

## **Preliminary investigation of a diverse megafossil floral assemblage from the middle Miocene of southern Mississippi, USA**

**Daniel M. McNair, Debra Z. Stults, Brian Axsmith,  
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### **ABSTRACT**

Our understanding of Miocene floras in eastern North America is hampered by the rarity of megafossil sites. An early report from the middle Miocene Hattiesburg Formation in Mississippi included palms and *Ulmus*. A later report listed *Taxodium*, *Salix*, either *Morus* or *Celtis*, and monocot fragments. The floral assemblage described here was recently recovered from along the Bouie River in southern Mississippi. Ferns are represented by complete *Salvinia* specimens including attached sporocarps, *Woodwardia*, and *Osmunda*. Conifers are represented by branchlets of *Taxodium*. Angiosperms include leaves attributable to the Lauraceae. *Platanus* is known from leaves, stipules, and fruits. Leaflets of *Sambucus* are common. *Cercis* is recognized from leaves with palmate venation and pulvini. Leaves of *Quercus* sections *Lobatae* and *Quercus* have been recovered. The Juglandaceae include fruits of *Juglans* and two species of *Carya*. *Morus*, *Populus*, and *Salix* leaves have been recovered. Of particular biogeographical interest is a seed of *Sargentodoxa*, which is the first record from the southeastern coastal plain of this current Chinese endemic. Monocots include *Cyperus* and two types of palm, including one with armed petioles. The first vegetative fossils of *Lemna* from North America have been identified. Because most of the fossils are related to plants still found in the region today, the climate was probably similar to that of the modern central Gulf Coastal Plain. This flora is now one of the most extensively known in the Neogene of southeastern North America and helps to fill a major gap in our understating of Miocene plant evolution.

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## INTRODUCTION

The Miocene Epoch is poorly represented in the megafossil plant record of the eastern United States, and the few scattered sites that have been described are generally not temporally well constrained. This is unfortunate, as the Miocene is widely considered a critical time in the evolution of modern plant communities, including such events as the rise to ecological dominance of  $C_4$  dominated grasslands (Bouchenak-Khelladi et al., 2014), the extirpation of several “Asian” taxa from North America (Manchester, 1999), and continued post-Eocene climatic deterioration (Graham, 2010). The only substantial site in the northeastern USA is the stratigraphically isolated Brandon Lignite in Vermont of probable early Miocene age (Tiffney, 1994). In the Mid-Atlantic region, a flora from the Brandywine Formation of Maryland was briefly documented (McCartan et al., 1990), but detailed descriptions are still ongoing (Stults et al., 2011). In the southeast, work on sinkhole floras from the late Miocene to early Pliocene of eastern Tennessee are now comparatively well documented (Gong et al., 2010). On the Gulf Coastal Plain, work on the middle Miocene Alum Bluff flora of the Florida Panhandle has documented a small megafossil flora (Corbett, 2004), expanding on earlier work by Berry (1916a).

Within Berry’s (1916a) account of the Alum Bluff paleoflora is a brief description of an assemblage from Hattiesburg, Mississippi, that he asserted was coeval with Alum Bluff, and included a poorly preserved palm (*Sabalites apalachicolensis*) and leaves attributed to *Ulmus*. Another small flora from the Hattiesburg Formation was described from fossils recovered during a groundwater survey (Brown, 1944). The plants were identified by the paleobotanist Roland Brown as probable *Taxodium*, *Salix*, either *Morus* or *Celtis*, and unidentified monocot fragments. None of the plant fossils mentioned in these reports were figured or described in any detail, and subsequent

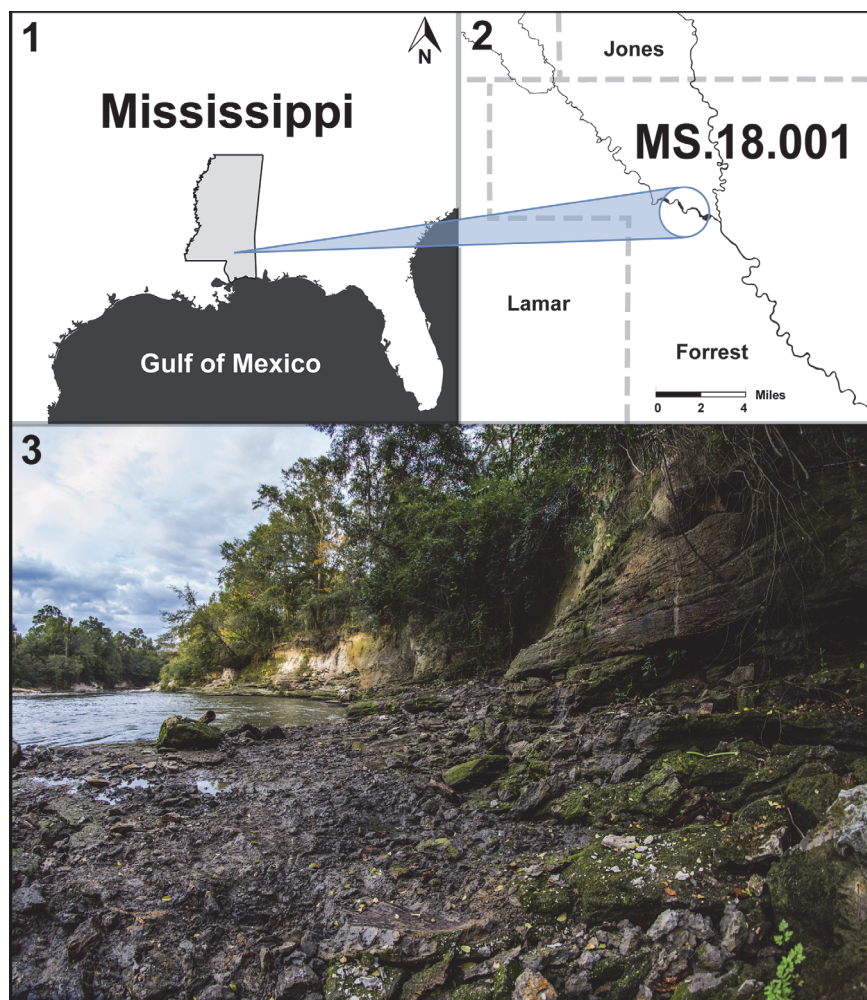
attempts at finding more specimens from these localities have not been successful.

Recent discoveries of fossil plants from previously unexplored exposures of the Hattiesburg Formation along the Bouie River (also commonly known as the Bowie River) in southern Mississippi are providing important information on plant diversity from this otherwise poorly known interval (Figures 1-3). Such sites are critical for expanding our understanding of plant evolution in this biodiverse part of North America. The following account should be considered preliminary, as several of the taxa require additional study and separate detailed publications. However, most components of the flora are presented below in considerable detail.

## GEOLOGICAL SETTING

The central Gulf Coastal Plain, including the Hattiesburg area, contains thick sequences of Neogene sediments, but their delineation has been historically controversial. As noted by Dockery and Thompson (2016), the sequence is mostly a monotonous series of fluvial and deltaic units, resulting in poorly constrained formational boundaries (Figure 3). In addition, extensive surface exposures are uncommon and are poor in diagnostic marine index fossils, making it difficult to place the Hattiesburg plant fossils in a precise stratigraphic and temporal context. Nevertheless, we propose that the site occurs in the uppermost Hattiesburg Formation and is of probable middle Miocene age based on several lines of evidence presented below.

The fossil site (MS. 18.001) occurs along both sides of the Bouie River, where the river makes a hard turn to the north just below the Glendale Avenue bridge on the northern border of the city of Hattiesburg, Mississippi (N 31.34969; W 89.30537) (Figure 2.2). Here, the river cut exposes about seven vertical meters of section along the eastern bank, with lower exposures present to the west (Figure 1.3). The site is attributed to the upper Hattiesburg Formation based on nearby well log data correlated with deeper well logs, which also



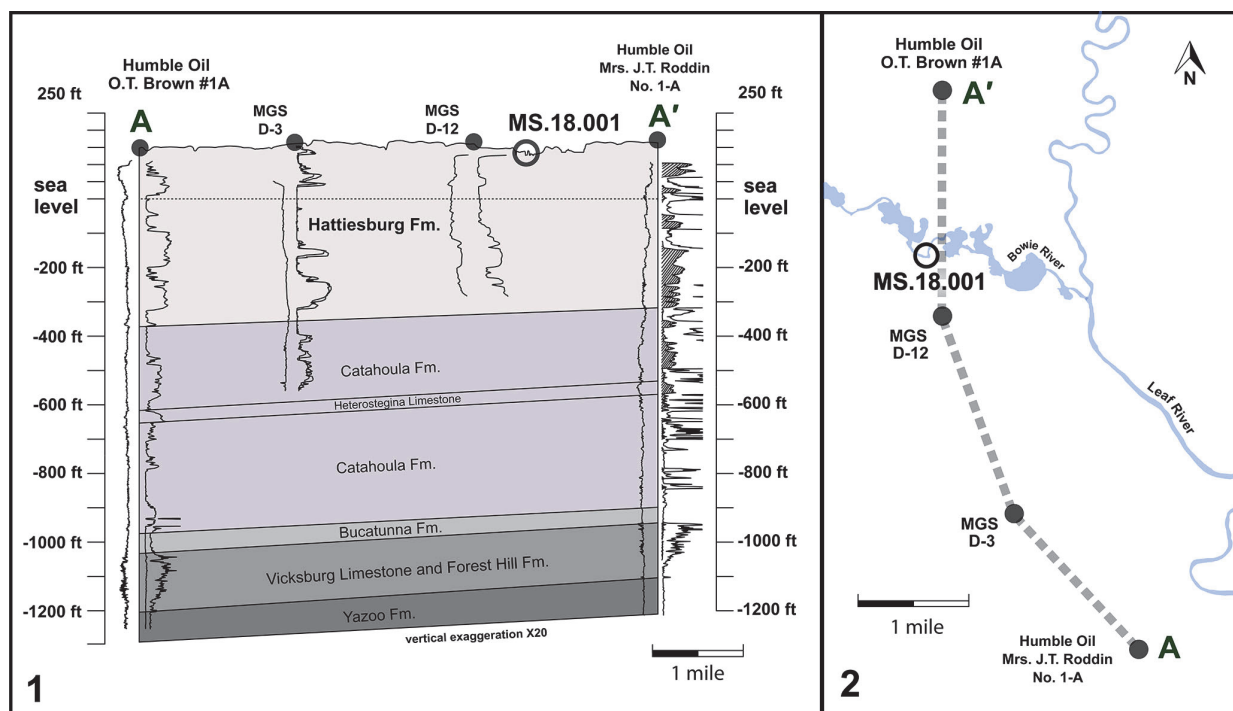
**FIGURE 1.** Maps and photograph of the study site (MS.18.001). **2,** Index maps showing the outline of the state of Mississippi and the location of the site (MS. 18.001). **3,** Field photograph looking north downstream showing the Bouie River cutting through the Hattiesburg Formation.

includes the stratigraphic relationship to underlying units (Figure 2).

The Hattiesburg Formation consists of thick channel sands separated by silty to fine-sandy clays in the middle, alluvial phase of the Grand Gulf Group. This portion of the post-Vicksburg prograding deltaic wedge overlies the Catahoula Formation of late Oligocene to early Miocene age (Foster, 1941) (Figures 2.1, 3). The Bouie River site is typical of the non-marine finer-grained sediments of the Grand Gulf Section. It consists of pyritic, gray-green colored, thinly-bedded to laminated alternating clays, silts, and fine-grained sands. This repetitive sequence is slightly carbonaceous to highly lignitic, with well-preserved fossil leaves and leaf hash along fissile partings and large, imbedded, lignitized logs. The depositional setting is likely an interfluvial over-bank deposit in

the lower distributary portion of a coastal river. The site is projected down-dip to be not far below the gradational contact with the overlying Pascagoula Formation (Figure 3).

A middle Miocene age designation is proposed for the Bouie River site based on correlations of this section to marine equivalents offshore. Also supporting this designation is a sparse collection of vertebrate material reported from other nearby Hattiesburg Formation outcrops. A strongly age-diagnostic example is a *Teleoceras medicornutum* tibia that was found as float in association with a fossil llama proximal phalanx on a Hattiesburg Formation outcrop on the Middle Fork of the Homochitto River near Meadville in Franklin County, Mississippi (Dockery and Thompson, 2016). *Teleoceras medicornutum* is a Barstovian, middle Miocene rhinoceros previously known from



**FIGURE 2.** Structural cross section and stratigraphic position. **1**, Structural cross section data showing the uppermost Oligocene at the top of the *Heterostegina* Limestone. The section above that unit is attributed to the Miocene. **2**, Corresponding map of A to A' well sites close to the study site (MS. 18.001).

the Fleming Formation, Burkeville fauna of the Gulf Coastal Plain of Texas (Prothero and Manning, 1987). Overlying the Hattiesburg Formation in Mississippi is the Pascagoula Formation, which contains the index fossil *Rangia johnsoni*, a late Miocene bivalve mollusk. The Pascagoula Formation also contains a sparse late Miocene vertebrate fauna in Stone County and Amite County, Mississippi, that may be correlative to the better documented Mauvilla Fauna of southern Alabama (Hulbert and Whitmore, 2006).

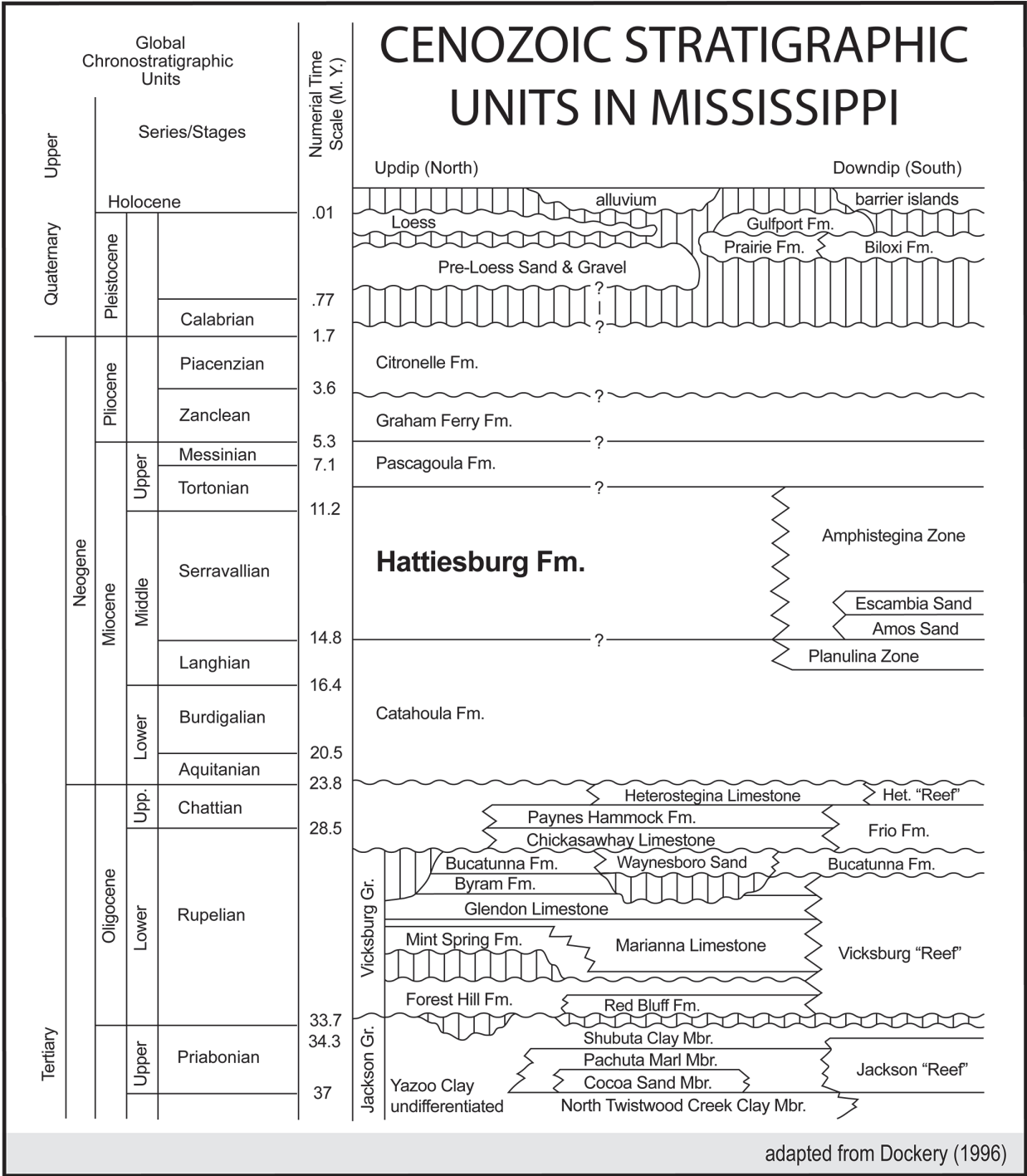
## MATERIALS AND METHODS

All of the described and figured specimens were collected from the Bouie River site in Hattiesburg, Mississippi (N 31.34969; W 89.30537), and are curated in the Mississippi Museum of Natural Science (MMNS) Paleontology Collection in Jackson, Mississippi. The descriptions are primarily based upon the figured specimens and include MMNS PB-82, 83, 84, 85, 86; MMNS 87.1, 87.2; MMNS 88.1, 88.2, 88.3, 88.4, 89, 90, 91, 92, 93, 94, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105.1, 105.2, 106, 107, 108, and 109. Specimen numbers are also listed in the corresponding figure captions.

The fossils are mostly impressions and some compressions recovered by splitting the matrix in which they are contained. A few specimens are represented by relatively uncompressed, three-dimensional seeds and fruits that emerged from the matrix when split. When needed, an assortment of needles and brushes was used to fully expose the plant organs. Fragmentary cuticles, when recoverable from the compressions, were obtained by maceration of the organic matter using various dilute concentrations of sodium hypochlorite. Specimens of wood consistent with the identifications here were examined and will be presented in a future publication.

Larger specimens were photographed on a copy stand using a Nikon D3200 digital SLR camera, with close-ups using a Tokina 100 mm lens. Micrographs were taken with a Zeiss Stemi 2000-C dissecting microscope on a Diagnostic Instruments boom stand, and a Zeiss Axio Imager 2 system. *Salvinia* sporocarp contents were obtained by removing them from the matrix surface with needles followed by mounting on stubs for SEM study using an FEI Quanta 200 environmental scanning electron microscope. The sporocarp contents were not sputter coated.





**FIGURE 3.** Select portion (uppermost Eocene through Holocene) of the stratigraphic units of Mississippi adapted from Dockery (1996). The Hattiesburg Formation is indicated in boldface. Data presented in this paper suggests a slightly older age (middle Miocene) for the upper part of the Hattiesburg Formation (see text for details).

The systematic identifications presented here are based primarily on herbarium reference material, living material, and various literature sources cited in the description section below. Classifications are based on Chase and Reveal (2009),

along with the Angiosperm Phylogeny Group (APG) IV (2016), Smith et al. (2006), and Reveal (1992, 2012). However, for readability and accessibility, taxa are also organized under informal but

widely-used groupings such as “ferns,” “conifers,” and “angiosperms.”

Leaf morphological descriptions are based as far as possible on the Manual of Leaf Architecture (Ellis et al., 2009). Nearly all the fossils are assignable to extant families and genera. In some cases where multiple lines of evidence support it, they are identified to the species level. A “cf.” designation preceding a name indicates that the fossil is a possible representative of the taxon, but more complete or better-preserved material is required for verification.

### SYSTEMATIC PALEOBOTANY

Subclass POLYPODIIDAE Cronquist, Takht. and Zimmerm., 1966

Order OSMUNDALES Bromhead, 1838

Family OSMUNDACEAE Martinov, 1820

Genus OSMUNDA Linnaeus, 1753

*OSMUNDA* sp. indet. cf. *spectabilis* Willdenow, 1810

Figure 4.1-2

**Description.** Two compressions and one impression fossil of sterile pinnules represent *Osmunda*. The pinnule apices are acute. A partial petiolule is visible at the basal end of the most complete pinnule (Figure 4.1). Approximately 10 teeth per cm occur along the thickened margin. From the pinnule mid-veins arise numerous, regularly-placed, closely-spaced lateral veins. Branching of the pinnule lateral veins occurs mostly near the mid-vein, less frequently midway to the margin, culminating in veinlets of the same gauge with parallel courses ending at the margin (Figure 4.2). The average distance between these parallel secondary veins is 332  $\mu$ m.

**Remarks.** The fossil record of the Osmundaceae extends back to the Permian Period (Hewitson, 1962; Tidwell and Ash, 1994), and many fossil examples demonstrate remarkable morphological stasis over hundreds of millions of years (Miller, 1967; Phipps et al. 1998; Vavrek et al., 2006; Bomfleur, 2014). Currently, the family contains four genera: *Leptopteris*, *Osmunda*, *Osmundastrum*, and *Todea* (Metzgar et al., 2008). Within genus *Osmunda* are three subgenera, *Claytosmunda*, *Osmunda*, and *Plenasium*. One character that differentiates subgenus *Osmunda* from *Claytosmunda* and *Plenasium* is the presence bipinnate leaves, a feature recognized when the pinnule is connected to the costa by a slender petiolule. While a direct connection to the costa is not visible in the Hattiesburg Formation fossil, the presence of a partial slender petiolule and smoothly rounded

petiole bases indicates a probable originally bipinnate frond like that of subgenus *Osmunda* species. Four species presently comprise subgenus *Osmunda*: *O. regalis* (European), *O. japonica* and *O. lancea* (southeastern Asia), and *O. spectabilis* (Western Hemisphere). Most authorities now accept that *O. spectabilis* is a separate species and not a variety or subspecies of *O. regalis* (Gray, 1856; Underwood, 1903; Löve and Löve, 1977; Arana and Ponce, 2015). *Osmunda spectabilis* occurs only in the Western Hemisphere, is phylogenetically distinct from the European *O. regalis*, and is contained within the clade including the Japanese species *O. japonica* and *O. lancea* (Metzgar et al., 2008; Arana and Ponce, 2015).

The Hattiesburg Formation fossils indicate affinity with the genus *Osmunda* (Cobb et al., 2005), and there are possible species level features when compared with similar extant forms of subgenus *Osmunda*. The pinnule lateral veins of *O. japonica* and *O. regalis* branch several times; *O. lancea* and *O. spectabilis* branch much less frequently (Hewitson, 1962), in accord with the Hattiesburg fossils. Our observations of living and herbarium material of *O. spectabilis* indicate lateral veins that branch nearer the midvein and exhibit a more uniform parallel course toward the margin (as in the Hattiesburg Formation fossils, and *O. lancea*), and a narrower distance between veinlets (Imaichi and Kato, 1992). Because the fossils occur within the extant range of *O. spectabilis* and considering the extremely long temporal range of many *Osmunda* species, we suggest that it is a representative of that species rather than *O. lancea* or an extinct form. At this point, affinity with *Telmatoblechnum serrulatum* (Blechnaceae) cannot be entirely ruled out due to convergence in leaf architecture. More complete material will be required to resolve the exact affinities of this fern.

Order POLYPODIALES Mett. ex A.B. Frank, 1877

Family BLECHNACEAE Newman, 1844

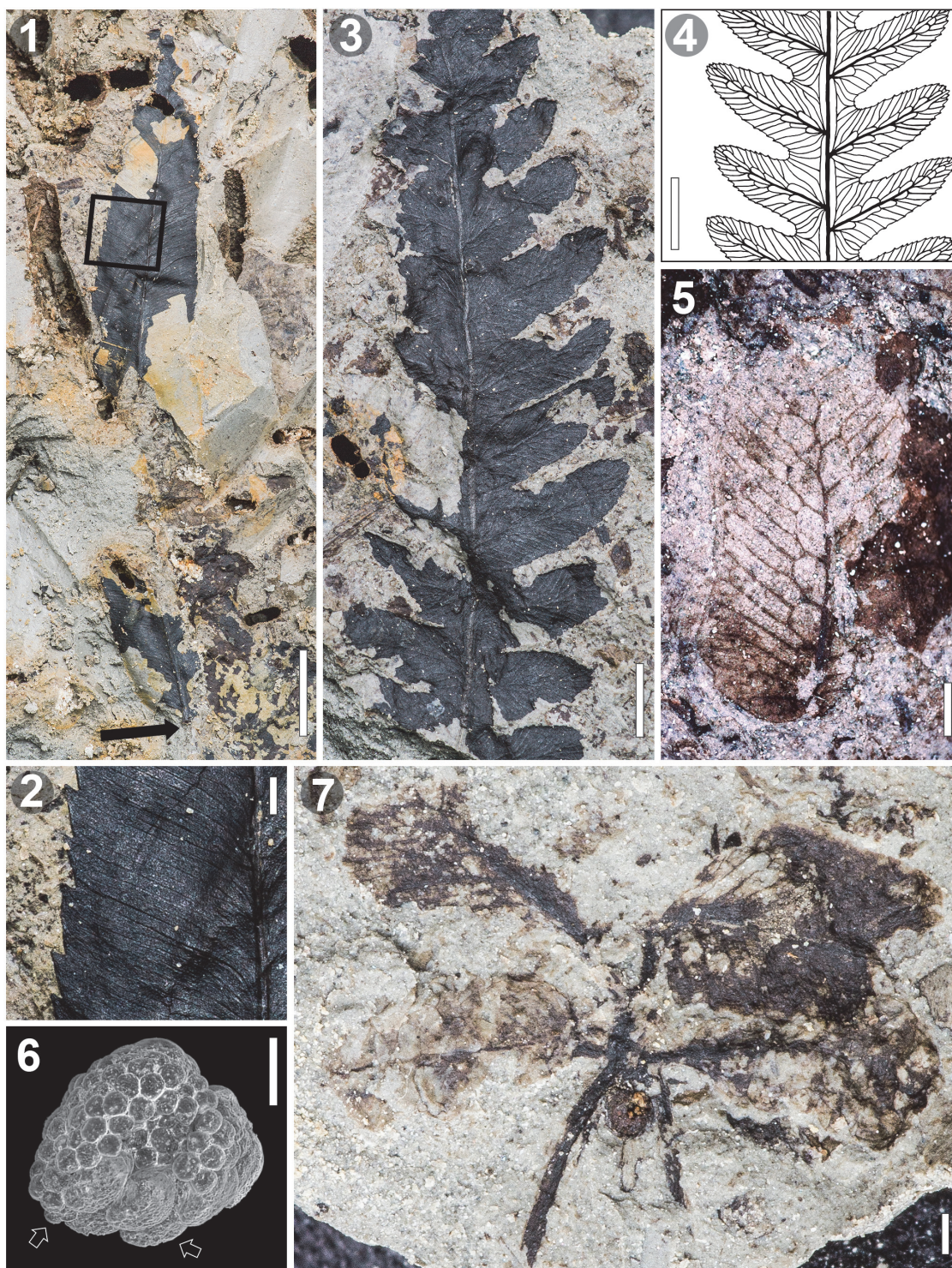
Genus WOODWARDIA Smith, 1793

*Woodwardia* sp. indet. cf. *virginica* (Linnaeus) Smith, 1793

Figure 4.3-4

**Description.** Two specimens of incomplete, sterile, pinnatifid pinnae comparable to *Woodwardia* cf. *virginica* have been recovered. Fronds were at least 5.3 cm long x 2.3 cm wide and 6.0 cm long x 1.3 cm wide. The largest pinnule on the first frond is 1.3 cm x 0.4 cm, and the largest pinnule lobe visible on the second frond is 1.0 cm x 0.2 cm. The pinnule lobes become smaller distally (Figure 4.3). On either side of the pinnule midvein, a secondary





**FIGURE 4.** Representative ferns from families Osmundaceae, Blechnaceae, and Salviniaceae. **1,** *Osmunda* sp. indet. cf. *spectabilis* (MMNS PB-82) with arrow indicating partial petiolule, scale bar equals 1 cm. **2,** Close-up of rectangle indicated in Figure 4.1 showing fairly parallel secondary veins that branch occasionally, scale bar equals 1 mm. **3,** *Woodwardia* sp. indet. cf. *virginica* frond (MMNS PB-83), scale bar equals 5 mm. **4,** Reconstruction of fossil *Woodwardia* venation (from MMNS PB-83), scale bar equals 5 mm. **5,** *Salvinia* sp. leaf showing venation (MMNS PB-84), scale bar equals 1 mm. **6,** *Salvinia* sp. SEM of partial sporocarp contents showing microsporangia (left arrow) and megasporangia (right arrow) (MMNS PB-85), scale bar equals 0.5 mm. **7,** *Salvinia* sp. (MMNS PB-86), entire plant with attached sporocarp (with typical yellow-orange coloration), scale bar equals 1 mm.



vein connects consecutive pinnule lobes. The secondary veins form areoles that parallel both sides of the pinnule midvein. Except for the pinnule lobe midvein, veins within the lobes appear to be of the same gauge. Exmedial veins reach the margin unbranched or fork once before terminating at the margin. Minute teeth occur on the pinnule margin (Figure 4.3-4).

**Remarks.** Fossils of *Woodwardia* (and *Woodwardites*, a name sometimes used for fossil representatives) are common in Cenozoic deposits in Europe, North America, and Asia (Smith, 1938; Collinson, 2001; Pigg et al., 2006). *Woodwardia virginica* has been definitively identified from the Miocene Yakima Canyon locality in Washington based on excellent reproductive and vegetative specimens (Pigg and Rothwell, 2001). Although fragmentary, the fronds from the Hattiesburg Formation are also very similar to those of *W. virginica*. Common features include the overall morphology, and distinctive venation features like the areoles paralleling the pinnule midvein and the basal secondary vein connecting the pinnules. Nevertheless, we employ the “cf.” designation pending the discovery of more complete material. The current distribution of *W. virginica* in North America forms a semi-circular pattern along the southern borders of the Great Lakes (except Lake Superior), running along the Atlantic Coastal Plain (from southern New Brunswick, Canada to the Florida peninsula), and then southwestward along the Gulf of Mexico Coastal Plain to East Texas (Cranfill, 1993+). This is the first suggested occurrence of the genus and species in the fossil record from within its current range.

Family SALVINIACEAE Martinov, 1820

Genus SALVINIA Séguier, 1754

*Salvinia* sp.

Figure 4.5-7

**Description.** Two specimens of nearly complete plants, including two sets of paired sterile leaves, connected filamentous leaves, and attached sporocarps have been found (Figure 4.7). Numerous floating leaves (often still characteristically paired on a rhizome fragment), several submerged filamentous leaves with attached sporocarps with characteristic elongate trichomes, and numerous unattached sporocarps have also been recovered. The floating leaves are obovate or oblong, measuring 8–10 x 6–8 mm, with round or slightly emarginate apices and round or slightly cordate bases (Figure 4.5). The mid-vein does not run an entire course to the apex but branches into looping veinlets. Areoles are present on both sides of the mid-

vein for its entire course. Evenly spaced veinlets arise from these areoles and diverge at approximately 45°, then form long loops that further divide into smaller loops near the margin. Evenly spaced trichome bases are visible, but the typical “egg-beater” trichomes are no longer attached. Also, many of the leaves probably represent the abaxial surface which lacks the trichomes. Filamentous leaves branch into hair-like segments. Internal components of the sporocarps are often orange in color and often contain both megasporangia and microsporangia (Figure 4.6-7).

**Remarks.** These fossils occur frequently with other aquatic plants such as *Lemna* and *Cyperus* described below. They appear most similar in size and overall morphology to *Salvinia minima*, but more study is required to acquire a more complete set of comparative features. Of particular interest is the finding that many of the fossil sporocarps from the Hattiesburg locality contain both megasporangia and microsporangia (mixed) (Figure 4.6). *Salvinia* is widely considered to have sporocarps containing only one of the sporangium types. However, Bierhorst (1971) noted that there is a tendency for some mixed development in the modern forms.

There has been some debate about whether extant *Salvinia* is native to North America. Although it has been treated as native in several floras, the earliest well-documented collection was made from populations in Florida in the 1930s, and its expansion from there has been well documented (Jacono et al., 2001). Nearly complete plants lacking sporocarps were described from the Eocene of Tennessee (Berry, 1925). This, along with the report here, indicates that *Salvinia* was a natural component of the southeastern flora at least from the Eocene to the middle Miocene. Globally, spore records of *Salvinia* are common in the fossil record, but vegetative remains are known from the Upper Cretaceous of Mexico, the Cretaceous/Paleogene of India, the Eocene of France, United States, and China, and the Miocene of Poland and Bohemia/Czech Republic (Collinson, 1991, 1996, 2001; Collinson et al., 2001; Wang et al., 2014).

Subclass PINIDAE Cronquist, Takht. and  
Zimmerm., 1966

Order CUPRESSALES Bromhead 1838

Family CUPRESSACEAE Richard ex Bartling,  
1830

Genus TAXODIUM (Linnaeus) Richard, 1810  
*Taxodium* sp.

Figure 5.1-2



**Description.** Leaves are about 5–18 x 1–1.5 mm, alternately attached on deciduous branchlets (Figure 5.1). Leaf apices are acute. Leaves have a single vascular strand. Stomata are transversely oriented to the primary vein (Figure 5.2).

**Remarks.** Leaf fossils are common at the site, but intact cuticle was very difficult to recover. No cones or cone scales have been found, so we refrain from a species level identification. *Taxodium* was previously reported from the Tallahala Creek Locality of the Hattiesburg Formation, although no figures were provided or mention made of what plant organs were examined (Brown, 1944). Acute leaf apices and perpendicularly orientated stomata separate *Taxodium* from other cupressaceous genera (Farjon, 2005; Mai et al., 2013) and are present in the Bouie River material. *Taxodium* was widespread in Eurasia and North America during the Paleogene and Neogene (Knobloch and Mai, 1986; Aulenback and LePage, 1998; Kunzmann et al., 2009). The distribution of the genus is relictual, currently found only in the southeastern United States (*T. distichum* and *T. ascendens*) and Mexico (*T. mucronatum*) (Kunzmann et al., 2009). In the southeastern Neogene fossil record, it is a common component of the Miocene Brandywine flora of Maryland and the Pliocene Citronelle Formation flora in south Alabama (Stults et al., 2011).

Order LAURALES Perleb, 1826

Family LAURACEAE de Jussieu, 1789

Gen. et sp. indet. cf. *Persea* Miller, 1754

Figure 5.3-7

**Description.** Two entire-margined lauraceous leaves with possible affinities to *Persea* were recovered. One is obovate (7.8 cm x 4.0 cm) (Figure 5.3) and one elliptical (8.6 cm x 3.4 cm). Bases are decurrent in both specimens. The apex is incomplete in the obovate specimen, but obtuse and appears to have been acuminate. The apex in the elliptical specimen is acute, acuminate. Primary venation is pinnate (Figure 5.4, 6). Secondary venation is difficult to categorize—somewhat brochidodromous to somewhat eucamptodromous. Secondary veins are non-arcuate, irregularly spaced, with angles diverging from the primary vein fairly consistently at about 45°. Intersecondaries are few, but when visible appear more obvious toward the apex. The marginal vein is substantial and categorized as a secondary vein. Tertiary venation is irregular reticulate. Fourth and fifth order veins in the obovate specimen are regular reticulate (Figure 5.4). Stomata are paracytic (Figure 5.5). Spherical oil bodies are visible in the mesophyll of the obovate specimen under light

microscopy (Figure 5.7) and under epifluorescence in the elliptical specimen.

**Remarks.** The features of these leaves clearly indicate affinity with the Lauraceae, especially the size and distribution of the oil bodies in the mesophyll (Watson and Dallwitz, 1992+). This feature is comparable to many extant species including *Lindera benzoin*, a common species of sandy riparian habitats of the southeastern United States. The paracytic stomatal complexes are also common for taxa within the Lauraceae (Watson and Dallwitz, 1992+; Christophel et al., 1996) (Figure 5.5). The regular reticulate fourth and fifth order venation is common in many taxa including *Persea*, as are the strong marginal secondary veins and apparent coriaceous texture. Overall, these fossils appear most similar to *Persea*, but until more information is available, we use the “cf.” designation.

Currently, there are about 50 genera and 2500–3000 species of Lauraceae, several genera of which (e.g., *Lindera*, *Litsea*, *Persea*, and *Sassafras*) show the classic disjunction between tropical/subtropical areas in southeastern Asia and North America (Chanderbali et al., 2001). However, *Ocotea* is the most speciose lauraceous genus in the neotropics (Chanderbali et al., 2001). Fossils of the family appear by the mid-Cretaceous, but the Asian/American disjunction of the *Perseae-Lauraeae* clade ensued with late Eocene cooling (Wolfe, 1975; Tiffney, 1985; Zheng, 1983; Drinnan et al., 1990; Eklund and Kvaček, 1998; Chanderbali et al., 2001). *Lindera*, *Persea*, and *Sassafras* have been reported from the Upper Pliocene of South Alabama (Stults and Axsmith, 2015).

Order DIPSICALES Juss. ex Bercht. and J. Presl, 1820

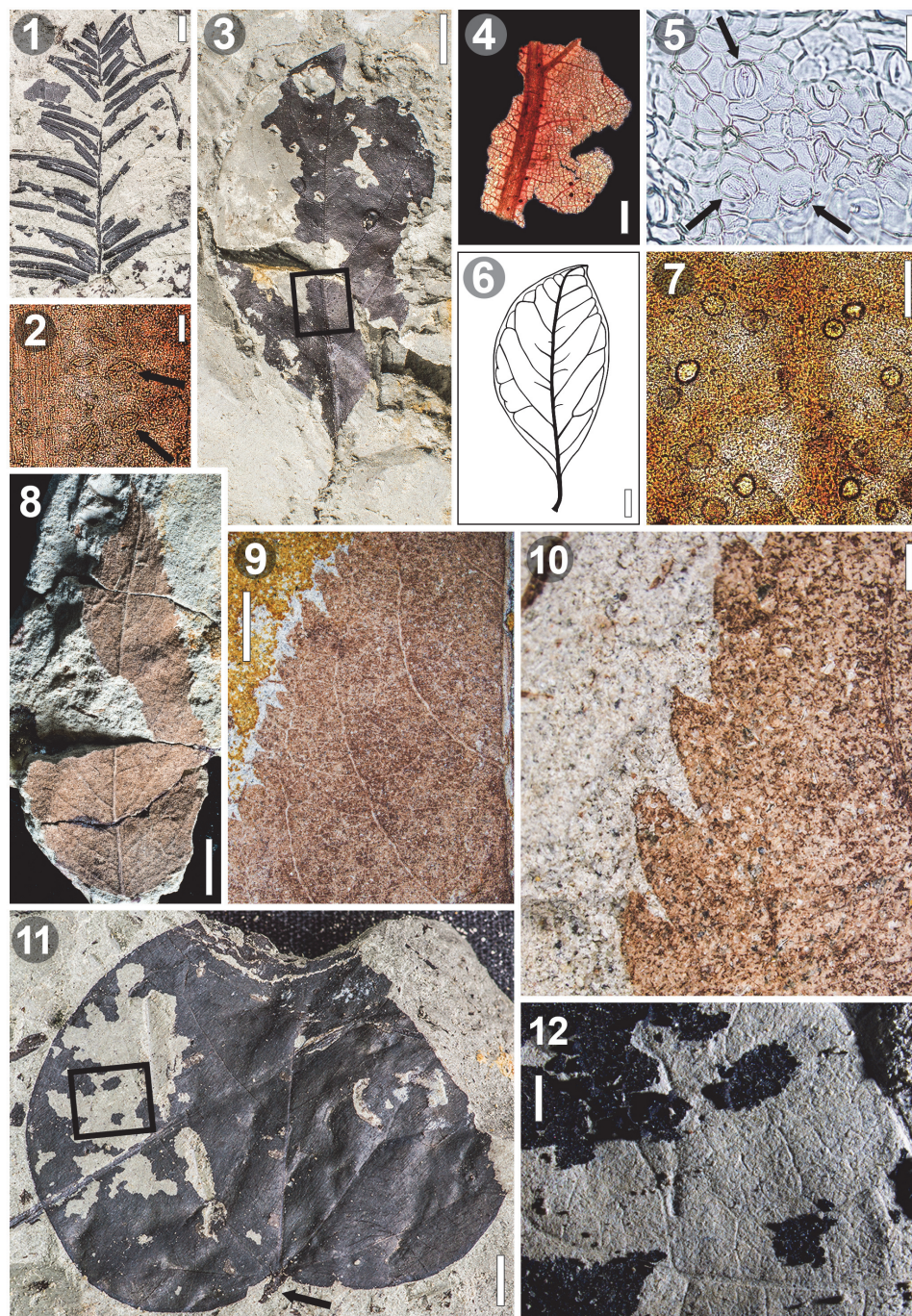
Family ADOXACEAE Meyer, 1839

Genus SAMBUCUS Linnaeus, 1753

*Sambucus* sp.

Figure 5.8-10

**Description.** Leaflets are mostly ovate, although a few are elliptic. Laminar width is generally symmetrical, but slight asymmetry occurs in several leaflets at the petiolule insertion point (a common feature of the leaflets of extant *Sambucus*) (Figure 5.8). Most leaflets are incomplete; however, width ranges of the original leaflets are about 2.0–4.3 cm. The smallest complete leaflet length is 4.3 cm, and larger specimens were greater than 7.2 cm long. Margins are unlobed and serrate (Figure 5.8-9). Leaflet bases are acute and convex. When a petiolule portion is present, the base appears to be decurrent. However, most of the fossil leaflets appear to have been sessile, recognizable by the



**FIGURE 5.** Representatives of gymnosperm family Cupressaceae and angiosperm families Lauraceae, Adoxaceae, and Fabaceae. **1**, *Taxodium* sp. branchlet (MMNS PB-87.1), scale bar equals 5 mm. **2**, *Taxodium* sp. lower cuticle showing stomata (MMNS PB-87.2), scale bar equals 0.05 mm. **3**, Lauraceae gen. et sp. indet. cf. *Persea* sp. nearly complete leaf (MMNS PB-88.1), scale bar equals 1 cm. **4**, Partial lamina extracted and cleared (MMNS PB-88.2) from the same fossil in Figure 5.3 with extraction area indicated by rectangle, scale bar equals 2 mm. **5**, Cuticle from the same fossil as in Figure 5.3 showing paracytic stomatal complexes indicated by arrows (MMNS PB-88.3), scale bar equals 0.05 mm. **6**, Reconstruction of venation features of the fossil in Figure 5.3. **7**, Oil bodies from the same fossil as in Figure 5.3 (MMNS PB-88.4), scale bar equals 2 mm. **8**, *Sambucus* sp. nearly complete leaflet (MMNS PB-89), scale bar 1 cm. **9**, *Sambucus* sp. partial lamina, venation close-up (MMNS PB-90), scale bar equals 5 mm. **10**, *Sambucus* sp. partial lamina, close-up of marginal teeth (MMNS PB-91), scale bar equals 1 mm. **11**, *Cercis* sp. partial leaf with pulvinus indicated with an arrow (MMNS PB-92), scale bar equals 5 mm. **12**, Close-up rectangle in Figure 5.11 showing impressions of higher order venation, scale bar equals 1 mm.

asymmetry at the basal end and lack of a petiolule. Apices are acute and straight to acuminate. Primary vein framework of the leaflets is pinnate. Secondary veins are mostly cladodromous, excurrent, irregularly spaced with inconsistent angles, and conspicuously arcuate. Intersecondaries are rare, and if present, observable only at the basal end. Third order veins are mixed percurrent with inconsistent angles. Fourth order venation is also mixed percurrent. Fifth order veins are sometimes observable, but difficult to characterize. The leaflet margins have one order of relatively large, serrated teeth, although an extraneous tooth is sometimes evident (a feature common in extant *Sambucus*). Teeth are regularly spaced with angular sinuses, straight to concave on the distal side and convex on the proximal side. Tooth apices are simple (more like that of *S. racemosa* rather than *S. canadensis*, which displays a setaceous tooth apex) (Figure 5.10). The number of teeth/cm is also more similar to *S. racemosa*.

**Remarks.** Twenty leaflets are assigned to *Sambucus* sp. making it the most common eudicot taxon in the collection. The genus *Sambucus* includes about 25 species of shrubs, small trees, and herbs distributed mainly in temperate and subtropical regions of the Northern Hemisphere, in both wet and dry soils (Little, 1977; Eriksson and Donoghue, 1997). Seven species occur in North America, three occurring in eastern portions of the continent. *Sambucus canadensis* (considered a subspecies of *S. nigra* by some) occurs mainly in the eastern United States and some areas west of the Mississippi River. *Sambucus racemosa* is widespread in North America but in the southeast is native only in Georgia, North Carolina, Virginia, Tennessee, Kentucky, and Arkansas. *Sambucus ebulus* inhabits only the northeastern portion of North America (Little, 1977; USDA GRIN online database, [www.ars-grin.gov](http://www.ars-grin.gov)).

The fossil record of *Sambucus* is based mostly on endocarps found in the Paleocene through Holocene of Europe, Asia, and North America (see references in table 4 of Huang et al., 2012). Leaves/leaflets have been less reliably recorded, but a North American record of a compound leaf and additional leaflets has been verified for the Eocene of Florissant, Colorado (MacGinitie, 1953; Manchester, 2001). Leaflets of *Sambucus* are easily disassociated from the overall compound leaf, as noted in natural populations of *S. canadensis* in southern Alabama (based mainly on personal observations of an extensive population along the floodplain of Muddy Creek in the Muddy

Creek Management Area of southern Mobile County, Alabama). These fossils are somewhat similar to those described as *Ulmus floridana* by Berry (1916a), which also occur at the Alum Bluff locality in Liberty County, Florida (Corbett, 2004). However, the leaves described here as *Sambucus* have prominent simple teeth. Additionally, the secondary veins are arched and the cladodromous organization appears variable and disorganized compared to secondary venation patterns typically seen in *Ulmus* or *Prunus*. Furthermore, these leaflets are different from *Prunus* leaves in lacking glands on the teeth or leaf base.

Order FABALES Bromhead, 1838

Family FABACEAE Lindley, 1836

Genus CERCIS Linnaeus, 1753

*Cercis* sp.

Figure 5.11-12

**Description.** One compression/impression fossil leaf is broadly ovate measuring 4.6 cm wide, but if assuming symmetry on both sides of mid-vein, the original leaf would have been about 5.1 cm wide (Figure 5.11). The leaf is un-lobed with an entire margin. The base is symmetrical, cordate. Venation is actinodromous consisting of five primary basal veins. Simple agrophic veins are exmedial to the outermost primary veins. One agrophic complex originates with a basal vein; therefore, six total basal veins are observable. Assuming symmetry, a seventh basal vein was probably present on the opposite agrophic complex. Major secondary venation is camptodromous to brochidodromous. Secondary interior veins are present between the major primary veins. Third order veins are mixed percurrent to irregular reticulate. Fourth and fifth order venation patterns are irregular reticulate (Figure 5.12). A 1.5 mm thickening of the petiole near the base is interpreted as a pulvinus (Figure 5.11).

**Remarks.** Observations of herbarium specimens of the four extant North American species of *Cercis* (*C. canadensis*, *C. mexicana*, *C. reniformis*, *C. occidentalis*) primarily show seven primary veins rather than five (as we describe for the Hattiesburg leaf fossil). However, examination of *C. canadensis* specimens in the USAM and USMS herbaria demonstrate that five to nine basal veins can be recognized, the determination of which to consider primary veins vs. non-primary basal veins possibly being dependent upon the size of the specimen. There are modern species in eastern Asia that appear predominately 5-veined (e.g., *C. racemosa*, Chen et al., 2010). The well-described fossil North American Eocene species *C. parvifolia* (Florissant of Colorado) also usually shows five primaries.



Apparently, this leaf venation character does not allow differentiation among the species of *Cercis* (Jia and Manchester, 2014). Agrophic veins appear in some herbarium specimens of *C. canadensis* but not in others. The only record of *Cercis* from eastern North America is identified as the extant species *C. canadensis* from the Pleistocene of North Carolina (Berry, 1926). The Bouie River site *Cercis* is significant in that it represents the oldest leaf fossil of the genus in eastern North America.

Order FAGALES Engl., 1892  
Family FAGACEAE Dumortier, 1829  
Genus QUERCUS Linnaeus, 1753  
Section *Lobatae* Loudon, 1830  
*Quercus* sp. 1  
Figure 6.1

**Description.** Three *Quercus* section *Lobatae* compression/impression leaf fossils are identified. Lobes are shallow. Bristle tips approximately 2 mm long occur on the lobe apices. Primary venation is pinnate. Some secondaries end in the lobe bristle tip, other secondaries are brochidodromous. Intersecondaries are present. Third order, fourth order, and fifth order veins are irregular reticulate. A fimbrial vein is present (Figure 6.1).

Section *Quercus* Hickel and Camus in Camus, 1938  
*Quercus* sp. 2  
Figure 6.2-3

**Description.** Leaves are obovate, ovate, or elliptical. Most have shallow lobes, but some have more definitive lobes. One mostly complete specimen is 6.6 cm long x 2.4 cm wide. Primary venation is pinnate. Some secondary veins terminate at the margin of lobe apex, other secondaries are brochidodromous or cladodromous. Secondary veins diverge at approximately 45°. Intersecondaries are present. Third and fourth order venation is irregular, reticulate. The petiole of one the attached leaves is 1 cm long. Several specimens have rounded lobes (Figure 6.3), while a few have pointed lobes with no evidence of bristles (Figure 6.2), so it appears that there may be at least two species of section *Quercus* in the collection.

**Remarks.** Six *Quercus* section *Quercus* leaf fossils are identified. Four are compression fossils (Figure 6.2), including one slab with two young leaves still attached to the stem (Figure 6.3). Two are impressions, one with a counterpart. Comparison of these leaves with *Quercus* species from the USAM and USMS herbaria suggest the possibility that oaks related to *Quercus alba* (those with rounded lobes) and *Quercus lyrata* (those with pointed lobes, but

no bristles) may be a part of this flora, but this is uncertain based on the available material. More leaf specimens and some reproductive structures will be needed for confident identification.

*Quercus* is widely distributed throughout the Northern Hemisphere, with its greatest diversity in the southeastern United States, the highlands of Mexico, montane subtropical Eurasia, and East Asia (Nixon, 1993, 1997). Presence or absence of lobes, in conjunction with the presence or absence of bristles are leaf characters useful in subgenus determination (Daghlian and Crepet, 1983). *Quercus* section *Lobatae* species have stiff bristles at the end of lobes/teeth, or if entire, at the end of the leaf apex (Daghlian and Crepet, 1983). *Quercus* section *Quercus* species (if lobed) usually have lobes without bristles, although the ends of the lobes may be pointed and mucronate (Nixon and Muller, 1997), as is the case with *Q. lyrata*. *Quercus* section *Protobalanus* usually has spiny teeth without bristles and is found mainly in the western U.S. (Manos, 1997). *Quercus* fruit and leaf fossils have been identified in North America from the middle Eocene of the West, while *Quercus* leaf and fruit records from the eastern portion of the continent occur in the late Miocene Brandywine flora and the late Pliocene Citronelle Formation flora (MacGinitie, 1941; Wolfe, 1973; Crepet and Daghlian, 1980; McCartan et al., 1990; Manchester, 1994; Stults, 2003). Records of section *Lobatae* fossil leaves have been recovered from the Oligocene of eastern Texas and from the Citronelle Formation of Alabama (Daghlian and Crepet, 1983; Stults, 2003). The Hattiesburg Formation fossils help to fill in a partial gap in the Miocene North American record of *Quercus* for both sections *Lobatae* and *Quercus*.

Family JUGLANDACEAE de Candolle in Perleb, 1818  
Genus JUGLANS Linnaeus, 1753  
Section RHYSOCARYON Dode, 1909a, 1909b  
*Juglans* sp.  
Figure 6.4

**Description.** Globose nut 3.1 cm long x 2.1 cm wide, but wider equatorially than axially. The nutshell is longitudinally grooved, and the surfaces between the grooves are slightly rugose to smooth (Figure 6.4 top). The nutshell is thick, measuring 3 mm at the equatorial section. The two-lobed kernel is preserved and visible within the nutshell (Figure 6.4 bottom).

**Remarks.** *Juglans* is divided into four sections by Manning (1978). The most recent molecular phylogeny by Aradhya et al. (2005) indicates that





**FIGURE 6.** Representatives of angiosperm families Fagaceae, Juglandaceae, Lardizabalaceae, and Moraceae. **1**, *Quercus* section *Lobatae* leaf (MMNS PB-93), scale bar equals 5 mm. **2**, *Quercus* section *Quercus* leaf (MMNS PB-94), scale bar equals 5 mm. **3**, Two *Quercus* section *Quercus* leaves attached to stem (MMNS PB-95), scale bar equals 5 mm. **4**, *Juglans* sp. complete nut with preserved kernel visible inside (MMNS PB-96), scale bar equals 5 mm. **5**, *Carya* sp. 1 complete nut (MMNS PB-98), scale bar equals 5 mm. **6**, *Carya* sp. 2 complete nut (MMNS PB-97), scale bar equals 5 mm. **7**, *Sargentodoxa* sp. complete seed from two angles (MMNS PB-99), scale bar equals 5 mm. **8**, *Morus* sp. nearly complete leaf (MMNS PB-100), scale bar equals 5 mm.

these sections are mostly monophyletic. However, section *Trachycaryon*, represented by one species (*Juglans cinerea*), is nested within section *Rhysocaryon*, which contains all of the New World *Juglans*. Aradhyia et al. (2005) also found little resolution among *Rhysocaryon* species, even though the clade as a whole was well-supported. Our material shows typical features of section *Rhysocaryon*, but its fewer grooves and smooth,

non-warty between-groove ridges are more like *Juglans major* or similar species extant in the western U.S. than to the extant eastern species *Juglans nigra*. There is no evidence for abrasion or long transport, suggesting that this is a real feature and not a taphonomic artifact. There is also evidence for deep ridges in the shell cross-section (Figure 6.4 top). The fossil is also dissimilar in these features to *Juglans cinerea*, whose distribution is

mainly east of the Mississippi River, but not reaching the Gulf of Mexico Coastal Plain. The precise relationships of this fossil will be considered in more detail in a forthcoming study. *Juglans* fruits have occasionally been found in western North American deposits dating back to the Eocene (Manchester, 1994). The fossils described here represent the first fossil record of *Juglans* fruit from eastern North America.

Genus *CARYA* Nuttall, 1818  
Section APOCARYA de Candolle, 1864  
*Carya* sp. 1 and 2  
Figures 6.5-6

**Description.** *Carya* sp. 1 fruit is longer and thinner, measuring 2.7 x 1.1 cm. The husk is four-valvate, but the sutures are more obviously flanged than in *Carya* sp. 2. The husk is also much thinner at approximately 0.51 mm thick. *Carya* sp. 2 fruit is oblong, measuring 2.0 x 1.5 cm. The husk is four-valvate, has slightly flanged sutures, and is 1.04 mm thick. The nutshell shows the quadrangular shape corresponding to the lines of dehiscence of the husk (Manchester, 1987).

**Remarks.** Fossil evidence suggests *Carya* evolved in North America at the end of the Cretaceous, approximately 67 Ma (Zhang et al., 2013). Two sections of the genus are recognized. This divergence apparently occurred 22 Ma, with one section corresponding to the species in East Asia and the other to those of eastern North America (Zhang et al., 2013). The current center of diversity for *Carya* is eastern North America (Thompson et al., 1999). However, until recently, the majority of North American *Carya* megafossils were identified from western localities (as early as the Eocene), where the genus no longer exists (Manchester, 1987, 1999; Zhang et al. 2013). The contemporary center of diversity for *Carya* is now producing a much-improved fossil record, with megafossils identified from the late Miocene Brandywine locality (northern Virginia), the Miocene-Pliocene Gray Fossil site (eastern Tennessee), and the Citronelle Formation (southern Alabama) (Berry, 1916b; McCartan et al., 1990; Huang et al. 2014; Stults and Axsmith, 2015). The new Miocene records from the Hattiesburg Formation described here help fill a Miocene gap for the biogeography of *Carya*. So far, no leaves of *Carya* have been recovered from the Bouie River site, but pollen is common and will be described in a forthcoming publication.

Order RANUNCULALES Dumortier, 1829  
Family LARDIZABALACEAE Brown, 1821  
Genus SARGENTODOXA Rehder and Wilson,

1913  
*Sargentodoxa* sp.  
Figure 6.7

**Description.** A single globose seed 6 mm long with a truncate apex and round base has been found. Diagnostic features include a smooth surface, thick seed coat (up to about 300  $\mu$ m) (Figure 6.7 top), a prominent hilar rim, and a central micropyle (Figure 6.7 bottom).

**Remarks.** *Sargentodoxa* is represented by a single species of vine (*S. cuneata*) found in parts of China, Laos, and Vietnam. It is recognizable by its distinctively smooth, shiny globose seed coat and prominent apical truncation (Tiffney, 1993). A review of the fossil record of the genus by Manchester et al. (2009) included seeds from the middle Eocene of Oregon, the late Eocene to late Oligocene of northwest Saxony, the early Miocene of Vermont, the middle Miocene of Germany, the uppermost Miocene-Lower Pliocene of Alsace, and the Pliocene of Italy. There is also a brief mention of *Sargentodoxa* seeds from the latest Miocene-earliest Pliocene Gray Fossil site in northeastern Tennessee (Gong et al., 2010). The Hattiesburg Formation seed expands the fossil record of the genus to the Gulf Coastal Plain of North America during the middle Miocene.

Order ROSALES Bercht. and J. Presl, 1820  
Family MORACEAE Gaudichaud-Beaupré, 1835  
Genus MORUS Linnaeus, 1753  
*Morus* sp.  
Figure 6.8

**Description.** The largest specimen is 4.5 cm long x 4.0 cm wide with three lobes; a smaller specimen is 4.2 cm long x 3.1 cm wide and not lobed. Leaf attachment is petiolate, a 0.8 cm petiole present on the smaller specimen. Leaf margins are toothed. Base angles are obtuse, base shape is asymmetrical in the large specimen, convex in the smaller fossils. Primary venation is palmate with three primary veins. Simple agrophic veins are present. Costal secondary veins are semicraspedodromous. Third order veins are usually straight percurrent or sinuous percurrent, but occasionally alternate percurrent. Fourth and fifth order venation is regular, reticulate. Teeth are regularly spaced, convex distally and proximally, approximately three teeth per centimeter, the principal tooth vein terminating at the non-glandular apex (Figure 6.8).

**Remarks.** *Morus* consists of 10–13 species. Four of these species (*M. celtidifolia*, *M. insignis*, *M. microphylla*, and *M. rubra*) are native to North America, but only *M. rubra* is native to eastern

North America (Nepal and Ferguson, 2012). *Morus celtidifolia* and *M. microphylla* are sister taxa to *M. rubra*, all three being sister to the Asian species of *Morus* (Nepal and Ferguson, 2012). Two previously published records for *Morus* are from the Alaskan Cenozoic and the New Jersey Pleistocene (Hollick, 1892; Keller et al., 1961).

Glen Brown (1944) sent specimens of Hattiesburg Formation plant fossils to paleobotanist Roland Brown who identified some as “*Morus* or *Celtis*.” Assuming our fossils are similar, we suggest that our material represents *Morus* rather than *Celtis* based on the following observations. Some *Celtis* leaves have similar venation to *Morus* (up to fourth and fifth orders), but *Celtis* leaves are more elongate with less regularly spaced teeth. To support this quantitatively, we performed a small study of L:W ratios between the two genera based on specimens in the USAM herbarium. Using 21 specimens for *Celtis* (which included *C. laevigata*, *C. occidentalis*, and *C. tenuifolia*), one mature leaf per sheet was selected that exhibited the least difference between length and width measures (i.e., least L:W ratio). Twenty specimens of *Morus* (including *M. alba*, *M. nigra*, and *M. rubra*) that showed the largest difference between length and width (e.g., largest L:W ratio) were measured. The mean L:W ratio for *Celtis* using specimens with the least L:W ratios was 2.2:1, whereas the mean L:W ratio for *Morus* using specimens with the largest L:W ratios was 1.6:1, showing a 40% difference even when using specimens biased to show as much overlap as possible. Another noteworthy difference between *Celtis* and *Morus* leaves is the lobation. *Morus* is typically lobed, whereas *Celtis* leaves are rarely lobed (Godfrey, 1988). The broad teeth that are convex both proximally and distally on the fossils are also more characteristic of *Morus* than *Celtis*. The circumscription of the family Moraceae currently includes 37 genera (Datwyler and Weiblen, 2004). Of these, only leaves of *Broussonetia*, which is currently native to Southeast Asia, has leaves that are similar to *Morus*, but with very hairy abaxial surfaces. However, unless reproductive material becomes available, *Morus* is most likely as the genus is present today in the same region.

Order PROTEALES Dumort., 1829  
Family PLATANACEAE Lestiboudois, 1826  
Genus PLATANUS Linnaeus, 1753  
*Platanus* sp.

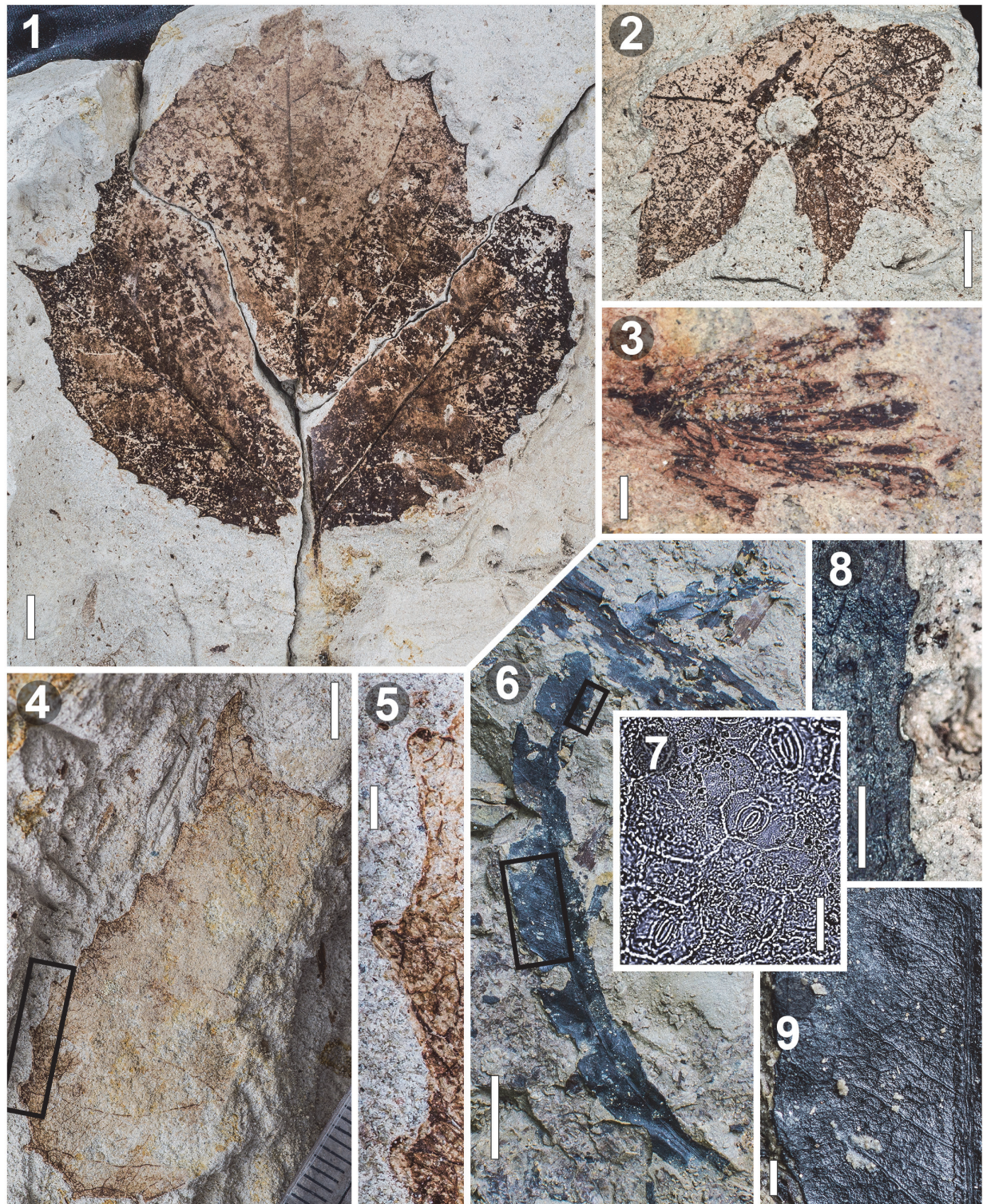
Figure 7.1-3

**Description.** Six *Platanus* compression leaf fossils (two complete and four partial specimens), one

partial fruiting head, and three foliose stipules are identified. The largest leaf specimen is 20.0 cm long x 20.5 cm wide (including a 2.6 cm petiole). Unfortunately, in this largest specimen, a small portion near the base is overlain by another leaf fossil masking the complete primary venation. A mostly complete smaller specimen 12.0 cm long x 13.0 cm wide, along with a fragmentary specimen (with a 1.7 cm petiole) provide evidence for the palinactinodromous primary venation typical of the genus (Figure 7.1). Margins are serrate/dentate with at least five lobes visible on the largest specimen; three large lobes and two shallow lobes are identifiable on the smaller complete specimen. Length/width ratios are approximately 1:1. Leaf bases are either obtuse/rounded or lobate, apices are acute. Compound agrophic veins are evident. Costal second order veins are craspedodromous, third order veins between costal secondaries are a percurrent mixture (straight, sinuous, alternate percurrent). Fourth order veins are irregular reticulate and more difficult to pinpoint than the fine meshwork of the fifth order veins, which are regular reticulate. Margins have simple teeth of one order, even though variable in size (Ellis et al., 2009). Rarely a small, secondary tooth is present. Teeth occur 1–3 per cm, smaller teeth are regularly spaced, while larger teeth are more often irregularly spaced. Sinuses between the teeth are rounded. Teeth are concave/straight both distally and proximally. Two mostly complete stipules with evidence of five pointed lobes and a few teeth between lobes, and one incomplete stipule showing three lobes and no teeth are recognized (Figure 7.2). Of the more complete stipule specimens, one measures 3.5 cm at its widest while the other measures 2.7 cm at its widest point. The larger stipule base displays the broad attachment that would have encircled the petiole. The partial fruiting head measures 1.9 cm; eight achenes are visible, and one achene shows a persistent style that is about 9 mm long x 1 mm wide. Hairs of the pappus are attached to the achene bases (Figure 7.3)

**Remarks.** The fossil record of *Platanus* fruits and leaves begins in the Paleocene of eastern Russia (Maslova, 1996; Manchester, 1999). Miocene records occur in western North America in the Clarkia and Succor Creek floras (Smiley and Rember, 1985; Fields, 1996). Probable fossils of *P. occidentalis* have been reported from the late Miocene Brandywine flora of Maryland, and definite *P. occidentalis* fossils have been identified from the Pliocene Citronelle Formation (McCartan et al., 1990; Stults and Axsmith, 2015). Of the three (or four)





**FIGURE 7.** Representatives of angiosperm families Platanaceae and Salicaceae. **1,** *Platanus* sp. nearly complete leaf (MMNS PB-101), scale bar equals 1 cm. **2,** *Platanus* sp. stipule (MMNS PB-102), scale bar equals 5 mm. **3,** *Platanus* sp. fruit section (MMNS PB-103), scale bar equals 1 mm. **4,** *Populus* sp. indet. cf. *deltoides* partial leaf (MMNS PB-104), scale bar equals 5 mm. **5,** Close-up of rectangle in Figure 7.4 showing teeth, scale bar equals 1 mm. **6,** *Salix* sp. partial lamina (MMNS PB-105.1), scale bar equals 1 cm. **7,** Lower cuticle fragment of the same fossil (MMNS PB-105.2), scale bar equals 0.02 mm. **8,** Close-up of Figure 7.6 (smaller) rectangle showing teeth, scale bar equals 1 mm. **9,** Close-up of Figure 7.6 (larger) rectangle showing venation, scale bar equals 1 mm.



species of *Platanus* currently found in North America, *P. racemosa* and *P. wrightii* (or possibly *P. racemosa* var. *wrightii*) occur in western regions, while *P. occidentalis* has a wide distribution along streams and rivers in eastern North America (Godfrey, 1988). The Mississippi fossils described here are very similar to *P. occidentalis* and occur within its current range; however, we refrain from a species level identification at this time based on their age and the low levels of morphological differentiation of most modern forms.

Order MALPIGHIALES Juss. ex Bercht. and J.  
Presl, 1820

Family SALICACEAE Mirbel, 1815

Genus *POPULUS* Linnaeus, 1753

*Populus* sp. indet. cf. *deltoides* Bartram ex  
Marshall, 1785

Figure 7.4-5

**Description.** The smaller leaves range from 2.6–4.1 cm. long x 3.4–3.6 cm. wide. One of the larger leaves is 6.5 cm long. The other larger leaf had an estimated width of 6.8 cm. The overall shape is ovate, and the margins are toothed. Four leaves have a truncate base, while one appears to be slightly cordate. Apices are acuminate, one extending into an elongated tip (Figure 7.4). Primary venation is pinnate. Compound agrophic veins are visible in two of the better-preserved smaller leaves. Second order venation is semi-craspedodromous, third order veins are mixed percurrent, fourth and fifth order venation is irregular reticulate. One order of regularly-spaced teeth is present, approximately 3–5 per cm, with distal flanks concave, straight, or convex and proximal flanks convex or straight. Several teeth are retroflexed. Salicoid teeth are visible on several specimens (Hickey and Wolfe, 1975; Wilkinson, 2007). Tooth sinuses are angular or rounded (Figure 7.5).

**Remarks.** The fossil record of *Populus* begins in North America in the late Paleocene and the genus spreads widely during the Eocene (Eckenwalder, 1980; Manchester et al., 2006). *Populus* species currently native to wet lowlands in the southeastern United States are *P. deltoides*, with its very wide, almost continent-wide distribution, and *P. heterophylla*, with a spottier distribution from parts of the United States east of the Mississippi River (Godfrey, 1988). *Populus deltoides* has a Pliocene fossil record from the Citronelle Formation of southern Alabama (Stults and Axsmith, 2011). *Populus heterophylla* leaves are distinct from those of *P. deltoides* based upon their lack of acuminate apices (Godfrey, 1988).

Three small leaves, two mostly complete and one partial, and two larger partial leaves were recovered from the Hattiesburg Formation. The petiole is evident on two of the small leaves. The specimens have acuminate apices, suggesting that *P. deltoides* or a possible precursor species existed along the Gulf of Mexico Coast by at least the middle Miocene.

Genus *SALIX* Linnaeus, 1753

*Salix* sp.

Figure 7.6-9

**Description.** One almost complete linear leaf measures 8.0 cm long x 0.8 cm wide (the original L:W ratio would have been >10:1 (Figure 7.6). Neither base nor apex are present. Although typified as linear (Ellis et al., 2009), the preserved basal portion of the leaf is wider than the apical portion. The abaxial cuticle obtained is fragmentary and not well preserved but contains paracytic stomata about 20 µm long and regular epidermal cells with straight to somewhat curved cell walls (Figure 7.7). These are common epidermal features among extant *Salix* species (Chen et al., 2008). One order of small teeth (6–7 per cm) is present (Figure 7.8). Tooth shapes are distally straight or concave and proximally straight or convex. Opaque tissue possibly representing a salicoid tooth is present on the apex. Between-teeth sinuses are angular or rounded. First order venation is pinnate. Second order venation is semicraspedodromous and some secondaries are arcuate. Third order venation is irregular reticulate (Figure 7.9).

**Remarks.** Teeth in *Salix* are variable, with some species maintaining a large spheroidal gland at the tooth apex while others lack a gland or the gland withers or abscises with age (Reinke, 1876; Weber, 1978; Wilkinson, 2007; Beuchler, 2014). We also note that herbarium samples of *Salix* may not have completely intact tooth apices potentially due to degradation during storage. We suggest that prior to fossilization or to the degrading processes before/during fossilization the tooth apices on the original leaf were probably spherulate. Of the approximately 450 species of *Salix* worldwide, 113 species occur in North America. Those found in the southeastern United States including southern Mississippi (Kartesz, 2015), Alabama, Florida, and Georgia (Godfrey, 1988) are *S. caroliniana*, *S. eriocephala*, *S. floridana*, *S. humilis*, *S. interior*, and *S. nigra*. Based on leaf dimensions, the specimen from the Hattiesburg Formation is most similar to extant *S. caroliniana*, *S. eriocephala*, *S. interior*, or *S. nigra*. Reproductive and vegetative fossils of *Salix* have been found in Eocene deposits of Wyom-

ming, North Dakota, Colorado, and Utah, Oligocene and Miocene deposits of Alaska, and Miocene deposits in Oregon (Hollick, 1936; MacGinitie, 1969; Hickey, 1977; Wing 1981; Collinson 1992; Fields, 1996). This is the first Miocene macrofossil record from the eastern portion of the continent. A Pliocene occurrence has been recorded from the Citronelle Formation of southern Alabama (Stults and Axsmith, 2015).

Order ALISMATALES R. Br. ex Bercht. and J. Presl, 1820

Family ARACEAE de Jussieu, 1789

Genus *LEMNA* Linnaeus, 1753

*Lemna* sp.

Figure 8.1-2

**Description.** Description of the Hattiesburg *Lemna* fossils follows traditional terminology for the genus whereby the leaf-like organs are referred to as fronds. However, we recognize that this term does not indicate homology to the fronds of ferns. All the recovered *Lemna* fossils from the Hattiesburg Formation contain five fronds and measure approximately 4.5–5.0 mm at their widest point (Figure 8.1). Sunken meristematic zones are observable, but as only one meristematic zone is evident per fossil, it would appear that four of the fronds are daughters. The daughter fronds of each fossil vary in size, some apparently as large as the original mother frond. No roots are visible, but this is likely an artifact of preservation. One impression fossil is particularly informative in showing one primary vein on opposite fronds, the cellular alignment of which is comparable to modern *Lemna* specimens (Figure 8.2).

**Remarks.** The entire plant body of *Lemna* species is highly modified, and true leaves do not exist for this group in any straightforward way and are referred to as fronds (Landolt et al., 1986; Bell, 1991; Bogner, 2009). The flattened plant body of *Lemna* consist of leaf lamina on the outermost portion, a combination of stem and leaf lamina proximally, and a proximal sunken meristematic zone from whence daughter fronds originate.

Three complete specimens and one partial specimen represent *Lemna* from the Hattiesburg Formation. They occur in direct association with many fossils of another floating aquatic plant, *Salvinia* and many examples of a wetland *Cyperus* sp. The report here of relatively complete vegetative fossils of *Lemna* is particularly significant, as previous records are known only from relatively poorly-preserved fossils from the early Miocene of the Czech Republic (the Bilina Mine) by Kvaček (2003). Seed records are known from the Oligo-

cene through Quaternary of Eurasia (Dorofeev, 1963). Vegetative remains of other Araceae taxa distantly related to *Lemna* consist of *Limnobiophyllum* from the Upper Cretaceous and Lower Paleogene of North America and the Miocene Bilina Mine locality in the Czech Republic and *Cobbania* from the Late Cretaceous of North America and East Asia (Stockey et al., 2007). *Limnobiophyllum* and *Lemna* coexisted during the Oligocene and Miocene, but only *Lemna* survives to the present day (Rothwell et al., 2004; Bogner, 2009).

Order ARECALES Bromhead, 1840

Family ARECACEAE Berchtold and Presl, 1820

Fossil palmate genus PALMACITES Brongniart, 1822 (emend. Read and Hickey, 1972)

Figure 8.3-4

**Description.** The leaf blade is fan-shaped (coryphoid) and induplicate. The leaf blade is palmate, as the costa does not extend into the leaf blade, rather the leaf segments arise at the petiole apex and extend toward the leaf apex. All palmate leaf segments display a prominent mid-rib. Up to two orders of parallel veins on either side of mid-rib are observable on some specimens as preservation permits. Maximum measurable petiole width is 1.6 cm. Some palmate specimens have attached petioles with well-spaced recurved spines (Figure 8.4).

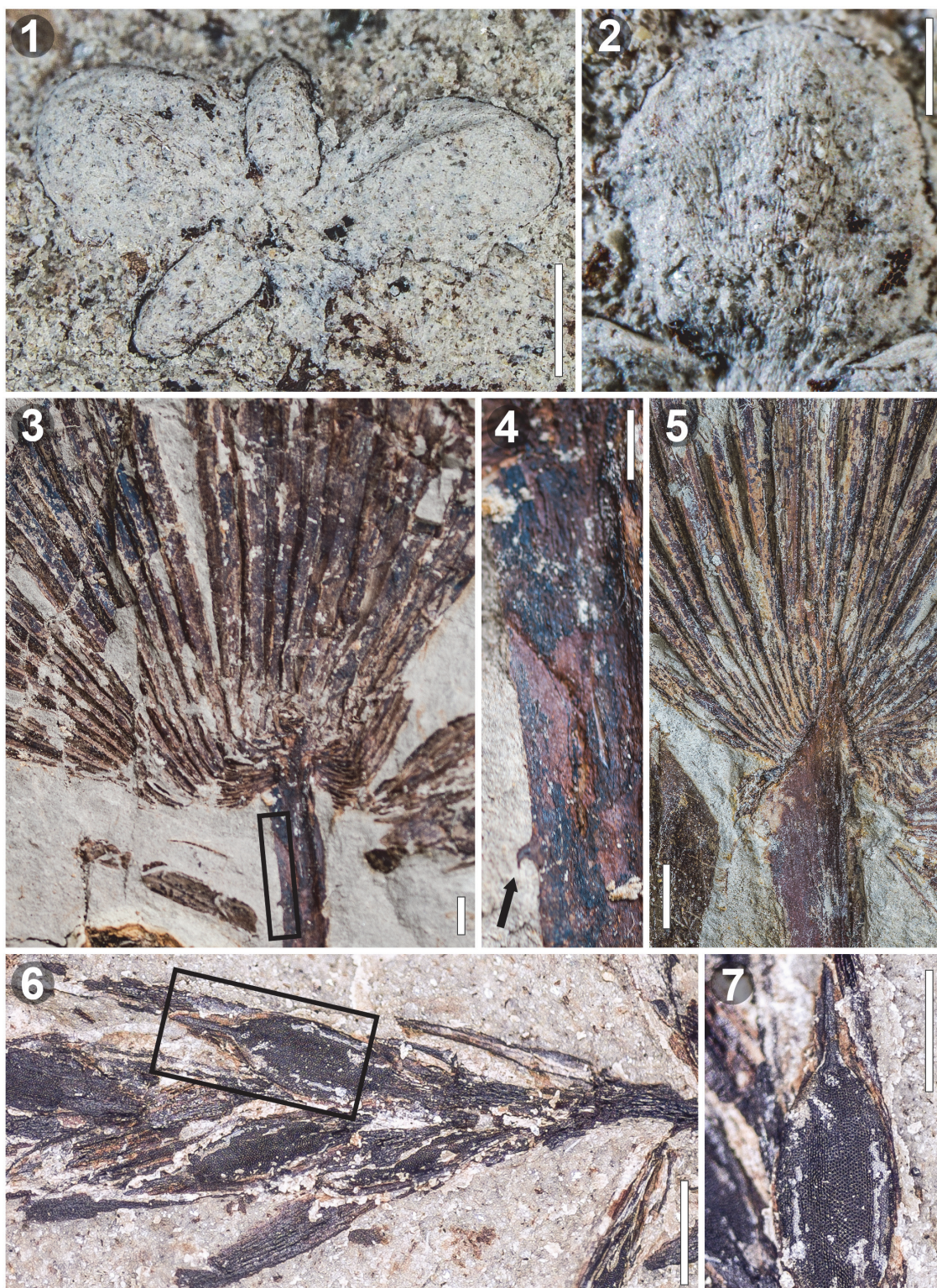
Fossil costapalmate genus SABALITES Saporta, 1865 (emend. Read and Hickey, 1972)

Figure 8.5

**Description.** The leaf blade is fan-shaped (coryphoid), induplicate. The leaf is costapalmate, as the costa extends for a distance into blade of leaf (Figure 8.5). Mid-rib of each leaf segment is prominent with up to two orders of parallel veins observable on many specimens. Petioles are unarmed. Maximum measurable petiole width is 2.9 cm.

**Remarks.** When describing palms, it should be recognized that the term palmate is a categorization on two levels; the first level of distinction is a leaf that is not pinnate (i.e., fan-shaped or coryphoid), and the second level is a comparison regarding the extension of the petiole into the coryphoid leaf blade itself (costapalmate vs. palmate). Costapalmate and palmate fossil leaves are recognized in this collection, primarily using definitions summarized in Read and Hickey (1972). The differential diagnosis is dependent upon the presence of an extended petiole (costa) into the leaf blade from which fused segments emerge at an acute angle vs. a leaf where the costal extension is not present, thus leaf segments originate from a single, centralized area at the top of the petiole. It has long been





**FIGURE 8.** Representative monocot families Lemnaceae, Arecaceae, and Cyperaceae. **1,** *Lemna* sp. multiple fronds (MMNS PB-106), scale bar equals 1 mm. **2,** Close-up of Figure 8.1 showing detail of single frond. **3,** *Palmacites* sp. showing partial leaf with palmate venation (MMNS PB-107), scale bar equals 1 cm. **4,** Close up Figure 8.3 showing tooth on petiole, scale bar equals 5 mm. **5,** *Sabalities* sp. showing partial leaf with costapalmate venation (MMNS PB-108), scale bar equals 1 cm. **6,** *Cyperus* sp. with multiple achenes (MMNS PB-109), scale bar equals 1.0 mm. **7,** Close-up of Figure 6.1 showing detail of the achene, scale bar equals 0.5 mm.



recognized as impossible to assign extant fan palm leaves to modern genera or species without the additional characters provided by fruit and/or flowers. Correlating fossil fan palm leaves with modern taxa is even more problematical; thus, we use the fossil form genera established for fan palms. However, we realize that any fossil record of palmate leaves with spines on the petioles may require a revision of the form genus *Palmacites* or establishment of a new fossil form genus, as palmate leaves with spines have not been previously recorded as *Palmacites*.

Interestingly, a dichotomous key within a field guide of extant palm genera of the Americas (Henderson et al., 1995) lists spines along the petiole as one of the first sub-categorizations (after discriminating between palmate and pinnate leaves) for discerning a genus from the Western Hemisphere. Within the Americas, only five genera match these criteria (i.e., palmate with armed petioles): *Acoelorrhaphe*, *Serenoa*, *Copernicia*, *Brahea*, and *Washingtonia*. From this list, *Washingtonia* and *Brahea* are associated with desert climates; additionally, *Washingtonia* is costapalmate and *Brahea* is shortly costapalmate. *Serenoa* is common to the southeastern United States occupying pinelands, prairies, and sand dunes (Henderson et al., 1995) and is a palmate leaf as there is no costal extension into the leaf blade. However, the petiolar teeth of *Serenoa* are small, fine, sharp, and more closely-spaced teeth than those of the *Palmacites* fossil. *Acoelorrhaphe* occupies swampy, coastal areas of the northern Caribbean while *Copernicia* is found in savannahs, woodlands and lowland areas of Cuba (Henderson et al., 1995; Dransfield et al., 2008). Both *Acoelorrhaphe* and *Copernicia* are palmate, and both have teeth that appear similar to those of the Hattiesburg Formation *Palmacites* fossil. Although proposing a direct evolutionary relationship of our fossil to a modern taxon is not yet feasible, it cannot be ruled out that the spinous *Palmacites* fossil is possibly ancestral to one of these genera, especially considering that the biogeographical history for sub-family Coryphoideae has been a significant factor in its current distributional patterns (Asmussen et al., 2006; Bjorholm et al., 2006).

Recent reviews of coryphoid palm species, including those currently limited to the New World, indicates that most New World genera are unarmed and palmate (Dransfield et al., 2008). As mentioned above, several Hattiesburg fossil specimens of palmate leaves that do not display spines on the petioles fit the original description of *Pal-*

*macites*. These could either represent a Miocene precursor to some other modern palmate form or could have lost the spines during preservation and recovery. This review also indicates that a conspicuous costapalmate extension is not representative of most New World genera. Currently, an unarmed, prominently costapalmate leaf would seem to indicate a relationship only with the tribe *Sabaleae*, genus *Sabal*. *Sabal* has 16 species confined to the New World, including the northern Gulf of Mexico Coastal Plain (Dransfield et al., 2008).

Included within the Hattiesburg Formation collection are many palm leaf fragments (currently undeterminable to palmate or costapalmate forms) indicating large dimensions of the original leaf. These include fragments of a palmate leaf with a length of more than 29 cm. Numerous isolated spinous palm petioles also occur in the collection. Isolated palm trunk fragments are common at the site, affirmed by features of the wood anatomy. These will be described in a forthcoming paper.

Palm leaves have been previously reported from the Hattiesburg Formation. Berry (1916a) reported fossils from a location in Forrest County, and Brown (1944) reported palm fragments from a locality on Tallahala Creek. From our data, including numerous records of palm leaves and stems from the Bouie River locality along with previous reports, palms were clearly a dominant feature of this delta-associated plant community. Palm fossils have also been reported from the Catahoula Formation of Mississippi (Berry, 1916c) and from the Alum Bluff locality of Florida (Berry, 1916a; Corbett, 2004). Berry (1916a) argued that the Alum Bluff and Hattiesburg palms represented the same species (*Sabalites apalachicolensis*), but this is difficult to determine based on the information provided (Corbett, 2004).

Palms have a fossil record extending back to the mid-Cretaceous; however, the fossil record of some common extant palm morphotypes is relatively rare (Read and Hickey, 1972). For example, palm leaves with armed petioles are common among extant taxa (e.g., *Licuala*, *Johannesteijsmannia*, *Pholidocarpus*, and *Pritchardiopsis*, and many more) (Dransfield et al., 2008), so it is surprising that there are few such fossil records (e.g., Pan et al., 2006), especially those showing petioles still attached to the leaf blades (Wang et al., 2015) as in the *Palmacites* specimens described here. Based on our observations of the Bouie River locality fossils, we suggest that palm fossils with armed petioles may be more common than currently thought, as we note that the spines can be



easily broken off during the collection of the fossils. Also, the matrix does not always clearly spit along a plane on which the petiolar spines occur.

Order POALES Small, 1903  
Family CYPERACEAE de Jussieu, 1789  
Genus CYPERUS Linnaeus, 1753

*Cyperus* sp.

Figure 8.6-7

**Description.** Numerous fossil spikelets, the longest approximately 2 cm, bearing florets distichously arranged on the rachilla are identified as a *Cyperus* sp. (Figure 8.6). Florets are approximately 3 mm in length (Figure 8.7). Achenes are biconvex or flattened with surfaces completely covered with evenly spaced, consistently small, rounded projections. Long persistent styles are approximately 1 mm in length.

**Remarks.** The apparently deciduous habit of the spikelets and their distichous arrangement along the rachilla indicate affinity with the genus *Cyperus*, with the caveat that the Cyperaceae are an exceedingly large family, notoriously difficult to identify to lower taxonomic levels in modern examples let alone from fragmentary fossils. However, we suggest that the slightly stipitate, oblong achenes with an apiculate apex (or partly persistent style?) and pitted surface are reminiscent of *Cyperus strigosus* and relatives, a common species of wetland areas in the southeastern U.S. These fossils occur on slabs with abundant *Salvinia* and *Lemna* remains, indicating a relatively quiet, freshwater depositional setting within the Hattiesburg Formation Bouie River locality section.

## DISCUSSION

It has long been realized that the eastern North American Neogene paleobotanical record is poor, especially in comparison with the better-known western record (Graham, 2010). The new Bouie River flora site described here helps to fill this significant gap in our understanding of North American paleobotany and biogeography. Prior to this study, only five taxa had been reported from the Hattiesburg Formation: *Sabalites* (an unarmed costapalmate palm), *Taxodium*, *Salix*, *Ulmus*, and *Morus/Celtis* (Berry, 1916a; Brown, 1944), and most of these were not figured. Here, we identify, describe, and figure 22 taxa. Some of these are identified down to section (i.e., within the genera *Quercus*, *Juglans*, and *Carya*), and some possibly to species (e.g., *Osmunda spectabilis*).

Several components from this flora are particularly significant from a taxonomic and biogeographical perspective as regional, continental, or even nearly global first records. For example, the first Gulf Coast record of the now endemic Asian genus *Sargentodoxa* represents a major paleobiogeographic expansion for this genus and supports the Miocene age determination in joint consideration with previous North American records (Tiffney, 1993; Manchester et al., 2009). The *Juglans* fruit described here is different from those of the two eastern North American extant species (i.e., *J. cinerea* and *J. nigra*); therefore, it represents an extinct or extirpated species. We also present some of the only Neogene fern records from eastern North America including *Osmunda*, the earliest and first fossil evidence of *Woodwardia* from its current range, and nearly entire plants of the floating fern *Salvinia*. This flora also makes a key contribution to the fossil record of the floating aroid genus *Lemna*, as there was only one previous vegetative record, and this was from the Miocene of the Czech Republic (Kvaček, 2003). We also report the earliest macrofossil record of *Cercis* from eastern North America and describe specimens representing two sections of *Quercus* that are currently major components of the regional extant forest.

With a few exceptions mentioned above, most of the Bouie River site fossil plants are similar to taxa present in the area today (e.g., *Carya*, *Cyperus*, *Morus*, *Platanus*, *Populus*, *Taxodium*, *Salix*, and *Sambucus*), which supports the idea that a generally similar precursor to the current Gulf Coast wetland flora was already established here since at least the middle Miocene. From a qualitative perspective, this suggests that the climate was also similar to now. The presence of abundant palms indicates that the climate was at least warm temperate. This issue will be addressed in a detailed quantitative analysis that will be undertaken once all of the identifications are finalized. However, like the late Pliocene Citronelle flora of Alabama, the Hattiesburg flora was relatively poor in *Pinus* (only pollen has been found to date from the Bouie River site) compared to this region today, which could indicate somewhat drier conditions than at present (Stults et al., 2010).

## CONCLUSION

The newly recognized Bouie River site of the Hattiesburg Formation has substantially increased our knowledge of the middle Miocene floras of the Gulf of Mexico Coastal Plain. Where previously only five taxa had been recognized, 22 are now acknowledged, including "exotics" and several

other taxa, which had no previous Miocene record from eastern North America. As additional older and younger sites are studied, the Bouie River flora will be an important window into developing a broader view of the evolution of the extant Gulf Coast flora. However, it is already apparent that the Bouie River site fossils, along with those of the Citronelle Formation (Stults and Axsmith, 2011, 2015) and other sites under study, support the concept of an early establishment of a flora generally similar to that of the modern Gulf Coast, but with the presence of several “exotic” taxa that subsequently disappear from North America during the late Pliocene (Graham, 2010). This also suggests that climates through this interval were similar to today and were relatively stable.

Although many of the plant fossils are described here in considerable detail, we still consider this research preliminary overall. Additional taxa are still being found with nearly every visit to the site, indicating that much more diversity awaits discovery. In addition, some of the taxa, such as the fern *Salvinia* and the palms, merit additional study as dedicated papers. Palynological analysis, which is yielding evidence of additional taxa not yet represented in the megafossil record, is ongoing. Stratigraphic work is also refining the formational boundaries and ages, which will allow better temporal constraint for Gulf Coast fossil floras (Dock-

ery and Thomson, 2016). In any case, it is becoming increasingly clear that the supposed paucity of Neogene plant megafossil sites in the southeastern USA compared to the well-known succession in western states may be at least in part due to poor exposure and historically inadequate prospecting and study.

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