposite percurrent. Teeth are of one order, uniformly placed 4–5 per cm, and usually occurring along the distal half of the lamina; no teeth or very few small teeth are noticeable basally. Between-teeth sinuses are angular; tooth shapes are straight distally/convex proximally. The principal tooth vein terminates at the tooth apex.

Site occurrence. Scarborough School.

Remarks. Today *Carya tomentosa* is common in upland sites throughout eastern North America.

Carya sp. 3
Figure 3.4, 3.7

Description. Three obovate and elliptical *Carya* leaflet specimens with characteristics not fitting well within those of either *C. aquatica* or *C. tomentosa* are present in the Citronelle Formation flora. They cannot confidently be assigned to any other species at this time. Laminae in these specimens may be symmetrical or asymmetrical; bases are

FIGURE 3. Representative Juglandaceae from the Citronelle Formation (continued). **1.** *Carya* cf. *aquatica* leaflet (UF 19315–062069), scale bar equals 5 mm. **2.** Epifluorescence micrograph of leaf from Figure 3.1, note peltate hairs, scale bar equals 125 µm. **3.** *Carya* cf. *tomentosa* leaflet (UF 19315–062070), scale bar equals 2 cm. **4.** *Carya* species #3 partial leaflet (UF 19210–062071), scale bar equals 5 mm. **5.** *Carya* cf. *aquatica* leaf margin of Figure 3.1, scale bar equals 2.5 mm, **6.** *Carya* cf. *tomentosa* leaf margin of Figure 3.2, scale bar equals 5 mm. **7.** *Carya* species #3 of Figure 3.4 leaf margin, scale bar equals 2.5 mm.

cuneate; apices are acute. Secondary veins are irregularly spaced with angles increasing basally (from 45º to almost 90º). Tertiary veins are mixed percurrent. Uniform-sized teeth are of one order, regularly spaced, approximately 5 per cm, appearing all along the leaf margin (tooth characters are the major features not comparing well with *C. aquatica* or *C. tomentosa*). Tooth sinuses are angular, shape is straight distally/convex proximally. Principal tooth vein terminates at the apex.

Site occurrence. Perdido Park.

Family remarks. Species of the Juglandaceae are successful in a warm temperate to subtropical North America, as records of both extinct and extant genera clearly demonstrate (Wing and Hickey, 1984; Manchester, 1991; Manchester and Dilcher 1997; Manos and Stone, 2001; Elliott et al., 2006;). *Carya* first appears in Eocene sediments in North America (Manchester, 1999). Seven species of *Carya* currently occur on the Gulf of Mexico Coastal Plain (Godfrey, 1988), making this region a major center of diversity of the genus. Fruits and leaves of the juglandaceous genus *Pterocarya* have been identified from the Citronelle Formation, but will be described in a separate publication.

Family LAURACEAE de Jussieu, 1789
Genus *LINDERA* Thunberg, 1783
Lindera sp.
Figure 4.1, 4.5

Description. *Lindera* is represented by one, simple, petiolate leaf specimen. The blade is obovate, 7.1 cm long and 3.1 cm wide, with a L:W ratio of 2.3:1. The slender petiole is 0.8 cm long. The margin is unlobed and entire. The base is acute, decurrent. The apex is acuminate, without a drip tip, as in modern *Lindera.* Primary vein framework is pinnate. Secondary venation is brochidodromous, excurrent, irregularly spaced and does not exhibit the arcuate state of *Persea.* This leaf can also be differentiated from *Persea* and *Magnolia* based on its less robust appearance, and thin marginal fimbrial veins (compared to the marginal secondary veins of *Persea* or *Magnolia*). Tertiary venation is irregular reticulate, although the presence of several intersecondary veins renders this determination difficult. Quaternary and quinternary veins are irregular, reticulate.

Site occurrence. Perdido Park.

Remarks. Of the approximately 100 *Lindera* species, the three North American species occur along streams, mesic woodlands, sandy areas, and swampy areas. Two species, *L. melissaefolia* and *L. subcoriacea* have restricted distributions; however, *L. benzoin* (Figure 4.2) is found throughout eastern North America. American *Lindera* species diverged from Asian counterparts in the middle Miocene (Chanderbali et al., 2001; Nie et al., 2007). *Lindera* has been reported from the Miocene Clarkia flora (Fields, 1996).

Genus *PERSEA* Miller, 1754
Persea sp.
Figure 4.3, 4.6

Description. *Persea* sp. is represented by one complete leaf from the Scarborough School site, and six complete to mostly complete specimens from the Perdido Park site. All specimens are elliptical. The two most complete specimen laminae measure 9.0 cm long X 2.4 cm wide and 7.2 cm long X 2.4 cm wide, L:W ratios approximate 3–3.8:1. Widths of incomplete specimens range from 2.8–3.0 cm. Bases are acute. Apices are acute, some are acuminate with drip tips. Primary venation is pinnate. Secondary veins are excurrent, arcuate, and weakly brochidodromous. Tertiary and quaternary veins are irregular reticulate, but the quinternary veins are mostly regular, reticulate. A perimarginal vein is present, but portions of the leaf also seem somewhat curled under as to appear revolute. One specimen presents this feature as a thickened area with the appearance of extraneous cuticle.

Site occurrence. Perdido Park and Scarborough School.

Remarks. Three species of *Persea* occur in the flora of North America today. *Persea humilis* is found on the Florida peninsula only, whereas *P. borbonia* and *P. palustris* are more widely distributed along areas of the Atlantic coastline of the mid- to southeastern United States and extending to east Texas. *Persea palustris* occupies swampy areas, whereas the other two species prefer drier settings. Biogeographic investigations of the family Lauraceae indicate that American members of *Persea* diverged from Asian counterparts with the onset of cooling at the Eocene-Oligocene boundary (~ 32 m.y.a.). Fossils of *Persea* have been reported from the western Miocene Clarkia and Succor Creek floras (Smiley and Rember, 1985; Fields, 1996).

Genus *SASSAFRAS* von Berchtold and Presl, 1825
Sassafras albidum (Nuttal, 1818) Nees von Esenbeck, 1836
Figure 4.4

Description. One bilobed leaf is attributed to *Sassafras albidum.* The overall outline is ovate with one lateral lobe. The original leaf was > 7 cm long.

FIGURE 4. Representative Lauraceae from the Citronelle Formation. **1.** *Lindera* sp. leaf (UF 19210–062072), scale bar equals 1 cm. **2.** Extant *Lindera* leaf from USAM herbarium for comparison with Figure 4.1, scale bar equals 1 cm. **3.** *Persea* sp. leaf (UF 19210–062073), scale bar equals 1 cm. **4.** *Sassafras albidum* leaf (UF 19210–062074), scale bar equals 1 cm. **5.** Close-up of Figure 4.1 *Lindera* leaf showing high order venation, scale bar equals 2.5 mm. **6.** Close-up of Figure 4.3 *Persea* leaf showing high order venation, scale bar equals 2.5 mm.

The main lobe has a width of 3 cm, whereas the lateral lobe is 1.5 cm wide. The base is missing. The apex of the central lobe is missing, but was probably rounded or acute. The apex of the lateral lobe is acute. It is difficult to categorize the primary venation, since the major veins to the lobes often do not diverge at the same point in other extant and fossil *Sassafras* specimens. The majority of *S. albidum* leaves are suprabasalactinodromous regardless of the number of lobes (usually from 1–3) (personal observation). In the Citronelle Formation fossil, the primary vein of the lateral lobe is smaller than the primary vein in the main lobe. Secondary veins are brochidodromous, forming long arches departing the midvein at angles of approximately 50–55°. There are many intersecondary veins perpendicular to the midvein in the basal half of the leaf, becoming parallel to the major secondaries in the apical portion. Tertiary veins are mixed percurrent. Quaternary veins are irregular reticulate. A fimbrial vein is evident.

Site occurrence. Perdido Park.

Remarks. There are only two or three modern species of *Sassafras, S. albidum* being the only species currently in North America. It has a wide distribution over much of the eastern portion of the continent. *Sassafras albidum* probably diverged from Asian counterparts in the middle Miocene (Chanderbali et al., 2001; Nie et al., 2008). Fossils of *Sassafras* have been reported from the western Miocene Clarkia and Succor Creek floras (Smiley and Rember, 1985; Fields, 1996).

Family MAGNOLIACEAE de Jussieu, 1789
Genus *LIRIODENDRON* Linnaeus, 1753
Liriodendron cf. *tulipifera* Linnaeus, 1753
Figure 5.1 – 5.2

Description. One partial leaf with marginal petiole attachment is identified as *Liriodendron,* probably *L. tulipifera*. A portion of the slender petiole (approximately 1 mm thick) is 1.1 cm in length, but was probably originally much longer. The original leaf was > 6.8 cm long and > 6.8 cm wide, and broadly concavo-convex with an obtuse base. Primary venation is pinnate. Simple agrophic veins form loops near the basal portion of the leaf (Figure 5.2). Proximal secondary veins are decurrent and arching. Thickened secondary veins are irregularly spaced with consistent 45° angles. Some intersecondaries are present. It is difficult to categorize the looping tertiaries; some appear percurrent, whereas others appear irregular, reticulate. However, the fourth order veins are clearly irregular, reticulate. A fimbrial vein is present. Unfortunately, the characteristic notched apex of the genus is not preserved on the fossil.

Site occurrence. Scarborough School.

Remarks. *Liriodendron tulipifera* occurs in woodlands and wetlands extending from southern Alabama and the Florida panhandle to Louisiana, northward to Illinois, Michigan, and Vermont. Populations common on the southeastern coastal plain typically have smaller leaves, shorter petioles, rounder lobes, and rounder bases than typical leaves of more northern populations (Godfrey, 1988; personal observation). The Citronelle Formation specimen is most similar to the extant southeastern variety in the observable features. Leaves and fruits of *Liriodendron* occur in the Miocene of Idaho (Baghai, 1988). The two extant *Liriodendron* species (the other being *L. chinense*) probably diverged in the middle Miocene (Parks and Wendel, 1990; Azuma et al., 2001; Nie et al., 2008).

Genus *MAGNOLIA* Linnaeus, 1753
Magnolia cf. *virginiana* Linnaeus, 1753
Figure 5.3–5.4

Description. Three specimens of *Magnolia* cf. *virginiana* leaf have been recovered from the Perdido Park site. These leaves are simple, petiolate, with marginal petiole attachment. They are either elliptical or obovate. The most complete obovate specimen is 12 cm long, the most complete elliptical specimen is 11.6 cm long and 3.0 cm wide (L:W ratio 4:1). Margins are unlobed, entire. Bases are acute, decurrent. Apices are acute, straight. Primary venation is pinnate. Secondary venation is simple brochidodromous, mostly decurrent, irregularly spaced, angles consistently ~ 30°. A perimarginal secondary vein is evident. Tertiary veins are irregular reticulate as are the quaternary and quinternary veins (Figure 5.4).

Site occurrence. Perdido Park.

Remarks. *Magnolia virginiana* occurs in swamps and bogs, mostly along the coastal plain from New Jersey to lower Florida and westward to east Texas, and also appears in Arkansas, Massachusetts, and New York. The family Magnoliaceae appears early in the macrofossil record, in existence as early as 93.5 to 110 m.y.a. (Tao and Zhang, 1992; Frumin and Friis, 1996, 1999). Fossil and molecular evidence suggest that the clade containing *M. virginiana* diverged in the early Oligocene. The genus *Magnolia* appears in western North America as early as the upper Paleocene, and in the southeast in the middle Eocene (Grote, 1989; Manchester, 1994; Azuma et al., 2001; Nie, et al., 2008). Seeds of *Magnolia* occur in the Mio-

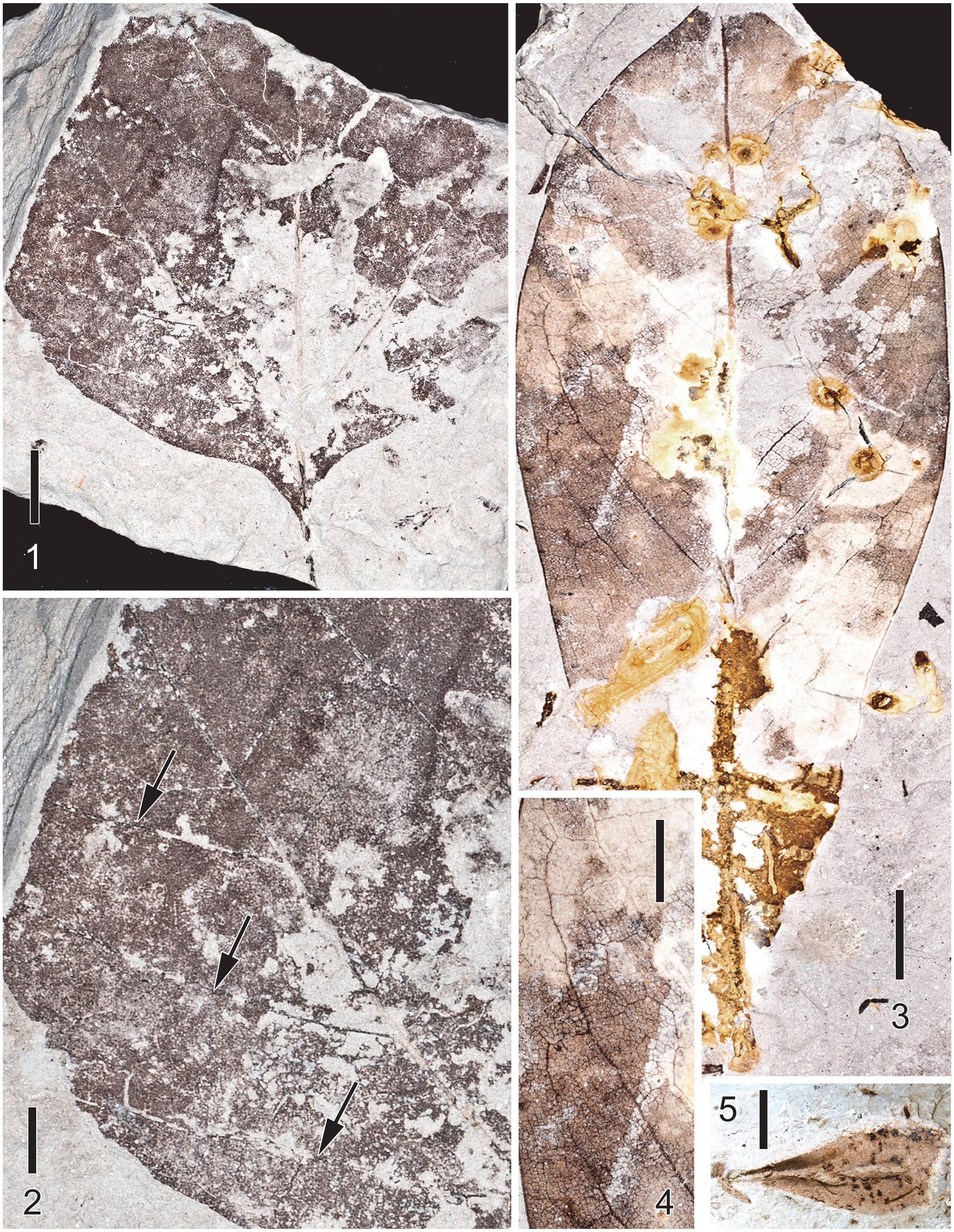

FIGURE 5. Representative Magnoliaceae and Oleaceae from the Citronelle Formation. **1.** *Liriodendron* cf. *tulipifera* partial leaf (UF 19315–062075), scale bar equals 1 cm. **2.** Close-up of Figure 5.1 *Liriodendron* leaf basal portion showing simple agrophic veins at arrows, scale bar equals 5 mm. **3.** *Magnolia* cf. *virginiana* leaf (UF 19210–062076), scale bar equals 1 cm. **4.** Close-up of Figure 5.3 *Magnolia* leaf showing details of fourth and fifth order veins, scale bar equals 5 mm. **5.** *Fraxinus* sp. fruit (UF 19413–062077), scale bar equals 5 mm.

cene Brandon Lignite of Vermont, and there is a fruit record from the Miocene Clarkia site of Idaho (Tiffney, 1977; Rember, 1991).

Family OLEACEAE Hoffmannsegg and Link, 1809
Genus *FRAXINUS* Linnaeus, 1753
Fraxinus sp.
Fruit
Figure 5.5

Description. A small (9.7 mm long, 4.1 mm wide) *Fraxinus* samara has been recovered from the Lambert Station site. A small part of the apical portion of the wing is missing. The fruit body is flattened, centrally positioned within the samara, and ~ 6.5 mm long. It is too fragmentary for meaningful specific comparisons.

Site occurrence. Lambert Station.

Remarks. Twenty native species of *Fraxinus* occur in North America, but only five of these (*F. americana, F. caroliniana, F. pennsylvanica, F. profunda*, and *F. quadrangulata*) occur in the southeastern United States. The earliest record of *Fraxinus* in North America is from the early Eocene of the west, and records continue into the middle Eocene Green River and Quilchana floras (Brown, 1940; MacGinitie, 1941; Matthews and Brooke, 1971). Middle Eocene records of *Fraxinus* fruits have been documented in Tennessee (Berry, 1916b; Call and Dilcher, 1992).

Leaflets
Figure 6.1–6.2

Description. Two ovate leaflets of *Fraxinus* are recognized in recent collections from the Citronelle Formation flora. One is probably a terminal leaflet, as indicated by petiolule length (2.2 cm). The most complete leaf is 9 cm long and 3.5 cm wide (L:W ~ 2.5:1). Margins are unlobed, crenate/serrate. Leaflet bases are decurrent, acute, asymmetrical. Apices are acuminate, one with a drip tip. Primary venation framework is pinnate. Secondary venation is festooned semicraspedodromous. Secondary veins are decurrent, irregularly spaced, with inconsistent angles. A few intersecondaries are present. Tertiary veins are irregular reticulate, as are the fourth and fifth order veins (Figure 6.2). One order of teeth is present, straight or concave distally and convex proximally, between-teeth sinuses are angular to rounded. The course of the principal tooth vein terminates at the nadir of the super-adjacent sinus, consistent with several extant species of *Fraxinus*.

Site Occurrence. Scarborough School and Perdido Park.

Remarks. A poorly preserved leaflet attributed *Fraxinus* sp. was reported from the Lambert Station site by Berry (1916a), but this determination is uncertain and the specimen was not observed in the NMNH collections.

Family PLATANACEAE Lestiboudois, 1826
Genus *PLATANUS* Linnaeus, 1753
Platanus occidentalis Linnaeus, 1753
Leaves
Figure 6.3

Description. Ten large leaves of this species are present at the Scarborough School site, whereas five smaller, possibly less mature leaves are present at Perdido Park. The larger specimens are > 15.0 cm long and ~ 18.0 cm wide. A complete smaller specimen (part and counterpart) is 6.1 wide and 6 cm long. L:W ratios for large and smaller leaves are ~ 1:1. Margins are lobed and serrate. The larger and smaller specimens differ somewhat in morphology as also seen in the extant species. For example, the larger leaves are usually strongly five-lobed, while the smaller leaves have three shallow lobes. Small, basal lobes occur on the larger leaves. Leaf bases are either cordate or lobate, regardless of leaf size. Apices of the lobes on large specimens are acute, while apices on smaller specimens are sometimes acute, sometimes obtuse. The primary venation of the larger leaves is mostly palinactinodromous, while the smaller leaves have actinodromous primary framework. Compound agrophic veins are evident on the smaller leaves. The margins have simple teeth, with 0–2 teeth per cm. One order of teeth is present, however, tooth sizes are variable on any given leaf. Teeth are irregularly spaced on the margin (as a whole), but are regularly spaced when comparing symmetry on either side of the lobes. Sinuses between the teeth are rounded. Teeth are convex/straight proximally, concave/straight distally.

Fruits
Figure 6.4

Description. Four *Platanus* fruiting heads have been found at the Red Bluff site. The most complete is 2.3 cm in diameter. Achenes with persistent styles are ~ 8 mm long and 2 mm wide. The receptacle is 9 mm wide. The fossil leaves and fruits are identical to those of the extant species *P. occidentalis*.

Site occurrence. Large leaves are from Scarborough School; small leaves are from Perdido Park; fruiting structures are from Red Bluff.

Remarks. Of the eight species of *Platanus*, three (or four) occur in North America. *Platanus race-*

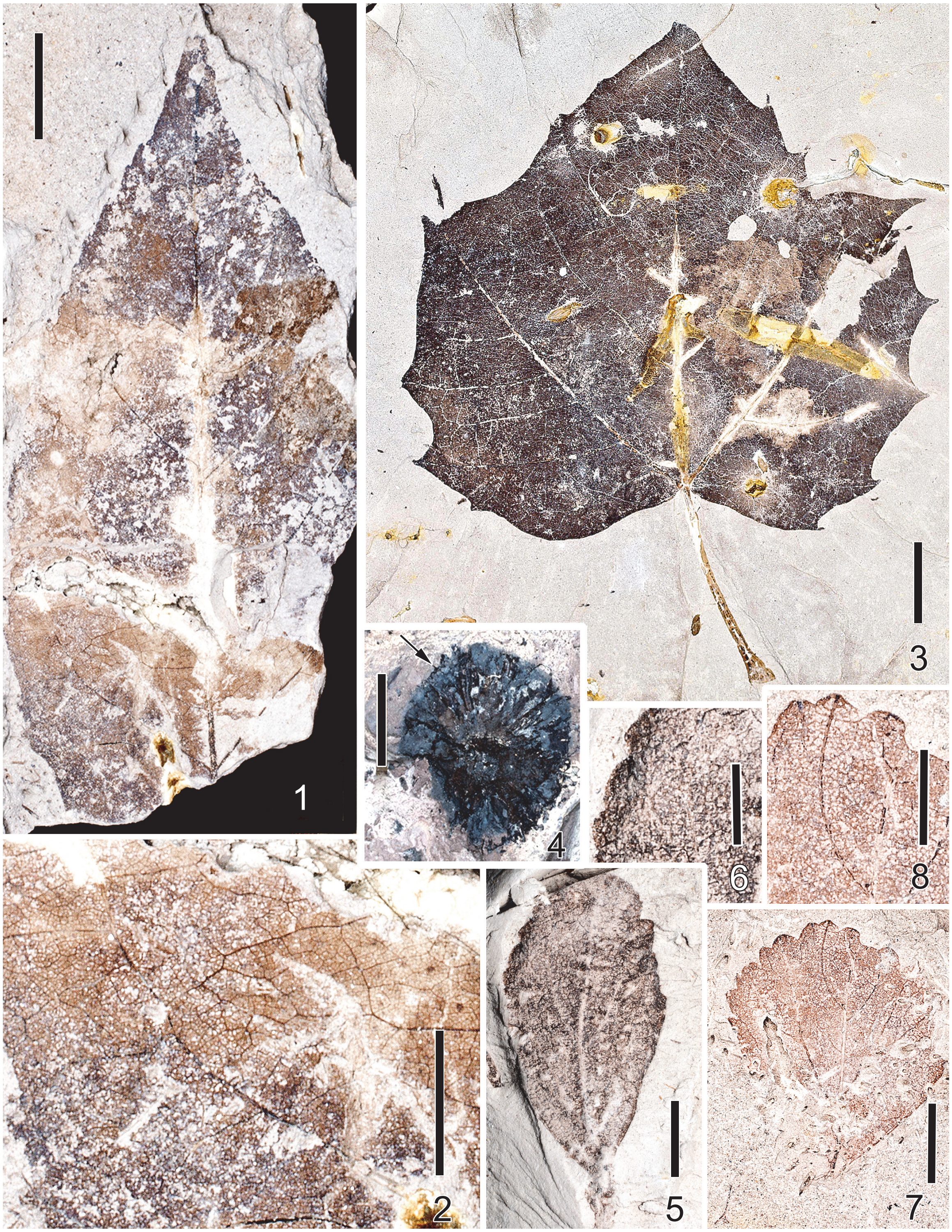

FIGURE 6. Representative Oleaceae (continued), Platanaceae, and Roseaceae from the Citronelle Formation. **1.** *Fraxinus* leaflet (UF 19210–062078), scale bar equals 1 cm. **2.** Close-up of Figure 6.1 *Fraxinus* leaflet showing higher order venation, scale bar equals 5 mm. **3.** *Platanus occidentalis* leaf (UF 19210–062079), scale bar equals 1 cm. **4.** *Platanus occidentalis* fruit (UF 19211–062080), showing persistent style at arrow, scale bar equals 1 cm. **5.** *Crataegus* leaf species 1 (UF19315–062081) similar to *C. spatulatha*, scale bar equals 5 mm. **6.** Close-up of Figure 6.5 *Crataegus* leaf showing higher order venation, scale bar equals 2.5 mm. **7.** *Crataegus* species #2 leaf (UF 19210–062082), wedge-shaped lamina similar to *C. floridana,* compare with Figure 7.1*,* scale bar equals 5 mm. **8.** Close-up of Figure 6.7 *Crataegus* leaf showing higher order venation, scale bar equals 2.5 mm.

mosa and *P. wrightii* (possibly *P. racemus* var. *wrightii)* are found primarily in areas of Arizona, California, and New Mexico, and also in northwestern Mexico. *Platanus mexicana* occurs in Mexico and Guatemala. *Platanus occidentalis* has a wide distribution along streams and rivers in eastern North America, from southern Maine to the panhandle of Florida, westward to south-central Texas, and northward to Iowa, Wisconsin, and Michigan.

The fossil record of *Platanus* in North America begins in the Paleocene (Manchester, 1999). *Platanus* is also present in the western Miocene Clarkia and Succor Creek floras (Smiley and Rember, 1985; Fields, 1996). The apparent divergence of *P. occidentalis* from *P. mexicana* occurred in the middle to late Miocene (Feng et al., 2005). Fossils of possible *P. occidentalis* have been reported from the Brandywine flora of Maryland (McCartan et al., 1990).

Family ROSACEAE de Jussieu, 1789
Genus *CRATAEGUS* Linnaeus, 1753
Crataegus sp. 1.
Figure 6.5–6.6

Description. One simple leaf, 2.0 cm long and 0.9 cm wide, obovate, L:W ratio 2:1, is attributed to *Crataegus*. Margin is shallowly lobed distally, crenations/serrations are also distal. Base is acute, decurrent. Apex is obtuse. Primary venation is pinnate. Secondary veins are craspedodromous, angles departing from the mid-rib at 30° to 40°. Tertiary, quaternary, and quinternary veins are irregular, reticulate. Crenations/serrations are irregularly spaced, sinuses angular, rounded teeth convex proximally and distally. This specimen is somewhat similar to extant *C. spathulata.*

Site Occurrence. Scarborough School.

Crataegus sp. 2.
Figure 6.7–6.8

Description. A second simple leaf is also attributed to *Crataegus*, but appears to represent a separate species. The leaf is ~ 1.5 cm long and 1.2 cm at its widest distally, obovate, L:W ratio 1:1. Margin unlobed, serrate. The base is missing, but was probably very narrow basally. Apex is obtuse. Primary framework is pinnate. Secondary venation is craspedodromous, veins departing the mid-rib at 20° to 30°. Tertiary through quintinary venation is irregular reticulate. Two orders of somewhat rounded teeth, sinuses angular, both orders of teeth convex proximally and distally.

Site occurrence. Perdido Park.

Remarks. This specimen appears similar to extant *Crataegus floridana,* which is sometimes considered a form of *C. flava* (Figure 7.1). Specific identification, even of extant species, can be challenging. *Crataegus* is well represented in North America with ~ 214 species, 41 of which occur today in the southeastern United States. Fossil genera similar to *Crataegus* occur in the early and middle Eocene Okanogan Highlands of eastern Washington, USA, and British Columbia, Canada. Some of the earliest records of the modern genus occur in the late Eocene Florissant flora of Colorado (Devore and Pigg, 2007); fruit records have been reported from European Miocene deposits (Kvacék and Walther, 2004). Leaves of *Crataegus* have been identified from the western Miocene floras of Clarkia and Succor Creek (Smiley and Rember, 1985; Fields, 1996). Europe or eastern North America is most probably the ancestral range of modern *Crataegus* species, with the modern species having an estimated divergence in the late Miocene (~ 14.3 Ma) (Lo et al., 2009).

Genus *RUBUS* Linnaeus, 1753
Rubus sp.
Figure 7.2

Description. This description is based on part and counterpart of a leaflet, 2.3 cm long and 0.9 cm wide, elliptic, L:W ratio 2.5:1. Margin is toothed. An asymmetrically inserted petiolule is 2 mm long. The base is convex, obtuse. The apex is obtuse, round. This specimen is probably a lateral leaflet because a small sub-basal lobe is present, as has been noticed in lateral leaflets of extant *R. argutus* and *R. cuneifolius*. Primary venation is pinnate. Secondary veins are excurrent, craspedodromous, and branch very near the margin. They are irregularly spaced, depart the primary vein mid-leaf at ~ 45°, angles become much wider proximally. Tertiary venation is mixed percurrent; quaternary and quinternary veins are irregular reticulate. First order teeth are regularly spaced with angular sinuses; distally they are straight; proximally they are usually convex, but may also be straight. The occurrence of a second order of teeth is irregular. Teeth are absent near the basal portion of the leaf, as is also recognized in many leaflets of extant *R. argutus* and *R. cuneifolius*. Principal tooth veins terminate at each tooth apex.

Site occurrence. Lambert Station.

Remarks. *Rubus* is a large genus that is well represented in North America today with ~ 237 species, 23 of which occur in the southeastern United States. As for *Crataegus,* fossils similar to *Rubus* occur in the early and middle Eocene Okanogan Highlands of eastern Washington, USA, and British Columbia, Canada. *Rubus* leaflets have been iden-

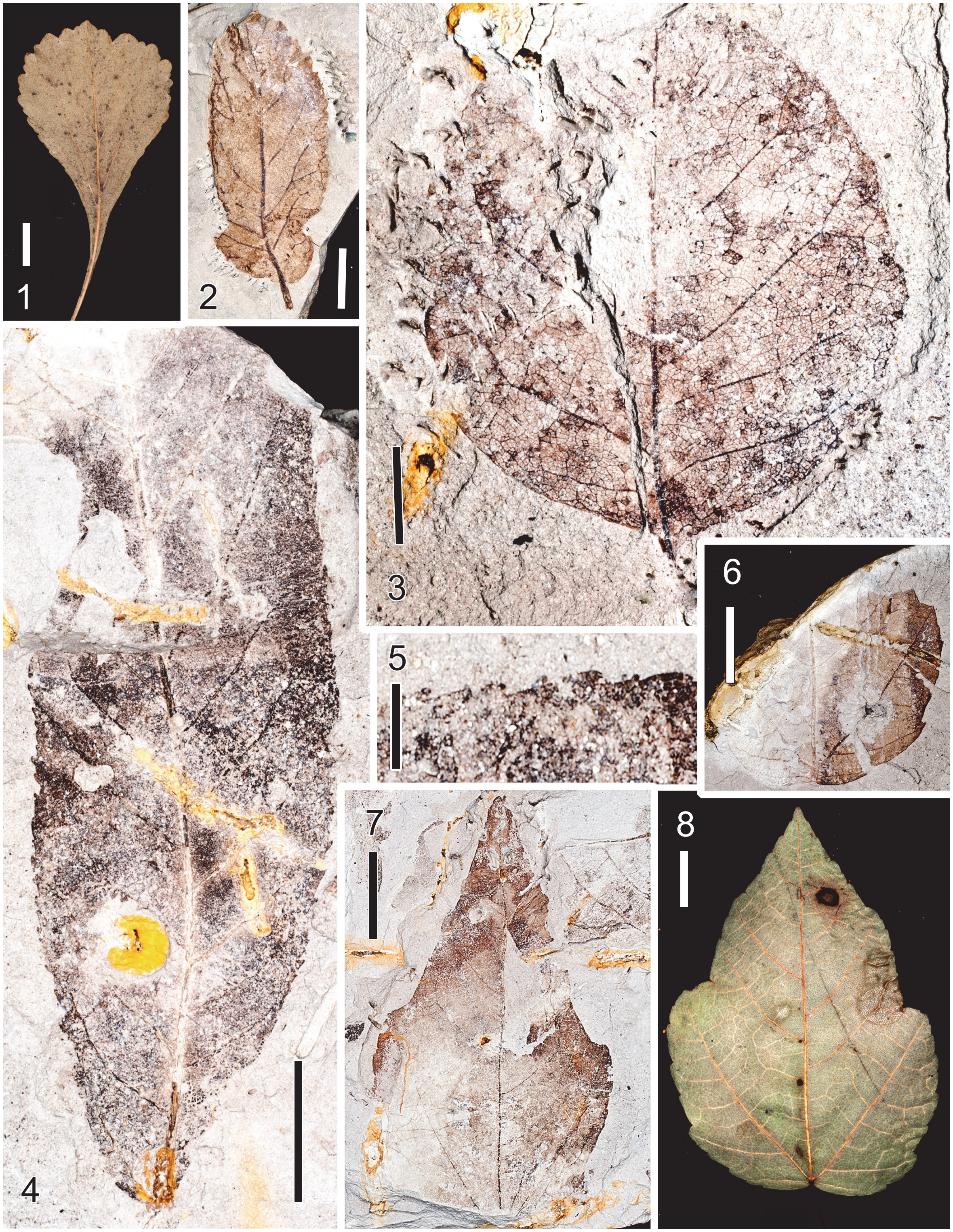

FIGURE 7. Representatives Rosaceae (continued), Salicaceae, Rutaceae, and Sapindaceae from the Citronelle Formation. **1.** Extant *Crataegus floridana* from USAM herbarium for comparison with Figure 6. 7, scale bar equals 5 mm. **2.** *Rubus* sp. leaf (UF 19413–062083), scale bar equals 5 mm. **3.** *Ptelea* cf. *trifoliata* leaf (UF 19210– 062084), scale bar equals 5 mm. **4.** *Salix* sp. leaf (UF 19210–062085), scale bar equals 1 cm. **5.** Close-up of Figure 7.4 *Salix* leaf margin showing salicoid teeth, scale bar equals 2.5 mm. **6.** *Acer* cf. *rubrum* basal portion of leaf (UF 19210–062087), scale bar equals 1 cm. **7.** *Acer* cf. *rubrum* leaf (UF 19210–062086), scale bar equals 1 cm. **8.** Extant *Acer rubrum* USAM herbarium for comparison with Figure 7.6–7, scale bar equals 1 cm.

tified from the western Succor Creek flora (Smiley and Rember, 1985; Fields, 1996).

Family RUTACEAE de Jussieu, 1789
Genus *PTELEA* Linnaeus, 1753
Ptelea cf. *trifoliata* Linnaeus, 1753
Figure 7.3

Description. One mostly complete leaflet is identified as *Ptelea*, possibly *P. trifoliata.* The leaflet is ovate and nearly circular (in the Gulf of Mexico Coastal Plain, this is a characteristic of many extant lateral leaflet specimens of this genus). The leaf is 2.6 cm long and 2.5 cm wide, L:W ratio of 1:1. The base is obtuse and decurrent. The apex is incomplete, but indications are that it was rounded. Margins are sinuous. No glands are visible, indicating that the fossil is displaying the abaxial surface of the leaf (glands are typical on the adaxial side of *P. trifoliata*). Primary venation is pinnate. Irregularly spaced secondary venation appears mixed; some secondaries are brochidodromous, whereas others are cladodromous. Secondaries also display both excurrent and decurrent departures from the midrib. Tertiary, quaternary, and quinternary veins are irregular reticulate. A fimbrial, perimarginal vein is present.

Site occurrence. Perdido Park.

Remarks. *Ptelea* is currently represented by three species in North America. *Ptelea aptera* and *P. crenulata* occur in California. *Ptelea trifoliata* occurs over a large portion of North America from Connecticut to central peninsular Florida, westward to Texas and parts of Mexico, northward to southern Ontario through Oklahoma, Arkansas, Missouri, Illinois, Indiana, and Ohio. The first reliable North American fossil records of *Ptelea* (based upon samaras) are from the middle Miocene of Idaho and Oregon (Dorf, 1936; Chaney and Axelrod, 1959; Call and Dilcher, 1995).

Family SALICACEAE Mirbel, 1815
Genus *SALIX* Linnaeus, 1753
Salix sp.
Figure 7.4–7.5

Description*.* *Salix* is identified from two oblong leaf fossils. A petiole is present on one specimen and is 8 mm long. The length of the complete specimen is 3.5 cm long and 1.3 cm wide, whereas an incomplete specimen is > 5.5 cm long with a width of 2 cm, L:W ratios approximately 3:1. Margin is unlobed, serrate. The bases are acute and slightly asymmetrical. The apex is preserved in one specimen and is acute and straight. Primary venation is pinnate. Secondary veins are semicraspedodromous, excurrent. Secondaries are noticeably arcuate near the basal end. Intersecondaries are present, but not prominent. Tertiary and quaternary veins are irregular reticulate. Teeth are of one order, present along the entire lamina. Teeth are small, regularly spaced, angular to rounded sinuses, convex/straight proximally, concave/straight distally, apices glandular (Figure 7.5).

Site occurrence. Scarborough School and Perdido Park.

Remarks. The genus *Salix* currently contains approximately 450 species worldwide, 113 of these occur in North America. Those occurring today in Alabama, Florida, and Georgia are *S. caroliniana, S. eriocephala, S. floridana, S. humilis,* and *S. nigra.* Reproductive specimens of *Salix* have been found in Eocene deposits of Wyoming and late Oligocene and early Miocene deposits of Alaska (Hollick, 1936; Wing 1981; Collinson 1992). Leaves of *Salix* have been described from Eocene deposits in Wyoming, North Dakota, Colorado, and Utah, and from Miocene deposits in Oregon (MacGinitie, 1969; Hickey, 1977; Wing, 1981; Collinson, 1992; Fields, 1996).

Family SAPINDACEAE de Jussieu, 1789
Genus *ACER* Linnaeus, 1753
Acer cf. *rubrum* L.
Figure 7.6–7.7

Description. Four partial specimens and one mostly complete specimen are similar to *Acer rubrum*. Leaves are simple, ovate, petioles slightly eccentric. Widths range from 3.0–5.0 cm. The most complete leaf is 5.8 cm long and 3.0 cm wide; L:W ratio of 2:1. Margins appear somewhat lobed, although the incision is less than 25% of the distance to the midvein. Margins are toothed. Bases are obtuse and rounded in some specimens, but somewhat cordate in others. Apices are acute and straight. Primary venation is basal actinodromous. Agrophic compound veins are evident. Major secondaries are craspedodromous/semicraspedodromous; a few intersecondaries are present. Tertiaries and quaternary veins are irregular reticulate, while quinternary veins are regular reticulate. Two orders of teeth are unequally distributed on the leaf margin. First order tooth sinuses are angular, teeth convex/straight proximally, convex/concave/straight distally. Secondary teeth when present have angular sinuses, teeth straight proximally, straight/concave distally. First order tooth apices are somewhat cassidate, as in the modern species (Figure 7.8).

Site occurrence. Perdido Park.

Remarks. *Acer rubrum* is common in floodplain forests from Canada to peninsular Florida, and occurring westward to east Texas. The ancestral species of *A. rubrum* and *A. saccharinum* apparently split from Asian clades during the late Oligocene to early Miocene, whereas these North American sister species apparently diverged from each other in the earlier Pliocene (Renner et al., 2008; Saeki et al., 2011).

Acer cf. *saccharinum* Linnaeus, 1753
Figure 8.1

Description. Two partial mesophyllic leaves indicate a second *Acer* species from the Citronelle Formation similar to *A. saccharinum*. Inferring mostly bilateral symmetry of the lamina on either side of the midvein, the size of larger specimen extrapolates to a leaf > 8.7 cm long and 6.4 cm wide. Margins are toothed. Base is truncate. Apex is not preserved. Primary venation is actinodromous or palinactinodromous. Six suprabasal veins are present, as are agrophic compound veins. Both interior secondary veins and intersecondary veins are present. Tertiary veins are irregular reticulate. Teeth are of one order, but differ in size, some very large. Tooth sinuses are mostly rounded, teeth convex/straight proximally, concave/straight distally. Several teeth are present basally, which differentiates these specimens from *A. saccharum*. Additionally, they can be distinguished from the palmately lobed, palinactinodromous leaves of *Platanus* based upon the much broader tooth-width of *Platanus* leaves, and the greater incision of the lobes in *Platanus* leaves.

Site occurrence. Scarborough School.

Remarks. There are 27 species of *Acer* currently in the flora of North America, seven of which have been introduced. Nine of these species occur within the southeastern United States; seven of which, including *A. saccharinum*, are wetland inhabitants.

Family SMILACACEAE Ventenat, 1799
Genus *SMILAX* Linnaeus, 1753
Smilax sp.
Figure 8.2–8.3

Description. One partial leaf represents *Smilax.* Margin is entire. Primary venation is basal acrodromous with five primary veins. Secondary veins are excurrent, and many arch from their respective primary veins. An intramarginal secondary vein is present in the basal region. Tertiary and quaternary veins are irregular reticulate (Figure 8.3).

Site occurrence. Lambert Station.

Remarks. There are 350 species of *Smilax*, 20 in the flora of North America, about half of which occur in the southeastern United States. Although the family is mainly pantropical, some species occur in southern South America, New Zealand, and temperate areas of the northern hemisphere (Vinnersten and Bremer, 2001). *Smilax* leaves have been described from middle Eocene sediments of western Tennessee, (Dilcher and Lott, 2005).

Family ULMACEAE Mirbel, 1815
Genus *ULMUS* Linnaeus, 1753
Ulmus cf. *alata* Michaux, 1803
Figure 8.4–8.5

Description. Five simple, ovate leaves are similar to specimens of modern *Ulmus alata*. Lamina lengths range from 2.5–4.2 cm and widths from 1.2–2.3 cm, L:W ratio 2:1. Margins are serrate. Bases are acute, some displaying an asymmetrical basal petiole insertion. Apices are acute and straight. Primary vein framework is pinnate. Secondary venation is craspedodromous, excurrent. Occasionally, second order veins branch just before reaching the margin. Spacing of secondaries is fairly uniform, but decreases somewhat basally. Angles of most secondary veins are ~ 45º, but angles increase proximally. Tertiary veins are difficult to discern, but appear to be irregular reticulate as are the fourth order veins. Teeth are of two orders with secondary teeth appearing on the basal side of the primary tooth. There are 3–5 first order teeth per cm. Tooth sinuses are angular, teeth usually convex/straight proximally, convex/straight distally. The first order teeth are about as wide as long, giving them a broad appearance. There are no extenuating tips on teeth apices (Figure 8.5).

Site occurrence. Lambert Station.

Remarks. Ten species of *Ulmus* occur in North America. Of these, *U. alata, U. americana, U. crassifolia*, and *U. rubra* occur in the southeastern United States. Fossil *Ulmus* leaves have been recorded from the western Miocene Succor Creek Flora, and possibly from the Miocene Clarkia site of Idaho (Smiley and Rember, 1985; Fields, 1996).

RESULTS

NLR Analyses Results

CoA. Climate intervals for each of the five individual Citronelle Formation fossil sites and the combined data are presented in Table 4. The results are compared with climate parameters from nearby modern sites (i.e., Baton Rouge, Louisiana; Mobile, Alabama; Pensacola, Florida). The taxa that were most influential in establishing the coexistence interval boundaries are shown in Table 5. It is

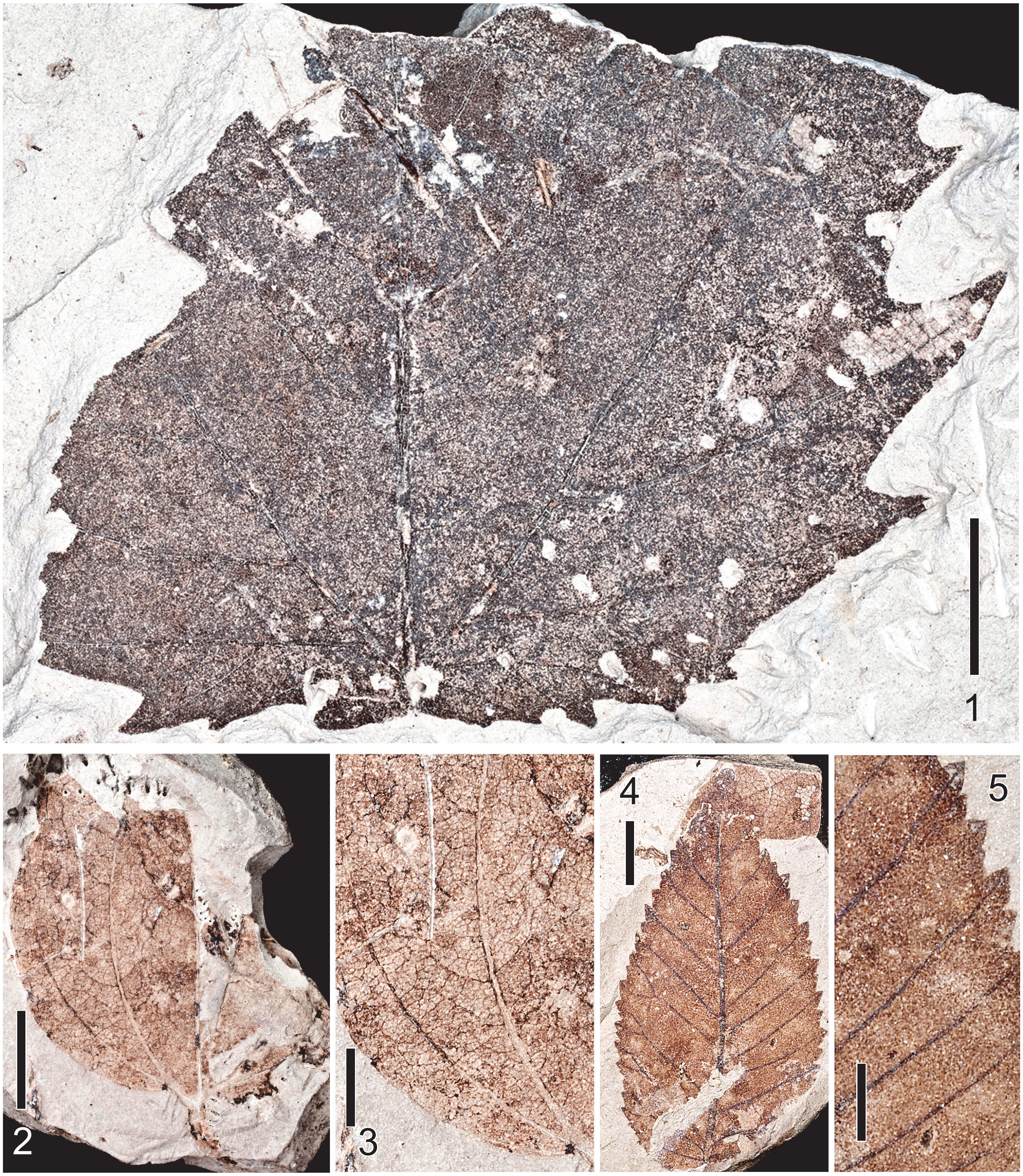

FIGURE 8. Representative Sapindaceae (continued), Smilicaceae, and Ulmaceae from the Citronelle Formation. **1.** *Acer* cf. *saccharinum* partial leaf (UF 19315–062088), scale bar equals 1 cm. **2**. *Smilax* sp. partial leaf (UF 19413–062089), scale bar equals 5 mm. **3.** Close-up of Figure 8.2 *Smilax* leaf showing higher order venation details, scale bar equals 2.5 mm. **4.** *Ulmus* sp. leaf (UF 19413–062090), scale bar equals 5 mm. **5**. Close-up of Figure 8.4 *Ulmus* leaf showing margin details and multiple orders of teeth, scale bar equals 2.5 mm.

TABLE 4. Coexistence Approach analysis (CoA) results and modern value comparisons. MAP, PWTM, PRDM, PWMM results are in mm/year. C.Form= Citronelle Formation combined sites, H=HMR site, LS=Lamberts Station site, PP=Perdido Park site, RB=Red Bluff site, Sc=Scarborough site , Baton Rouge, Mobile, and Pensacola are modern sites. See text for details.

Site	MAT °C	CMMT °C	WMMT °C	MAP	PWTM	PDRM	PWMM
C.Form	14.4-20.8	4.3-12.6	25.6-27.9	1122-1250	142-146	50-55	99-142
HMR	13.6-21.1	4.3-13.3	25.6-27.9	961-1355	109-195	50-55	99-176
LS	13.3-21.1	-0.1-12.6	25.6-27.9	897-1258	109-146	50-55	84-142
PP	14.4-21.1	3.7-13.3	25.6-28.1	1122-1355	142-192	43-61	142-177
RB	13.3-21.1	-0.1-12.6	25.6-27.9	897-1520	109-185	50-55	84-172
Sc	13.3-20.8	0.7-12.6	25.6-27.9	1003-1250	116-146	50-61	94-142
Baton Rouge	19.8	9.9	27.9	1547	170	89	170
Mobile	19.3	10.5	27.5	1684	183	83	166
Pensacola	19.8	10.3	27.8	1580	188	89	188

TABLE 5. Citronelle Formation taxa establishing Coexistence Approach analysis (CoA) interval boundaries.

	MAP1122 250 mm	PWTM 142 46 mm	PDRM 50 55 mm	PWMM 99 142 mm
Established Min-value	*Persea* sp.	*Gordonia* sp.	*Planera aquatica*	*Gordonia* sp.
Established Max-value	*Carya aquatica* *Populus deltoides*	*Carya aquatica*	*Carpinus* sp.	*Carya aquatica*

	MAT 14.4 - 20.8°C	CMMT 4.3 - 12.6°C	WMMT 25.6 - 27.9°C
Established Min-value	*Gordonia* sp. *Persea* sp. *Quercus. virginiana*	*Cyrilla racemiflora* *Gordonia* sp. *Persea* sp.	*Persea* sp. *Taxodium distichum* *Quercus virginiana*
Established Max-value	*Acer sacharinium* *Vaccinium* sp.	*Carya aquatica*	*Cyrilla racemiflora* *Nyssa* sp.

important to note that in several instances multiple taxa established a single boundary (e.g., *Gordonia* sp., *Persea* sp., and *Quercus virginiana* established the low end of the MAT range).

The MAT and WMMT values are consistent between fossil sites. The lower boundaries of the range of each individual MAT differ only by about 1° C, and the high boundaries by even less. The WMMTs are very similar among the sites. The combined mean MAT for the coexistence interval is 17.6° C (Table 4). The CoA analysis indicates that the late Pliocene MAT was close to current regional values, as the current MAT occurs within the higher end of each fossil MAT interval (seen in the figures for Baton Rouge, Mobile, and Pensacola). The CMMT between sites, however, are more variable and reveal how only one or two fossils can influence the results. The CMMT ranges for the HMR and Perdido Park sites are warmer than those for Lambert Station, Red Bluff, and Scarborough School due to the presence of the frost-sensitive taxa *Cyrilla racemiflora* (at HMR) and *Gordonia* (at Perdido Park) (Table 5).

Overall precipitation values obtained for the Citronelle flora are somewhat variable. The floras of the Lambert Station and Red Bluff sites indicate a drier setting. Precipitation during the driest months was not significantly different from site to site. Interestingly, the CoA analysis indicates that the warmest months were not necessarily the wettest, unlike the current climate in the region today. In fact, this analysis indicates that the fossil MAP overall (1122–1250 mm) was lower than current values (1684 mm for Mobile) and more similar to that of the southeastern Atlantic Coastal Plain, the central Florida peninsula, and a small area of the eastern Texas Gulf Coastal Plain. Today, no areas in the entire state of Alabama have a MAP as low as that indicated by the CoA analysis for the late Pliocene (NOAA, 1971–2000) (Table 4).

BA/MCRT. The BA/MCRT approach focuses on climatic intervals between the 10th and 90th percen-

TABLE 6. Coexistence Approach analysis (CoA), Bioclimatic Analysis/Mutual Climate Range Technique (BA/MCRT), Leaf Margin Analysis (LMA) results comparisons.

Method	MATºC	WMMTºC July MT	CMMTºC Jan MT	MAP mm	PWMM mm July MP	PDRM mm Jan MP
CoA	14.4 - 20.8	25.6 - 27.9	4.3 - 12.6	1122 - 1250	99 - 142	50 - 55
BA/MCRT	18	27	5-7.4	1190 - 1325	125	85 - 105
LMA	19.3 +/- 2.6					
Current Mobile, AL	19.3	27.5	10.5	1684	166	83

tiles (Thompson et al., 1999a, 1999b, 2000; Fang et al., 2011) (Table 6). In some instances, a single estimate is acquired rather than an interval. When necessary, data outside of the 10th and 90th percentiles, but still within established climate parameters per taxon, were used here. For example, a conservative MAT estimate of ~ 18º C was acquired from the 10th percentile of *Quercus virginiana* and within the 100th percentile of *Acer saccharinum*. This violated the 90th percentile suggestion detailed in the method section, but as both species currently exist in Alabama, Georgia, and Florida, it would be problematic to suggest that they would not have coexisted during the late Pliocene. Interestingly, this is congruent with the mid-range MAT estimate of 17.6º C in the CoA analysis (Table 4). July MT of BA/MCRT is considered comparable to WMMT of the CoA analysis and was approximately 27º C, which is congruent with the 90th percentile of *A. saccharinum* and the 10th percentile of *Q. virginiana* (Table 6). *Clethra* was not used for either the MAT or July MT estimate, as the Thompson et al. (2000) climate values are based on the more northern species *C. acuminata*, which tolerates much cooler temperatures than the southeastern species *C. alnifolia* (Godfrey 1988). January MT of the BA/MCRT is considered comparable to CMMT of the CoA analysis. This temperature parameter could be regarded as less robust in this analysis, as the 10th percentiles for *Quercus virginiana, Cyrilla racemiflora, Gordonia,* and *Persea* are all outside the 90th percentile for *Acer saccharinum*; however, they are all within the 100th percentile of that species. Consequently, it is apparent that climate data for the Pliocene and Recent Gulf of Mexico Coastal Plain requires consideration of the more outlying, but still valid, climatic ranges when estimating intervals for this region. A January MT interval of 5.0–7.4º C would be between the upper 90th and lower 10th percentiles of these taxa (Table 6).

A MAP estimated interval of 1190–1325 mm is based on the lowest 10th percentile of *Planera aquatica* and the highest 90th percentile of *Populus deltoides* (Table 6). July MP of the BA/MCRT is comparable to the precipitation warm month (PWMM) parameter of the CoA analysis. A July MP singular value of ~ 125 mm is based on the 10th percentile of *Cyrilla racemiflora* and the 90th percentiles of *Populus deltoides* and *Acer saccharinum.* January MP of BA/MCRT is comparable to the driest month precipitation (PDRM) value of the CoA analysis, with the interval of approximately 85–105 mm based on the 10th percentiles of *Clethra, Cyrilla, Planera aquatica*, and *Nyssa aquatica*, and the 90th percentile of *Gordonia*.

Comparison of NLR analyses. Table 6 summarizes the climatic values for both NLR analyses based on the taxa identified from the Citronelle Formation. The mid-range MAT value of the CoA analysis and the single MAT value obtained for the BA/MCRT are in close agreement, as are the CoA WMMT and BA/MCRT July MT values. The BA/MCRT Jan MT interval is within the CMMT of the larger CoA analysis interval. The current WMMT for the Mobile area is ~28º C and the CMMT is ~11º C (Table 4). The BA/MCRT approach produces a WMMT of ~27º C and CMMT of ~ 6º C for the Citronelle flora. This higher level of seasonality in a mid-latitude terrestrial setting is in sharp contrast with several previous studies from the marine record of the North Atlantic region indicating that Pliocene temperatures showed less annual variability than occurring now (Knowles et al., 2009; Williams et al., 2009).

Precipitation values obtained with the BA/MCRT technique indicate possibly wetter conditions than the CoA analysis. The July MP of BA/MCRT is the midpoint of the CoA PWWM. The Jan MP of BA/MCRT is identical to the current PDRM, although the CoA PDRM indicates drier conditions. Both NLR techniques indicate drier conditions than presently occur in the area. The BA/MCRT analy-

TABLE 7. CLAMP results and modern value comparisons. GRIDMet3brAZ climate values from CLAMP website (clamp.ibcas.ac.cn/ Clampset2.html). GSP (growing season precipitation) is in mm. LGS (length of growing season) is in months. Sc= Scarborough site, PP = Perdido Park, C. Form = Combined Citronelle Formation sites. [a] = Modern values from NOAA Climatography of the United States No. 81 (01 Alabama). [b] = Removed three coldest months (period between first freeze of season to last freeze of season) according to NOAA for adjusted LGS and GSP.

Site	MAT C°; 2SD	WMMT C°; 2SD	CMMT C° 2SD	LGS; 2SD	GSP; 1SD
Sc	11.8; 9.5 - 14.1	23.1	1.5; -2.3 - 5.3	7.0; 5.6 - 8.4	728; 527 - 929
PP	13.9; 11.6 - 16.2	22.8	5.6; 1.8 - 9.4	7.9; 6.5 - 9.3	1055; 854 - 1256
C.Form.	13.4; 11.1 - 15.7	23.3	4.3; 0.5 - 8.1	7.7; 6.3 - 9.1	946; 745 - 1147
Mobile, AL[a]	19.3	27.5	10.1	12	1683
Mobile, AL[b]				9	1289

sis also suggests a less seasonal annual distribution of precipitation.

Physiognomic Analyses Results

LMA. Using the regression equation of Kowalski and Dilcher (2003) and the standard deviation calculation method of Wilf (1997), the MAT calculated from the combined 47 scored leaf morphotaxa of the Citronelle flora is 19.3° +/- 2.6°. Although this range is rather wide, the 19.3° value exactly matches the current MAT of the Mobile Alabama area. Comparison with the NLR derived MAT results is found in Table 6.

CLAMP. The CLAMP analysis results with standard deviation values are shown in Table 7. Two standard deviation ranges are shown for MAT, WMMT, CMMT, and LGS. Since the uncertainties for precipitation results are large, one SD range is listed for GSP. These ranges are compared to current climate data from Mobile, Alabama, obtained from NOAA (1971–2000). The results indicate that MAT and CMMT conditions were cooler, whereas the WMMT was similar to the current value. A cooler MAT is not entirely unexpected, as CLAMP studies using modern vegetation have shown that the predicted MATs and CMMTs are typically a reflection of a microenvironment rather than a regional assessment, and that fossil floras are likely to indicate wetter and cooler environments (Yang et al., 2007). Additionally, evapotranspirational cooling during drier winter months in generally warm environments is likely to indicate a lower than actual CMMT. CLAMP estimated WMMTs are usually closer to observed WMMTs (Spicer et al., 2011). These factors could result in an overestimation of seasonality.

Wolfe (1993) defined a growing season as any month where the temperature was ≥ 10°C, a definition based upon a delineation of forested areas vs. tundra. Under this definition, the current growing season in the Mobile region encompasses the entire year, which is much longer than CLAMP predicted results for the Citronelle flora of 6.3–9.1 months (Table 7). An alternative definition of a growing season in a region with adequate precipitation is based on the difference in the number of months between the last frost and the subsequent first frost (Carter and Seaquist, 1984). In the current Mobile area, the last frost of the winter season typically occurs in February, and the first frost of the winter season typically occurs around November (Gallup, 1979). This delimits the modern growing season to approximately nine months, which falls within the upper CLAMP predicted limits for the Citronelle Formation flora. It is unlikely that warmth-requiring, cold-sensitive taxa identified from the Citronelle Formation (e.g., *Cyrilla racemiflora, Gordonia* sp., and *Begonia* sp.), could have occurred within an area with a cooler climate and significantly shorter growing season than now as predicted by CLAMP (Stults and Axsmith, 2011a, b).

The precipitation results obtained here are considerably lower (nearly half) than modern regional values and are possibly the result of a coastal flora anomaly within the CLAMP method discussed in more detail below. However, under the alternative growing season definition of Carter and Seaquist (1984) (shown in last row, 5th column of Table 7), the modified CLAMP predicted GSP results (results in last row, 6th column in Table 7) are much closer to current precipitation values, and also comparable to the range of precipitation values predicted in the CoA analysis.

DISCUSSION

Floral Composition

The descriptions of 23 woody angiosperm taxa here are important in part because there is so little information on Neogene plants from eastern North America, especially based on macrofossils. In fact there are only five known macrofossil sites that provide points of comparison with the Citronelle Formation flora, and none of them are late Pliocene. The oldest is the Brandon Lignite of Vermont, which is now widely considered lower Miocene (Tiffney, 1994). The flora is rather similar to that of the southeastern U.S. today, and shares several genera with the Citronelle flora, including some indicating warm temperatures (e.g., *Cyrilla*, *Gordonia* and *Persea*). As expected due to its greater age, the Brandon Lignite contains more taxa now confined to Asia than does the Citronelle flora.

At this time there are only four comparable southeastern sites producing substantial macrofossils. The late Miocene Brandywine flora near Washington D.C. is known from one locality that was only briefly exposed. Although an extensive list of taxa was produced (McCartan et al., 1990), only the *Taxodium distichum* fossils have been described and figured in detail (Stults et al., 2011). The floral composition, at least at the generic level, is similar to that of the Citronelle flora with 16 shared taxa based on macrofossil and four more based on pollen. The Asian endemics of the Citronelle flora also occur in the Brandywine flora (*Pterocarya* and *Trapa*); however, the Brandywine flora also includes the Asian taxa *Alangium* and *Zelkova*. The Gray Fossil site in northeastern Tennessee represents a late Miocene to early Pliocene montane community around a lacustrine sinkhole setting (Ochoa et al., 2012). Although sharing several genera with the Citronelle flora, such as *Carya*, *Quercus*, and *Vitis*, species level studies of the Gray flora are revealing a surprisingly high level of affinity with Asian forms (Gong et al., 2010; Huang et al., 2014). Because of the significant differences in age, depositional environment, and physiographic setting, detailed comparisons of the two floras are limited. Other nearby Neogene localities include the Hattiesburg Formation and Alum Bluff floras (Berry, 1916c); however, these are currently under reinvestigation and cannot be readily compared to the Citronelle flora at this time. The palynoflora of Alum Bluff suggests a warm temperate flora with some Eurasian elements such as *Paliurus* (Jarzen et al., 2010).

Paleoclimate Analyses

Comparison of method results. The multipronged approach taken here was required, as serious criticisms have been leveled against most quantitative paleoclimate methods. For example, Grimm and Denk (2012) concluded that a CoA analysis can rarely provide significant resolution, and noted that the Palaeoflora Database contained errors with respect to the climate tolerances of NLRs. This is the main justification for employing the BA/MCRT method here, as it typically provides narrower ranges (Kotthoff et al., 2014). Also, Little et al. (2010) propose that the assumptions underlying CLAMP underestimate the role of phylogenetic signal in leaf morphology relative to physiological factors. These criticisms were considered in evaluating the results of this study.

In some cases (CoA and CLAMP) it was possible to perform site-by-site and combined analyses, but the combined data is more reliable at this time (also see Greenwood et al., 2005). This is because the precise relative ages of the sites are unknown due to poor outcrop, rapid facies changes, the lenticular nature of the plant-bearing clays, and lack of materials for absolute dating. The depositional environments include meandering river systems, floodplain channel fills, and estuarine/near shore marine settings (Otvos, 1997) that would preserve a diverse taxonomic assemblage representing a more regional (rather than localized) climate signal. There is also prior evidence that the Pliocene warm interval was relatively uniform, which would mitigate undesirable averaging effects of a combined analysis that could mask potential temporal trends. For example, the amplitudes of climate-oscillating cycles, such as Milankovitch cycles, are generally attenuated during extended warm periods (Draut et al., 2003). Climate attenuation probably occurred during the Pliocene warm interval, as the amplitude of such cycles increased only after intensification of Northern Hemisphere glaciations commenced approximately 2.75 Ma (Ravelo et al., 2004). However, some caution in interpreting the results is still in order, as Prescott et al. (2014) present some evidence of greater climate variability during this time than previously realized.

The LMA MAT result matches the current MAT of the Mobile, Alabama area, although the standard error is still rather broad. It also mostly overlaps the CoA analysis and BA/MCRT values, but is considerably higher than the CLAMP MAT result (Tables 6, 7). The high and low climate interval boundaries of the CoA analysis are more consistent from site to site compared with the CLAMP 2 SD intervals (Tables 4, 7). For example, the lower boundaries of MAT based on the CoA analysis vary by 1.1° C, and the higher boundaries by 0.3° C. By comparison, the 2 SD boundaries between the CLAMP sites vary by 2.1° C. A similar result was found when comparing MAP of the CoA analysis with the GSP of CLAMP. The CoA analysis lower boundaries between sites vary by 225 mm and the higher boundaries vary by 270 mm. For the CLAMP analysis results, the 1SD boundaries vary by 327 mm. The greater disparity in the CLAMP results are probably due to the method's tendency to reflect differing microclimates (Spicer et al., 2011), which could vary somewhat from site to site due to the complex facies changes within the Citronelle Formation (Otvos, 2004). This result may indicate that the LMA and CoA analyses are providing a better regional climate signal, and justifies the use of combining all of the sites in the BA/MCRT analysis. This also suggests that it is desirable to employ multiple sites in a CLAMP analysis to better estimate the regional climate signal.

Comparisons with modern flora and conditions. The overall similarity of the Citronelle Formation and modern floras is consistent with the relatively young age of the Citronelle flora and the basic similarity of physiographic conditions to the recent during the late Pliocene (Piacenzian) of the northern Gulf of Mexico Coastal Plain. These include the nearby Gulf of Mexico, which would provide some temperature amelioration, a tectonically passive continental margin, and mostly lowland areas dominated by sandy, marshy, lagoonal, and deltaic environments (Donnelly, 1975; Martin, 1975; Uchupi, 1975; Smith et al., 1994; Balsillie and Donoghue, 2004). Potentially significant differences during the Pliocene affecting the region include sea levels as much as 25 m higher, lack of an intact Florida peninsula, and the ongoing formation of the Central American isthmus (Keigwin, 1982; Keller et al., 1989; Otvos, 1997, 1998). The results of this study are in general agreement with the qualitative climate trends seen in the Pinecrest Beds palynoflora of Florida (3.5–2.5 Ma), which indicate that temperatures in the southeast were comparable to modern values (Willard, 1994). However, as discussed above, the mid-Piacenzian global climate was warmer than the recent, although the causes and distribution of this warmth remain somewhat controversial (Dowsett et al., 1992; Van der Burgh et al., 1993; Crowley et al., 1996; Dowsett et al., 1996; Kurschner et al., 1996; Raymo et al., 1996; Hill et al., 2014).

Despite the overall taxonomic similarity of the Citronelle Formation and modern floras, the Citronelle flora contains several "exotic" taxa that provide conflicting data and require some consideration. Such fossils are often dismissed as misleading climatic outliers for several compelling reasons (Utescher et al., 2014), but some of them could be providing valuable climatic and ecological signals. For example, a *Begonia* sp., a mainly tropical genus, has been identified from the Citronelle Formation along with white pine pollen and macrofossils, which would suggest cooler temperatures (Forrest et al., 2005; Stults et al., 2010; Stults and Axsmith, 2011a). The *Begonia* is based on a single specimen and could represent a more cold tolerant extinct form, but the pines are more difficult to interpret. Today, hard pines (subgenus *Diploxylon*) dominate many southeastern forests to the complete exclusion of white pines (subgenus *Haploxylon*), and their abundant, robust needles are conducive to fossilization. Nevertheless, no macrofossils clearly attributable to the hard pines have been found in the Citronelle flora, and their pollen is never more than 23% of the pine pollen spectrum at any site (Stults et al., 2010). A few white pine macrofossils have been found at one site, and their pollen component ranges from 77 to 100% of the total *Pinus* palynoflora. This indicates that pines were not nearly as commonly found as in the region today region today, and that the ones present were predominantly white pines. It is interesting in this context that white pine (*P. strobus*) today prefers drier, warmer conditions, and may expand its future range due to anthropogenic global warming (Jacobson and Dieffenbacherkrall, 1995). The white pine dominance in the Citronelle flora supports this scenario based on the drier conditions indicated by the CoA, BA/MCRT, and CLAMP results.

Although exotic taxa raise interesting questions, it is currently difficult to fully assess their impact, as most of the Citronelle flora taxa are common to the area today and include several that would require a climate at least as warm as the recent (i.e., *Cyrilla racemiflora*, *Carya aquatica*, *Nyssa aquatica, Quercus virginiana*, and others). This relative taxonomic stability since the Pliocene on the Northern Gulf of Mexico Coastal Plain is contrary to what occurred elsewhere (i.e., Europe, inland Mio-Pliocene sites of North America) and is probably a result of the region being spared from the major climatic deterioration that occurred to the north during the Pleistocene (Delcourt and Delcourt, 1993; Stults, 2011; Ochoa et al., 2012). Accordingly, the LMA, CoA analysis, and BA/MCRT results obtained here appear to be more robust proxies than those obtained from CLAMP, as their temperature estimates are closer to modern values and the precipitation values are only slightly drier.

Comparisons with other proxy data. Data from various marine proxies such as cheilostome bryozoans, mollusks, and ostracods support warmer ocean water temperatures and less seasonality for mid-Piacenzian southeastern U.S. coastal localities (Dowsett and Cronin, 1990; Cronin and Dowsett, 1996; Knowles et al., 2009; Williams et al., 2009). Although increased seasonality due to periodic seasonal upwelling (possibly resulting from tectonic influences associated with the closing of the Central American Straits) has been noted from southwestern Florida, most studies indicate less seasonality or temperatures similar to the present for this area (Cronin and Dowsett, 1990, 1996; Knowles et al., 2009; Williams et al., 2009). Climate models (Haywood et al., 2009) indicate that mid-Piacenzian mean summer temperatures for the southeastern U.S. were similar to current values, whereas winter seasons were slightly warmer (i.e., less seasonality). These models also indicate that regional precipitation values during the winter months were lower, whereas precipitation during the summer months was possibly similar to or somewhat lower than today (Haywood et al., 2009). These proxy values, in combination with the preceding argument based on the taxonomic composition of the Citronelle flora, also indicate that the NLR-based analyses (CoA analysis and BA/MCRT) and LMA appear more reliable than the CLAMP results for this region.

CONCLUSIONS

The taxonomic descriptions here support Berry's (1916a) finding that the Citronelle flora was similar to the extant flora of southern Alabama. Based on this, Berry (1916a) also asserted that the climatic and physiographic aspects of the Pliocene were similar to those occurring in the region today. The quantitative values obtained in this study generally support this conclusion and provide an explicit framework for future investigations. Importantly, the drier climate signal obtained using several relevant methods is probably real and may not have been recognized otherwise.

The CoA approach originally suffered from errors in the Palaeoflora Database regarding NLR climate requirements, but the inclusion of additional taxa and their climate tolerances as reported from other reliable resources have partially remedied this problem (Xia et al., 2009; Jacques et al., 2011; Liu et al., 2011). Nevertheless, Grimm and Denk (2012) have shown that even when corrected, the data produce large ranges of limited use. Recent modifications, such as the BA/MCRT analysis used here (Kotthoff et al., 2014), generally provide tighter intervals and improved resolution.

Furthermore, Wolfe (1979, 1993) noted problems with the physiognomic approaches to climate reconstruction when calibrating warm temperate to subtropical floras of the southeastern United States, possibly due to the lower-than-expected percentage of entire-margined, broad-leaved species. In addition there are relatively few reference sites for this region in the reference database. Although more recent studies have expanded the CLAMP database, subtropical and tropical sites are still under-represented (Spicer et al., 2011) and none of the additions include Gulf of Mexico Coastal Plain floras. It is likely that such improvement to the database will eventually result in greater utility of the CLAMP method in this region, but the significantly lower MAT and precipitation values obtained in this study remain suspect.

Considering the results of all the quantitative analyses presented here, in addition to prior qualitative estimates, independent proxy data, and the relatively young age of the Citronelle Formation flora, the best results were obtained from the LMA and NLR-based approaches. The BA/MCRT results in particular are most compelling. Therefore, the MAT for this region during the late Pliocene (mid-Piacenzian) was likely ~ 18° C compared to the current value of 19.3° C. Based on the CoA and BA/MCRT method results the MAP was approximately 1190–1250 mm, which is drier than the current 1603 mm value. The drier conditions are consistent with the dominance of white pine in the Citronelle flora (Jacobson and Dieffenbacherkrall, 1995), but the slightly lower estimated MAT is unexpected based on abundant independent evidence of global warmth at this time, even at lower latitudes (Haywood et al., 2005). However, the uppermost MAT CoA analysis interval boundary and the upper value of the LMA are 1.5° C and 2.6° C above the current MAT, respectively. Evidence of greater climate variability during this time than previously suggested could also be a factor (Prescott et al., 2014).

Studies of this type are fraught with difficulties, including taphonomic biases, lack of precise stratigraphic control, difficulties in correctly identifying NLRs, and controversies regarding the various climate estimation techniques themselves. Nevertheless, it is important to attempt such analyses in new areas to extend the methods and test them against one another and other independent proxies. The results obtained here are mostly reasonable, especially those of the NLR-based and LMA results, and suggest avenues of future research. In particular, ongoing investigations are uncovering a considerable number of new megafossil and palynological sites in this region ranging from the Eocene to the Pleistocene that promise to put the Citronelle flora in a more complete temporal context and fill many more gaps in our understanding of the Gulf Coast vegetational history.

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