



## Evidence of white pine (*Pinus* subgenus *Strobus*) dominance from the Pliocene Northeastern Gulf of Mexico Coastal Plain

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### ABSTRACT

Plant fossils from the Citronelle Formation provide a rare window into the Pliocene flora and climate of the northeastern Gulf of Mexico Coastal Plain. Many of the taxa recovered to date inhabit the region today. However, analysis of *Pinus* pollen grains and fascicles indicates that the dominant pines were members of *Pinus* subgenus *Strobus* (i.e., “white pines”). The fascicles have a small, bulbous base lacking a sheath, and bear four or five long, slender needles. These features are typical of white pines. Although macrofossils are rare, 77 to 100% of the dispersed *Pinus* pollen grains from five localities have sacchi continuous with the corpus and verrucae on the cappula, which are characteristics of white pines. This is remarkable, as the northeastern Gulf of Mexico Coastal Plain today is devoid of white pines, and is instead considered a center of diversity for *Pinus* subgenus *Pinus* section *Pinus* subsection *Australes*. Today, *Pinus strobus* is the only white pine in the eastern North America and its southernmost distribution only extends into the mountains of Georgia, about 600 km north of the fossil sites. The historical biogeographic relationships of *P. strobus* to other North American forms are unclear. For example, its close relative, *Pinus chiapensis*, is present in northeastern Mexico and Central America. The current disjunction between *P. strobus* and *P. chiapensis* is 2400 km and includes an arid barrier to dispersal. *P. chiapensis* is also associated with several other species showing a similar biogeographic pattern. The fossils described here indicate that white pines were more widespread in North America in the recent geological past than previously thought, and imply possible connections between disjunct species that would not be suspected if only current species' ranges and ecological tolerances were considered.

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### 1. Introduction

The fossil record of pines from the Cretaceous to the Recent is generally considered good. However, their fossil record from the Neogene of eastern North America is very limited, and several biogeographical questions – such as the timing and route of *Pinus* migration into Mexico and Central America – remain controversial (for review see Graham, 1999). Here we report on the unexpected occurrence of white pine (*Pinus* subgenus *Strobus*) macrofossils and abundant associated dispersed pollen from several localities of the Pliocene Citronelle Formation in coastal Alabama and Florida, USA and discuss the potential implications of these findings for our understanding of *Pinus* biogeography.

The poor state of knowledge regarding the Neogene history of *Pinus* in eastern North America is symptomatic of the general paucity

of fossil plant localities from this time and place. What information exists has been gleaned from only a few microfloras and even fewer macrofloras (Gray, 1960; McCartan et al., 1990; Graham, 1999; Farlow et al., 2001; Hansen et al., 2001; Stults and Axsmith, 2009; Liu and Jacques, 2010). Therefore, additional research, including ongoing study of the mid-late Pliocene Citronelle Formation along the Gulf of Mexico Coastal Plain, is needed to broaden our understanding of events during this important time when global vegetation changes, such as the C<sub>3</sub> to C<sub>4</sub> plant transition, and further climate deterioration had started (Cerling et al., 1997; Zachos et al., 2000).

Despite the discovery of white pine remains reported here, many of the taxa thus far, e.g. *Taxodium*, *Pinus*, *Smilax*, *Acer*, *Betula*, *Carpinus*, *Castanea*, *Quercus*, *Carya*, *Nyssa*, *Ulmus*, etc., recovered from the Citronelle Formation still inhabit the region today (Berry, 1916; Stults and Axsmith, 2009). This is unsurprising for several reasons: 1) the mid-late Pliocene is relatively recent, so it is reasonable to predict that many genera and species would be the same (Reid, 1920; Barghoorn, 1951); 2) the region lies on a passive coastal margin not conducive to geologic events that would cause geographic separation and genetic isolation; and 3) the region lies within the moderating influence of the

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Gulf of Mexico and remained relatively climatically stable during the Pleistocene (Delcourt and Delcourt, 1993).

As important as the documentation of plant taxa of the Citronelle Formation still inhabiting the region is, discoveries of unexpected taxa are significant and intriguing. The discovery of the predominance of white pines (subgenus *Strobus*) falls into this category, because the northeastern Gulf of Mexico Coastal Plain today is devoid of white pines and is considered a center of diversity for hard pines (subgenus *Pinus*) – especially those within subsection *Australes*. It also raises new questions as to how these fossils fit into the Neogene biogeography of white pines on the North American continent.

### 1.1. Brief review of *Pinus* history and biogeography

Due to the abundance, diversity, and economic importance of *Pinus*, the evolution and biogeography of the genus have been a significant research focus of botanists (e.g., Axelrod, 1986; Millar, 1993; Richardson and Rundel, 1998). *Pinus* contains approximately 111 species that are widely distributed predominantly within the Northern Hemisphere. The genus comprises a large proportion of worldwide extant gymnosperm diversity, and makes up about half of the species diversity of the family Pinaceae (Richardson and Rundel, 1998). While most modern pines occupy temperate and cool temperate regions of the Northern Hemisphere, a few occur in warmer, tropical areas (Critchfield and Little, 1966). *Pinus* tends to dominate where edaphic conditions coincide with its physiologic adaptations to cooler, arid environments – it has a competitive edge over angiosperms in these areas (Farjon, 1996). While the distribution of the genus is extensive, only certain regions contain many species. These include Mexico and Central America, California, and the southeastern United States in North America with about seventy species. China and the rest of eastern Asia house about twenty-five species (Price et al., 1998).

*Pinus* diverged early within the family Pinaceae as indicated by phylogenetic analyses and the fossil record (Miller, 1976; Farjon and Styles, 1997; Stankiewicz et al., 1997; Wang et al., 2000; Otto et al., 2007). Some interpretations of the Late Triassic *Composostrobus neotericus* suggest that the ancestors of the Pinaceae may have evolved by that time (Delevoryas and Hope, 1987), while macrofossils identifiable to the genus *Pinus* are recognizable by the beginning of the Cretaceous (Alvin, 1960). The origin and early species radiation of *Pinus* probably occurred in conjunction with the onset of increased seasonality and aridity during the Early Cretaceous (Axelrod, 1986). Early pine fossils support a warm, temperate eastern North American and/or possibly a warm western European site of origination. However, the diversity of pine fossils in eastern Asia provides some support for that region as an alternative. Nonetheless, by the end of the Mesozoic, the genus had become widespread and dominant throughout the middle latitudes of Laurasia (Miller, 1976; Millar, 1993). Fossil data also indicate that by this time the genus had diverged into its two subgenera, *Pinus* and *Strobus*. Subgenus *Strobus* (“haploxyton” or white pines) is characterized by the presence of one fibrovascular bundle per needle, while subgenus *Pinus* (“diploxyton” or red pines) is characterized by two fibrovascular bundles per needle, in addition to other morphological/anatomical features. Many of the extant subsections of the genus (*Australes*, *Canarienses*, *Cembroides*, *Gerardiana*, *Pineae*, *Pinus*, *Ponderosae*, and *Strobi*) appeared by the Late Cretaceous (Millar and Kinloch, 1991).

Although pines are now subordinate to angiosperms in most temperate and warm temperate regions, the fossil record indicates that they were abundant in these areas prior to the Cretaceous angiosperm radiation. The increased warmth and humidity of the Paleocene and Eocene placed them at a competitive disadvantage with angiosperms, which originated in such climates (Millar, 1993). As the angiosperms became dominant, pines were relegated to cooler, drier regions and on poor soils. Thus, pines survived in several refugia:

high-latitude localities in the Northern Hemisphere; warmer, but drier low latitudes in the southeastern United States and southeastern Asia; and high altitude regions in the middle latitudes, especially in western North America (Millar, 1993).

Regional contraction into refugia significantly affected *Pinus* evolution, as it promoted environmental heterogeneity and genetic isolation. Paleogene orogenies in the Northern Hemisphere, particularly the Laramide and Sevier orogenies in western North America, produced similar evolutionary effects (Millar, 1993). Subsequently, the cooler, drier early Oligocene climates forced many angiosperm range contractions, allowing pines to expand into regions they had occupied during the Mesozoic. When pines rebounded, they did so with a more diverse array of species, some of which were the probable direct ancestors of modern species (Millar, 1993). These episodes of environmental heterogeneity and genetic isolation are considered especially relevant for understanding the origin of pine species in regions that are now considered secondary centers of *Pinus* diversification, such as Mexico and Central America with 47 endemic species (Farjon and Styles, 1997; Perry et al., 1998). The similarity between the Mexican species *Pinus chiapensis* and *Pinus strobus* of eastern North America is a particularly striking and controversial example of the complexity of *Pinus* biogeography that the fossils described here may help elucidate.

## 2. Geological setting, materials and methods

The Citronelle Formation is a low-lying formation of the coastal southeastern United States occurring in areas between the panhandle of Florida and eastern Texas. It consists mostly of oxidized sands with few organic remains; however, rare and scattered unoxidized clay lenses sometimes contain plant fossils. Otvos (2005) provides compelling evidence that the Citronelle depositional environment was mainly a braided river system, but notes that muddy units at several localities indicate some deep meandering river channels. Several localities, such as Scarborough and Perdido Park (Table 1), also include estuarine facies (Stults et al., 2002).

Outcrops of the Citronelle Formation are generally poor because of low topographic relief, abundant modern vegetation cover, limited lateral continuity of facies with potential marker beds, and the lack of index fossils. Furthermore, sediments of the Citronelle Formation can be easily confused with those of similar underlying Miocene and overlying Pleistocene deposits. A Pliocene age was originally proposed based mainly on plant fossils (Berry, 1916; Matson 1916); however, several later workers proposed a Pleistocene or Miocene age (see historical review in Otvos, 1998). Otvos (1997) presented a synthesis of evidence indicating that the Citronelle Formation is Pliocene, and was deposited sometime between 3.4 to 2.7 mya.

**Table 1**  
Citronelle Formation localities with relative percentages of haploxyton and diploxyton pollen.

Site with GPS coordinates	Haploxyton (%)	Diploxyton (%)
Scarborough School (AL) 30° 43.74' N, 88° 8.57' W.	90	10
Lambert's Station (AL) 31° 1.73' N, 88° 12.23' W.	82	18
Red Bluff (AL) 30° 20.61' N, 87° 29.12' W	77	23
Perdido Park (AL) 30° 24.05' N, 87° 26.97' W.	84	16
<sup>a</sup> HMR Constr. (AL) 30° 50.95' N, 88° 7.60' W.	91	9
Joiner Pit (FL) 30° 36.79' N, 86° 59.93' W.	100	0

<sup>a</sup> Denotes site where many of the pine pollen grains were not of sufficient quality to clearly allow this distinction and should be treated with caution.

Eighteen plant taxa were originally described from the Citronelle Formation (Berry, 1916), some of which were ascribed to extant species (e.g., *Planera aquatica* J. F. Gmel., *Quercus nigra* L.) or considered their immediate precursors, and others were recognized as extinct (e.g., *Trapa alabamensis* Berry). Included in this initial assessment were specimens described as wingless pine seeds and pine needle fragments. We have examined these putative *Pinus* fossils in the collections of the National Museum of Natural History and consider this identification questionable.

Recently, pine fascicles with attached needles have been recovered from one site in southwest Alabama and are preserved as impressions/compressions (Plate IA). In some cases, dégagement revealed additional features and finer details under the dissecting microscope. The cuticles are not well preserved and epifluorescence did not produce useful results. *Pinus* pollen has been recovered from clays at several sites in southwest Alabama and northwest Florida (Table 1; Fig. 1) by processing using standard palynological methods (Faegri and Iversen, 1989). All studied specimens are deposited in the University of South Alabama (USAM) paleobotanical collections.

### 3. Results

#### 3.1. Fossil descriptions

##### 3.1.1. Macrofossils

Six fascicles of *Pinus* have been recovered from the Citronelle Formation (USAM # Sc12e, Sc14a, Sc34c, and Sc47a–c). Short, bulbous, sheathless (deciduous) fascicle bases (approximately 1 × 1 mm) are present on three specimens. Four to five needles are apparent per fascicle (four needles per fascicle on four of the

specimens and five needles per fascicle can definitely be seen on one specimen (Plate IA); five per fascicle possibly demonstrated on another). Only one specimen has the needles preserved all the way to the tip and is 8.6 cm long. Needle widths are consistent over entire needle lengths, varying between 0.5 and 0.75 mm. The fossil fascicles display characteristics consistent with herbarium samples of the species *P. strobus* in the University of South Alabama herbarium (USAM) (Plate IB).

##### 3.1.2. Microfossils

Palynological analysis from six localities (Table 1; Fig. 1) in the Citronelle Formation supports the macrofossil evidence for the occurrence of white pines (subgenus *Strobus*) along the Pliocene Gulf of Mexico Coastal Plain. In addition, the pollen evidence indicates that they were widespread and the dominant pines. Verrucae characteristic of the cappula of subgenus *Strobus* pollen (i.e. haploxylyon-type) (Kapp et al., 2002) are observable on many of the pollen grains (Plate 1C–D). Additionally, many of the pollen grains have semicircular sacci that are approximately continuous with the corpus, providing further support for subgenus *Strobus* affinities (Weir and Thurston, 1977).

The proportions of haploxylyon-type vs. diploxylyon-type *Pinus* pollen grains per site are tabulated in Table 1. Only those grains that were sufficiently cleared, of good quality, and clearly demonstrated diagnostic features were included. Haploxylyon-type grains dominate all assemblages with a low of only 77%. Three sites contain over 90% haploxylyon-type pollen. Grains of *Carya* are the next most common (Plate 1C). A representative pollen diagram based on the Scarborough School site, which produced the fascicles is presented in Fig. 2.

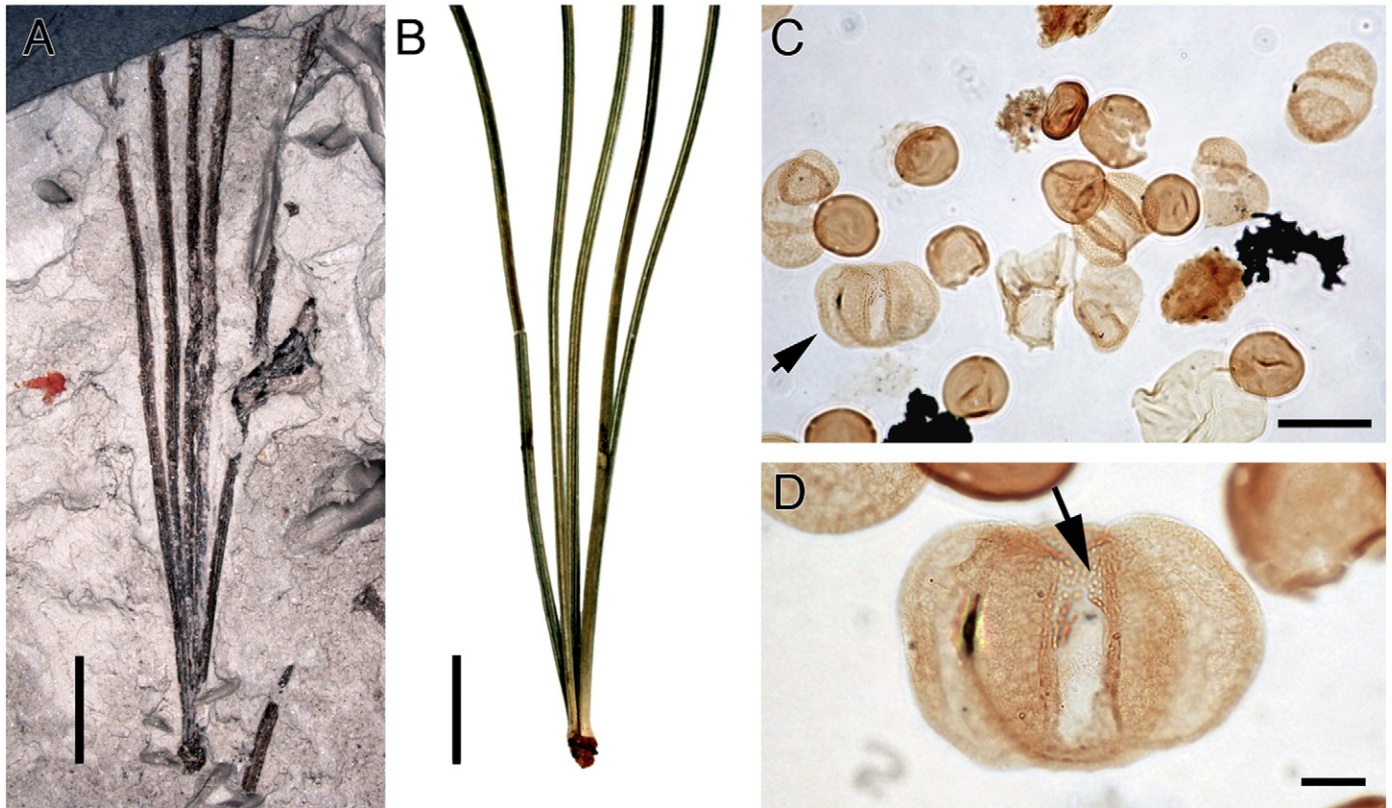


Plate I. Fossil and extant *Pinus*.

- (A). Fossil *Pinus* fascicle with five attached needles from the Pliocene Citronelle Formation of southern Alabama. Scale bar = 2.0 mm (#Sc34c).  
 (B). Modern *Pinus strobus* fascicle from Georgia. Note similarity to fossil in A. Scale bar = 2.0 mm.  
 (C). Typical palynological preparation slide field from Citronelle Formation. This example is from the site that produced the fascicle in A. Note the abundant *Carya* (round) and *Pinus* grains. Arrow indicates the *Pinus* grain detailed in D. Scale bar = 50.0 μm.  
 (D). *Pinus* pollen grain referable to subgenus *Strobus*. Note the broadly attached sacci and verrucae (arrow) on the leptoma. Scale bar = 10.0 μm.

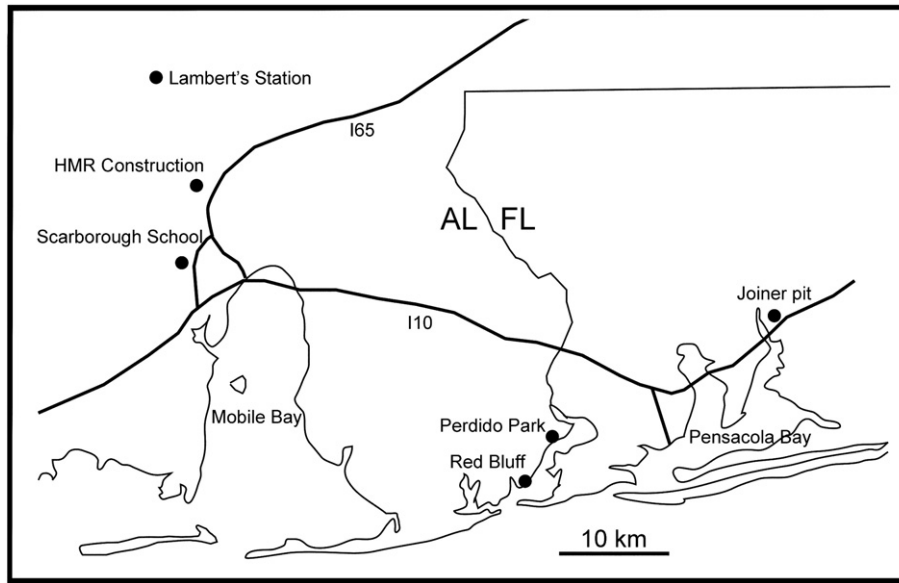


Fig. 1. Map showing Citronelle Formation plant fossil localities (dots). The precise GPS coordinates can be found in Table 1.

3.2. Remarks

The macrofossils consist of impressions with some organic residue and, therefore, cannot be sectioned to determine the number of fibrovascular bundles per needle. However, all observable features support assignment of these fossils to *Pinus* subgenus *Strobus*. These include the number of needles per fascicle (i.e., five with those with four probably representing a lost needle), the absence of a sheath, and the short, bulbous fascicle base. Faint serrations are visible on edges of extant *Pinus strobus* that cannot reliably be seen on the fossils, but this is probably due to the relatively coarse matrix. The fossil needle measurements are in accord with published records of *P. strobus*, which range from 6 to 14 cm long and approximately 0.5 mm wide (Vidakovic, 1991). Although these fossils cannot be assigned definitively to the species *P. strobus*, affinities with *Pinus* subgenus *Strobus* are clear.

4. Discussion

The southeastern coastal plain, including the northern Gulf of Mexico coast, is currently an area of *Pinus* diversity. Seven species are found there: *P. clausa*, *P. echinata*, *P. elliottii*, *P. glabra*, *P. palustris*, *P. serotina*, and *P. taeda* (Godfrey, 1988), all of which are of the subgenus *Pinus* with 2–3 needles per fascicle, persistent sheaths, and needle widths greater than or equal to 1 mm. Therefore, the fossils from the Citronelle Formation indicating that the dominant pines along the

Pliocene northeastern Gulf of Mexico Coastal Plain were of the subgenus *Strobus* is remarkable and unexpected. The only pine species of subgenus *Strobus* currently occurring anywhere near the northeastern Gulf of Mexico Coastal Plain is *Pinus strobus*. While the range of *P. strobus* is broad (Fig. 3) – occurring from Newfoundland to southeastern Manitoba, south into Iowa and Illinois, extending eastward again over the entire Appalachian Mountain region as far south as northernmost Georgia – it does not occur anywhere along the northeastern Gulf of Mexico Coast (Critchfield and Little, 1966; Flora of North America Editorial Committee, 1993).

Because *P. strobus* is the only haploxylon pine in eastern North America, the presence and dominance of haploxylon-type pines from the Citronelle Formation have important potential implications for our understanding of the biogeography of *Pinus* subgenus *Strobus* on the North American continent. As noted above, the southeastern U.S. Coastal Plain is considered a center of pine diversity, but the diversity of pines in Mexico and Central America is even greater. If pines originated in the warm temperate areas of Laurasia, their current presence in the warm temperate region of the northeastern Gulf of Mexico Coastal Plain is not surprising. However, there has been much speculation regarding the appearance of pine species in subtropical and tropical Mexico and Central America and the route of migration that may have established them there. *Pinus* diversity in tropical areas of Mexico and Central America is currently regarded as resulting from relatively recent secondary speciation events, as there is no fossil

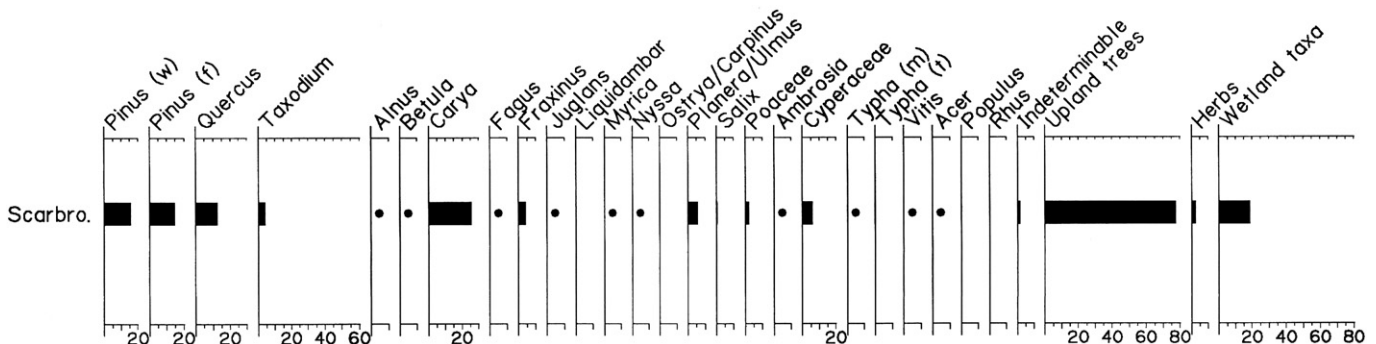


Fig. 2. Pollen percentage diagram of Scarborough School locality (AL) 30° 43.74' N, 88° 8.57' W. 83% of the *Pinus* grains are attributable to *Pinus* subgenus *Strobus*. (w) = whole grains, (f) = 50% or more complete grains.



**Fig. 3.** Map of North America showing the current range of *Pinus strobus* (hatched) and *Pinus chiapensis* (solid in box). The arrow indicates the Mobile, Alabama area in which the studied Citronelle Formation outcrops occur. Redrawn and modified from Thompson et al. (1999).

evidence of pines in these regions until the Miocene (Graham, 1999, 2003).

For some time, ecologists have been challenged by the remarkable similarities between *Pinus strobus* of eastern North America and another haploxylon-type pine in Mexico and parts of Central America, i.e., *Pinus chiapensis*. *Pinus chiapensis* occurs in portions of Puebla, Chiapas, Oaxaca Guerrero, and Veracruz at elevations varying from 500 to 2250 m with 1500 to 3000 mm annual precipitation (Styles, 1993). Until fairly recently *P. chiapensis* was considered to be simply a variant of *P. strobus*. It has four or five slender, finely serrated, intermediate-length needles (6–12 cm) in a deciduous sheath, small, bulbous fascicle bases, and other features in common with *P. strobus* (Perry, 1991). Thus, observable features of the pine macrofossils from the Citronelle Formation are also consistent with *P. chiapensis* needles and fascicles. Curiously though, there is now a 2400 km disjunction between *P. strobus* and *P. chiapensis* that includes a large arid area from southern Texas into northeastern Mexico, which would be a further obstacle to dispersal (Martin and Harrell, 1957).

*Pinus chiapensis* is currently considered by many to be a separate species from *Pinus strobus* due to slight differences in the morphology of cone scales, differences in the nature of needle serrations, slight differences in needle width, ecological differences, and enormous geographical separation (Andresen, 1964; Styles, 1993). Species status of *P. chiapensis* is also supported by recent molecular studies (Syring et al., 2007). These molecular studies also indicate a genetic distinction between *P. chiapensis* and other Mexican white pines (Castro-Felix et al., 2008) and a close relationship between *P. chiapensis* and *P. strobus* (Gernandt et al., 2005).

The disjunct relationship between warm temperate taxa of the southeastern United States and the eastern escarpment of Mexico and Central America has long been of interest to biogeographers (e.g., Steyermark, 1950; Sharp, 1951; Braun, 1955; Martin and Harrell, 1957). Other species that occur with *P. chiapensis* also show this pattern, such as *Liquidambar styraciflua*, *Nyssa sylvatica*, *Carpinus caroliniana*, *Ostrya virginiana*, and the *Acer saccharum* group (Braun, 1955; Martin and Harrell, 1957). It's important to note that several of these taxa are also recorded from the Citronelle Formation, e.g., *Nyssa*, *Liquidambar*, *Carpinus*, and *Acer* (Stults, 2003).

There has been much discussion as to when elements of the Eastern Deciduous Forest flora became incorporated into parts of Latin America. Some, such as Axelrod (1986), argued that it occurred at least during the Eocene when these taxa were more widely distributed. Cenozoic maps of North America do not show obvious barriers to migration during that time (Smith et al., 1994; Scotese, 2004). Others contend that these taxa moved south to escape the climatic deterioration of the Pleistocene (Sharp, 1953). However, the large zone of aridity in the southwest had already developed and would have posed a major deterrent to plant migration (Martin and Harrell, 1957). Graham (1999) points out that fossil evidence for these taxa in Latin America is not present until the Mid-Miocene when overall global cooling begins. Furthermore, the evidence becomes more prevalent in the Pliocene indicating a relatively north to south direction in plant migration. Our identification of fossil white pines from the Citronelle Formation, and the indication that they were the predominant pines within this formation, requires seriously considering that the northeastern Gulf of Mexico Coastal Plain may have served as a link between primary and secondary centers of *Pinus* diversity in North America (Fig. 3).

## 5. Conclusion

Based on the pine fossils from the Citronelle Formation reported here, it appears that sometime between the mid-Pliocene and today, pine populations along the northeastern Gulf of Mexico Coastal Plain changed from being composed mostly of subgenus *Strobus* to entirely subgenus *Pinus* species. Without this paleobotanical evidence, the fact that white pines were more widespread in North America in the recent geological past than previously thought would not have been suspected. This is particularly intriguing because, for the most part, the angiosperm taxa identified from the Citronelle Formation are the same, or similar to those in the region today (Stults, 2003). These findings also call into question the hypothesis that species of *Pinus* section *Australes* have been dominant in the southeastern United States since the Eocene (Millar, 1993).

There is no clear understanding as to when the predominance of subgenus *Strobus* along the northeastern Gulf of Mexico Coastal Plain waned. Macrofossil evidence does not support the presence of the subgenus in the area from at least 18,000 yrs BP to the present. (Jackson et al., 1997), while pollen evidence suggests that a very small percentage of haploxylon-type pines may have existed slightly to the north of the Citronelle Formation as recently as 2000 years BP (Delcourt, 1980; Delcourt et al., 1983). It is possible that the current exclusion of *P. strobus* from the northeastern Gulf of Mexico Coastal Plains may be due to precipitation requirements rather than temperature, as the species prefers somewhat drier conditions than exist in the region today (Jacobson and Dieffenbacher-Krall, 1995). Although, as indicated previously, abundant precipitation does not deter *P. chiapensis*, and may suggest that the Citronelle pines are more closely related to that species. The presence of a haploxylon-type pine on the northeastern Gulf of Mexico Coastal Plain during the mid-Pliocene does not appear to indicate a cooler climate for the area as most of the other taxa currently identified from the Citronelle Formation are identical or very similar to the warm temperate to subtropical taxa occupying the area today. Additionally, preliminary climate studies on the Citronelle Formation indicate temperatures similar to what exists in the region today (Stults, 2003).

The fossils described here imply possible connections between disjunct species that would not be suspected if only current species ranges and ecological tolerances were considered. The recovery of additional material including ovulate cones would be required to definitively link the Citronelle white pines with modern species. It is significant in this context that the molecular study by Syring et al. (2007), which supported a close relationship between *P. strobus* and *P. chiapensis*, also implicated the western North American species

*P. monticola* but was unable to resolve which species was the progenitor of this triad. The fossils described here suggest that this could be due to a recent range contraction in one or more of these species, or that the progenitor was an extinct species perhaps represented by the Alabama and Florida fossils. In any case, these fossils clearly show that white pines were more widely distributed in the eastern United States during the Neogene than previously realized. They also significantly reduce the 2400 km disjunction between the white pines of the eastern United States and Mexico, and may provide part of the long-sought paleobotanical link and time constraint between primary and secondary regions of North American *Pinus* diversity.

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