Review of Palaeobotany and Palynology 155 (2009) 25–31

Contents lists available at ScienceDirect

Review of Palaeobotany and Palynology

journal homepage: www.elsevier.com/locate/revpalbo

Betulaceae from the Pliocene and Pleistocene of Southwest Alabama, Southeastern United States

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ARTICLE INFO

Article history:
Received 10 July 2008
Received in revised form 5 January 2009
Accepted 12 January 2009
Available online 22 January 2009

Keywords:
Betula
Betulaceae
Carpinus
Citronelle Formation
Pleistocene
Pliocene

ABSTRACT

Recent investigations of mid-Pliocene Citronelle Formation sites and a Pleistocene terrace deposit in southwestern Alabama have yielded fossils of the Betulaceae. Trullate (shield-shaped) leaves with evenly spaced, craspedodromous secondary veins and distinctively serrated margins indicate that *Betula nigra* was part of the Gulf Coast vegetation for at least the last three million years. This determination is supported by the presence of small, membranous-winged fruits and a tri-lobed catkin bract. Previous reports of a supposed ancestral species, *B. prenigra*, from the Citronelle Formation are reconsidered in light of the present findings and rejected. Oblong/ovate leaves with craspedodromous secondary veins, serrated margins, and acute/acuminate apices from the Citronelle Formation are assigned to *Carpinus caroliniana*. A characteristic nutlet bract of *Carpinus* was previously described from this formation, and here a staminate catkin with typical *Carpinus*-like bracts and *in situ* pollen provides additional support. A nutlet bract from the Pleistocene site confirms that *C. caroliniana* has been consistently present in this region. Some leaves suggestive of *Ostrya* were found but their identification is inconclusive. All sites produce *Alnus* pollen but no macrofossils were found. Of the ten species of Betulaceae in the southeastern United States today, only *Alnus serrulata, Betula nigra, Carpinus caroliniana*, and *Ostrya virginiana* frequent the Gulf of Mexico Coastal Plain. Our findings confirm that *Betula nigra* and *Carpinus caroliniana* were clearly established in the area by the mid-Pliocene and persisted to the recent, probably due to regional climatic stability.

1. Introduction

Considering the evolutionary, ecological, and economic significance of the Eastern Deciduous Forest of eastern North America, it is unfortunate that the fossil record of this biome is so poor, especially for the Neogene and Pleistocene. This situation compromises our ability to confidently reconstruct the recent evolution, biogeography, and climate history of this important floristic region. The paucity of information regarding the history of forests on the Southeastern Coastal Plain is particularly troubling, as this area is a significant locus of botanical diversity and endemism (Christensen, 2000). Scattered Miocene and Pliocene palynofloras have been documented from this region (e.g., Groot, 1991; Litwin and Andrle, 1992; Willard et al., 1993); however, substantial megafloras are known only from a brief account of the Miocene Brandywine flora in Maryland (McCartan et al., 1990), the recently discovered Late Miocene or Early Pliocene Gray Fossil locality in Tennessee (Shunk et al., 2006), and the mid-Pliocene Citronelle flora of south Alabama (Berry, 1916; Stults et al., 2002; Stults, 2003).

In 1916, Berry described eighteen taxa from the Citronelle Formation, some of which he ascribed to extant species (e.g., *Planera aquatica* J. F. Gmel., *Quercus nigra* L.) and some of which he designated as extinct species (e.g., *Trapa alabamensis* Berry). This list was used as support for application of a Pliocene age to the Citronelle Formation (Matson, 1916). Included in Berry's assessment were two leaves identified as *Betula prenigra* Berry which, identified as such, suggests they were immediate precursors of the extant *B. nigra* L.

Preliminary research on the Citronelle Formation by the authors (Stults et al., 2002; Stults, 2003) at Berry's original localities and several new ones has revealed a remarkable megafossil plant assemblage, and indicates that Berry's (1916) account barely scratched the surface of the palaeobotanical potential of the formation. One of the main goals of this ongoing research is to document the plant diversity of the Citronelle Formation and its importance to understanding the palaeoecology of the Late Neogene of eastern North America. Here, a description of the Betulaceae is presented that follows up on an earlier study (Stults et al., 2002) and includes information on several Pleistocene occurrences as well.

The Betulaceae is a woody angiosperm family within the Fagales consisting of six genera and between 125 and 150 species, most of which inhabit cool temperate and boreal regions in North America, Europe, and Asia (Abbe, 1935). The majority of species occur in Asia (Li and Skvortsov, 2001), 33 species occur in North America north of Mexico (Furlow, 1997), while a few species are present in the cooler,

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doi:10.1016/j.revpalbo.2009.01.001

montane regions of Mexico, Central America, and South America. Of the ten species of Betulaceae recognized in the lower latitudes and warm temperate areas of the southeastern United States (Furlow, 1990), eight are relatively common to the region, and only four (*Alnus serrulata* (Ait.) Willd., *Betula nigra* L., *Carpinus caroliniana* Walt., and *Ostrya virginiana* (Mill.) K. Koch.) extend into subtropical areas of the Gulf of Mexico Coastal Plain (Thompson et al., 1999).

Morphological phylogenetic studies typically recognize two subfamilies of the Betulaceae: the Betuloideae, composed of *Alnus* and *Betula*, and the Coryloideae, which includes *Carpinus*, *Corylus*, *Ostrya*, and *Ostryopsis* (Hall, 1952; Hardin and Bell, 1986). Recent studies based on molecular, morphological and palaeontological data also recognize these two clades (Chen et al., 1999; Yoo and Wen, 2002). The palynological record suggests that the Betulaceae probably originated in the temperate zones of Laurasia during the Cretaceous (Bratzeva, 1967; Miki, 1977; Sun et al., 1979; Muller, 1981). Macrofossils, including reproductive structures, of the extinct genera *Palaeocarpinus* and *Cranea* have been found in Paleocene deposits in Europe, China, and western North America (Crane, 1981; Crane et al., 1990; Sun and Stockey, 1992; Manchester and Chen, 1996; Manchester and Guo, 1996; Manchester and Chen, 1998; Pigg et al., 2003). Remains of the extinct genus *Asterocarpinus* have been recovered from the Oligocene of western North America (Manchester and Crane, 1987). Fossils of extant genera of the Betulaceae first appear in the Late Paleocene of Asia (Budantsev, 1982) and the Eocene of Europe (Chandler, 1963).

In North America, fossils of extant genera of the Betulaceae first appear in the Eocene, with reliable records of *Alnus* in the Early Eocene and Middle Eocene from Wyoming and Oregon (Crane, 1989), and *Betula* from the Middle Eocene of British Columbia and Oregon (Crane and Stockey, 1987; Meyer and Manchester, 1997). The earliest reliable North American records of the derived genera, *Carpinus* and *Ostrya,* appear later in Middle Eocene and Oligocene western sites (Wehr, 1995; Meyer and Manchester, 1997; Manchester, 1999; Pigg et al., 2003). Curiously, reliable post-Eocene *Carpinus* fossil records are unknown from North America until recently (Manchester, 1999; Stults et al., 2002).

In contrast to the records of western North America and Europe, the fossil record of the Betulaceae in eastern North America is poor, especially from the Neogene, due to the paucity of significant macrofossil plant sites from this time and place. Berry (1916) assigned two leaves from the Citronelle Formation to *Betula*, and Stults et al. (2002) documented the first unambiguous, post-Eocene record of *Carpinus* in North America based on a nutlet bract from the Citronelle Formation. Berry (1907) also described leaves of *B. nigra* and *C. caroliniana* from Pleistocene deposits in Russell County, Alabama.

Continued reinvestigation of the Citronelle Formation flora by the authors has resulted in the discovery of several taxa, some of which represent first records (e.g., *Liquidambar styraciflua* L. and *Platanus occidentalis* L.) (Stults, 2003). In this paper, leaves, fruits and a catkin bract identical to those of the extant species *B. nigra* are described. In addition to demonstrating the morphological stasis of this species for at least the last 3 million years, these fossils call Berry's (1916) *B. prenigra* identification into question. Also described from the Citronelle Formation are leaves and a catkin with *in situ* pollen referable to *C. caroliniana* from the same locality as the nutlet bract described previously (Stults et al., 2002). Finally, *B. nigra* leaves and a *C. caroliniana* nutlet bract are described from a Pleistocene terrace deposit from the banks of the Mobile River in south Alabama. In addition to providing the earliest records of these taxa, the fossils described here confirm that *B. nigra* and *C. caroliniana* have been important components of the southeastern U.S. vegetation since at least the mid-Pliocene.

2. Geological sites, materials and methods

The Pliocene fossils were collected from clay and siltstone at two Citronelle Formation exposures in southwest Alabama. One site occurs on the eastern shore of Perdido Bay in Baldwin County, Alabama (30°24.05′ N, 87°26.97′ W). This new locality is informally known as Perdido Park and is about 7 km north of Berry's (1916) Red Bluff site. The second site is in central Mobile County, Alabama and is informally known as Scarborough (30° 43.74′N, 88° 8.57′ W). It also produced the nutlet bract of *Carpinus* described previously (Stults et al.2002) and refigured here (Plate II, 3). As is typical of the Citronelle Formation, the sediments at all sites are dominated by highly weathered sand; however, the plant fossils occur in relatively uncommon, unoxidized clay and siltstone units.

The age and depositional environment of the Citronelle Formation have been controversial issues due to poor outcrops resulting from low topographic relief; lush modern vegetation cover; limited lateral continuity of facies and potential marker beds; and paucity of age-diagnostic fossils. Matson (1916) assigned a Pliocene age based mainly on Berry's plant identifications; however, several later workers proposed Pleistocene or Miocene designations (see historical review in Otvos, 1998). Otvos (1997) presented a synthesis of evidence from several sources clearly indicating that the Citronelle Formation is Pliocene, and was deposited between 3.4 and 2.7 mya. Otvos (2005) also provided compelling evidence that the Citronelle depositional environment was mainly a braided river system, but noted that muddy units at several localities indicate some deep meandering river channels. Several localities, such as Scarborough and Perdido Park, also include estuarine facies (Stults, 2003).

The Pleistocene fossils were recovered from a layer of silty clay within a terrace deposit at the base of a high bluff along the Mobile River in Mobile County, Alabama (31°01.45′ N, 88°01.25′ W). This site is informally known as Buck's Landing. The terrace deposits in this region remain poorly understood and dated. In order to better understand the age and nature of this deposit, a sediment sample from the plant-bearing unit was collected, shielded from light, and subjected to luminescence dating (Aitken 1985, 1998) at the Luminescence Dating Research Laboratory at the University of Illinois at Chicago. Two age analyses were performed. The first was under infrared excitation, which preferentially accesses the time-dependent signal from feldspars. The second was under blue light excitation, which accesses the quartz-based signal. The resolved ages on these two minerals were approximately 82 and 85 ka, respectively, and may be correlative with late stage 5 of the marine oxygen isotope record (Steve Forman, University of Illinois, personal communication, 2007).

The plant fossils are preserved as impression/compressions; however, the cuticles are not well preserved. Most of the fossils were observed directly on the matrix surface, but in some cases, dégagement under a dissecting microscope revealed additional features and finer details. Regular light microscopy, cross-polarization, and epifluorescence microscopy were utilized. Epifluorescence using a Nikon B3A filter produced results on some specimens without obvious organic material present (e.g., Plate I, 1–2). Although regular epidermal cells could not be seen (except those immediately surrounding the guard cells and occasionally on the major veins), guard cells and peltate trichomes were observed on the surfaces of several leaves from the Scarborough site (e.g., Plate I, 6). Apparently, enough organic residue remained on the matrix surface to epifluoresce. Pollen grains were removed from the *Carpinus* catkin using a fine needle with a small amount of glycerin jelly on the tip, transferred to slide, and examined using light microscopy.

Modern material used for comparative purposes came from the University of South Alabama (USAM) herbarium and additional locally collected specimens. Modern leaf samples were soaked in sodium hypochlorite to allow disintegration of the mesophyll enabling separation of abaxial and adaxial cuticles for epidermal comparisons. All of the specimens are deposited in the palaeobotanical portion of the USAM, except the previously described *Carpinus* nutlet bract, which is deposited in the National Museum of Natural History collections.