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Acknowledgements

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A SOUTHEASTERN NORTH AMERICA RIVER COMMUNITY FORTY-THOUSAND YEARS AGO

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ABSTRACT

Understanding how past communities have been shaped by environmental alterations can provide insight into the impacts of future climate change. Local climate and river systems have changed significantly over the last glacial maximum, but little is known about the communities of the Georgian Coastal Plain earlier in the period. Plant fossils from Coffee Bluff, a Quaternary organic river deposit of the Ocmulgee River in southeastern Georgia, were used to determine past environmental and climatic conditions. The paleoflora were found imbedded in a mud matrix and were removed by a slaking method; they were later identified and separated to respective ecological environments. Of the eleven species identified, one was a wetland species (marsh sedges), while the remaining ten were woodland species. From using the coexistence approach with the plant fossils and aligning their growing conditions, we suggest that Coffee Bluff was a stream/riverine habitat with loamy and well-drained soils; local climate was humid, with temperatures and annual precipitation ranging from 10 to 21°C and 1016 to 1524 mm, respectively. Few gymnosperm specimens were recovered in the material, though groups like conifers were dominant in the coastal plain environment during the late Pleistocene. It is most likely that there were fewer conifer trees near the collection area.

Keywords. paleobotany, Ocmulgee River, coastal plain, Quaternary, late-Pleistocene, riverine

INTRODUCTION

The state of Georgia is divided into five distinct geographic regions as follows: Appalachian Plateau, Ridge and Valley, Blue Ridge, Piedmont, and Coastal Plain (Figure 1). The northwestern portion of the state (consisting of the Blue Ridge, Ridge and Valley, and Appalachian Plateau regions) is mountainous and has many different pine (*Pinus*) species. Before the end of the late glacial maximum, pine species dominated the area (Watts 1970, 1980; see Table I for a list of geologic

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periods and respective timeframes). The Piedmont region is mainly composed of igneous formations, and thus yields sparse fossil specimens since they are typically not left intact after igneous rock formation. Exceptions lie in some cases, such as the Cretaceous charcoal angiosperm preservations found in Buffalo Creek (Keller et al. 1996). The Coastal Plain region, conversely, has a rich diversity in formations and fossil flora and fauna. At the beginning of the Paleogene, 66 to 56 million years ago (Eargle 1955), the Coastal Plain region was inundated and thus fossilized marine organisms can be found in this area of the state (Rich et al. 2011).

River systems, climate, and local communities have changed significantly over the last glacial maximum (~50–10 ka). The last forty-thousand years exhibited increased glacier growth in tandem with decreased temperatures in North America (Clark et al. 2009), which was sufficient enough to result in more variable climates (Williams 2009). From roughly thirty-two thousand years ago, the climate was cold and ecological settings consisted of savannah plains with *Pinus* (Leigh 2008). Additionally, the eastern coast of Georgia, such as the area of St. Catherine's Island, acted as a refuge for both northern and southern plant and tree species, and allowed these northern species to succeed in an atypical environment (Rich et al. 2015). Maximum glacial volume was achieved during the last twenty-one thousand years (Hughes et al. 2013). Not only did glacial ice cover much of the available land for plant colonization, it precipitated a drop in sea level, which affected nearby environments (Clark et al. 2009). From thirty to sixteen thousand years ago, the river system was high-energy due to the colder temperatures (Leigh 2008). The northern flanks of these rivers had eolian dunes, which formed from western winds and were produced due to climate during that time period (Ivester and Leigh 2003). This type of river system was distinct in having high velocity flow and maintaining little vegetation (Rust 1977). Plant taxa were significantly affected by climate fluctuations during this time (Liu et al. 2013). The appearance of interstadial periods after glacial periods allowed such groups to invade previously inaccessible regions, such as areas that were once occupied by glaciers (Watts 1980; Grimm et al. 2006). Groups such as *Pinus* were able to occupy near areas that were once considered as poor habitat (Watts 1973; Whitehead 1973; Whitehead 1981).

From the end-late glacial maximum to four and a half thousand years ago (in the Holocene), there was an increase in temperature and rainfall, though both increased independently of the other (Jouzel et al. 1987; Prentice et al. 1991). This worldwide temperature rise affected the biodiversity of environments, particularly when it comes to plant species. For example, tree taxa transferred to higher latitudes, which altered the overall floral composition of affected environments (Davis et al. 2001). Oak-and pine-dominated open woodland environments were significantly reduced during this time (LaMoreaux et al. 2009). After four and a half thousand years ago additional cooling resulted in drier conditions, which meant increased fire occurrences allowed for pine to overcome oak as the dominant tree in the southern environment (LaMoreaux et al. 2009). The river systems from eleven to five thousand years ago were low energy, since temperatures were much warmer than previous years (Leigh 2008). Because of the slower flow velocity of this river system, the rivers were stabilized from the plant growth without any disruption from the water movement (Rust 1977), which aided in the aforementioned plant dispersal.

Less is known about the climate and community structure of the Georgian coastal plain region earlier in the late glacial maximum, specifically prior to 40ka (Watts 1980). Although the overall river energy intensity of the entire Coastal Plain has been documented as high and braided (Leigh et al. 2004), there are fewer understandings of local climate. In particular, there is a distinct absence of a palynological and plant macrofossil record in the Coastal Plain during this time interval (Markewich and Markewich 1994).

Discovery of new plant fossils may help reveal more information about local Georgian Coastal Plain communities towards the start of the late glacial maximum. These plant fossils were extracted from a mud deposit in the banks of the Ocmulgee River (Coffee Bluff), located in southeastern Georgia (Figure 1). Archaeologists Dr. Dennis Blanton and Mr. Frankie Snow originally recovered the mud material during an archaeological expedition in 2006, sponsored by the Fernbank Museum of Natural History in Decatur, Georgia. While searching for remains of a seventeenth-century Spanish mission, Blanton discovered the deposit (Blanton and Snow 2010). The deposit itself was exposed at a time of drought-induced low water in the eroding Coffee Bluff exposure, extending a few inches above the water's edge. It was composed of dark, organic-rich sediment, containing obvious floral macrofossils (Thieme and Blanton 2007). Both archaeologists knew that this deposit could have scientific significance, so they extracted the mud from the site, and then housed the material at South Georgia State College and Fernbank Museum for future examination. With permission from the museum, we undertook the opportunity to work with this overlooked collection of Quaternary aged plant fossils.

The goal of this study was to determine the community structure, and the local climate of Coffee Bluff during the late Quaternary. We identified the fossil flora from the locality and then used the identifications to align the flora with the associated ecological and growing conditions. By doing so, we are able to reveal more information about riverine habitats and local climates of early late glacial maximum coastal plain environments.

LOCALITY INFORMATION

In the bluff exposure, the organic deposit is roughly 3 m below the current floodplain level (Figure 2). The deposit itself is about 28 m wide and may have been part of a channel or slough, as it has a basin-like cross section. There is very coarse sediment on top of the deposit, with other cross-bedded sand and clay deposits located above them (Figure 3b and 3a, respectively). These sediment types are indicative of a fining-upward sequence above the mud deposit, in which finer grained rock overlay coarser grained rock on top of the entire profile. This sequence reflects significant and sometimes abrupt changes in streamflow character, specifically from low to high energy, and then gradually declining in energy again. The specific lithology and stratigraphy of Coffee Bluff can be seen in Figure 4. The original profile is in Figure 5. The age of the deposit was determined from preserved wood in the organic deposit (Figure 6). A radiocarbon dating determined the age to be approximately forty-two thousand years old, placing the deposit within the Pleistocene (lab number: beta-220769, measured radiocarbon age: 38700 ± 420 BP, conventional radiocarbon age: 42,664 ± 162 BP).

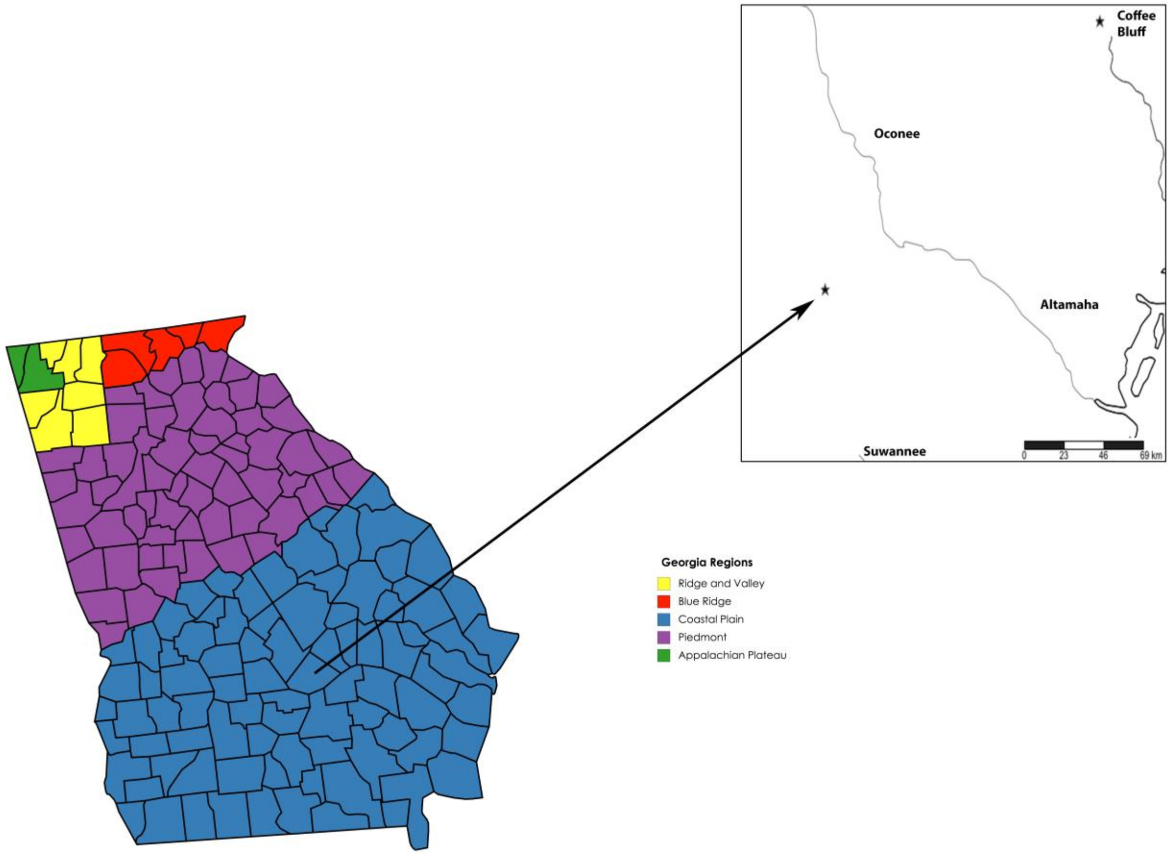

Figure 1. Map of Georgia regions. The arrow points from Telfair county to the Coffee Bluff locality. The region map was created with mapchart.net; the locality map was made with simplemappr (Shorthouse 2010).

Table I. Geologic ages of the Cenozoic (GSA 2018)

Period	Epoch	Age (million years, Ma)
Quaternary	Holocene	12,000 (0.012 Ma) to present
Quaternary	Pleistocene	2.58 to 0.012 Ma
Neogene	Pliocene	5.33 to 2.58 Ma
Neogene	Miocene	23.03 to 5.33 Ma
Paleogene	Oligocene	33.9 to 23.03 Ma
Paleogene	Eocene	56 to 33.9 Ma
Paleogene	Paleocene	66 to 56 Ma

Figure 2. An overview of Coffee Bluff. The arrow indicates the organic deposit.

Figure 3. a) The upper section of Coffee Bluff; b) The lower section of Coffee Bluff.

EXTRACTION METHODOLOGY

Different methodologies have been proposed for extracting plant fossils from matrixes of variable strengths; strategies range from solely heating the material to using hydrochloric acid (Tiffney 1990). For the Coffee Bluff paleobotanical material, we decided to use a technique called *slaking*. In this method, the material is dried for a period of time, with care taken to not dehydrate the plant fossils completely. The material is then immersed in hot water (Tiffney 1990). We modified the original slaking methodology of Tiffney (1990) by increasing the temperature but decreasing the amount of time the samples were exposed, in the hopes that more fossils could be removed without significant damage to them.

Because the mud material was submerged in water-filled buckets, the material was dried in segments. Each segment of material was put on a plastic plate and was placed outside in summer temperatures (~27–32°C) for an hour. This amount of time was ideal to reduce the water content of the samples but prevented the embedded fossils from becoming brittle. After the drying interval, the material was placed into the top container of an assortment of sieves, with sizes of 5, 10, 60, and 230 (Figure 7) and washed with warm water to remove mud material and retain fossil material. Fossils extracted from the mud were stored in containers with

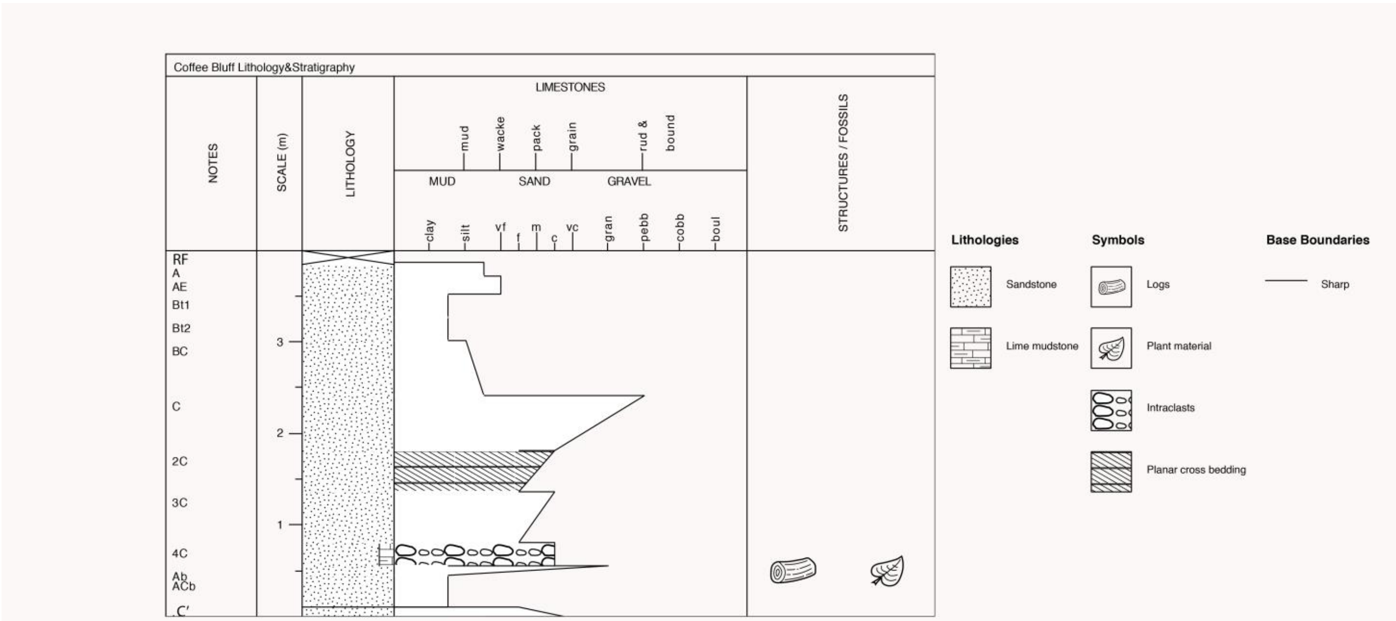

Figure 4. Lithology and stratigraphy of Coffee Bluff. RF (0-15 cm) is road fill, top of the bluff with highly mixed/disturbed sediment. A (15–30 cm) is sandy loam, with weak/fine sub-angular blocky sediment structure. AE (30–50 cm) is loamy sand, with medium to fine subangular block sediment structure. Bt1 (50–75 cm) is sandy clay loam, with weak/medium subangular blocky sediment structure; also a few sand-sized muscovite flakes. Bt2 (75–100 cm) is sandy clay loam, with subangular blocky sediment structure. BC (100–160 cm) is loamy sand, with weak/medium to fine subangular blocky to massive sediment structure. C (160–220 cm) is loamy coarse sand with 1 cm pebbles, weakly bedded with jointing. 2C (220–265 cm) is variable fine to coarse loamy sand, with intensely cross-bedding. 3C (265–320 cm) is fine to coarse loamy sand, interspersed with kaolin clay. 4C (320–345 cm) is coarse loamy sand, with large clasts and limestone fragments. Ab (345–355 cm) is mucky loamy sand that grades into clay loam at the bottom of the section; it also contains abundant plant material, including log and seeds. ACb (355–390 cm) is mucky clay loam, with highly decomposed organic material. C' (390 cm) is medium sand with fine (common) and medium (few) size gravel, also quartz sand. The stratigraphy column was made with the SedLog program (Zervas et al. 2009).

glycerol to preserve the integrity of the plant structures. To note, after drying the material, the extraction process was conducted inside to prevent contamination from extraneous sources.

For identification, we examined plant fossils with a computer USB microscope (Mustech USB Digital Microscope) for species-specific characteristics. Martin and Barkley's 1961 *Seed Identification Manual* and the modern seed collection at the Lamont-Doherty Earth Observatory were used to identify the individuals. A photo was taken of each fossil plant species (see *Paleontology*) using a Nikon SMZ18 stereoscopic microscope with a Nikon DS-Ri2 camera under 1.0x and 2.0x objective lenses and the fossils were separated into distinct species vials.

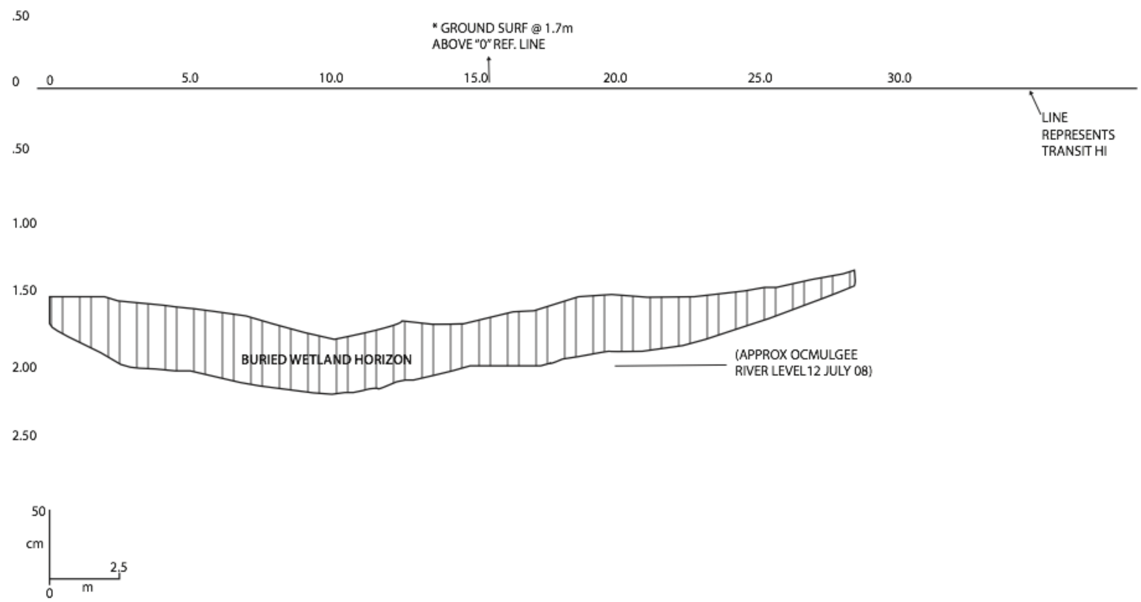

Figure 5. The original profile of Coffee Bluff. The top line in the profile represents the transect top. The profile is used with permission from Frankie Snow.

RESULTS

Eleven species of plants were identified. The recognized plants show a wide range of diversity, including seeds of trees, vines, and wetland sedges, as well as conifer needles. We have organized the recorded species and their physical descriptions below by plant grouping and associated environment. The latter includes wetlands and woodlands.

The wetlands flora contained a marsh sedge, the true sedge (*Carex* sp.). In the woodland flora, only woody plants were recorded; non-woody plants did not make up any portion of the material. The woody plants consisted of several species of oak, e.g. Spanish oak, *Quercus falcata*. Although the *Carpinus carolinana* specimen is very similar in morphology to *Ostrya virginiana*, *Ostrya* does not occupy the same spatial range within Coffee Bluff (Burns and Honkala 1965). One pine specimen was recorded, but only the leaf fascicle was recovered; we speculate that it belongs to *Pinus taeda* (loblolly pine), due to its leaf length and number of leaves in the fascicle (Burns and Honkala 1965). The following are the plant species identified:

Wetlands

Marsh sedges: *Carex* sp. (true sedges) [Plate 1a]

Woodlands

Woody flowering plants (angiosperms): *Carpinus carolinana* [Plate 2a], *Carya aquatica* (water hickory) [Plate 2b], *Fagus grandifolia* (American beech)

Figure 6. Wood from the deposit used to determine Pleistocene age (~42ka), indicated by the arrow.

Figure 7. a) Stacked sieves for fossil retention, b) Sieves for fossil sorting. Sizes are arranged from right to left: 5, 10, 60, 230.

2c], *Ilex* sp. (holly) [Plate 2d], *Quercus alba* (white oak) [Plate 2e)], *Quercus falcata* (Spanish oak) [Plate 2f], *Quercus palustris* (pin oak) [Plate 2g], *Staphlea* *trifolia* (American bladdernut) [Plate 2h], *Vitis* sp. (grapevine) [Plate 2i]; Woody non-flowering plants: (Gymnosperms: *Pinus taeda* (loblolly pine) needle [Plate 3j].

DISCUSSION

The present specimens suggest that Coffee Bluff was predominantly a stable habitat for trees, as more than seventy percent of the included species are woody plants (eight trees, specifically). Most if not all of the tree species are mesophytic and grow optimally in well-drained soils. Some trees like *Carpinus carolinana* can tolerate flooding, although they do not typically grow in flooded environments (Furlow 1987; Delcourt and Delcourt 1994); others such as *Quercus palustris* will die if exposed to permanent flooding (Fowells 1965). Most of the species grow in loamy soils, which was present in the matrix.

The coexistence approach (Mosbrugger and Utescher 1997) can be used to infer past climate based on the modern temperature and precipitation ranges of plants that have persisted from that time period to the modern age. From the plant specimens present, we can infer that the mean annual temperature during 42 ka in Coffee Bluff was likely between 10 and 21°C; mean annual precipitation was likely between 1016 and 1524 mm (Fowells 1965; Burns and Honkala 1990). The tree species also have recorded major and minor associations with each other. A major association in a plant series occurs more often in the association, while a plant in a minor association occurs less often. Major associations include *Q. falcata/Q. alba, Q. falcata/F. grandifolia, Q. alba/C. aquatica, C. caroliana/Q. alba, C. caroliana/Q. palustris,* and *C. caroliana/Q. falcata*; minor associations include *F. grandifolia/Q. alba, Q. palustris/Q. falcata, Q. palustris/F. grandifolia, P. echinata/Q. falcata,* and *C. caroliana/F. grandifolia* (Fowells 1965; Burns and Honkala 1990).

From our analysis, it is likely that the Coffee Bluff habitat was stream-based. The low organic content of the material matrix is an indication of a streaming river rather than a stationary pond (or a swamp as well), and the presence of woody root pieces (Figure 6) shows that trees were able to thrive in the habitat conditions (Abernethy and Rutherfurd 2001; Bertoldi et al. 2011).

A lack of a concrete pollen record prior to roughly the last forty thousand years in the North American southeast has made it difficult to divulge accurate climate information (Leigh 2008). However, the stable fluvial conditions in Coffee Bluff during this time and the presence of macrofossils from our study lends some ideas about the local climate and environment. Previous studies have suggested that the climate was likely cooler from the marine isotope stage (Lowe and Walker 1998), and the appearance of trees like *Quercus* and *Fagus* suggests cooler temperatures in the area (Bennett 1985; Leigh 2008). The addition of palynological studies will greatly aid to understanding past climate in this area.

It should be of notice that there is a distinct lack of non-angiosperm woody plants in the deposit. Despite groups like pine (*Pinus*) and bald cypress (*Taxodium*) that make up a significant portion of woody plants in southeast North America during this time (Davis 1983), these plants are not well represented in the Coffee Bluff deposit. These trees were dominant in southeast North America during the mid to end of the Pleistocene (40ka years), representing up to seventy-five percent of local tree populations (Jimenez-Moreno et al. 2010). There have been periods in the late Cenozoic when gymnosperm trees were no longer as highly represented in ecosystems, but these periods are in the mid Holocene (8–5ka), much younger than this study's fossil plants (Springer et al. 2010). Fire is a well-known mechanism for driving change in the coastal plain environment (Noss et al. 2015); however, no charcoal remains were found in the fossil material. Fire was most likely a driver in denser forests but might not have been as prevalent in river-adjacent ecosystems. The presence of the *Pinus taeda* fascicle confirms that conifers were in the area, but the reasoning for why fewer conifer specimens were present among the fossil angiosperm seeds is debatable. The fossil site may not have had nearby gymnosperm trees for deposition, but the explanation is too difficult to determine without additional clues.

CONCLUSION

A lack of credible macrofossil and palynological records in the early stages of the last glacial maximum have prevented many from determining habitat structure and climate of southeastern North America. Our study uncovered fossils of eleven plant species from Coffee Bluff, a riverine locality radiocarbon-dated to almost 43ka. Based on the identification of the plant fossils, we believe that Coffee Bluff was a stream-based habitat, with loamy and well-drained soils. Local climate was humid (10 to 21^{o}C and 1016 to 1524 mm of rainfall annually), significantly warmer compared with the climate during the Quaternary/Holocene boundary and the last glacial maximum. These results, along with future studies, will help to reconstruct southeastern habitats and local climate in southeastern North America during the mid to end of the Pleistocene.

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PALEONTOLOGY

Here are the descriptions and pictures of the fossil flora discussed in the *Results*.

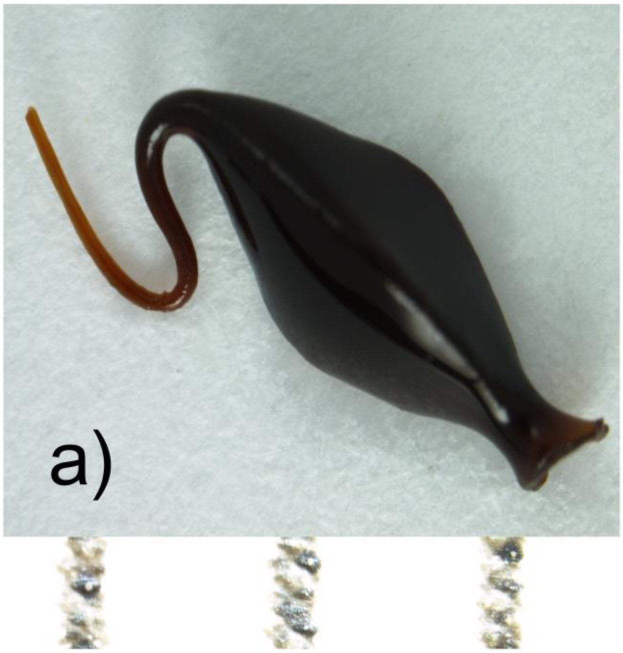

Plate 1. Marsh sedge: a) *Carex* sp. (Lineaus). The distance between each pair of lines represents 1 mm.

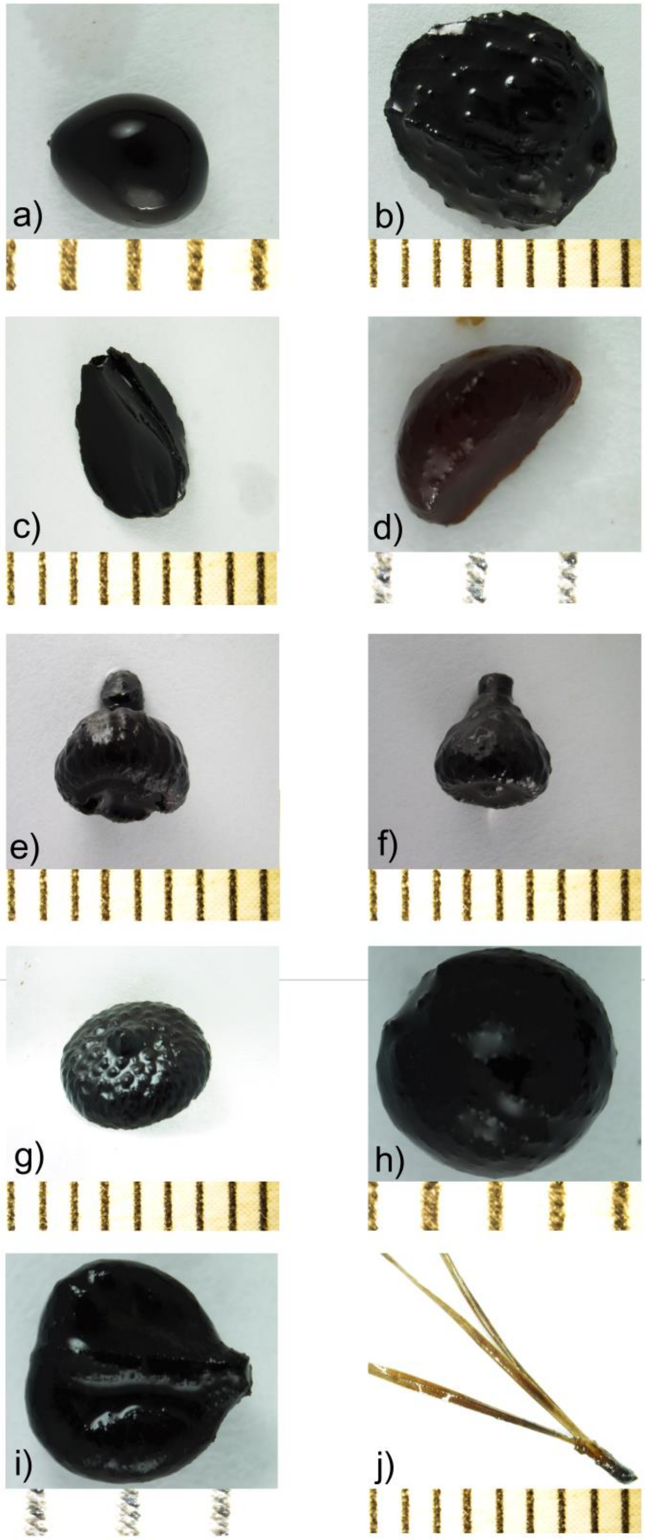

Plate 2. Woody plants (angiosperms): a) *Carpinus caroliniana* (Walter), b) *Carya aquatica* (Nuttall), c) *Fagus grandifolia* (Ehrhart), d) *Ilex* sp. (Lineaus), e) *Quercus alba* (Lineaus), f) *Quercus falcata* (Michaux), g) *Quercus palustris* (Münchh/Hausyater), h) *Staphylea trifolia* (Lineaus), i) *Vitis* sp. (Lineaus). Gymnosperms: j) *Pinus taeda* (Linaeus). The distance between each pair of lines represents 1 mm.

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