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Systematics, Climate, and Ecology of Fossil and Extant Nyssa (Nyssaceae, Cornales) and Implications of Nyssa grayensis sp. nov. from the Gray Fossil Site, Northeast Tennessee

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Systematics, Climate, and Ecology of Fossil and Extant *Nyssa* (Nyssaceae, Cornales) and

Implications of *Nyssa grayensis* sp. nov. from the Gray Fossil Site, Northeast Tennessee

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by

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ABSTRACT

Systematics, Climate, and Ecology of Fossil and Extant *Nyssa* (Nyssaceae, Cornales) and

Implications of *Nyssa grayensis* sp. nov. from the Gray Fossil Site, Northeast Tennessee

by

Nathan R. Noll

The Late Hemphillian (latest Miocene or earliest Pliocene, 7-4.5 Ma) Gray Fossil Site in

northeastern Tennessee is interpreted to represent a lacustrine paleokarst fed by a river or

stream. This research focuses on the morphological and systematic relations of *Nyssa*

endocarps (fruit pits) from the fossil site to extinct and extant *Nyssa* species. A

combination of metric and nonmetric traits allows recognition of a new species: *Nyssa*

grayensis sp. nov. This fossil species shares the most similarities with the extant *Nyssa*

ogeche Bartram ex Marshall from southeast North America and the Eocene fossil *Nyssa*

eolignitica Berry from western Tennessee. Affinities with *Nyssa ogeche* Bartram ex

Marshall suggest a warmer winter climate than the present and periodically fluctuating

water levels. Fossil vertebrates (*Alligator*, *Heloderma*, *Hesperotestudo*) and plants (Fossil

relatives of *Ilex vomitoria, Quercus virginiana, Taxodium, Acer leucoderme*) with

modern counterparts distributed in areas with mild winters support this interpretation.

ACKNOWLEDGEMENTS

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CHAPTER 1

INTRODUCTION

The Gray Fossil Site (GFS) in the Southern Appalachians of northeast Tennessee is interpreted to have been a series of coalesced sinkholes that developed into a lacustrine environment, at one point reaching a surface area of 1.8-2.0 ha and a depth up to 39 m (Wallace and Wang 2004; Shunk et al. 2006). The sediments are dominated by clay, silt, and fine-grained sands with interspersed deposits of gravel that may have been deposited by a stream that fed the small lake.

The occurrence of the short-faced bear *Plionarctos* and the rhinocerid *Teleoceras* has been used to constrain the age of the uppermost layers of the fossil site to the Late Hemphillian (latest Miocene to Early Pliocene; ca. 7-4.5 Ma) land mammal age (Parmalee et al. 2002; Wallace and Wang 2004). This age makes the Gray Fossil Site especially important because Neogene fossil sites in eastern North America are very rare, especially toward the coast. The only other significant Neogene megafloras in the eastern United States are the early Miocene (~20 Ma) Brandon Lignite in Vermont (Tiffney 1994), the Late Miocene or early Pliocene Brandywine Formation in Maryland (McCartan et al. 1990), and the Pliocene (~2.7-3.4 Ma) Citronelle Formation of Alabama, Florida, and surrounding areas in the Gulf Coast (Stults et al. 2010; Stults and Axsmith 2011a; Stults and Axsmith 2011b; Stults et al. 2011). The Pipe Creek Sinkhole is more inland than the above mentioned sites but is also of closer proximity to the GFS than fossil sites in the Great Plains. Like the GFS, the Pipe Creek Sinkhole in Indiana is Late Hemphillian in age based on the co-occurrence of *Plionarctos* and *Teleoceras* (Farlow et al. 2001; Farlow and Argast 2006).

The age of the GFS also falls within an important nearly global transition of plants being dominated by a C3 photosynthetic pathway to plants being dominated by the C4 photosynthetic pathway (DeSantis and Wallace 2008). Floras from this time are typically characterized to have been grasslands based on paleobotanical remains, tooth crown morphology of vertebrates, and isotopic signatures of bone and teeth (MacFadden 1999), but this representation is made with a poor understanding of the fossil record in eastern North America. The dominant plant macrofossils and pollen at the GFS are *Quercus* (oak) and *Carya* (hickory) followed by *Pinus* revealing a forest or forest-woodland setting (Ochoa et al. 2012). The common presence of vines such as *Vitis* (grape) (Gong et al. 2010), *Sinomenium* (moon-seed) (Liu and Jacques 2010), and *Sargentodoxa* (blood-vine) (Ochoa et al. 2012) further support the presence of a forested setting.

The presence of *Tapirus* at the GFS supports the presence of a forested setting as extant tapirs in both the new world and old world prefer closed canopy forests (DeSantis and Wallace 2008). The isotopic signatures from *Tapirus polkensis* Olsen, Tayassuidae, and Camelidae from the GFS suggest a browse-rich diet of C3 plants (DeSantis and Wallace 2008). A fragment of a Gomphotheriidae (Shovel-tusked proboscidean) tusk has an isotopic signature suggesting a C4 graze diet, meaning that this individual likely had access to a grassland or prairie environment at some point during its life (DeSantis and Wallace 2008). Poaceae (grass-family) pollen is not common at the GFS and much of the grass pollen present is believed to be from the native bamboo *Arundinaria* (Ochoa et al. 2012), although the presence of woodland prairies restricted in area or geologically short-lived may be hard to detect within an overall forested history of the fossil site.

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Gomphotheres, like modern members of the order Proboscidea (elephants and their relatives), likely traveled long distances during their life, so it is not clear if the animals grazed locally or if they consumed grasses or other C4-plants elswhere.

Aquatic plants and hydrophilic plants are found at the site, including Nymphaceae (water lilies), Cyperaceae (sedges), *Taxodium*, *Cicuta* type pollen (poison hemlock), *Liquidambar* (sweet gum), *Betula* (Birch), *Arundinaria* (river cane), and *Salix* (willow) (Ochoa et al. 2012), supporting the presence of a lacustrine environment. Aquatic and hydrophilic fauna are found as well, including Centrarchidae (sun-fish and bass), Castoridae (beaver), Bivalvia (clams), aquatic Gastropoda (snails), *Rana* (ranid frogs), *Alligator*, and multiple types of Testudines (turtles) (Boardman and Schubert 2011). The abundance of vertebrae from lungless plethodontid salamanders indicates that the terrestrial environment surrounding the sinkholes was moist enough, at least seasonally, for survival of these animals (Mead et al. 2012).

Previously unreported endocarps (fruit pits) of *Nyssa*, another plant genus with hydrophilic species, have been recovered at the GFS. This adds to the Miocene and Pliocene reports of *Nyssa* in eastern North America previously recorded at the Citronelle Formation of Alabama (Stultz and Axsmith 2011a) and the Brandon Lignite (Eyde and Barghoorn 1963). Within Tennessee the only fossils of *Nyssa* reported are from the Eocene Claiborne Group in West Tennessee (Dilcher and McQuade 1967).

Fossil and rbcL molecular clock data (Figure 1) support a rapid diversification of the basal eudicots during the Early Cretaceous (124-120 Ma) followed by the evolution of the core eudicots (120-115 Ma) (Anderson et al. 2005). *Nyssa* falls within the asterid clade of the core eudicots, which has been estimated to have arisen by 112-109 Ma

(Anderson et al. 2005). The order Cornales is believed to be one of the earliest diverging clades within the asterids, originating between circa 109 and 97 Ma (Anderson et al. 2005). The antiquity of cornalean taxa is supported by fossils of *Hironoia fusiformis* Takashi, Crane et Manchester (Cornaceae) from the Cretaceous Futaba Group (ca. 87 Ma) in Japan (Takahashi et al. 2002).

The genus *Nyssa* was once placed in the family Cornaceae but is now placed in a separate family, Nyssaceae. This family includes the extant genera *Campotheca* and *Davidia* as well as some extinct fossil genera (Wen and Stuessy 1993; Eyde 1997). The molecular data from Xiang et al. (2011) supports monophyly of Nyssaceae and suggests that *Nyssa* and *Camptotheca* may have diverged from each other during the late Cretaceous or early Paleocene (Figure 1). *Mastixia* and *Diplopanax* (Mastixiaceae) are closely related to the Nyssaceae. These extant genera and their extinct counterparts have been frequently termed the "Mastixiods" (Xiang et al. 1998).

FIGURE 1: Phylogeny And Molecular Clock Of The Cornales. Modified from Xiang et al (2011).

Nyssa-like pollen has been found in France and North America from the Paleocene, but the oldest known Asian *Nyssa* fossils are from the Oligocene (Wen and Stuessy 1993). *Nyssa* macrofossils are common throughout the Northern Hemisphere starting in the Eocene (Wen and Stuessy 1993). The earliest *Nyssa* endocarps are known from the Lower Eocene London Clay floras (Wen and Stuessy 1993). While *Nyssa* was once wide-spread throughout the Northern Hemisphere, the 7 extant species of *Nyssa* have a disjunct distribution (Figure 2), nearly all extant members naturally occur in eastern North America or eastern Asia (Wen and Stuessy 1993). One species, *Nyssa talamancana* Hammel and Zamora, is found in Central America and Panama (Hammel

and Zamora 1990). *Nyssa javanica* (Blume) Wangerin extends just south of the equator in Java and the surrounding islands (Eyde 1963).

Figure 2: The Distribution of Extant *Nyssa* Species. Modified from Wen and Stuessy (1993)

The extant species of *Nyssa* in North America are *Nyssa sylvatica* Marshall, *Nyssa ogeche* Bartram ex Marshall, and *Nyssa aquatica* Linnaeus (Eyde 1997). *Nyssa sylvatica* Marshall was formerly split into several species including *Nyssa biflora* Walter and *Nyssa ursina* Small, but these taxa are now considered varieties of *Nyssa sylvatica* Marshall (Wen and Stuessy 1993; Eyde 1997). Eyde (1997) suggested that there are at least 4 valid species of *Nyssa* in Asia, including *N. javanica* (Blume) Wangerin, *N. shangszeensis* Fang and Soong, *N. shweliensis* (Smith) Airy-Shaw, and *N. sinensis* Oliver. The Qin and Phengklai (2007) description of the genus in the Flora of China

recognizes 3 additional species, *N. leptophylla* Fang and Chen, *N. yunnanensis* Yin ex

Qin & Phengklai*, and *N. wenshanensis* Fang and Soong. Wang et al. (2012) used

morphological and molecular characters to show that the only distinct Asian species are

Nyssa sinensis Oliver, *Nyssa javanica* (Blume) Wangerin, and *Nyssa yunnanensis* Yin ex

Qin & Phengklai, with *N. shangszeensis*, *N. shweliensis*, *N. wenshanensis*, and *N.

leptophylla* reduced to synonyms of *Nyssa sinensis* Oliver.

Previously undescribed *Nyssa* endocarps have been recovered from the Mio-

Pliocene Gray Fossil Site. The goals of this research were to a) determine the *Nyssa* taxon

or taxa that are most similar to the fossil species at the Gray Fossil Site; b) offer

environmental, climatological, and ecological interpretations of the GFS based on the

systematic relations of the fossils; and c) compare the interpretations based on the *Nyssa*

fossils with evidence from other plant fossils, animal fossils, and geological observations.

Some of the best information about the fossil species of *Nyssa* may be held in the

living species. The sizes of fruits and seeds of some species have been correlated with

climatic conditions, environmental settings, and disperser sizes. Jordano (1995) found

that fruit sizes are positively correlated with disperser size across a variety of angiosperm

families. Eriksson et al. (2000) found that larger fruit sizes are favored by closed-forest

vegetation compared to more open environments. Climate also appears to play a role in

the size of many fruit species. Nakanishi (1996) found that the average size of fruits in

warm-temperate regions of Japan were larger than fruits from cold-temperate regions,

and Moles et al. (2007) found a negative correlation between latitude and fruit size in a

study including 11,481 species from around the globe. Because there is a large range of

fruit and endocarp sizes among both the extant and extinct species of *Nyssa*, the relation

of the fruit and endocarp dimensions of modern species with climatic conditions were investigated in this study. The relatively large sizes of the *Nyssa* endocarps from the Gray Fossil Site raise questions about the climatic and ecological significance of fruit size in this species.

CHAPTER 2

MATERIAL AND METHODS

The fossils used in this study were collected from sediments excavated from the Late Hemphillian (Latest Miocene to Earliest Pliocene) Gray Fossil Site located in Washington County of northeastern Tennessee (36.5°N, 82.5°W). The majority of the specimens were recovered during postexcavation screen-washing and screen-picking, although some specimens were recovered during excavation or from within field jackets surrounding vertebrate remains. The screen-washed sediments were from undisturbed laminated sediments composed mostly of organic rich clay-sized sediments, with periodic lenses of sand and silt. Some of the *Nyssa* fossils were recovered from within the coarser-grained lenses. The fossils were recovered within the same horizon as many other plants such as *Quercus*, *Carya*, *Vitis*, and *Sinomenium*. The fossils were also recovered within the same horizon as vertebrate remains including *Tapirus*, Tayasuidae, *Pristinailarus*, *Arctomeles*, turtles, fish, and many others. The methods used to separate the fossil materials were based on Tiffney (1990).

The fossils were separated from the clay using 1.7 mm meshed screen-washing boxes and air dried before being packaged into bags. Initial separations of plant and animal macro- and micro-fossils were made. Fossils preliminarily identified as *Nyssa*, based on shape, surface sculpture (ridges and grooves), and the presence of valves, were screen picked from the separated bulk plant fossils and saved for further identification. Fragments appearing similar to *Nyssa* were saved for further identification to limit collection bias. Excavation data including the quadrant numbers, test pit numbers, and dates were recorded for each of the 19 fossils from the Gray Fossil Site (Table 1a). Fossil

endocarps were prepared by placing them in 100% ethanol and running them in an

ultrasonic cleaner for 5-10 minutes to help remove adhering sediments.

Table 1a: *Nyssa* Fossils from the Gray Fossil Site

Catalog Number	Field Data
ETMNH 14024	9/13/007-002 C1-3, from small jacket with scapula
ETMNH 14025	10/13/06 001 K1-3
ETMNH 14026	Big Boy Skull 9.24.04.006
ETMNH 14027	From ETMNH 11639, Field number 061009, TP-2-2004 Sq AD 10-5-06
ETMNH 14028	TP-2-2004 SqE-10
ETMNH 14029	TP-2-2004 Spring cleanup 2007
ETMNH 14030	TP-2-2004 SqE-10
ETMNH 14031	TP-2-2004 SqT-10
ETMNH 14032	TP-2-2004 Sq-Q, Started 2-8-09
ETMNH 14033	TP-2-2004 Wall collapse
ETMNH 14034	No data, Screened June 2007
ETMNH 14035	TP-2-2004 Sq-W-10
ETMNH 14036	TP-3-2011, 371-103, 8-10-11-u4
ETMNH 14037	TP-2-2004 SQ-U, 7-14-06, Shell fragments surrounding specimen, with clay and silt
ETMNH 14038	TP-2-2004 SQ A and W 7/24/06 Near and under "snapir" tapir individual with articulated vertebrae
ETMNH 14039	TP-2-2004 SQA 7/17/06, found with ETMNH 14040, surrounded by sand and silt
ETMNH 14040	TP-2-2004 SQA 7/17/06, found with ETMNH 14039
ETMNH 14041	10-11-11-01 A1-4, F.J.
ETMNH 14042	From ETMNH 11639, Field Number 061009

Modern material for comparison were examined at or loaned from the Duke

University Herbarium and the University of Florida (UF) Paleobotany modern

comparative collection. Fallen fruits were collected from the arboretum of the University

of Florida, Gainesville; the East Tennessee State University Arboretum; Smith Lake

Oxbow, NC; Willow Spring Park in Johnson City, TN; the W.B. Clark Preserve, TN; the

arboretum of the Kunming Botanical Institute in Kunming, Yunnan Province, China; and

specimens of *Nyssa talamancana* Hammel and Zamora from the personal collections of

Dr. Hammel collected in Limón, Costa Rica (9°38'30"N, 83°08'30"W). The data from

these specimens were supplemented by the herbarium specimens studied by Eyde (1963)

and the data collected by Wang et al. (2012). The modern Nyssaceae specimens used in

this study are listed in Table 1b and with a more detailed list provided in Table 8

(Appendix, pg 120). Subspecies of *Nyssa* were not separated in the analyses. Consistent

differences between *N. sylvatica* var. *sylvatica* and var. *biflora* were not observed in the

study, although the largest endocarps within this species came from *N. sylvatica* var.

biflora. The other, less commonly accepted varieties used in this study also lacked

consistent differences. In preliminary phylogenetic analysis shared by Dr. Jenny Xiang

the various varieties of *N. sylvatica* were intermixed. Further investigation should be

made in order to determine the roles of genetic and environmental differences in these

varieties.

Table 1b: Specimens of Extant *Nyssa* Species Used in This Study

Taxon	Varieties	# Whole Fruit	# Endocarps
Nyssa sylvatica Marshall	*N. sylvatica* var. *sylvatica*	316	356
	N. sylvatica var. *biflora*	24	24
	N. sylvatica var. *ursine*	2	2
	N. sylvatica var. *caroliniana*	2	2
	N. sylvatica var. *bicolor*	0	3
	Total for all varieties	344	387
Nyssa sinensis Oliver	N/A	200	220
Nyssa aquatica Linnaeus	N/A	17	40
Nyssa ogeche Bartram ex Marshall	N/A	46	79
Nyssa talamancana Hammel and Zamora	N/A	6, plus data from Hammel and Zamora (1997)	4, plus data from Hammel and Zamora (1997)
Nyssa javanica (Blume)	N/A	50 from	50 from

Table 1b (continued)

Wangerin		Wang et al. (2012)	Wang et al. (2012)
Nyssa yunnanensis Yin ex Qin & Phengklai	N/A	50 from Wang et al. (2012)	50 from Wang et al. (2012)
Complete list of localities and herbarium or catalog numbers provided in Table 8, Appendix. Maximum dimensions of fruits and endocarps include specimens reported by Eyde (1997); Hammel and Zamora (1990); and Wang et al. (2012).			

After initial measurements, specimens representing modern comparative material (fresh and dried fruits) were soaked overnight in a dilute (10%) solution of NaOH, prepared by adding 10.0 mg of pure NaOH pellets to 100 mL of distilled water. This helped soften the fleshy covering surrounding the endocarps. Soaked fruits were found to provide an accurate estimate of original fruit size. After removing the bulk fleshy tissue, the endocarps were scrubbed with a toothbrush, placed in ethanol, and left in the ultrasonic cleaner for 5-10 minutes. Both the fossil and modern specimens used in SEM analysis were soaked in 100% acetone to draw out water and ethanol, then placed under negative pressure (-25 psi) for at least 3 days to allow degassing. When cross-sections of fruit were made, specimens were partially embedded in Ward's bio-plastic liquid casting plastic to assist cutting. Pieces of the endocarps 1cm or smaller were mounted on SEM stubs using acid free double sided sticky tape or double sided copper tape and gold sputter coated within a chamber of Argon gas using an EMITECH K500X. Because sections of *Nyssa talamancana* were larger than the preferred size, a wire-bridging method from Lametschwandtner et al. (1980) was used to avoid charge build up. Small pieces of copper wire were connected between the top of the specimen and the metal plate before sputter coating. SEM analysis was conducted using the Zeiss DSM 940 SEM. Specimens were examined for structural similarities and differences among the fossil and extant species. Some of the character states examined included size and shape

of the endocarp and germination valve, the position of vascular bundles relative to grooves and ridges, and the orientation of fibers throughout the endocarp.

Figure 3: Schematic Drawing of a *Nyssa* Fruit. Outer layers cut away to expose the endocarp. The labeled parts include the pedicel (P), the fleshy mesocarp (M), endocarp (E), grooves (G), Ribs or ridges (R), and the germination valve (V).

The traits of fossil *Nyssa* species used in systematic comparisons and the construction of a key to the extant and extinct *Nyssa* were based on the original photographs and descriptions of the holotypes and taxonomic revisions (Table 2). Descriptions of *Nyssa* published in a non-Latin alphabet were transcribed using Lexilogos Multilingual Keyboard (Negre 2002-2012), and translated using Google Translate (Google 2012). Additional traits noted by Eyde (1997) were also sometimes

noted in the key. When possible, the size range of a fossil fruit included the size range of

all specimens attributed to that species rather than those at the type locality alone.

Table 2: *Nyssa* Fossil Fruit Species and Sources Used to Construct the "Key to *Nyssa* Fruit Species"

Species:	Sources:	Age and Location of Type Specimen:
Nyssa aspratilis Eyde & Barghoorn (Nyssa rugosa Miki non Weber) (n=13)	Eyde and Barghoorn (1963); Miki (1956)	Pliocene Honshû, Japan
Nyssa bilocularis (Reid & Chandler) Chandler (n=3; n=4)	Chandler (1961); Reid and Chandler 1933; Eyde (1997)	Eocene London Clay, England
Nyssa boveyana Chandler (n=24)	Chandler (1957); Eyde (1997)	Mid. Oligocene Bovey Tracey, Devon, England
Nyssa brandoniana (Lesquereux) Eyde and Barghoorn (n=50)	Lesquereux (1861); Eyde and Barghoorn (1963)	Early Miocene, Brandon, Vermont
Nyssa eolignitica Berry (n=7)	Berry (1916); Berry (1930); Dilcher and McQuade (1967)	Eocene, Henry Co., Western TN
Nyssa fissilis (Lesquereux) Eyde and Barghoorn (n=750)	Lesquereux (1861); Eyde and Barghoorn (1963)	Early Miocene Brandon, Vermont
Nyssa complanata Eyde and Barghoorn (n=250)	Eyde and Barghoorn (1963); Eyde (1997)	Early Miocene Brandon, Vermont
Nyssa cooperi Chandler (n=1)	Chandler (1961)	Eocene London Clay, England
Nyssa disseminata (Ludwig) Kirchheimer (n=5; n=3)	Ludwig (1857); Mai (1965); Mai (1973); Mai and Walther (1978); Stachurska et al. (1971)	Villafranchian (Upper Pliocene- Lower Pleistocene) Berlin, Germany
Nyssa lescurii (Hitchcock) Perkins (n=13, ~50 identified total)	Hitchcock (1862); Perkins (1904); Eyde and Barghoorn (1963)	Early Miocene Brandon, Vermont
Nyssa magnifica (Knowlton) Berry (n=1)	Knowlton (1926); Berry (1929); Eyde and Barghoorn (1963)	Miocene Spokane, Washington
Nyssa multilocularis (Reid & Chandler) comb. nov. (n=5)	Reid and Chandler (1933)	Eocene London Clay, England
Nyssa ornithobroma Unger (n=4; n=10)	Unger (1860); Mai (1973); Mai and Gregor (1982); Mai (1964); Bůzek (1960); Bůzek (1971)	Lower Rhine Basin, Westphalia, Germany

Table 2 (continued)

Nyssa oviformis Reid (n=2)	Reid (1927)	Brittany, France
Nyssa pachycarpa Miki (n=73)	Miki (1956)	Pliocene Honshû, Japan
Nyssa scottii Manchester (n=6)	Manchester (1994)	Clarno, Oregon
Nyssa spatulata (Scott) Manchester (n=4; n=25)	Manchester (1994); Scott (1954)	Eocene, London Clay (Name revision published with description of Clarno, Oregon specimens)
Nyssa texana Berry (n=11)	Berry (1924); Eyde and Barghoorn (1963)	Eocene Two miles SW of Lufkin, TX

Macroscopic and microscopic features of the endocarps from the Gray Fossil Site and each of the extant *Nyssa* species were studied and photographed using an Olympus-SZX12 stereomicroscope and a MicroFire-Optronics camera. Because the fossil endocarps and most of the endocarps of extant species were too large to photograph the entire specimen, a Canon PowerShot SD870 IS Digital Elph was used to photograph the specimens.

Macro-features analyzed in this report include endocarp dimensions, proportions of morphological features, types of vasculature and associated surface ornamentation, and the number of surficial grooves and ridges. Macroscopic features of specimens were measured using a Fisher Scientific scale bar and digital calipers.

Metric traits of the extant species were compared with climate data from the modern range of these species. The modern climatic averages used in the study (Table 5) were gathered from the climate profiles of cities on the Weather2 website based on data from "World Meteorological Organization GTS land, ship and data buoy observations; Global weather satellite imagery from both polar orbiting and geostationary satellites; NCEP Global Forecast System atmospheric mode output (to 16 days); ECMWF atmospheric

model output; and the Japan Meteorological Agency atmospheric model for northern Asia (Weather2 website 2012)". Definitions of the climatic variables for the sake of this study are listed in Table 3. Correlation coefficients and associated P-values were calculated using MINITAB. Correlations were made with fruit and endocarp dimensions against climatic and latitudinal variables (Table 7).

The Pearson's correlation coefficient (r), P-value (P), and r^2 values were used to test the strength of the correlations and hypothesis testing. The absolute value of the Pearson's correlation can be between 0.0 and 1, with the value of 1 being a perfect correlation. Values of r greater than about .80 are generally considered to have high correlation, and values between .60 and .80 usually indicate good correlation (Jeng et al. 2000). The sign of the r value indicates directionality of the correlation with negative values indicating an inverse relationship. The P-values of the correlations were adjusted by multiplying the original P-values by 124, the number of comparisons between climate and fruit size made. This method is based on the Bonferroni Correction procedure described in Holm (1979) and is used to make the statistical interpretations more conservative.

Climatic interpretations based on the proposed systematic relations of the *Nyssa* fossils from the GFS, and the sizes of the fossil endocarps, were compared with other sources of climatic data. These separate pieces of climatic evidence include climatic estimates calculated by Dr. Liu using the Coexistence Approach (originally developed by Mosbrugger and Utescher 1997), the distribution of plants and animal taxa with related taxa preserved at the Gray Fossil Site, and the climatic interpretations of Zachos et al. (2001; 2008).

Table 3: Definitions Of Variables Used To Correlate Climate With Endocarp Size

Variable:	Definition Used:
North Low	Coldest month mean low temperature for the coldest point in the geographic range of the species.
North Latitude	The northernmost latitude reported for a species.
South Latitude	The southernmost latitude reported for a species.
Cold Month Mean	The average of the high and low temperature of the coldest month for the coldest point in the geographic range of the species.
Record Low	The absolute minimum low temperature for the coldest point in the geographic range of the species.
Mid. Latitude	The midpoint between the most northern and most southern latitudes of the distribution.
Mid. Main Distribution	Middle latitude for the main distribution excluding isolated outliers of *Nyssa sylvatica* Marshall in Chiapas Mexico and the Florida Keys.
Latitudinal Breadth	Difference in the northern and southern extreme for a species.
Stone	An inner layer of fruit (endocarp) which is lignified or "woody."
Max. Stone Length	The maximum stone length of a species within +/- one SD of the mean.
Min. Stone Length	The minimum Stone length a species' mature fruit.
Mean Fruit Width	The mean width of a complete fruit including the mesocarp and exocarp.

CHAPTER 3

RESULTS AND DISCUSSION: *Nyssa grayensis sp. nov.*

Systematic Description of *Nyssa grayensis sp. nov.*

The combination of metric and nonmetric traits found in the *Nyssa* specimens

from the Gray fossil site are found to be unique and a new species is recognized as

follows:

Order Cornales Dumortier 1829
Family Nyssaceae Jussieu ex Dumortier 1829
Genus *Nyssa* Linnaeus 1753

Nyssa grayensis sp. nov. Noll et al. (Plates 1-3)
Holotype: ETMNH 14024
Paratypes: ETMNH 14025-14042
Repository: East Tennessee State University and General Shale Natural History Museum
Fossil Collections.
Type Locality: The Gray Fossil Site, Washington County, northeastern Tennessee, USA
(36.5°N, 82.5°W).
Stratigraphic position: near the top layer of the laminated black clay.
Age: Late Hemphillian (7–4.5 Ma, latest Miocene to earliest Pliocene).
Etymology: The specific epithet 'grayensis' has been chosen in reference to the type
locality; The Gray Fossil Site.

Specific Diagnosis: Endocarp with 2 (-3) locules and one triangular valve per locule,
within the apical half of the endocarp. Outline fusiform with apical and basal ends
usually tapering steeply. 17-20 (-23) vascular grooves on the surface, sometimes partially
obscured by an outermost layer(s) of transverse fibers. Posessing a central axis without
vasculature. Prominent vascular groove running from apex to base and aligned with the
center of the valve. Grooves tending to have clusters of two or more bundles, or closely
paired grooves. Endcarp length ranging from (21.5-) 25.0-33.3 mm long. Endcarp width
circa 11-15 mm, though somewhat flattened. Many layers of longitudinal fibers forming
the innermost layer of the endocarp, central portion of endocarp wall composed of
randomly oriented fibers.

Description: Endocarps with 2 locules (n=17), or less frequently 3 locules (n=2). Mean
endocarp length 28.02 mm, SD= 2.85, n=13. Smallest endocarp (ETMNH 14029) 21.5
mm long, with the second smallest complete endocarp having a length of 25.0 mm.
Longest complete endocarp (ETMNH 14025) 33.3 mm long. Mean width of complete
endocarps 13.2 mm, SD=1.4, n=13. Length to (maximum) width ratio ranges from 1.79
to 2.56, with a mean of 2.15, SD=.26, N=13. Six of 19 endocarps incomplete along their
length, reaching minimum lengths of 17.1-22.0 mm and maximum widths of at least

11.0-15.0 mm. Endocarps composed of fibers. Fibers tangentially arranged, perpendicular to the length of the endocarp in the outside layers of the endocarp, longitudinally arranged in the innermost (avg. 12-15 fibers; circa 110-150 μm) layers on the inside of the endocarp (Figures 28-29; 38-39), and randomly arranged between these layers (Figures 8-9). Fibers surrounding vascular bundles running parallel with the bundles. Outermost layers of the endocarp often cover some of the grooves and bundles. Prismatic crystals <0.1 mm to >1.5 mm scattered amongst the fibers. Endocarps usually having at least 17 grooves, sometimes as many as 23, mean 18.9; SD= 1.51, n=17. Grooves often having multiple vascular bundles grouped together within them. Ridge width highly variable, sometimes less than 1 mm wide when grooves are closely paired, or up to several mm wide when further spaced apart. Ridges sometimes quite narrow when the bundles are close together, especially toward the ends of the endocarp. Outline of endocarp fusiform with apex and base steeply arching to a point. Dorso-ventrally compressed, but exaggerated by compression. Apex of endocarp often having a raised rim. The valves of the endocarp extend between 29.9-50.0% (mean =37.63, SD=7.03) of the length of the endocarp toward the base. Base of the valves ranging from 7.9-12.1 mm (mean=9.7mm, SD=1.65, n=7) wide.

Plate 1

ETMNH 14024

ETMNH 14025

ETMNH 14026

ETMNH 14027

ETMNH 14028

ETMNH 14029

10 mm

Plate 2

ETMNH 14030

ETMNH 14031

ETMNH 14032

ETMNH 14033

ETMNH 14034

ETMNH 14035

10 mm

Plate 3

ETMNH 14036

ETMNH 14037

ETMNH 14038

ETMNH 14039

ETMNH 14040

ETMNH 14041

ETMNH 14042

10 mm

Distinguishing *Nyssa* from Related Genera

The fossil fruits reported in this study are characterized by endocarps composed of fibers, triangular apical germination valves within the apical half of the endocarp, the absence of an axial vascular bundle, and 1 to 4 single seeded locules. This combination of traits is only known from the cornalean genus *Nyssa* (Eyde 1997; Manchester et al. 2007). Vascular bundles run on or shallowly within the surface of *Nyssa* endocarps, causing grooves and ridges in most extant and fossil species (Eyde and Braghoorn 1963). The Nyssaceae can be distinguished from the Cornalean families Hydrangeaceae, Hydrostachyaceae, and Loasaceae by the lack of germination valves as well the presence of grooves and ridges on their surfaces (Manchester et al. 2007). These 3 families differ from all other members of the Cornales by having multiple seeds per locule (Fan and Xiang 2003). The Nyssaceae and Mastixiaceae (*Mastixia*, *Diplopanax*, and extinct relatives) have sometimes been placed within the family Cornaceae along with *Cornus* (Wen and Stuessy 1993; Eyde 1997). In the Mastixiaceae and Nyssaceae, however, the endocarps are both composed of fibers, whereas *Cornus*, *Alangium, Curtisia*, and *Grubbia* have endocarps composed of isodiametric to slightly elongate sclereids (Xiang et al. 2005). These morphological differences are supported by molecular studies (Fan and Xiang 2003). The fibers in all known extant and fossil *Nyssa* species are more or less randomly oriented within the central portion of the endocarp wall (Figures 4-10; 40).

Figure 4: Randomly Oriented Fibers in the Extant Species *Nyssa talamancana* Hammel and Zamora

Figure 5: SEM Image of Randomly Oriented Fibers of *Nyssa talamancana* Hammel and Zamora in Section View.

Figure 6: SEM Image of Fibers of a *Nyssa sinensis* Oliver Endocarp in Section View. Single layer of longitudinal fibers and transition from circumlocular fibers to randomly oriented fibers in a *Nyssa sinensis* Oliver endocarp.

Figure 7: Randomly Oriented Fibers Toward the Central Portion of the Endocarp Wall in *Nyssa sylvatica* Marshall.

Figure 8: SEM Image of Randomly Oriented Fibers of *Nyssa grayensis* sp. nov. The longitudinal fibers from inside the locule have broken away to expose this layer.

Figure 9: Close-up of the Randomly Oriented Fibers of *Nyssa grayensis* sp. nov.

Figure 10: SEM Image of Randomly Oriented Fibers of *Nyssa grayensis* sp. nov. from the Central Portion of the Endocarp Wall in Section View.

The endocarps of *Cornus* often split parallel to the long axis of the fruit with a flange or shutter (Hill 1933; Hill 1937) but lack defined germination valves found in the Nyssaceae. *Alangium*, the sister taxa to *Cornus,* contains germination valves as well (Fan and Xiang 2003). Members of *Cornus* subgenus *Cornus* have cavities densely spread throughout their wall and septum (Manchester et al. 2010), a trait that is not reported in any *Nyssa* species. The genus *Curtisia*, within the monogeneric family Curtisiaceae, has germination valves that dehisce down the entire length of the endocarp and has an axillary vascular bundle that is absent from the Nyssaceae and Mastixiaceae (Manchester et al. 2007). The Mastixiaceae can be distinguished from *Nyssa* based upon their valves extending down the entire length of the endocarp, and by endocarps that have inward folds visible both externally and as a ridge within the locules (Eyde and Xiang 1990;

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Manchester et al. 2007). Additionally, *Diplopanax* has a woody mesocarp, and the endocarp is only known to be one seeded and without septal partitions (Eyde and Xiang 1990).

The extant genera of Nyssaceae are united by fruits with endocarps composed of variously oriented tracts of fibers, germination valves that are pointed toward the apex, a single germination valve per seed locule, the lack of a central vascular canal (axillary vascular bundle), vascular bundles on the surface of the endocarp, and seeds with moderately copious endosperm (Wen and Stuessy 1993; Eyde 1997). *Camptotheca* can be distinguished from *Nyssa* by having thin endocarps that are hardly stony (Cronquist and Takhtajan 1992; Manchester et al. 1999), a higher length to width ratio, large numbers of fruits collected in heads, and endocarps roughly triangular in cross section (Manchester et al. 1999; Manchester et al. 2002). The fossil records of other Nyssaceae genera (e.g. *Nyssa,* fossils similar to *Camptotheca*) have shown a pattern of reducing their locule number over time, whereas *Davidia* has retained a high number of seed locules within the endocarp (Figure 11).

Modern *Davidia* species have 5-6(-7) seed locules (Manchester 2002). Often many of the locules in extant *Davida* are reduced in size and contain aborted seeds (Eyde 1963). The endocarps of *Davidia* are roughly circular in section, have raised vascular bundles, have a smaller length to width ratio than *Camptotheca*, and have germination valves (Figures 12-13) that extend down the length of the endocarp (Hill 1937; Eyde 1997). Manchester et al. (1999) discuss the affinities of the extinct genus *Amersinia* with the extant genera of Nyssaceae. This genus is treated as a member of the Nyssaceae in the key presented in this paper. Like *Camptotheca*, *Amersinia* fruits have an endocarp

surrounded by a pericarp that forms wing-like projections (Manchester et al. 1999).

Amersinia lacks a distinct central vascular canal but has transeptal vascular bundles

associated with each locule that are absent from the other Nyssaceae (Manchester et al.

1999). The species also differs from the extant *Camptotheca* by having 3 to 4 locules

while the extant *Camptotheca* has 1 or, less frequently, 2 locules (Manchester et al.

1999).

Figure 11: Illustration Of A *Davidia* Endocarp Showing Valves That Dehisce Down Most of its Length. Two fertile locules and several reduced locules are visible in the cross-sectional view. Modified from Hill (1933)

The thick-walled woody endocarps of *Nyssa* generally have 1-4 single-seeded

locules depending on the species, with one germination valve per locule located within

roughly the apical one half to one-third of the endocarp (Eyde 1997). The endocarps of

Nyssa can have vascular bundles sunken into grooves on the surface (which are less pronounced in some species resulting in a fairly smooth endocarp), or vascular bundles that are raised on thin ridges (Eyde 1997). The fruits occur singly or in small clusters rather than the globose fruit heads with dozens of narrow fruits seen in *Camptotheca* (Figure 12). *Nyssa* endocarps are round in section or sometimes dorso-ventrally compressed (Wen and Stuessy 1993; Eyde 1997).

Figure 12: Immature Fruit Heads of *Camptotheca acuminata* Decne. UF 1260

Figure 13: Mature Fruits of *Camptotheca acuminata* Decne. UF 1058

Inter-Specific Variation and Species Identification

The endocarps of the various extant and extinct species of *Nyssa* are generally

distinguished from each other based on the nature of their vasculature (e.g. raised

bundles, sunken bundles, or smooth surfaces), size, locule number, and shape (Eyde

1997). In addition, during these investigations certain species were found to have

vascular bundles grouped in clusters rather than single vascular bundles per groove

(Figures 43-44). Some forms were found to have bundles obscured from view beneath the

surface, or bundles that deviated from the parallel orientation of the grooves and ridges,

adding diversity to the 3 main types of vasculature. The topographic relief and the shapes

of grooves and ridges also varied considerably between species. A key to the fruit of all

validly recognized extant and fossil *Nyssa* species was created based on morphological

and metric traits (pg 73). Whenever possible, multiple traits were used for each couplet in

the key. Some species were found to have endocarp traits that were either variable or

inconspicuous. In these circumstances a species was included in both divisions of couplets and separated based on other traits in subsequent couplets.

<div align="center">Comparisons with Extant Species</div>

Nyssa grayensis Noll et al. sp. nov. can easily be distinguished from all of the extant species of *Nyssa*. The vascular bundles of *Nyssa grayensis* sp. nov. are situated within grooves on the surface of the endocarps. The specimens have deeper and wider grooves aligned with the midpoint of each valve. The grooves centered along the valves run from the apex to the base of the endocarp. *Nyssa javanica* (Blume) Wangerin and *Nyssa aquatica* Linnaeus differ in having a ridge running down the center of the endocarp (Eyde 1963). All of the vascular bundles are situated on the endocarp ridges in *Nyssa aquatica* Linnaeus and are mostly unattached and above the ridges in *Nyssa javanica* (Blume) Wangerin. The endocarps of *Nyssa javanica* (Blume) Wangerin are mostly smooth, with 1.44 +/- .050 ribs on their surface at the 95% confidence interval (Wang et al. 2012). *Nyssa yunnanensis* Yin ex Qin and Phengklai also has a low number of endocarp ribs, reported as 4.40 +/- .94 by Wang et al. (2012). Eyde (1963) reports that *Nyssa aquatica* Linnaeus generally has about 10 ridges. All of the *Nyssa aquatica* Linnaeus specimens examined during this study have 9 or 10 ridges. Eyde (1963) reported 7-12 vascular grooves on the surfaces of *Nyssa sylvatica* Marshal and *Nyssa sinensis* Oliver. *Nyssa sinensis* Oliver is reported to have between 7.59 +/- .17 and 9.87 +/- .060 ribs at the 95% confidence interval by Wang et al. (2012).

Almost all of the endocarps of both *Nyssa sylvatica* Marshall and *Nyssa sinensis* Oliver examined in this study had nine distinct grooves on the surface, although many specimens had a few additional grooves that extended a portion of the length of the

endocarp and were generally fainter. *Nyssa talamancana* Hammel and Zamora is reported

to have 9-12 grooves with vascular bundles within them (Hammel and Zamora 1990).

Most of the grooves of *Nyssa talamancana* endocarps examined during this study had

groups of more than one vascular bundle, or had closely grouped grooves with bundles

next to them (Figure 16). The vascular bundles were obscured until the endocarp had

dried and split along the bundles (Figure 15). Many of the bundles stayed obscured after

drying but were visible in section.

Figure 14: Comparison of the Fossil *Nyssa* Endocarps from Gray with Extant Species. *Nyssa grayensis* sp. nov. (B) and the extant species *Nyssa talamancana* Hammel and Zamora (A); *Nyssa ogeche* Bartram ex Marshall with (C2) and without (C1) the mesocarp wings; *Nyssa aquatica* Linnaeus (D); *Nyssa sinensis* Oliver (E); *Nyssa sylvatica* Marshall (F). Endocarps shown with apical valves toward the top of the photograph.

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Figure 15: A *Nyssa talamancana* Hammel and Zamora Endocarp Before and After Dehydration. Note the vascular bundles are not visible until the surface has split along the bundles as the specimen dried

Figure 16: SEM Image of a Pair of Vascular Bundles in *Nyssa talamancana* Hammel and Zamora beneath the Surface. Outer surface on the left side.

Nyssa ogeche Bartram ex Marshall can have 9 to as many as 15 vascular bundles (Eyde 1963). Although the *Nyssa ogeche* Bartram ex Marshall specimens examined in this study had 9 or 10 main grooves with 1 or 2 bundles in them, they often had additional bundles that deviated from the grooves. Most specimens had one to several bundles that were beneath the outer surface of the endocarp, sometimes including bundles within the endocarp ridges. In some cases more than one bundle were grouped together. *Nyssa grayensis* sp. nov. has 17-23 grooves on the surface which is most similar to *Nyssa talamancana* Hammel and Zamora and *Nyssa ogeche* Bartram ex Marshall among the extant species.

Figure 17: A Vascular Bundle Mostly beneath the Surface of a *Nyssa ogeche* Bartram ex Marshall Endocarp. Specimen from Gainesville, FL.

Figure 18: A Vascular Bundle Completely Obscured beneath the Surface of a *Nyssa ogeche* Bartram ex Marshall Endocarp. Specimen from Gainseville, FL.

Figure 19: SEM Image of Vascular Bundles Obscured beneath the Surface of *Nyssa grayensis* sp. nov. ETMNH 14042

Figure 20: Vascular Bundles Obscured below the Surface Of *Nyssa grayensis* sp. nov. Under a Light Microscope. Visible on ETMNH 14027 where the outer surface has broken away.

The valve shape of *Nyssa grayensis* sp. nov. is triangular and roughly equilateral with straight to gently curved edges (Figure 22). This differs from *Nyssa aquatica* Linnaeus that has an acuminate germination valve that narrows quickly toward the apex (Figure 21). The valves of the other extant *Nyssa* species such as *Nyssa ogeche* Bartram ex Marshall are more similar in shape to the valves of *Nyssa grayensis* sp. nov.

Figure 21: A *Nyssa aquatica* Linnaeus Endocarp from Richmond, NC. The outline of the valve with an attenuate shape is clearly visible. Vascular bundles are raised on the ridges

ETMNH 14024   15.7 mm

Figure 22: Valve Shape on *Nyssa grayensis* sp. nov. Notice the pronounced groove centered in the middle of both valves and running the length of the endocarp.

Figure 23: Valve Shape of *Nyssa ogeche* Bartram ex Marshall.

The shape of the endocarp is most similar to *Nyssa ogeche* Bartram ex Marshall that also tapers to points on both ends. *Nyssa aquatica* Linnaeus is also pointed on both ends, but most endocarps are obovate with the widest point above the midline (Figure 21). The other extant species of *Nyssa* are more or less rounded on both ends.

Nyssa grayensis sp. nov. also differs in size from the extant *Nyssa* species. *Nyssa talamancana* Hammel and Zamora is considerably larger with most endocarps between 37 and 52 mm and occasionally up to 55 mm long (Hammel and Zamora 1999). The average lengths of *Nyssa aquatica* Linnaeus and *Nyssa ogeche* Bartram ex Marshall are 21 and 23 mm respectively with ranges of 14.0-28.3 mm and 14.7-29.3 mm (Eyde 1963). The *Nyssa aquatica* Linnaeus and *Nyssa ogeche* Bartram ex Marshall specimens examined during this study all fell within those ranges but had mean lengths of 23.1 and 24.4 mm respectively. The beak-like extensions on the apex of *Nyssa aquatica* Linnaeus

were included in these measurements, as well as the conical projections of *Nyssa ogeche* Bartram ex Marshall. *Nyssa yunnanensis* Yin ex Qin & Phengklai endocarps are 16.18 (SD = 1.02) mm long and *Nyssa javanica* (Blume) Wangerin endocarps are 14.67 (SD= .21) mm long (Wang et al. 2012). The largest known *Nyssa javanica* (Blume) Wangerin endocarp is 29.8 x 15.2 mm, but normally they are rarely more than 17.8 mm long (Eyde 1963). The *Nyssa sylvatica* Marshall and *Nyssa sinensis* Oliver endocarps examined during this study as well as those measured by Eyde (1963) and Wang et al. (2012) rarely reached much over 10 mm long. The smallest specimen of *Nyssa grayensis* sp. nov. is 21.5 x 12.0 mm, and is much smaller than the second smallest specimen (25.0 x 11.0 mm). The largest complete specimen from the GFS is 33.3 x 13.0 mm. This makes *Nyssa grayensis* sp. nov. considerably smaller than *Nyssa talamancana* Hammel and Zamora, but larger than the average size of the other extant species.

Figure 24: Boxplot of Extant *Nyssa* Stone or Endocarp Lengths in Comparison to *Nyssa grayensis* sp. nov. Diamonds represent mean values and ranges of species with the upper and lower quartiles unavailable.

Endocarp locule numbers are important distinguishing factors of the extant species as well. *Nyssa grayensis* sp. nov. has 2 locules, or rarely 3 locules. The extant species *Nyssa javanica* (Blume) Wangerin, *Nyssa yunnanensis* Yin ex Qin & Phengklai, and *Nyssa aquatica* Linnaeus are strictly one seeded (Eyde 1963; Wen and Stuessy 1993; Wang et al. 2012). Of specimens examined for this study, 35 of the *Nyssa ogeche* Bartram ex Marshall, 150 of the *Nyssa sinensis* Oliver, and 100 of the *Nyssa sylvatica* Marshall fruits observed were sliced to determine locule number.

Nyssa ogeche Bartram ex Marshall was found to frequently have 2 locules, 71% were unilocular and the remainders were bilocular. 52% of *Nyssa sinensis* Oliver endocarps had one locule and 48% were bilocular. Only one bilocular specimen of *Nyssa sylvatica* Marshall has ever been reported (Eyde 1963), and none were observed in this study. Both trilocular and bilocular forms are common for *Nyssa talamancana* Hammel and Zamora. Hammel and Zamora (1997) report that tetralocular forms of this species are also occasionally found.

The wall thickness of *Nyssa talamancana* Hammel and Zamora is much greater than in *Nyssa grayensis* sp. nov. and in any extant species. The wall easily exceeds 4 mm of thickness from the center of the valve to the locule, and 6 mm from the lateral edge of the locule to the lateral edge of the endocarp. The endocarp wall on the sides with the valves is thickest toward the center, contributing to the crescent or C-shaped locules. C-shaped locules are not found in *Nyssa grayensis* sp. nov or any other extant species. *Nyssa javanica* (Blume) Wangerin, however, has several ridges on the surfaces of the locules (Eyde 1963; Figure 27) resulting in a roughly w-shaped locule. Bilocular

endocarps of *Nyssa grayensis* sp. nov. with exposed locules have compressed, roughly D-shaped locules with a straight inner septum and an outer wall with an even thickness.

Figure 25: A Cross-Section of *Nyssa talamancana* Hammel and Zamora Showing Crescent-Shaped Locules That Result from the Valves Thickening toward the Midline.

Figure 26: Cross-Section Showing the Roughly "D" Shaped Locule of *Nyssa ogeche* Bartram ex Marshall with an Even Wall Thickness.

Figure 27: A Thin-Section Of *Nyssa javanica* (Blume) Wangerin. Modified from Eyde (1963).

The arrangement of fibers in the inner, outer, and central portions of *Nyssa* endocarps generally differ from each other. Transverse fibers arranged approximately perpendicular to the long axis are also found in the outer layer of the endocarp of *Nyssa grayensis* sp. nov. and all of the extant *Nyssa* except for *Nyssa javanica* (Blume) Wangerin (Eyde 1963) and possibly *Nysssa yunnanensis* Yin ex Qin and Phengklai for which this trait has not yet been investigated. *Nyssa javanica* (Blume) Wangerin also lacks longitudinal fibers on the inside of the locule (Eyde 1963). Nyssa ogeche Bartram ex Marshall, *Nyssa talamancana* Hammel and Zamora, *Nyssa aquatica* Linnaeus, *Nyssa sylvatica* Marshall, and *Nyssa sinensis* Oliver were all found to have a single layer of longitudinal fibers lining the locule, followed by a layer of circumlocular fibers and randomly oriented fibers within the central portion of the endocarp wall. The arrangement of fibers in *Nyssa grayensis* sp. nov. endocarps was similar to the majority of the extant species in having an outer layer of transversely arranged fibers, inner

longitudinal fibers surrounded by circumlocular fibers, and a central layer of randomly oriented fibers. *Nyssa grayensis* sp. nov. differs from all of these species, however, by having a ~12-15 fiber thick layer of longitudinal fibers rather than a single row of longitudinal fibers lining the locule.

Figure 28: SEM Image of the Outermost Transverse Fibers of *Nyssa grayensis* sp. nov. They are arranged roughly perpendicular to the long axis of the endocarp.

Figure 29: SEM Image of the Outer Tangential Fibers of *Nyssa grayensis* sp. nov. Viewed in Cross-Section.

Figure 30: SEM Image of the Outer Tangential Fibers of a *Nyssa talamancana* Hammel and Zamora Endocarp. Also see Figure 16.

Figure 31: SEM Image of Outer Transverse Fibers of *Nyssa sylvatica* Marshall. In section view.

Figure 32: SEM Image of Tangential Fibers on the Outer Surface of *Nyssa sinensis* Oliver.

As discussed in the previous paragraphs, *Nyssa grayensis* sp. nov. shares several similarities with *Nyssa ogeche* Bartram ex Marshall and *Nyssa talamancana* Hammel and Zamora that are not present in the other extant species. *Nyssa ogeche* Bartram ex Marshall is probably most closely related to *Nyssa grayensis sp.* nov. based on the similar D-shaped locules (opposed to "C-shaped" in *N. talmancana*), more similar size, similar wall thickness, and endocarp shape with tapers at both ends. *Nyssa grayensis* sp. nov. sometimes has thin, sharp ridges, especially near the ends of the endocarp. *Nyssa ogeche* Bartram ex Marshall consistently has sharp ridges down the entire endocarp, but only broad flat ridges were found on *Nyssa talamancana* Hammel and Zamora.

Although *Nyssa ogeche* Bartram ex Marshall can have a similar shape to *Nyssa grayensis* sp. nov. it can be distinguished based on the tall height of the ridges (often exceeding 2 mm without the mesocarp wings) and the uneven height of these ridges along their length, which become taller toward the middle. In addition *Nyssa ogeche* Bartram ex Marshall has a single layer of longitudinal fibers surrounding the endocarp locule (Figure 37), whereas *Nyssa grayensis* sp. nov. has a thick group of longitudinal fibers (circa 12-15 fibers thick) lining the endocarp wall.

Figure 33: SEM Image of Fiber Arrangement in *Nyssa aquatica* Linnaeus. Single layer of longitudinal fibers (bottom of the image), followed by longitudinal fibers that become more randomly oriented toward the center of the endocarp wall, and become arranged transversely toward the surface (top).

Figure 34: Close-up of the Fibers in *Nyssa aquatica* Linnaeus. Same specimen as shown above. Single layer of longitudinal fibers on the bottom of the image, followed by longitudinal fibers that become more randomly oriented toward the center of the endocarp wall.

Figure 35: SEM Image of the Longitudinal Fibers That Line the Locule of *Nyssa sylvatica* Marshall, Followed by Circumlocular Fibers.

Figure 36: Single Layer of Longitudinal Fibers Lining the *Nyssa talamancana* Hammel and Zamora Endocarp Locule, Followed by Circumlocular Fibers.

Figure 37: SEM Image of the Inner Two Layers of Fibers of a *Nyssa ogeche* Bartram ex Marshall Endocarp. An inner layer of longitudinal fibers (L) and a layer of circumlocular fibers (C).

Figure 38: Close-Up SEM Image of Longitudinally Arranged Fibers Lining the Locule of *Nyssa grayensis* sp. nov.

Figure 39: An SEM Image Showing All of the Fiber Layers of a *Nyssa grayensis* sp. nov. ENDOCARP. Longitudinal fibers (L) followed by roughly circumlocular (C) fibers that transition into randomly oriented fibers (R) in *Nyssa grayensis* sp. nov.

Figure 40: A Schematic Diagram Showing the Arrangement of Fibers in the Wall of *Nyssa grayensis* sp. nov. (L) longitudinal; (C) circumlocular; (R) randomly arranged; (T) transverse.

Comparisons with Extinct Species

As with the extant species, differences in vascularization and surface texture are important characters to distinguish among extinct *Nyssa* species. The surfaces of *Nyssa magnifica* (Knowlton) Berry, *Nyssa brandoniana* (Lesquereux) Eyde and Barghoorn, *Nyssa spatulata* (Scott) Manchester, and *Nyssa multilocularis* (Reid & Chandler) comb. nov. have fairly smooth endocarp surfaces with few or no vascular bundles adhering to their surfaces, similar to the extant *Nyssa javanica* (Blume) Wangerin (Berry 1929; Eyde and Barghoorn 1963; Reid and Chandler 1993; Manchester 1994). Like *Nyssa aquatica* Linnaeus the extinct species *Nyssa boveyana* Chandler and *Nyssa fissilis* (Lesquereux) Eyde and Barghoorn have raised bundles (Chandler 1957; Eyde and Barghoorn 1963). Although the original description of *Nyssa boveyana* Chandler says that the endocarps have sunken bundles the type specimen has vascular bundles raised on ridges (Eyde 1997). The description in the key presented here relies on the traits of the type specimen for *Nyssa boveyana* Chandler. All of the *Nyssa* endocarps originally designated as *Nyssa boveyana* Chandler are smaller and less pointed than *Nyssa grayensis* sp. nov. *Nyssa ornithobroma* Unger has mostly sunken bundles within about 10 grooves but usually has bundles raised on ridges toward the apex of the endocarp (Mai 1965; Eyde 1997). The valves of *Nyssa ornithobroma* Unger are acuminate as in *Nyssa aquatica* Linnaeus (Figure 41; Mai 1973). The endocarps also have a smaller maximum size than *Nyssa grayensis* sp. nov. and most specimens identified as *Nyssa ornithobroma* Unger are much smaller than the smallest *Nyssa grayensis* sp. nov. (Mai and Gregor 1982). This species also differs in being reported to have 1-4 locules and a tendency to be obovate in outline (Eyde 1997).

Figure 41: A Comparison of the Variation of Valve Morphology in *Nyssa disseminata* (Ludwig) Kirchheimer AND *Nyssa ornithobroma* Unger. Modified from Mai (1973).

The remaining species have endocarps with sunken bundles similar to *Nyssa grayensis* sp. nov. The species *Nyssa eolignitica* Dilcher & McQuade, *Nyssa texana* Berry, *Nyssa lescurii* (Hitchcock) Perkins, and *Nyssa pachycarpa* Miki share the most similarities with *Nyssa grayensis* sp. nov. Each of these species has in common an outer layer of transverse fibers and vascular bundles tending to be grouped in clusters. All of the species except *Nyssa texana* Berry have forms with more than one locule. The species *Nyssa lescurii* (Hitchcock) Perkins and *Nyssa pachycarpa* Miki can be distinguished by their thick endocarp walls (often up to 3 mm) and smaller size (Miki 1956; Eyde and Barghoorn 1963). The larger of these species *Nyssa lescurii* (Hitchcock) Perkins is smaller than *Nyssa grayensis* sp. nov (13.5-24 cm long) and is found in both unilocular and bilocular forms (Eyde and Barghoorn 1963). *Nyssa texana* Berry is known to be a similar size as *Nyssa grayensis* sp. nov. (22-30 mm long) but is only known to be unilocular (Berry 1924; Eyde and Barghoorn 1963). *Nyssa eolignitica* Berry (including

N. wilcoxiana Berry) shares the most similarities with *Nyssa grayensis* sp. nov. This species is also bilocular or less frequently trilocular, can have a large number of grooves on the surface (10-15 or occasionally more) with bundles frequently grouped in pairs, and have a similar arrangement of fibers throughout the endocarp (Berry 1916; Berry 1930; Dilcher and McQuade 1967). Both *Nyssa eolignitica* Berry and *Nyssa lescurrii* (Hitchcock) Perkins *Nyssa lescurii* (Hitchcock) Perkins have a group of longitudinal fibers lining their locules which is about 3 fibers thick on average (Eyde and Braghoorn 1963; Dilcher and McQuade 1967) compared to roughly 12 to 15 fibers thick in *Nyssa grayensis* sp. nov. The size of *Nyssa eolignitica* Berry overlaps *Nyssa grayensis*, although it includes endocarps of much smaller sizes and has a smaller maximum size. The largest reported specimens are from the Puryear Clay Pit, Tennessee, reaching 26 mm (Berry 1916), compared to *Nyssa grayensis* sp. nov. with a specimen as long as 33.3 mm. These specimens are all rounded on both ends (Berry 1916). Berry (1930) recognized *Nyssa wilcoxiana* Berry, a similar form found at the same site that is reported to be 16-22.5 mm long. This species was placed as a synonym of *Nyssa eolignitica* Berry by Dilcher and McQuade (1967) who reported endocarps between 16-22 mm long. The endocarps of *Nyssa eolignitica* Berry are rounded on both ends, or sometimes broadly pointed on one end, and the valves are rarely externally visible (Berry 1916; Berry 1930; Dilcher and McQuade 1967), compared to the endocarps of *Nyssa grayensis* sp. nov. that are fusiform with both ends generally being acutely pointed. The endocarps usually have clearly visible valves. The age difference also supports separation of the species. The fossils are from the Claiborne Group, which is Middle Eocene in age based on macrofossils (Russel and Parks 1975) and supported by palynological studies (Potter and

Dilcher 1980). The Claiborne Group in Texas falls within the Uintan land mammal age based on the remains of the tillodont *Anchippodus riparius* Leidy (Westgate 1990), which constrains the age to ~46.5-40 Ma (Middle Eocene) (Williams and Kirk 2008). Using a conservative estimate the ages of the fossils at Gray are separated by at least 33 million years. Magallón and Sanderson (2001) model speciation rates within the Cornales as being between .0486 (under absence of extinction) and .0678 per million years (under high extinction rates). Thus the probability of speciation not occurring per million years would be between 1-.0486 = .9514 and 1-.0678= .9322. Using the conservative age difference of 33 million years, the probability of a typical species within the Cornales to speciate before the age of the Gray Fossil Site would be between at least $(1-(.9514^{33}) \times 100) = 81.6\%$ and $(1-(.9322^{33}) \times 100) = 90.1\%$. *Nyssa eolignitica* Berry has the most similarities to *Nyssa grayensis* sp. nov. out of any modern or fossil species and could represent an ancestral form. *Nyssa grayensis* sp. nov. has a larger amount of longitudinal fibers, however, which seems contradictory to the evolutionary trend in longitudinal fiber numbers. The modern species analyzed in this study all had a layer of longitudinal fibers that was mostly one fiber thick (Figures 33-37). Sections of *Nyssa javanica* (Blume) Wangerin in Eyde (1963) lacked longitudinal fibers.

Figure 42: A Bundle within a Groove on the Surface of *Nyssa grayensis* sp. nov. ETMNH 14025

Figure 43: A Pair of Vascular Bundle Traces on a *Nyssa grayensis* sp. nov. Endocarp. ETMNH 14025

Figure 44: A Pair of Vascular Bundle Traces within a Groove on another *Nyssa grayensis* sp. nov. Endocarp. ETMNH 14040

Interestingly a conical projection interpreted to be a stylar remnant and a calyx rim are found at the apex of *Nyssa eolignitica* Berry, *Nyssa lescurii* (Hitchcock) Perkins, *Nyssa pachycarpa* Miki (Eyde and Barghoorn 1963; Dilcher and McQuade 1967; Eyde 1997). These features are also present on *Nyssa talamancana* Hammel and Zamora and *Nyssa ogeche* Bartram ex Marshall (Figure 15, Figure 45; Hammel and Zamora 1990). This shared trait along with the paired bundles, transverse fibers on the outermost layers of the endocarp, and multi-locular states suggest that these taxa share a closer common ancestor than other members of *Nyssa*. Clear evidence of an apical projection hasn't been found on *Nyssa grayensis* sp. nov, although the apex often has a flattened area that may have held an apical projection. Many of the endocarps have what appears to be a rim surrounding this area. Based on the similar locule number, the arrangement of the inner and outer-most layers of fibers, bundle arrangement, and roughly similar size, *Nyssa eolignitica* Berry appears to be the closest extinct relative of *Nyssa grayensis* sp. nov.

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Figure 45: An Immature *Nyssa ogeche* Bartram ex Marshall Endocarp with Most of the Mesocarp Removed. A conical projection interpreted to be a stylar remnant is visible at the apex.

Figure 46: Apex of *Nyssa grayensis* sp. nov. with a Possible Attachment Site for an Apical Projection. ETMNH 14025

Table 4: Comparisons of Taxa Similar to *Nyssa grayensis* sp. nov.

Taxon	Trait	Similarities	Differences
Nyssa ogeche Bartram ex Marshall	Size	Similar size range.	Upper limit of length range slightly smaller.
	Shape	Similar shape with both ends tapering to a point. Similar D-shaped locules.	

Table 4 (continued)

	Locule Number	Can be bi-locular, but most frequently unilocular. Not reported tri-locular.	*N. grayensis* most frequently bi-locular. Sometimes tri-loclular. Not known to be unilocular.
	Vasculature and Surface Topography	Can have a large number of vascular bundles. A portion of the bundles below the surface of the outermost transverse fibers. Bundles sometimes paired. Bundles not strictly straight and parallel to the length of the endocarp. Ridges between bundles can be thin or broad. Pronounced groove running down the center of the endocarp, centered at the valve(s).	Grooves and ridges more prominent and having greater topographic relief. Upper range of the number of vascular bundles smaller. Ridges usually taller toward the center and more variable in height.
	Valves	Similar valve shape.	
	Fiber Layers		Only one layer of longitudinal fibers making up the innermost portion of the endocarp.
Nyssa eolignitica Berry	Size	Overlapping size range	Larger endocarps closer to the length of small *N. grayensis* specimens.
	Shape	Elongate. Locules D-shaped.	Tend to be rounded on the ends.

Table 4 (continued)

	Locule Number	Can be Bi- or tri-locular.	Sometimes unilocular.
	Vasculature and Surface Topography	Paired bundles appear to be common.	Valves rarely externally visible
	Fiber Layers	More than one inner layer of longitudinally arranged fibers.	Thinner layer of longitudinal fibers (circa three fibers thick).
	Other		Much older (Eocene).
Nyssa lescurii (Hitchcock) Perkins	Size	Slight size overlap.	Largest endocarps close to the length of small *N. grayensis* endocarps.
	Shape	Elongate.	Tending to be rounded on the ends. Locules C-shaped.
	Locule Number	Can have bi-locular or tri-locular forms	Trilocular forms common
	Vasculature and Surface Topography	Bundles often paired.	Less grooves from vascular bundles
	Valves		Valves usually not externally visible
	Fiber Layers	Transverse fibers often grouped in a sinuous manner resulting in a wrinkled surface.	
Nyssa pachycarpa Miki	Size	Transverse fibers often grouped in a sinuous manner resulting in a wrinkled surface.	Largest specimens shorter than the smallest *N. grayensis* specimens

Table 4 (continued)

	Shape		Sometimes nearly globose. generally rounded on both ends
	Locule Number	Can be bilocular	Non-bilocular forms not reported
	Vasculature and Surface Topography	Paired bundles common.	Less grooves (about 10).
	Valve	Similar valve shape.	
	Fiber layers	Transverse fibers often grouped in a sinuous manner resulting in a wrinkled surface	
Nyssa talamancana Hammel and Zamora	Size		Much larger (can exceed 50 mm length). Size ranges do not overlap.
	Shape		Tend to be more rounded on the ends. C-shaped locules.
	Locule Number	Can be 2 or 3 locular.	Sometimes known to have four locules
	Vasculature and Surface Texture	Paired bundles common. Have bundles obscured by outer layer of transverse fibers.	
	Valves		Valves usually not externally visible.
	Fiber Layers	Transverse fibers often grouped in a sinuous manner resulting in a wrinkled surface.	Much thicker endocarp wall. Single layer of inner longitudinal fibers.
Nyssa texana Berry	Size Shape	Overlapping Size range.	Tending to be

Table 4 (continued)

			rounded on the ends.
	Locule Number		Appearing to only be unilocular.
	Vasculature and Surface Topography	Paired bundles common. Similar large number of grooves for vascular bundles.	
	Other		Much older (Eocene)

Key to The Fruits of the Extant and Extinct Nyssaceae Genera

1 Fruit samara-like, endocarp thin and hardly lignified and surrounded by a soft parenchymatous pericarp formed into wings. Fruit in head-like clusters of >35 fruits.…………...……………………………………………………...….(2)

+ Fruit with lignified endocarps and fleshy pericarp without wings. Fruit in clusters of 1-5 fruits...……………………………………………………….……(3)

2 Fruits unilocular or rarely bilocular. Fruit highly elongate with a length to width ratio of about 4/1……………...……………………………………*Camptotheca*

+ Fruits trilocular or tetralocular. Fruit wider, with length to width ratio usually less than 4/1………………………………………………….…*Amersinia*

3 Endocarp with 6-10 locules, of which many are often sterile by seed abortion and reduced in size. Dehiscence valves trigonal and extending nearly the entire length of the endocarp...*Davidia*

+ Endocarp with 1-4 locules, valves trigonal and roughly equilateral. Valves limited to the apical 1/2 to 1/3 of the endocarp…..………………………………….*Nyssa*

Key to the endocarps of Extant and Extinct *Nyssa*

(extant species names in bold)

1   Endocarp with grooves and ridges…………………………………………………(2)

+   Endocarp surface mostly smooth. Few grooves and ridges or vascular bundles

leaving few marks on or between the ribs..*Nyssa* Key 3

2   Endocarp with vascular bundles sunken in grooves, or on the crests of ridges, but

not both……………………………………………...…………………………….3

+   Endocarp with vascular bundles mostly sunken in grooves except near the

apex……………………………………………….………..*Nyssa ornithobroma* Unger

3   Endocarp with vascular bundles mostly sunken in grooves…..………*Nyssa* Key 1

+   Endocarp vascular bundles mostly raised along the crests of ridges

………………………………………………………………………...…*Nyssa* Key 2

Nyssa Key 1- Endocarps with Vascular Bundles Mostly Sunken in Grooves

1   Endocarp with four locules (or locule number known to be variable in endocarp

morphotype and having up to 4 locules)……………………….……..…………(2)

+   Endocarp having less than 4 locules (or locule number variable and known to

sometimes have less than 4 locules)...…..………………………………………(5)

2   Endocarp fairly smooth with bundles generally not adhering, or adhering only

along the midline of the valve…………………………………………..…….(3)

+   Endocarp with distinct grooves and ribs……………………………….….(4)

3   Endocarp with 3 or 4 locules. Endocarp circa 12.3-15 mm long by 6.2-9.5mm

wide. Valves attenuate at base, ovate or acuminate. Endocarp relatively smooth

with bundles generally not adhering except along the midline of the locules that

bear a more prominent groove.

……………………………… *Nyssa multilocularis* (Reid & Chandler) comb. nov.

+   Endocarp with three locules or variable with 3 to 4 locules. Endocarp circa

20.1-30.0 mm long and 12.0-21.5 mm wide. Valves elliptical in outline. Locules

C shaped with the outer wall of the endocarp thickest toward the middle.

Endocarp fairly smooth, usually lacking distinct traces of vascular bundles

between the ribs. ……………………..………*Nyssa spatulata* (Scott) Manchester

4   Endocarp with one to 4 locules. Endocarp circa 7-23.4 mm long and 4-12 mm

wide. Valves acuminate and narrowing toward the apex. Ribs often becoming

sharp toward the apex with vascular bundles sometimes on the ridges near the

apex. Often obovate with the widest point above (toward the apex) of the

midline…………………..……..............................……*Nyssa ornithobroma* Unger

+   Endocarp with two to 4 locules. Endocarp circa 5.6-11.8 mm long and 3.2-8.8

mm wide. Ribs blunt or rounded and not having vascular bundles upon them.

Endocarp very rarely obovate.……....…….*Nyssa complanata* Eyde and Barghoorn

5   Endocarp having 3 locules or variable and known to have up to 3

locules…………………………………………………………...…………….(6)

+   Endocarp with less than 3 locules or variable and known to sometimes have

less than 3 locules………………..……………………………………….…(14)

6   Endocarp fairly smooth with bundles generally not adhering, or adhering only along the midline of the valve…………………………………………..…….(7)

+   Endocarp with distinct grooves and ribs………………………………..….(8)

7   Endocarp with 3 or 4 locules. Endocarp circa 12.3-15 mm long by 6.2-9.5mm wide. Valves attenuate at base, ovoid or acuminate. Endocarp relatively smooth with bundles generally not adhering except along the midline of the locules which bear a more prominent groove.

………………………………… *Nyssa multilocularis* (Reid & Chandler) comb. nov.

+   Endocarp with 3 locules or variable with 3 to 4 locules. Endocarp circa 20.1-30.0 mm long and 12.0-21.5 mm wide. Valves elliptical in outline. Locules C shaped with the outer wall of the endocarp thickest toward the middle. Endocarp fairly smooth, usually lacking distinct traces of vascular bundles   between the ribs.

………………….………………..………*Nyssa spatulata* (Scott) Manchester

8   Endocarp with attenuate germination valve that narrows toward the apex. Endocarp surface clearly ribbed. Ribs often becoming sharp toward the apex with vascular bundles sometimes on the ridges near the apex.

…………..*Nyssa ornithobroma* Unger

+   Endocarp with triangular valve that is not attenuate…………...……………..(9)

9   Endocarp circa 37-52 mm in length

…………………………………....……*Nyssa talamancana* **Hammel & Zamora**

+   Endocarp lessa than 37 mm long…………………………………………..(10)

10   Endocarp less than 12 mm long…………………………………………(11)

+	Endocarp less than 37 mm long but greater than 12 mm long………………..(12)

11	Base of endocarp squared and only slightly rounded, forming nearly a right angle

 with the sides of the fruit. (Holotype only known specimen, 9.5 mm long by 6.25

mm wide)………………………………………………*Nyssa cooperi* Chandler

+	Base of endocarp bluntly pointed or rounded. Endocarp between circa 5.6-11.8

mm long and 3.2-8.8 mm wide……..…….*Nyssa complanata* Eyde and Barghoorn

12	Endocarp coarsely ribbed. Ribs mostly evenly spaced and about the same size as

the interspaced grooves. Endocarp consistently trilocular. Length of endocarp

ranging from 12.6-16.5 mm long and 6.1-9.5 mm wide

…………………………………………………….……..*Nyssa scottii* Manchester

+	Endocarp ribs and grooves of different sizes. Ribs varying from narrow to wide,

often on the same specimen. Endocarp morphotype usually bilocular, but

sometimes trilocular. Endocarp consistently at least 16 mm long

………………………………………………………………………..(13)

13	Endocarp oblong to elliptical. Frequently rounded on both ends, occasionally

broadly pointed (obtuse) towards the apex. Valves rarely visible on the surface.

Endocarps ranging from 16-22.5 (-26) mm long and 4.5-12mm wide. 10-15

grooves on the surface of the endocarp. Group of longitudinal fibers lining the

locule about 3 fibers thick…...…………..……….…………*Nyssa eolignitica* Berry

+	Endocarp fusiform with both ends acute. Base of the endocarp rarely slightly less

pointed. Valves normally clearly visible on surface of the endocarp with a more

pronounced groove running from the center of the valve to the base of the fruit.

Endocarp (21.5-) 25-33.3 mm long. 17-21(-23) vascular bundles on the surface of

the endocarp. Group of longitudinal fibers lining the locule about twelve to fifteen

fibers thick …………………………...………..….….……*Nyssa grayensis* sp. nov.

14   Endocarp bilocular or locule number variable and known to have up to at least

two locules...(15)

+   Endocarp unilocular or locule number variable and known to have a single locule.

…………………………………………………………...………...….……(30)

15   Endocarp 37-52 mm long with 2-3 "C" shaped locules

…………………...……………….……**Nyssa talamancana** **Hammel & Zamora**

+   Endocarp less than 35 mm long.….……………………….….………………(16)

16   Endocarp less than 14.5 mm long or length of morphotype variable and known to

sometimes be less than 14.5 mm long.………………………………………...(17)

+   Endocarp greater than 14.5 mm long or length of morphotype variable and known

to sometimes be greater than 14.5 mm long…...……………………………….(23)

17   Endocarp with conically shaped apical projection. Endocarp thick walled (up to 3

mm)……………………………………………………………….…….......(18)

+   Endocarp lacking apical projection. Endocarp usually .5-1.5 mm thick...……..(19)

18   Endocarp usually dorso-ventrally compressed. Valves clearly visible externally.

Circa 10 ribs on the surface. Endocarp 10-20 mm long by 10-20 mm wide.

Consistently bilocular……….………............………………..*Nyssa pachycarpa* Miki

+   Endocarp usually circular in cross-section. Valves usually not visible externally.

Circa 10-15 ribs on the endocarp surface. Endocarp 13.5-24 mm long by 7-13.5

mm wide. Both unilocular and bilocular forms common

…………………………………………………*Nyssa lescurii* (Hitchcock) Perkins

19   Endocarp with 1 to 4 acuminate germination valves which narrows toward

the apex. Ribs often becoming sharp toward the apex with vascular bundles

sometimes on the ridges near the apex. Endocarp ranging from 6-23.4 mm long

and 4-12 mm wide………………………………… *Nyssa ornithobroma* Unger

+   Endocarp valves not narrowing toward the apex. Vascular bundles between ribs

the entire length of the endocarp. Endocarp consistently less than 14.5mm long

and less than 9 mm wide……………………….…………………………(20)

20   Base of endocarp internally having multiple vascular strands possibly remnants of

a receptacle tip. Endocarps having 2-4 locules in the same population. Smaller

endocarps of morphotype usually curved laterally so that one edge is somewhat

concave and the other edge is more convex. Large endocarps often having a

length to width ratio greater than two. 10-15 ribs on the surface of the endocarp.

…………………………………..………............……*Nyssa complanata* Lesquereux

+   Endocarp lacking multiple vascular strands. Endocarp with no more than 2

locules. Endocarp not laterally bent regaurdless of size……………….………(21)

21   Endocarps unilocular or very rarely bilocular. Grooves wider than vascular

strands that rest within them. 10-15 ribs.

...………………………………….…..*Nyssa disseminata* (Ludwig) Kirchheimer

+   Endocarps unilocular or bilocular. Usually 9-10 distinctive grooves. Sometimes

up to 12 grooves with 2 to 3 grooves less pronounced and visible for only a

portion of the length of the endocarp. Endocarps having a length to width   ratio

less than 2.

………………………………………………………………………………(22)

22   Endocarps very rarely bilocular. Endocarps ranging in size from 7.5-12.8 mm but most frequently less than 8.5-9.0 mm. Ventral wall of the endocarp up to twice as thick as the dorsal side bearing the germination valve. Dorsal side of the endocarp more flattened and ventral side more visibly convex…………………………………………………*Nyssa sylvatica* **Marshall**

+   Endocarps usually both unilocular and bilocular in an assemblage of fruits from a single tree. Endocarps ranging from 8-14.2 mm, but most frequently greater than 9.5 mm. Ventral walls of unilocular endocarps up to twice as thick and more rounded than the dorsal side. Curvature of dorsal and ventral sides about the same when the endocarp contains 2 fully developed locules, but more curved ventrally when the ventral locule is abortive and reduced in size. Bilocular endocarps usually more flattened on one or both lateral edges and roughly perpendicular to the dorsal and ventral sides.

…………………………………………………………*Nyssa sinensis* **Oliver**

23   Endocarp with 1 to 4 attenuate germination valves which narrow toward the apex. Ribs often becoming sharp toward the apex with vascular bundles   sometimes on the ridges near the apex. Endocarp ranging from 6-23.4 mm long and 4-12 mm wide………………………….………………...……*Nyssa ornithobroma* Unger

+   Consistently less than 4 germination valves. Valves not attenuate. Endocarps consistently at least 10 mm long………………………………………………….(24)

24   Endocarp with 9-12 (-15) very prominent (2-5 mm tall) pointed ridges that support papery mesocarp wings. Mesocarp wings more vulnerable to decomposition but sometimes persistent in the fossil record. Ridges of variable

thicknesses and heights, often tallest toward the center of the endocarp. Apex of endocarp steeply narrowing above the valve as an elongate extension. A conical projection is attached at the end of the extension. Unilocular forms most common, but bilocular forms not rare…………………***Nyssa ogeche* Bartram ex Marshall**

+ Endocarp with between 8 and 20 ridges which are rounded or fairly pointed but less than 2 mm tall. Mesocarp wings not reported. Ridge height fairly uniform. Thickness of ridges variable or consistent. Apex of endocarp not elongate. Conical projection at apex present or absent…………………………………..(25)

25 Endocarp irregularly rugose. Surface very rough. Endocarp consistently bilocular. 10-20mm long by circa 10 mm wide.

………..……*Nyssa aspratilis* Eyde & Barghoorn (*Nyssa rugosa* Miki non Weber)

+ Endocarp ribs fairly smooth or surface wavy with longitudinally oriented wrinkles..……………………………………………………….………………(26)

26 Endocarp thick walled, reaching up to 3 mm thick. Conical apical projection present. Ten to fifteen ribs……………………………………………………………………………..(27)

+ Endocarp wall usually .5-1.5 mm thick. Conical apical projection present or absent…………………………………………………………………….…….(28)

27 Endocarp round in section. Endocarp having 10-15 ribs. Both 1 and 2 locular forms commonly found together. Valves rarely visible externally. Endocarps 13.5-24 mm long by 7-13.5 mm wide.

………………………………………………*Nyssa lescurii* (Hitchcock) Perkins

+	Endocarp somewhat flattened. Endocarp usually having 10 ribs. Endocarps consistently one locular. Valves usually visible externally. Endocarps 10-20 mm long by 10-20 mm wide...…………………………………*Nyssa pachycarpa* Miki
28	Endocarp with 8-10 broad ribs with vascular bundles between them. A smooth external covering present on the endocarp, obscuring the underlying vascular bundles in places. Endocarp only reported to have 2 locules. Endocarps up to 18.5 mm long by 10 mm wide. Endocarp ovate, broader at the base and narrower toward the apex. Valves clearly visible on the surface. …………….....………………… *Nyssa bilocularis* (Reid & Chandler) Chandler
+	Endocarp with at least ten ridges and grooves. Endocarp bilocular or trilocular. Endocarps not typically ovate……………………….……………………(29)
29	Endocarp oblong to elliptical. Frequently rounded on both ends, occasionally broadly pointed (obtuse) towards the apex. Valves rarely visible on the surface. Endocarps ranging from 16-22.5 (-26) mm long and 4.5-12mm wide. 10-15 grooves on the surface of the endocarp. Group of longitudinal fibers lining the locule about three fibers thick……………….....………..*Nyssa eolignitica* Berry
+	Endocarp fusiform with both ends usually acute. Base of the endocarp rarely slightly less pointed. Valves normally clearly visible on surface of the endocarp with a more pronounced groove running from the center of the valve to the base of the fruit. Endocarp (21.5-) 25-33.3mm long. 17-21(-23) vascular bundles on the surface of the endocarp. Group of longitudinal fibers lining the locule about 12-15 fibers thick…………………………..………….*Nyssa grayensis* sp. nov.

30   Endocarp having (3-) 4-5 (-6) ribs; mostly on the dorsal side. Endocarp dorso-

ventrally compressed. Basal and apical ends arching gently toward the dorsal side.

Dorsal side thinner-walled and less curved along its length. Endocarp thickness

and width greater toward the base. Consistently unilocular.

……………………………...……..*Nyssa yunnanensis* **Yin ex Qin & Phengklai**

+   Endocarp having more than 6 ribs, rarely less than 8 ribs. Endocarp straight

or arching………………………………………………………………………(31)

31   Endocarp with 1 to 4 acuminate germination valves that narrows toward the apex.

Ribs often becoming sharp toward the apex with vascular bundles sometimes on

the ridges near the apex. Endocarp ranging from 6-23.4 mm long and 4-12 mm

wide……………..………………………………..………*Nyssa ornithobroma* Unger

+   Valves not acuminate. Endocarp with consistently less than 3 locules.

Vascular bundles not raised near the apex…………………………………..(32)

32   Endocarp with conically shaped apical projection. Endocarp between circa 13.5-

29.3 mm long…………………………………………………………..…………(33)

+   Endocarp without conically shaped apical projection. Endocarp between circa 4.7-

30 mm long..…………………………………………………………….…..(34)

33   Endocarp with 9-12 (-15) very prominent (2-5 mm tall) pointed ridges that

support papery mesocarp wings. Mesocarp wings more vulnerable to

decomposition but sometimes persistent in the fossil record. Ridges of variable

thicknesses and heights, often tallest toward the center of the endocarp. Apex of

endocarp steeply narrowing above the valve as an elongate extension. Conical

projection attached at the end of the extension. Unilocular forms most common,

but bilocular forms not rare. Average length circa 23mm, ranging from 14.7-29.3 mm. Endocarp wall usually less than 1.5 mm thick.

……………………………...……….…….*Nyssa ogeche* **Bartram ex Marshall**

\+ Endocarp with 10-15 rounded or flat ribs. Mesocarp wings not known. Ridges not varying drastically in height . Both ends of endocarp usually more or less rounded. Both unilocular and bilocular forms common. Ranging from 13.5-24 mm long. Endocarp thick-walled, up to 3 mm thick.

………………………………………………*Nyssa lescurii* (Hitchcock) Perkins

34 Endocarp 22-30 mm long. 12-15 thick grooves which appear to have held more than one vascular bundle. Endocarp unilocular………………..*Nyssa texana* Berry

\+ Endocarp between circa 4.7-18 mm long. Endocarp grooves generally holding a single vascular bundle. Endocarp unilocular (or morphotype containing both unilocular and bilocular forms)...…………………………………………………(35)

35 Endocarp wall thick, reaching up to 3 mm. Endocarp wall thinner near the valve, reaching about 1.3 mm. 10-12 shallow grooves on the surface.

………………………………………………......……………*Nyssa oviformis* Reid

\+ Endocarp wall usually .5-1.5 mm thick . Endocarp with dorso-ventral compression. Endocarp less than 15 mm long and less than 8 mm broad at widest point. 8-12 shallow or deep grooves on surface……………………….……….(36)

36 Endocarp highly sculptured with grooves wider than vascular strands that rest within them. 10-15 ribs. Endocarps unilocular or very rarely bilocular. 6-14mm long and 3-7 mm wide.………..………*Nyssa disseminata* (Ludwig) Kirchheimer

+ Endocarp with 8-12 shallow and narrow grooves approximately the same size of the vascular bundles……….……………………………………………………..(37)

37 Endocarp usually rounded on both ends. Endocarp unilocular or found in both unilocular and bilocular forms……………………………..…………………..(38)

+ Apex of the endocarp frequently tapered to a point. Endocarps only reported as unilocular. Endocarps ranging from 4.7-9.9 mm long and 2-5 mm wide. 3-5 vascular bundles on the ventral side and 5-6 on vascular bundles on the dorsal side.………………….………….……..……….*Nyssa sibirica* Dorofeev ex Zhilin

38 Endocarps usually both unilocular and bilocular in an assemblage of fruits from a single tree. Endocarps ranging from 8-14.2 mm long and 5-7.5 mm wide, but most frequently greater than 9.5 mm long. Ventral walls of unilocular endocarps up to twice as thick and more rounded than the dorsal side. Curvature of dorsal and ventral sides about the same when the endocarp contains 2 fully developed locules, but more curved ventrally when the ventral locule is abortive and reduced in size. Bilocular endocarps usually more flattened on one or both lateral edges and roughly perpendicular to the dorsal and ventral sides. Sometimes up to 12 grooves with 2 to 3 grooves less pronounced and visible for only a portion of the length of the endocarp……..…………….……………………*Nyssa sinensis* **Oliver**

+ Endocarps very rarely bilocular. Endocarps ranging in size from 7.5-12.8 mm long and 5-7 mm wide but most frequently less than 8.5-9.0 mm long.Ventral wall of the endocarp up to twice as thick as the dorsal side bearing the germination valve. Dorsal side of the endocarp more flattened and ventral side more visibly convex. Sometimes up to 12 grooves with 2 to 3 grooves less pronounced and

visible for only a portion of the length of the endocarp

……………………………………………….………*Nyssa sylvatica* **Marshall**

Nyssa Key 2- Endocarps with Vascular Bundles Mostly Raised on the Crests of

Ridges

1   Endocarp mostly smooth, usually having a dorsal ridge and 2 less distinct dorsal

ridges to the sides. Occasionally some small grooves or a single sharp ridge

on the ventral side. Vascular bundles positioned above the ridges but not

attached…………………………….……...*Nyssa javanica* **(Blume) Wangerin**

+   Endocarp with 9-15 distinct sharp ridges. Vascular bundles running along

ridges.....……………………….…………………………………….…..(2)

2   Endocarp greater than 9 mm wide. Length at least 14.8 mm long and usually over

20 mm. Endocarp often obovate, and usually having a mucronate-shaped apex.

…………………………………….……………………………………..(3)

+   Endocarp 3-9 mm broad and 5.6-20 mm long. Endocarp usually sub-ovoid or less

frequently sub-obovoid. 10-14 sharp ridges and 1-3 locules. Endocarp frequently

arched dorso-ventrally and less convex on dorsal side. Apex not mucronate.

……………………….………………………………….*Nyssa boveyana* Chandler

3   Endocarp with one locule. Valve acuminate, narrowing steeply toward the apex.

Endocarp 14.8-28.3 long, usually about 21 mm long. Endocarp about 9.4-11.2

mm at the widest point. About 10 sharp ridges.

……………………….………….……………...…….*Nyssa aquatica* **Linnaeus**

+ Endocarp bilocular or trilocular, most frequently bilocular. One locule sometimes abortive and greatly reduced in size. Base of endocarp enlarged and ranging from 5-15mm thick. Valve not acuminate. Endocarp ranging from 17-44 mm long and 13-28 mm wide.…………………*Nyssa fissilis* (Lesquereux) Eyde and Barghoorn

Nyssa Key 3- Endocarps with Few Traces of Vascular Bundles on the Surfaces

1   Endocarp with one locule………………………………..…………………(2)

+   Endocarp with at least three locules. Valve narrow at base and ovoid or sub-ovoid with an acuminate or mucronate tip………………………………………..(4)

2   Endocarp with a ridge in the center of the valve. Endocarp lacking beak like extension at the apex…………….……………………………………………(3)

+   Endocarp lacking ridge along the center of the locule. Three grooves near the apex. Endocarp having beak like extension at the apex. Endocarp circa 40x23 mm…….………………………………….*Nyssa magnifica* (Knowlton) Berry

3   Valve within the apical 1/3 portion of the endocarp. Valve not acuminate. Locule with a broad dorsal groove and 2 smaller dorsal grooves. Ventral portion of locule wall with broad internal ridge. Locule roughly "M" shaped from these ridges. 8.9-17.8 mm long and 6.2-10.9 mm wide. Very rarely up to 29.8 mm long and 19.2 mm wide..…………..…………..…..***Nyssa javanica* (Blume) Wangerin**

+   Valve extending at least 1/2 of the length of the endocarp from the apex. Valve wide at base and possessing an acuminate or mucronate apex. Locule surface lacking ridges. 24-45 mm long and   18-30 mm wide. Endocarp wall about 2 mm thick toward apex and 4 mm thick near base.

…………………………...*Nyssa brandoniana* (Lesquereux) Eyde and Barghoorn

4   Endocarp with mucronate-shaped apex. Ridges present in the center of the valves.
Endocarp consistently having 3 "c"-shaped locules. Valve length over half the
length of the endocarp. Endocarp 23-25 mm long and 12-16 mm.

...……………………………………………….*Nyssa spatulata* (Scott) Manchester

+   Apex of endocarp not mucronate. Endocarp fairly smooth without vascular
bundles adhering between the ribs except along the midline of the locules that
usually bear a more prominent groove. Endocarp with 3 or 4 locules. Valve
length about one third the length of the endocarp. Endocarp circa 12.3-15 mm
long by 6.2-9.5mm wide.

…………………………….……….*Nyssa multilocularis* (Reid & Chandler) comb. nov.

Climatic and Biogeographic Implications

Isotopic signatures from benthic foraminifera presented in Zachos et al. (2001;
2008) suggest that the average global temperature during the Miocene-Pliocene was
warmer than the present. According to geological studies of the Atlantic and Gulf Coast
Plains the sea level may have been as much as 100 m higher than the present during the
late Hemphillian (Van Arsdale et al. 2007) when the Gray Fossil Site was actively being
deposited. Based on modern topography (Figure 47), sea transgression would have likely
resulted in an inward movement of the coastline and intrusion of the sea up the
Mississippi River valley. The sea may have extended up the Mississippi River valley as
far north as western Tennessee and Virginia (Van Arsdale et al. 2007; Figure 47,
Williams et al. 2002). Mid-latitude bodies of water act as a thermal buffer (Newell 1979),

so the higher sea levels would have helped reduce winter cooling at the GFS. Winter

temperatures and precipitation are some of the most important factors influencing the

distribution of plants and animals (Woodward and Williams 1987; Carpenter et al. 1993).

Figure 47: An Estimation of the Paleoshore-Line During 100 Meter Higher Sea
Levels Based on Modern Topography. Modified from Williams (2002).

Fossil floras and faunas provide a source of climatic information that can be used

to test other climate data and provide more detailed information about local and regional

climates. In particular, quantitative data from the coexistence approach and other proxies

provide a source for quantitative climate data that is required for climatic modeling.

When the climatic requirements of modern representatives of coexisting fossil flora are

plotted on a graph, the climatic requirements of the taxa are usually in good agreement

with each other (Tiffney and Manchester 2001). The fossil record suggests that

migrations of plant species toward climatic conditions they are adapted to occur more

frequently than adaptation to new climatic conditions (Tiffney and Manchester 2001).

Many of the taxa found at the GFS (e.g. *Sinomenium*, *Vitis*, *Pristinailarus*) are most closely related to species in Asia (Wallace and Wang 2004; Gong et al. 2010; Liu and Jacques 2012), showing that these elements survived the milder environments in SE Asia but went extinct locally. We would also expect the boundaries of some surviving species to move southward. Areas closer to the Atlantic coast also currently have milder winter temperatures than more inland areas, which allow many species to survive at higher latitudes compared to areas further inland (Gilliam and Christensen 1986). Areas within the Atlantic Coastal Plain also have rainy and humid summers (Gilliam and Christensen 1986).

Based on the similarities described in the previous sections, *Nyssa grayensis* sp. nov. appears to be part of a group of closely related *Nyssa* that includes the fossil species *Nyssa eolignitica* Berry from the mid Eocene of western Tennessee, *Nyssa lescurii* (Hitchcock) Perkins from the early Miocene Brandon Lignite, *Nyssa pachycarpa* Miki from several Pliocene localities in Japan, the extant *Nyssa ogeche* Bartram ex Marshall, and the extant *Nyssa talamancana* Hammel and Zamora from Costa Rica and Panama. Out of these species, the fossil species *Nyssa eolignitica* Berry and *Nyssa ogeche* Bartram ex Marshall are the most similar to *Nyssa grayensis* sp. nov. The distribution of the fossils and extant species shows that the group was once more widespread and found in fairly high northern latitudes but became limited to more southern latitudes as the climate deteriorated. Similar scenarios are suggested by other plant and animal taxa at the GFS. The *Nyssa* subgroup also appears to be of American origin, with the only Eurasian endocarps fitting the morphology being those of the Pliocene *Nyssa pachycarpa* Miki (Miki 1956) and the Oligocene *Nyssa* cf. pachycarpa from Siberia reported in Dorofeev

(1963). This suggests that members of the group spread between North America and Eurasia by at least the Oligocene.

Fossils tentatively identified as being most similar to the extant *Ilex vomitoria* Solander ex Aiton (Ochoa et al. 2012), *Quercus virginiana* Miller (Zavada, personal communication), *Taxodium* sp. (Ochoa et al. 2012), and *Acer leucoderme* Small (Liu, personal communication) are found at the GFS. The modern distribution of *Taxodium* includes the Atlantic Coastal Plain, the Mississippi Valley floodplains, and portions of Mexico and Guatemala (Stults et al. 2011; Figure 48). *Quercus virginiana* Miller is found along the Atlantic Coastal Plain south to Florida, west to Texas, and in portions of Mexico (Cavender-Bares et al. 2011). *Ilex vomitoria* Solander ex Aiton is found along the coastal plain and an isolated pocket in Chiapas, Mexico (González-Espinosa et al. 2006; Little 2006). *Acer leucoderme* Small is distributed in the southeastern United States, with most of the range located in the Coastal Plain south of Virginia (Figure 51). *Ehretia* (Boraginaceae) has recently been discovered at the GFS, and is most similar to the Central American form (Liu, personal communication). The co-occurrence of these taxa suggest that during the deposition of the upper layers of the GFS the climate was fairly rainy or humid during the summer, and winter temperatures were milder, perhaps similar to the modern Coastal Plain. The presence of these species also supports the southern and coastward push of the northern limit of these species during climatic deterioration.

Figure 48: The Modern Distribution of *Taxodium distichum* (Linnaeus) Richard (in Blue) and *Taxodium mucronatum* Tenore (in Green). Modified from Little (2006).

Figure 49: The Modern Distribution of *Quercus virginiana* Miller. Modified from Little (2006).

Figure 50: The Modern Distribution of *Ilex vomitoria* Solander ex Aiton. Modified from Little (2006).

Figure 51: The Modern Distribution of *Acer leucoderme* Small. Modified from Little (2006).

Animals remains found at the GFS tell a similar story. This is especially true for herpetofauna. The *Alligator* remains from the Gray Fossil Site show some distinction from extant species, but *Alligator mississippiensis* (Daudin) Snyder is likely the nearest living relative (Schubert, personal communications). The coldest climate zones where *A. mississippiensis* is found today are near the mean and minimum January isotherms of 7.2°C (45°F) and -1°C (34°F) respectively, with the minimum isotherm apparently controlling the distribution of modern populations (Mead et al. 2012). The modern distribution of *Alligator mississippiensis* (Daudin) Snyder is shown in Figure 52. Notice in Figures (48-51) all of these species modern distributions that overlap the distribution of *Alligator*. Members of the genus *Heloderma* are not active at temperatures much below 24°C (75°F) (Mead et al. 2012). Morphological studies of *Heloderma* osteoderms from the Gray Fossil Site reveal a closest similarity with the extant species *H. horridum* Wiegmann (Mead et al. 2012). Ecologically *H. horridum* Wiegmann is most fitting based on the forested environment interpreted to have dominated the Gray Fossil Site. The range of this species currently extends from the southern Sonora southward along the western coast of Mexico to Guatemala in tropical dry forests, tropical deciduous forests, pine-oak woodlands, and tropical thornscrubs (Mead et al. 2012). *Hesperotestudo* sp. found at the GFS (Schubert 2011) is a gopherine tortoise genus related to the extant gopherine tortoise *Gopherus* (Morafka and Berry 2002). One of the extant species *Gopherus polyphemus* Daudin is found in the southeastern coastal plain (Figure 54) today, whearas the other species are found in the Mojave Desert, Texas, and parts of Mexico (Morafka and Berry 2002). *Hesperotestudo* may have had similar climatic requirements.

Figure 52: The Modern Distribution of *Alligator mississippiensis* Daudin. Modified from NatureServe (2012).

Figure 53: The Distribution of the Subspecies of *Heloderma suspectum* Cope and *Heloderma horridum* Wiegmann. Modified from Douglas et al. (2010).

Figure 54: The Range of an Extant Gopherine Tortoise *Gopherus polyphemus* Daudin. Modified From Smith et al. (2006)

The presence of *Pristinailurus bristoli* Wallace and Wang at the Gray Fossil Site (Wallace and Wang 2004) may also have climatic and environmental significance. The extant red panda *Ailurus fulgens* Cuvier lives in areas between 10°C to 25°C and 350-150 cm of annual rainfall (Roberts and Gittleman 1984). In general these areas have well-drained moist soils suitable to bamboo growth (Roberts and Gittleman 1984). *Arundinaria sp.* has been reported at the Gray Fossil Site (Ochoa et al. 2012) and may have been an important component of the diet of *Pristinailurus bristoli* Wallace and Wang.

Similar to the nearest living relatives of a number of other plants and animals at the Gray Fossil Site, Nyssa ogeche Bartram ex Marshall, the proposed nearest living relative of *Nyssa grayensis* sp. nov. is found in the southeastern United States today. While the climatic inferences of a single taxon may not be reliable, together these taxa

provide strong support for mild-winters at the Gray Fossil Site during the time the fossils were being deposited. This is not surprising considering independent data such as isotopic studies that suggest the average global temperatures were warmer than the present during the Late Miocene and Early Pliocene.

<div align="center">Fruit Size and Climate</div>

Several size parameters of complete fruit and endocarps were compared with latitudinal and climate data of the extant *Nyssa* species. After adjusting the P-values (values listed as P*124) using the Bonferroni correction procedure (Holm 1979), the only variables to have statistically significant correlations were the fruit width and stone widths with the north low and north latitude. Stone length and southern latitude did not form statistically significant correlations with the other variables.

Table 5: Climate and Latitude Data for the Ranges of Extant *Nyssa* Species

Taxon	North Low (°C)	Mean North Limit (°C)	Record Low (°C)	North Lat. (°)	South Lat. (°)	Mid. Lat. (°)	Mid. Main Distrib (°)	Lat. Breadth (°C)	North Limit Loc.	South Limit Loc.
Nyssa javanica (Blume) Wangerin	2	5.5	-8	27.2830	0.0000	13.64	13.64	27.2830	Baisha, China	Java
Nyssa sinensis Oliver	-7	-1.5	20	35.7886	21.9600	28.74	28.74	13.8300	Liangshan, China	Longzhou China
Nyssa sylvatica Marshall	-11	-7.0	-27	44.3106	16.4100	30.36	36.09	27.9000	Augusta, Maine	Chiapas, Mexico
Nyssa yunnanensis Yin ex Qin & Phengklai	12	19.0	2	22.7000	22.7000	22.70	22.70	0.1000	Jinghong, China	Jinghong, China
Nyssa aquatica Linnaeus	-5	1.0	-26	39.7319	29.3000	34.52	34.52	10.4300	Murfreesboro, IL	Inglis, FL
Nyssa ogeche Bartram ex Marshall	5	16.0	-8	32.8039	29.3100	31.05	31.05	3.5309	Millen, GA	Inglis, FL

Table 5 (continued)

Nyssa talamancana Hammel and Zamora	21	20.0	14	9.6830	9.3333	9.51	9.51	0.3500	Limon, Costa Rica	Chiriqui Grande
Ranges from Qin and Phengklai (2007); Kartesz (2012); Eyde (1963). Climate data from Weather2 (2012)										

While there may be unknown factors (e.g. atmospheric content, ecological relations) that play a role in the relation of fruit size and climate, the large size of the fruits at the GFS may have climatic implications. Using the MINITAB regression analysis function on the data from the north limit low and mean stone width, a mean stone width of 13 mm would predict a north limit low of 8.08°C +/- 6.2°C at the 95 percent confidence interval and 8.08°C +/- 15.36 °C at the 95% prediction interval. Because compression may have increased the mean widths slightly, this calculation was also made assuming a mean width of 11 mm, which coincidentally is also the width of the smallest *Nyssa* endocarp at the GFS. The degree at which the maximum width of the bilocular endocarps can increase during flattening is more limited by the septum. The value of 11 mm predicts a north limit low of 2.82°C +/- 5.31°C and 2.82°C +/- 15.02 within the 95% correlation and prediction intervals. Using a minimum endocarp length of 21 mm, the north limit low is predicted to be 7.43°C +/- 6.95°C at the 95% confidence interval and 7.43 °C +/- 17.52°C at the 95% prediction interval. If a mean endocarp length of 28.0 mm is used, a north limit low of 8.46 °C +/- 8.8 °C and 8.46 °C +/- 20.87°C are predicted for the 95% confidence interval and the 95% prediction interval respectively. The cold month mean temperature for the northernmost portion of the range based on a mean stone width of 13 mm was 12.35 °C +/- 8.2 °C at the 95% confidence interval and 12.35 °C +/- 20.12 °C. The values were 7.90 °C +/- 6.96 °C and 7.90 °C +/- 19.69 °C after assuming a mean stone width of 11 mm.

Table 6: Fruit Measurements of Extant *Nyssa* Species

Taxon	Mean Stone Length (mm)	Min. Stone Length (mm)	Max. Stone Length (mm)	Mean Fruit Width (mm)	Mean Stone Width (mm)
Nyssa javanica (Blume) Wangerin (Wang et al., 2012; n=50)	14.67	14.46	14.88	15.27	12.74
Nyssa sinensis Oliver	10.51	8.00	14.20	8.61	6.97
Nyssa sylvatica Marshall	9.54	7.50	12.80	7.97	5.40
Nyssa yunnanensis Yin ex Qin & Phengklai (Wang et al., 2012; n=50)	16.18	15.16	17.20	15.80	12.48
Nyssa aquatica Linnaeus	23.10	14.80	28.30	12.70	11.15
Nyssa ogeche Bartram ex Marshall	24.04	14.70	29.30	15.19	10.23
Nyssa talamancana Hammel and Zamora	45.00	37.00	52.00	25.00	17.00 (16-22)

Although the total variation of each *Nyssa* species can be great, individuals of any single modern species do not show a significant gradation in size related to latitude. Caution should still be used because the low number (n=19) of specimens found at the GFS represent a small subsample of the true diversity of the species. The modern range of some *Nyssa* species may also be smaller due to anthropogenic changes to environments. Climatic field data directly collected from the plant localities would improve the accuracy of the correlation. However, the fact that latitude also shows correlation with fruit size supports a general conclusion that climate and fruit size are related in the modern members of this genus. It should also be noted that the climatic parameters predicted represent the climatic conditions of the northernmost extent of a species range and thus would provide minimum temperature conditions for the GFS. Still, these results are in good agreement with the systematic relation of *Nyssa grayensis* sp.

nov with the extant species *Nyssa ogeche* Bartram ex Marshall which has a subtropical to

tropical range. *Nyssa ogeche* Bartram ex Marshall has a north limit low of 5.0 °C in

Jenkins Co., Georgia (Table 5). The best fits for the north limit low based on various

metric variables also mostly group near 7-8 °C that is similar to the northern limit of the

extant *Alligator* and other animal and plant species at the GFS. These data are also in

good agreement with climatic calculations made by Dr. Liu using climatic requirements

of the nearest living relatives of plants at the GFS and the Coexistence Approach (CA).

The CA estimates a cold month mean temperature at the GFS of 2.9-7.1°C (Liu, Personal

Communication).

Table 7: Correlation of Fruit Sizes with Climatic and Latitudinal Variables

Correlation Tested (Stared correlations statistically significant adjusted P-value)	Pearson Correlation	P-value	Adjusted P-value (P*124)	R-squared
Mean Fruit Width Vs. North Low*	.948	.001	0.124	.8994
Mean Fruit Width Vs. North Latitude*	-.927	.003	0.372	.8592
Mean Fruit Width Vs. Record Low*	.910	.004	0.496	.8283
Mean Stone Width Vs. North Low*	.897	.006	0.744	.8054
Mean Stone Width Vs. North Latitude*	-.895	.006	0.744	.8013
Min. Stone Length Vs. North Latitude	-.870	.011	1.364	--
Min. Stone Length Vs. North Low	.863	.012	1.488	--
Mean Stone Width Vs. Record Low	.847	.016	1.984	--
Mean Fruit Width Vs. Cold Month Mean	.843	.017	2.108	--
Mean Stone Width Vs. Mid. Main Distribution	-.822	.023	2.852	--
Min. Stone Length Vs. Record Low	.818	.025	3.100	--
Mean Stone Length Vs. North Low	.804	.029	3.596	--
Mean Fruit Width Vs. Mid. Main Distribution	-.801	.030	3.720	--
Mean Stone Width Vs. Cold Month Mean	.795	.033	4.092	--
Mean Stone Length Vs. North	-.771	.042	5.208	--

Table 7 (continued)

Latitude				
Mean Fruit Width Vs. Mid. Latitude	-.757	.049	6.076	--
Mean Stone Width Vs. Mid. Latitude	-.751	.052	6.448	--
Min Stone Length Vs. Mid. Main Distribution	-.736	.059	7.316	--
Mean Stone Length Vs. Record Low	.735	.060	7.440	--
Max. Stone Length Vs. North Low	.717	.069	8.556	--
Min. Stone Length Vs. Mid. Latitude	-.713	.072	8.928	--
Max. Stone Length Vs. North Latitude	-.668	.101	12.524	--
Max. Stone Length Vs. Cold Month Mean	.614	.142	17.608	--
Mean Fruit Width Vs. Latitudinal Breadth	-.604	.151	18.724	--
Mean Stone Length Vs. Mid. Latitude	-.554	.197	24.428	--
Max. Stone Length Vs. Mid. Latitude	-.422	.345	42.780	--
Mean Stone Width Vs. Southern Latitude	-.362	.425	52.700	--
Mean Fruit Width Vs. Southern Latitude	-.338	.458	56.792	--
Min. Stone Length Vs. South Latitude	-.321	.482	59.768	--
Mean Stone Length Vs. South Latitude	-.147	.753	93.372	--
Max. Stone Length Vs. South Latitude	-.026	.956	118.544	--

Figure 55: Boxplots Of *Nyssa* Fruit Widths

Figure 56: Boxplot of *Nyssa* Stone Widths

Figure 57: Scatterplot of Mean Fruit Width Correlated with North Limit Low Temperature.

Figure 58: Scatterplot of Mean Stone Width Correlated with North Limit Low Temperature.

The results of this study suggest that fruit sizes of the extant *Nyssa* species are directly or indirectly related to climate and latitude. Other taxa have previously been shown to have a relation between fruit or seed size and climate. *Arctostaphylos* species found in lower minimum latitudes typically have larger fruit sizes (Simpson 2009). Moles and Westoby (2003) found that mean seed mass across 2706 species declined with increasing latitude. It is possible that growing season or other metabolic advantages control this correlation. Larger seeds may have several advantages including a larger food and water reserve to combat drought, growth through soil and leaf litter, deep shade, and low soil nutrients (Westoby et al. 2002). Because animals often play a role in fruit dispersal, this correlation could be the indirect result of the distribution of faunal sizes and diversity. Herrera et al. (2002) found that in addition to the impacts of frugivores, the size of other parts of the plant may impact fruit size. In their study fruit-size showed a significant positive correlation with leaf size (Herrera et al. 2002). Larger fruits may be preferred by some large dispersers, whereas dispersal ability is also limited by an animal's gape size. These factors must also be balanced by the energy investments. There may be a tradeoff between fruit size and total fruit production per tree. *Fragaria* (strawberry) plants with larger fruit numbers usually have smaller fruits (Rindom and Hansen 1995). The density of fruit on the branches of *Nyssa* species is high on the species with small fruits (e.g. *N. sylvatica* and *N. sinensis*), and the fruit often occur in clusters of multiple fruits. Larger-fruited species observed in this study (e.g. *N. talamancana*, *N. ogeche*, and *N. aquatica*) had a single fruit per infructesence.

Mammalian and Avian frugivores are known to be more diverse in the tropics (Alroy et al. 2000), suggesting that fruit size will be less of a limiting factor in warmer environments. The modern diversity of birds in North America decreases drastically with increasing latitude. In the higher latitudes of the boreal zone, birds have a diversity of less than 100 species within the region, compared to 300 species in central Mexico, and 600 species in the new world tropics near the equator (MacArthur 1969; Hawkins et al. 2003).

Frugivore size and fruit size appear to be clearly related to each other. Pratt and Stiles (1985) note that the range of both bird sizes and fruit sizes are both greater in the tropics. Fruit and bird studies in Mexico have suggested that intermediate sized fruits attract the most birds (Kantak 1979). Wheelright (1985) shows that the frequency distribution of bird gape sizes in Costa Rica mirrors the frequency distribution of bird gape sizes. The smallest size of fruit eaten by a species, however, is not correlated with bird size; Wheelright (1985) found that even large birds will eat the smallest fruits as well.

Fruit dispersal by animals is also noted to decrease with increasing latitude (Herrera 2002). Terborgh et al. (1990) suggest that as many as 85% of tropical plant species depend on vertebrate dispersers in the Amazon, and Fleming et al. (1987) state that the tropics as a whole have between 50% to over 90% of plant species with a dependence on frugivores. Over 90% of tropical rainforest plants enclose their seeds in a fleshy covering compared to 45% percent in tropical dry forests and 35% percent in temperate forests (Jordano 1995; Galetti et al. 2011). Márquez et al. (2004) studied the relation of birds and fleshy fruited plant diversity across Europe with an emphasis on overwintering birds and winter-fruiting plants. They found that birds affected the

diversity of fleshy fruited plants about twice as much as fleshy fruited plants control the diversity of birds. They also found that the influence of birds on plant diversity was 4 times as great as environmental factors.

Fruit width is expected to be more of a dietary limit than fruit length. *Nyssa* fruit and stone widths form statistically significant correlations with the north low and north latitude of the species, supporting the possibility that frugivores have an impact on *Nyssa* fruit size. The fact that the northern limits (temperature and latitude) of the range correlate with fruit size, but the southern limits do not would agree with the idea that the size needs to be small enough to accommodate dispersers throughout the entire range. While some large birds are found far north (e.g. waterfowl and large galliform game-birds) and some potential medium and large sized mammalian dispersers of *Nyssa* (e.g. opossum, raccoon, bear) are found even in high northern latitudes, the diversity of animals filling this niche is lower than in the tropics (Rybczynski and Riker 1981; Fleming et al. 1987). Water-fowl are also more common in lacustrine and fluvial environments where the larger-fruited (*N. ogeche* and *N. aquatica*) North American species are found. In lower latitudes a greater diversity will also remain present during the fall when most types of *Nyssa* ripen. As an example the distribution of *Aix sponsa* Linnaeus (wood duck) extends far north during the summer but is mainly restricted to the southern United States, especially toward the coast and Mississippi River Valley after migration in the fall (Figure 58).

In addition to the likely relations between the extant *Nyssa ogeche* Bartram ex Marshall and the presence of many taxa with nearest living relatives found in the southeastern United States, the size of *Nyssa grayensis* sp. nov. endocarps may be related

to the climate being warmer than the present when the Mio-Pliocene Gray Fossil Site was being deposited. The size and distribution of dispersers of *Nyssa* species may also play a role in the fruit sizes of extant and extinct *Nyssa* species. The distribution of dispersing species, especially those of migratory birds, may play a role in the relationship between fruit size and climate.

Figure 59: The Winter Distribution of *Aix sponsa* Linnaeus. Modified from Sauer et al. (2011)

Environmental Implications

The relation of *Nyssa grayensis* sp. nov. to the extant *Nyssa ogeche* Bartram ex Marshall, a species that inhabits lacustrine environments and fluvial margins and the extinct *Nyssa eolignitica* Berry, a species whose remains were deposited in fluvial sediments, suggests *Nyssa grayensis* sp. nov. probably had a similar habitat, i.e. lowland forests. This is supported by the deposition of the newly described endocarps in the clay and silt lenses that infill the GFS sinkhole, and the hydrophilic taxa that are deposited in the same strata. The modern large-fruited *Nyssa* species of North America (*Nyssa*

aquatica Linnaeus and *Nyssa ogeche* Bartram ex Marshall) are frequently found

associated with *Taxodium*, which has similar habitat and climatic preferences. Similarly,

fossil *Taxodium* and *Nyssa* are also found together very frequently (Dorofeev 1963; Elsik

and Dilcher 1974; Mai 2001; Kvaček et al. 2004; Stults and Axsmith 2011a; and many

others).

Periodic flooding is important to *Nyssa aquatica* Linnaeus and *Nyssa ogeche*

Bartram ex Marshall and decreased inundation due to dam construction in some areas has

resulted in declines of these species in back swamps (Stallins et al. 2010). The survival of

Nyssa seedlings is very poor when the moisture conditions are not ideal (Campbell et al.

2001). The American *Nyssa* species *Nyssa ogeche* Bartram ex Marshall, *Nyssa aquatica*

Linnaeus, and *Nyssa sylvatica* Marshall var. *biflora*, as well as *Taxodium*, are shown to

grow best when flooding conditions occur either periodically or frequently (Keeland and

Sharitz 2011). All of these species can grow completely submerged in water for long

periods of time (Hook et al. 1971; Keeley 1979; Stallins et al. 2010; Keeland and Sharitz

2011) due to anaerobic respiration abilities in the roots. This gives *Nyssa* and *Taxodium* a

special niche that most species of trees cannot inhabit. The seeds of *Nyssa* and *Taxodium*

have been known to remain viable after submersion for a year or more; however, the

seeds of neither taxon can germinate under the water (Demaree 1932; DeBell and Naylor

1972; Keeley 1979; Johnson 1990). This means that the plants require not only a wet

environment but fluctuating water levels. For this reason *Nyssa* species thrive in

floodplain environments. The periodic lenses of silt and sand support the presence of

fluctuating water levels at the GFS. *Nyssa* species are also tolerant of both shade and

light, making them less vulnerable to disturbances (Abrams 2007). Watts et al. (2012)

found that the survival of *Taxodium* during fires was also high in wetland environments.

CHAPTER 4

SUMMARY AND CONCLUSIONS

The presence of *Nyssa* at the Gray Fossil Site supports the interpretation of the depositional environment as a sinkhole fed by a river or stream, and with water levels that fluctuated depending on fluvial input and other factors (e.g. beaver dams, collapses). While the endocarp morphology of *Nyssa grayensis* sp. nov is distinct from previously named species, morphological and anatomical similarities suggest the fossil species most similar to *Nyssa grayensis* sp. nov. is *Nyssa eolignitica* Berry. The extant species most similar to *Nyssa grayensis* sp. nov. is *Nyssa ogeche* Bartram ex Marshall.

The affinities of *Nyssa grayensis* sp. nov. with *Nyssa ogeche* Bartram ex Marshall suggest *Nyssa grayensis* sp. nov likely lived in areas with mild winters and seasonally high rainfall or high humidity. The extant species *Nyssa talamancana* Hammel and Zamora also shares several similarities with *Nyssa grayensis* sp. nov. and is found in areas of high rainfall and humidity as well in. Based on the correlation of fruit size of extant species with climate, the large size of the endocarps also supports the species requirement of a warm climate. The stronger positive correlation of endocarp and whole-fruit width with climate supports the idea that frugivore gape size influences the evolution of *Nyssa* fruit width. Other plant and animal taxa at the GFS support the inference that the climate and environment were more similar to the modern climates near the Mid-Atlantic and Gulf of Mexico coastal plains. Higher sea levels than the present would have placed the fossil site much closer to the ocean than present and likely had an important impact on the regional climate. All of the pieces of evidence point

toward a climate with mild winters during the time the Mio-Pliocene deposits of the Gray Fossil Site were forming. This is not surprising since global studies suggest the climate was warmer than the present during the Late Miocene and Early Pliocene.

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APPENDIX

Table 8: Data On Specimens of Extant *Nyssa* Species Used in This Study

Source	Taxon/taxa	ID	Number of specimens observed	Original Source of Fruit
DUKE (Duke University Herbarium)	*Nyssa aquatica* Linnaeus	184077	1 endocarp (and 9 whole fruits)	Near road NC 1417
DUKE	*Nyssa aquatica* Linnaeus	359512	1 endocarp (and 4 whole fruits)	Sandy Island , NC
DUKE	*Nyssa aquatica* Linnaeus	149126	1 endocarp (and 4 whole fruits)	Jasper Co., Tx
DUKE	Nyssa ogeche Bartram ex Marshall	57535	4	Waycross, Ware Co., GA
DUKE	Nyssa ogeche Bartram ex Marshall	359887	6	Nassau Co., Florida, St. Mary's River
DUKE	Nyssa ogeche Bartram ex Marshall	359918	6	Nassau Co., Florida, St. Mary's River
DUKE	*Nyssa sylvatica* Marshall var. *biflora*	160079	4	Brunswik Co., NC
DUKE	*Nyssa sylvatica* Marshall var. *biflora*	364360	4	Old Mill Pond off Goodwill Rd.in NC
DUKE	*Nyssa sylvatica* Marshall var. *biflora*	350435	4	border of Swamp on US 1, North Carolina
DUKE	*Nyssa sylvatica* Marshall var. *biflora*	183867	4	Franklin Co., FL
DUKE	*Nyssa sylvatica* Marshall var. *biflora*	374160	4	Amite Co., Mississippi
DUKE	*Nyssa sylvatica* Marshall var. *sylvatica*	229635	4	Durham Co., NC
DUKE	*Nyssa sylvatica* Marshall var. *sylvatica*	382821	4	Granville Co., NC
DUKE	*Nyssa sylvatica* Marshall var. *sylvatica*	374159	4	Amite Co., Mississippi
DUKE	*Nyssa sylvatica* Marshall var. *sylvatica*	222335	4	Allegan Co., Clyde Twp, Michigan
DUKE	*Nyssa sylvatica* Marshall var. *sylvatica*	80240	2	Bridgeport, Newyork
DUKE	*Nyssa sylvatica* Marshall var. *sylvatica*	197435	2	Chiapas, Mexico
DUKE	*Nyssa sylvatica* Marshall var. *caroliniana*	84973	2	Harrison Co., Indiana

Table 8 (continued)

DUKE	*Nyssa sylvatica* Marshall var. *ursina*	364772	2	Liberty Co., Florida
W.B.Clark Preserve, State Natural Area	*Nyssa aquatica* Linnaeus	Previous Year's Fruit	10	Wolf River Floodplain, Fayette Co., TN
UF Paleobotany Comparative Collection	*Nyssa aquatica* Linnaeus	Richard and Eyde 10-28-1988 State Park, VA	3	State Park VA
UF Paleobotany Comparative Collection	*Nyssa ogeche* Bartram ex Marshall	UF 1619	13	N/A
UF Paleobotany Comparative Collection	*Nyssa sinensis* Oliver	UF 1027;; U.S. Herbarium Number 1575307, from Richard Eyde	9	China
UF Paleobotany Comparative Collection	*Nyssa ogeche* Bartram ex Marshall	UF 1503	3	UF Campus near McCarty Hall, Gainesville, FL
UF Paleobotany Comparative Collection	*Nyssa sinensis* Oliver	UF 1030; U.S. Herbarium # 599343	13	China
UF Paleobotany Comparative Collection	*Nyssa aquatica* Linnaeus	0554	9	N/A
UF Paleobotany Comparative Collection	*Nyssa sylvatica* Marshall	UF 1810	4	N/A
UF Paleobotany Comparative Collection	*Nyssa sylvatica* Marshall	UF 0552; June 23 1996	33 stones	Putnam, Co., Little Orange Lake, Florida
UF Paleobotany Comparative Collection	*Camptotheca acuminata* Decaisne	UF 1260; Collected by Kokawa and Manchester,	2 fruit heads	Osaka City University Campus; Japan
UF Paleobotany Comparative Collection	*Nyssa sylvatica* Marshall "bicolor"	UF 0999, Jarzen, D.M, 10-33-1999	3	Georgia
UF Paleobotany Comparative Collection	*Camptotheca acuminata* Decaisne	UF 1249; UF 1250; UF 1251;	3 Vials of Fruit Preserved in alcohol	Cultivated trees in Nachadoches, Texas
UF Paleobotany Comparative Collection	*Nyssa sylvatica* Marshall	UF 0553	3	N/A
UF Paleobotany	*Camptotheca acuminata* Decaisne	UF 1058; Dilcher and Kokau 11-27-	64	Osaka, Japan

Table 8 (continued)

Comparative Collection		1986		
UF Paleobotany Comparative Collection	*Nyssa sinensis* Oliver	UF 1029; R.C. Ching 2131; China July 16-25, 1924; U.S. Herbarium # 1246978; From Richard Eyde	4	China
UF Paleobotany Comparative Collection	*Nyssa sinensis* Oliver	UF 1031; Y.W. Taom 967; China; U.S. Herbarium # 3009262, From Richard Eyde	2	China
Smith Lake Oxbow, Richmond, V.A.	*Nyssa aquatica* Linnaeus	Previous year's fruit in leaf litter	5	Smith Lake Oxbow, Richmond, V.A.
UF Arboretum	*Nyssa ogeche* Bartram ex Marshall	Previous year's fruit from leaf litter; Summer 2011	17	Gainesville, FL
UF Arboretum	*Nyssa ogeche* Bartram ex Marshall	Fresh Fruit; September 2010	30	Gainesville, FL
ETSU Arboretum	*Nyssa sinensis* Oliver	Fallen Fruit September 2011	200 fruit/endocarps	Johnson City, TN
ETSU Arboretum	*Nyssa sylvatica* Marshall	Fallen Fruit September 2011	100 fruit/endocarps	Johnson City, TN
Willow Springs Park	*Nyssa sylvatica* Marshall	Fallen Fruit 2011	200 fruit/endocarps	Johnson City, TN
K.I.B Botanical Garden	*Nyssa sinensis* Oliver	Collected by Tao, Su. Kunming Botanical Institute Botanical Garden; 2010	14	Yunnan Province, Kunming, China
Wang et al. (2012)	*Nyssa sinensis* Oliver; *Nyssa javanica* (Blume) Wangerin; *Nyssa yunnanensis* Yin ex Qin & Phengklai	Fruit from type localities and herbarium specimens listed in text	*N. sinensis* (n=200); *N. javanica* (n=50); *N. yunnanensis* (n=50)	China, See text
Eyde (1963)	*Camptotheca acuminata* Decaisne; *Davidia involucrata* Baillon; *Nyssa sinensis* Oliver; *Nyssa sylvatica* Marshall; *Nyssa javanica* (Blume) Wangerin; *Nyssa aquatica* Linnaeus; *Nyssa ogeche* Bartram ex Marshall;	Herbarium specimens listed in text	See text	Natural sites in Asia and the U.S. and cultivated specimens in arboretums

Table 8 (continued)

Personal Collections of Dr. Barry Hammel	*Nyssa talamancana* Hammel and Zamora	Fruit collected from Limon Costa Rica	4	Limon, Costa Rica
DUKE	*Nyssa talamancana* Hammel and Zamora	346575	2	Limon, Costa Rica
Hammel and Zamora (1990)	*Nyssa talamancana* Hammel and Zamora	Fruit described in text; and See Figures (14-16)	See text	Sites in Panama and Costa Rica, See text

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