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Discovery of bald cypress fossil leaves at the Gray Fossil Site, Tennessee and their ecological significance.

Sara Brandon
East Tennessee State University

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Abstract

This study focuses on fossil *Taxodium* leaves found at the Gray Fossil Site in northeastern Tennessee where many 7-4.5 million year old plants and animals have been recovered. Identification of the leaves is based on comparison of leaf morphology and confirmed by leaf anatomy. The ecological implications of the fossil are discussed to understand the paleoecology and paleoclimate at the Gray site. It is concluded that the fossil plant along with many other plants lived by a large sinkhole lake under a little warmer-than-today's climate condition.

Keywords: *Taxodium*, Gray Fossil Site, bald cypress

1. Introduction

Taxodium is a genus within the family Cupressaceae that is commonly referred to as bald cypress (Farjon 2005). *Taxodium* is a winter deciduous conifer that grows in wet riparian areas with high humidity such as freshwater swamps and flood plains that are characteristic of the Southeastern United States (Kunzmann et al. 2009; Farjon 2005). *Taxodium* growth is inhibited by salinity over 1%, which keeps it from growing in areas that are flooded by seawater (Farjon 2005). A characteristic of the genus is the buttressed base and the pneumatophores, otherwise known as knees, which grow up and out of the water in these areas (Farjon 2005). These knees are an extension of the root system that is buried in permanently wet habitats (Farjon 2005).

The fossil record reflects that *Taxodium* from the Late Cretaceous of Europe and North America are the oldest known specimens of the genus (Farjon 2005; Kunzmann et al. 2009). A more varied and spread out *Taxodium* record has also been identified from Europe and North America during the Paleogene and Neogene (Kunzmann et al. 2009). Material recognized as *Taxodium* in the Miocene and into the Pliocene has been connected to riparian environments (Kunzmann et al. 2009). In the Tertiary fossil records *Taxodium* is common from the Western United States and extends down into the southeastern part of the country (Chaney 1950).

Taxodiaceae as a family was separated from Cupressaceae *sensu stricto* (s.s.) in the past based on the differing arrangement of leaves on a branch, or phyllotaxis, as shown by R. Pilger in 1926 (Farjon 2005). Through further morphological and anatomical analysis it has been noted that the two families can be merged as reflected by J.E. Eckenwalder in 1976 (Farjon 2005). The result of combining the two families of conifers is one family, Cupressaceae *sensu lato* (s.l.), which includes the genera from Taxodiaceae such as *Taxodium, Glyptostrobus, Metasequoia,* and *Sequoia* (Farjon 2005).

This paper focuses on a comparison of the characteristics of some of the genera of Cupressaceae s.l., including *Taxodium*, *Glyptostrobus*, *Metasequoia*, and *Sequoia*. Through comparison of these species, identification of the fossil specimen from the Gray Fossil Site as *Taxodium* is made possible. Once identification is confirmed, the information about the genus *Taxodium* is used to discuss the ecological implications of the finding of this fossil specimen at the Gray Fossil Site. Identification as *Taxodium* will support the current reconstruction of the Gray Fossil Site as a forested area including a ponded environment.

2. Materials and Methods

Gray Fossil Site

The fossil material was collected at the Gray Fossil Site of Washington County in northeastern Tennessee (Figure 1). Gray Fossil Site was exposed in May of 2000 during a road construction project (Shunk et al. 2006). The site has been characterized as a paleosinkhole that has filled by a deposit of clay, silt, and sand about 40 m thick (Wallace and Wang 2004). Findings of vertebrate species such as the tapir (*Tapirus polkensis*), rhino (*Teleoceras*), and the short-faced bear (*Plionarctos*) and floral species such as oak (*Quercus*), hickory (*Carya*), and pine (*Pinus*) suggest a forested area surrounded the sinkhole lakes between 7 and 4.5 million years ago in the late Miocene to early Pliocene (DeSantis and Wallace 2008; Wallace and Wang 2004).

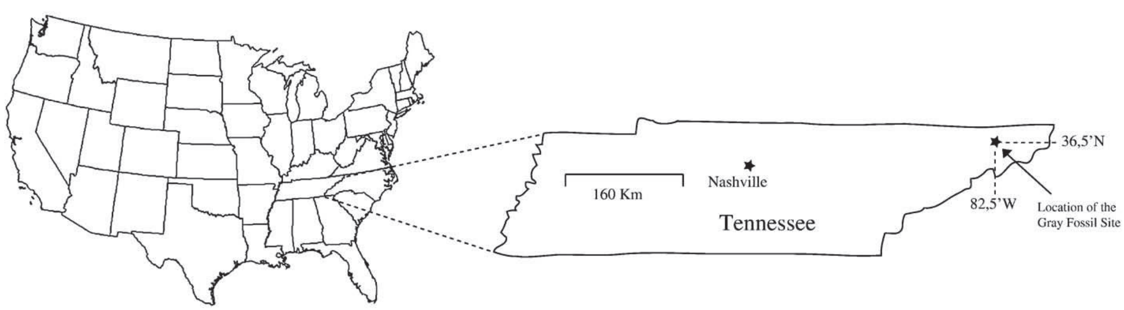


Figure 1: Location of Gray Fossil Site (after Liu and Jacques 2010)

Cuticle Analysis

Gymnosperms within the same family, such as Cupressaceae, have similar morphological characteristics that can make identification difficult (Kerp 1990). Differences between these genera are found in the microscopic features (Kerp 1990). The cuticle of these leaves can reflect the imprint of the epidermis, where specific patterns of epidermal cells and stomata are seen by different species of plants (Kerp 1990). A layer of dark material identifies fossils of gymnosperms with preserved cuticles (Kerp 1990).

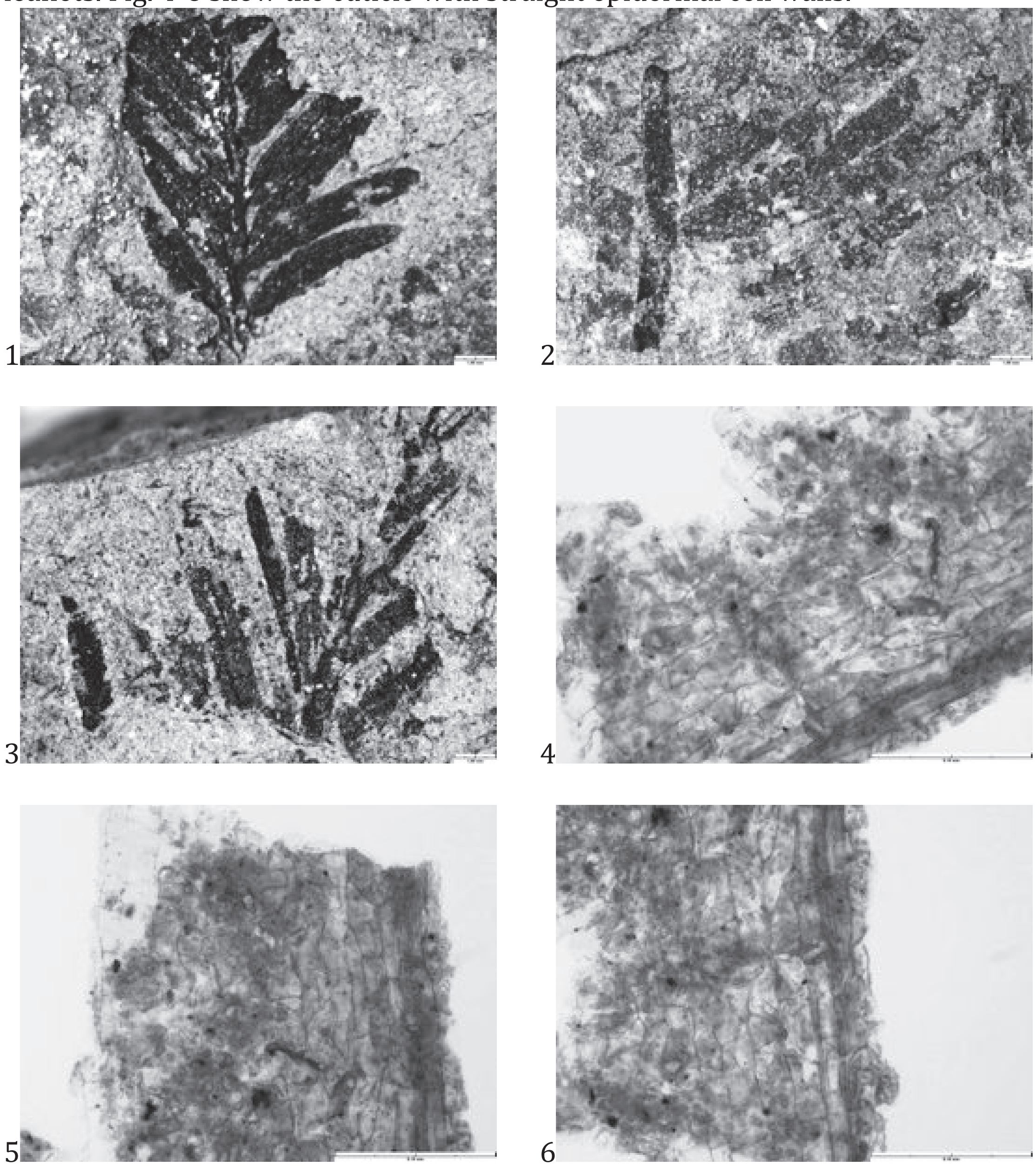
Thickness of the cuticle is important when choosing how to process the fossilized cuticle, since evergreen cuticles are thicker than those of deciduous trees (McElwain and Chaloner 1996). Once the cuticle has been processed by an oxidation technique, the characteristics of the cuticle can be used to identify the fossil (Kerp 1990). Shape and orientation as well as the type of walls and corners of the epidermal cells are used in characterization of the cuticle (Kerp 1990). Stomata, the pores in the leaves to facilitate gas exchange and water loss, are also an identifying factor (McElwain and Chaloner 1996; Kerp 1990). The stomata are characterized by orientation, types of surrounding cells, and frequency (Kerp 1990). Information gathered from the details of the cuticle not only identifies the fossil, but it also contributes to understanding the environment that the fossil came from (McElwain and Chaloner 1996).

Lab Process

Samples were taken from the fossil leaves using water on a brush and a dissecting needle to remove small pieces of the cuticle. Specimens were placed in concentrated nitric acid (HNO_3) overnight. The cuticle material was washed with distilled water and left immersed in distilled water for one week in a covered beaker. The oxidation process was not complete, and the samples were again immersed in HNO_3 for 2 hours. Once washed with distilled water, the cuticle was placed on a slide and viewed with OLYMPUS-SZX12 microscope. Digital images were taken using an attached Microfire camera. Measurements were made from the digital images using ImageJ (Version 1.46r).

3. Results

Plate 1: Images of fossil specimens (1-3) and cuticle (4-6). Scale bars: Fig. 1-3 = 1.0 mm, Fig. 4-6 = 0.1 mm. Fig. 1-3 show portions of a leaf with alternate attachment of leaflets. Fig. 4-6 show the cuticle with straight epidermal cell walls.



Fossil Description

The fossil specimens, shown in Plate 1 (Fig. 1-3), consist of linear leaves. The leaves are arranged in an alternate, or spiraled, manner around the stem. The leaf apex of the fossil specimen is acute, with leaf dimensions averaging at 4.3 mm long by 0.8 mm wide. The cuticle, shown in Plate 1 (Fig. 4-6), is characterized by straight epidermal cell walls with an average proportion of length to width of 2.9 to 1. No stomata could be recovered in the process.

4. Comparison and Discussion

The simple leaves of gymnosperms differentiate these trees from angiosperms (Farjon 2005). Based upon this fact, the specimen was immediately identified as a conifer. Cupressaceae has a widespread fossil record, with leafy cupressaceous fossils common in the Northern Hemisphere (Farjon 2005). The specimen was further classified as Cupressaceae based upon the identification of linear leaves, seen in mature leaves of the family Cupressaceae (Farjon 2005). Similar genera within this family are compared to identify the specimen.

Comparisons

Taxodium

Three types of leaves are present on a tree of *Taxodium*: linear, scale, and linear-subtulate (Farjon 2005). The linear leaves of *Taxodium* are characterized by a spiral phyllotaxy and acute apex of the leaves with dimensions averaging around 3-17 mm long by 0.7-1.5 mm wide (Chaney 1950; Kunzmann et al. 2009). Epidermal cell walls of *Taxodium* are straight, with a length: width ratio of 2-3:1 (Kunzmann et al. 2009). Stomata are distributed amphisotmatically in an orientation transverse to the midvein of the linear leaf (Farjon 2005).

Glyptostrobus

Linear, scale, and linear-subtulate leaves grow on *Glyptostrobus* (Farjon 2005; Ma et al. 2004). The linear leaves have an acute apex and a spiral phyllotaxy with dimensions of 15-30 mm long by 1.5-3 mm wide (Ma et al. 2004). The stomata are distributed amphisomatically in bands parallel to the midvein, and epidermal cells have an average length to width ratio of 4.2:1 with straight cell walls (Ma et al. 2004)

Metasequoia

The linear leaves of *Metasequoia* are on the branch in a decussate arrangement (Leng et al. 2001; Chaney 1950). Scale leaves are also present on trees in this genus (Farjon 2005). Linear leaves have an obtuse apex and have average dimensions of 8-35 mm long by 1-2.5 mm wide (Leng et al. 2001). Epidermal cells have a length to width ratio of 2.5:1, and the cell walls are undulate (Leng et al. 2001). The stomata have a hypostomatic distribution in bands parallel to the midvein (Leng et al. 2001; Chaney 1950).

Sequoia

Linear and scale leaves grow on *Sequoia*, with linear leaves growing in a spiral phyllotaxy (Ma and Li 2002; Farjon 2005). The linear leaves have dimensions on average of 3-23 mm long by 0.7-2.2 mm wide and an obtuse apex (Ma and Li 2002). Epidermal cells have straight walls and a length to width ratio ranging from 1:1 to 17:1 (Ma and Li 2002). Stomata can be amphistomatic or hypostomatic in a band parallel to the midvein (Ma and Li 2002).

Table 1: Comparison of Fossil with Genera of Cupressaceae

	Sequoia	*Metasequoia*	*Taxodium*	*Glyptostrobus*	Specimen
Leaf Shape	linear	linear	linear	linear	linear
	scale	scale	scale	scale	
			linear-subulate	linear-subulate	
Phyllotaxy	spiral	decussate	spiral	spiral	spiral
Leaf Apex	obtuse	obtuse	acute	acute	acute
Leaf Dimensions (mm) aver.	3-23 x 0.7-2.2	8-35 x 1.0-2.5	3-17 x 0.7-1.5	15-30 x 1.5-3	4.3 x 0.8
	evergreen	deciduous	deciduous	evergreen	
Walls of Epidermal Cells	straight	undulate	straight	straight	straight
Epidermal Cell Wall Proportions aver.	1:1 to 17:1	2.5:1	2-3:1	4.2:1	2.9:1
Stomata Distribution	amphistomatic	hypostomatic	amphistomatic	amphistomatic	
	hypostomatic				
Stomata Orientation	parallel	parallel	transverse	parallel	

Identification as *Taxodium*

The morphology and anatomy of the specimen support identification as *Taxodium*, shown in Table 1. The cuticle anatomy of the stomata was not observable with the sample, but there is enough evidence from the morphology to rule out other genera within Cupressaceae, based on phyllotaxy and leaf apex. The fossil exhibited an alternate, or spiral, leaf attachment, ruling out the possibility of identification as *Metasequoia*. *Sequoia* is not a correct identification based upon the leaf apex, which is obtuse instead of the acute apex of the fossil. The specimen is similar to *Glyptostrobus* in most characteristics except dimensions, but lab methods were able to rule out this genus. *Glyptostrobus* is an evergreen genus, but as such would have a thick cuticle for protection through the colder seasons. The cuticle of the specimen was thin, easily dissolving away during the first several attempts of oxidation in the lab. This suggests that the specimen would be from a deciduous tree, like *Taxodium*.

5. Ecological Significance

The variety of fossils discovered at the Gray Fossil Site has concluded that the area was a pond surrounded by a forested environment (Wallace and Wang 2004). The fossils also place the site in late Miocene to early Pliocene (7-4.5 million years ago) (Wallace and Wang 2004), which coincides with the change from C_3 to C_4 dominant flora (DeSantis and Wallace 2008). Species typically found in C_4 grasslands have not been found at the site, suggesting that the area served as a refugium for the animals present during the transition (Wallace and Wang 2004; DeSantis and Wallace 2008). Based on analysis of findings from the site, C_3 vegetation was dominantly present, with some C_4 grassland areas adjacent to the refuge site (DeSantis and Wallace 2008). *Taxodium* is found mixed with genera such as *Pinus* and *Quercus*, which were also found at the Gray Fossil Site within the forested area (Farjon 2005; Wallace and Wang 2004). The habitat of *Taxodium* is like that of the Gray Fossil Site, being a riparian environment (Kunzmann et al. 2009; Wallace and Wang 2004). Therefore, the identification of this fossil as *Taxodium* is ecologically consistent with the present interpretation of the Gray Fossil Site.

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