THE GENUS *NYSSA* (CORNACEAE) IN NORTH AMERICA: A REVISION

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ABSTRACT

The genus *Nyssa* has been the subject of bibliographic and taxonomic confusion for more than two centuries. This revisionary research reviews the nomenclatural history, ecological research, and certain evolutionary relationships of the genus. In an associated study that combined foliar flavonoids with traditional taxonomic exomorphic features, habit, and habitat characteristics of the North American *Nyssa*, a distinct monophyly for five taxa was revealed. A clarification of species separation between *N. sylvatica* and *N. biflora* is expanded to include habitat and morphological features. A new key, new species descriptions, and recently compiled distribution maps of the five North American *Nyssa* species also are presented. The five North American *Nyssa* taxa are: *Nyssa aquatica* L., *N. biflora* Walt., *N. ogeche* Bartr. ex Marsh., *N. sylvatica* Marsh., and *N. ursina* Small.

INTRODUCTION

A number of major taxonomic problems have occurred throughout the systematic history of North American members of the genus *Nyssa* (Rickett 1945; Eyde 1959; 1963; 1966). Some of the problems have been associated with difficulties in correlating species with habitats while other problems have involved the synonymy of the genus. Many authors have recognized at least two morphological varieties of *Nyssa sylvatica* Marsh. in which the two most variant forms have been associated with either lowland hydric or upland mesic habitats. Other authors have recognized as many as four varieties of *N. sylvatica*.

The systematic delineations also have been questionable with regard to the *Nyssa biflora* Walt. and *N. ursina* Small correlation. Some authors have considered *N. ursina* to be a separate species (Small 1927; Rickett 1945; Clewell 1985), while other authors have considered it to be an ecologically induced variant of *N. biflora* or *N. sylvatica* var. *biflora* (Kurz & Godfrey 1962; Eyde 1966; Godfrey & Wooton 1981; Godfrey 1988).

Certain taxonomic and bibliographic problems have occurred with *Nyssa ogeche* Bartr. ex Marsh. and *N. acuminata* Small. It is now generally agreed that *N. acuminata* is only a phenotypic variation of *N. ogeche* (Eyles 1941; Little 1979) induced by ecologically stressful situations primarily produced by fire (Eyde 1966) and/or drought.

In many herbaria, a problem exists in that *Nyssa aquatica* L. often is separated

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from *N. uniflora* Wangenh. Eyde (1964a) appears to have clarified the nomenclatural problems and *N. aquatica* usually is recognized as having nomenclatural precedence and synonomy with N. *uniflora*.

Close taxonomic and phylogenetic affinities long have been recognized between *Nyssa* and *Cornus* and, although *Nyssa* is the genus under examination in this research, *Cornus* is discussed with regard to phylogenetic outgroup comparison. Also, the genus *Garrya* has been associated with both *Nyssa* and *Cornus* (Holm 1909; Moseley & Beeks 1955; Eyde 1964b) and, therefore, *Garrya lindheimeri* Torr. is discussed.

Due to the lack of availability of material, the disjunct populations of *Nyssa sylvatica* in Mexico were not examined for flavonoids. However, the traditional morphological characters and the distribution of *N. sylvatica* in Mexico were examined from numerous herbarium specimens.

PREVIOUS WORK

Nomenclature of the Genus

First cited in *Systema Naturae* (Linnaeus 1735), the name *Nyssa* was applied to a genus but no species were recognized (Eyde 1959). In *Species Plantarum*, Linnaeus (1753) recognized one species, *N. aquatica*, that had been determined from several specimens of both *N. aquatica* and *N. sylvatica* (Eyde 1964a). Other authors would later determine that this species was a *nomen confusum* (Rickett 1945; Eyde 1964a). For at least the next two centuries, nomenclatural controversy was to become very common for members of the genus *Nyssa*.

In 1785, Humphrey Marshall published his recognition of *Nyssa sylvatica* (Little 1979), although Thomas Walter (1788) independently described the same species as *N. multiflora* only three years later. Also in 1785, Marshall published the name *N. ogeche* (Little 1979), which William Bartram had assigned to that taxon but had never validly published. Bartram referred to it as *N. coccinea*. Friederich von Wangenheim (1787) published his account of *N. uniflora*, but this name has been placed in synonomy under *N. aquatica* (Eyde 1964a).

In 1788, Walter was the first to recognize *Nyssa biflora* as a separate species. Walter (1788) also described *N. multiflora*, as mentioned above, *N. capitata*, which is synonymous with *N. ogeche*, and supported von Wangenheim's *N. uniflora*. Nine years later, Jean de Lamarck published Jean Poiret's description of *N. caroliniana*, now another synonym for *N. sylvatica* (Rickett 1945; Little 1979).

In 1893, C. S. Sargent lowered *Nyssa biflora* to varietal status under *N. sylvatica* (Eyde 1963), and twelve years later elevated it back to *N. biflora*. In 1903, J.K. Small published his account of *N. acuminata* (Small 1903), which today is recognized only as an ecological variant of *N. ogeche* (Eyde 1966; Little 1979).

The most recent publication of a new tupelo species was *Nyssa ursina* (Small 1927). Small published the description three years after collecting numerous specimens near Port St. Joe, Florida. Many authors have failed to recognize *N. ursina* as a true species. Rather, they have viewed it only as a phenotypic variant of either *N. sylvatica* var. *biflora* or *N. biflora* (Kurz & Godfrey 1962; Eyde 1966; Godfrey & Wooton 1981).

Many other varieties of *Nyssa* have been published, although today none of those varieties are generally accepted by botanists other than *N. sylvatica* var. *biflora*. Other varieties of *N. sylvatica* include var. *caroliniana*, var. *dilatata*, and var. *typica* (Fernald 1935; 1950). In 1878, Sereno Watson published the synonym *N. multiflora* var. *sylvatica* (Rickett 1945).

Theodore Holm (1909) reviewed root, stem, and leaf features of *Nyssa sylvatica*. Holm also cited his recognition of three species of *Nyssa* in North America, and their affinities to *Cornus* and *Garrya*.

A problem with leaf dentation variability in *Nyssa sylvatica* has encouraged some authors to recognize varieties *caroliniana* and *dilatata* (Fernald 1935; 1950; Steyermark 1963). However, Holm observed that dentation did not depend upon the positions of the leaves on the tree. Rather, leaf dentation appeared to occur more frequently on young trees and, on older trees, there appeared to be no order to the degree of dentation. Holm also was impressed by the variability of leaves in *N. sylvatica* as being almost as striking as the heterophylly in *Sassafras* (Holm 1909).

Although common names vary greatly in usage (Jones & Luchsinger 1986), the name "tupelo" has been applied to all species of *Nyssa* at various times in the literature. Most frequently, the name "water tupelo" has been referred to *N. aquatica*; "swamp tupelo" has been referred to *N. biflora*; "ogeche-lime" to *N. ogeche*; "dwarf tupelo" to *N. ursina*; and "blackgum," "sourgum," "pepperidge," or "black tupelo" to *N. sylvatica*. Unfortunately, some of the names have been used to refer to more than one species, and some of the names have been liberally interchanged among the species.

In this century, the first significant systematic effort that delineated *Nyssa* was completed by Rickett (1945). Rickett compiled the most thorough synonomy of the North American species, but tended toward splitting the group and thus recognized *N. sylvatica*, *N. biflora*, *N. ursina*, *N. uniflora*, *N. ogeche*, and *N. acuminata*. Little (1979) also compiled a recent synonomy of the North American species.

The most comprehensive systematic work of the genus was a survey of all known extant *Nyssa* species (Eyde 1963) in which Eyde detailed species characteristics and distributions. Eyde & Barghoorn (1963) also reviewed species characteristics, phylogenetic affinities, and nomenclatural synonomies of the extinct nyssoids. In a review of the taxa of the southeastern United States, Eyde suggested *N. biflora* deserved varietal status, because the differences that separated it from *N. sylvatica* were not as great as those that distinguished undisputed species of *Nyssa* (Eyde 1966). Also, he suggested that others may want to treat *N. biflora* as a subspecies.

In Clark's *Woody Plants of Alabama* (1971), three species and one variety of *Nyssa* are recognized: *N. aquatica*, *N. sylvatica*, *N. ogeche*, and *N. sylvatica* var. *biflora*. Clark acknowledged Eyde's citation of *N. ogeche* occurring in Alabama, but observed that no Alabama specimens had been examined. Clark stated that *Nyssa* taxa are very wide-ranging and variable and *N. biflora* appears to deserve ecotypic status. While reviewing some of Clark's specimens, many that had been identified as *N. sylvatica* var. *biflora* were annotated as *N. sylvatica*.

In a recent publication (Eyde 1988), extensive evidence was given for the replacement of *Nyssa* into the Cornaceae. Eyde believed that the Nyssaceae had been accidentally and erroneously separated from the Cornaceae (Wangerin 1907; 1910), and that Wangerin probably would have corrected the error, if not for his untimely death (Eyde 1988). Likewise, Eyde probably would have further promoted returning *Nyssa* to Cornaceae, if not for his untimely death.

Many features commonly cited as supporting separation of Nyssaceae and Cornaceae recently have been compromised by related genera exhibiting characteristics of both families. Many of these cornaceous genera were unknown by Wangerin, due to their rarity of collection and remoteness of location (Eyde 1988). In addition to at least two species of *Cornus* having alternate leaf arrangement (a feature shared with *Nyssa*), *Mastixia*, *Davidia*, and *Camptotheca* share many features intermediate between *Cornus* and *Nyssa* (Eyde 1963). Also, the recent recognition and placement of the "fossil" *Diplopanax* into subfamily Mastixioidae of Cornaceae, contributes yet another genus that exhibits characters between *Cornus* and *Nyssa* (Eyde & Qiuyun 1990). Therefore, this research means to encourage the replacement of *Nyssa* into the Cornaceae.

Ecological Research

Over the past five decades, much research has been published about the genus *Nyssa* regarding ecological, environmental, developmental, and phytosociological variables. Many studies appear to have been motivated by lumbering interests because those works review the difficulties encountered in reaching pure stands of *Nyssa* and problems involving regeneration and growth of large stands.

Two articles that examined the frequency of distribution and quantity of *Nyssa* and associated taxa, also cited observations on water quality, ratios of particulate matter to water at varying depths, and hydrogen ion concentrations of water in tupelo swamps in Louisiana and Alabama (Hall & Penfound 1939; 1943). Another study examined comparative wood structure in tupelo "knees" (Penfound 1934).

Nyssa sylvatica was used as an indicator plant in determining relative cobalt concentrations within various soil types (Kubota et al. 1960). The authors found that high concentrations of cobalt in soil are transmitted to high concentrations in the leaves of *N. sylvatica*. Although *Nyssa* was not known to be a forage plant of cattle, low concentrations of cobalt in *Nyssa* were translated to represent a nutritional deficiency of cobalt in cattle.

A large amount of tupelo research has centered on flood tolerance and physiological adaptations of *Nyssa* in floodplain and swamp habitats. Many of those studies made comparisons between aquatic *Nyssa* species and other lowland or aquatic tree taxa (Gill 1970; Hook & Brown 1973; Keeley 1979; Donovan et al. 1988).

A study of soil and site factors affecting the growth of tupelo stands in southeastern Georgia (Applequist 1959) was another project encouraged by lumbering concerns. The objectives of the research were to correlate soil and site factors to the quality and quantity of growth and yield. Applequist found that growth and development of *Nyssa biflora*, *N. aquatica*, and *Taxodium distichum* are dependent primarily upon large quantities of water. The evidence suggested that these three species not only tolerate extensive flooding, but actually thrive on it.

Associated with Applequist's research was his particularly significant citation of many species-specific characteristics of the species of *Nyssa*. Although he recognized that taxonomic problems existed in the literature, Applequist established an independent list of character differences. Applequist found *N. biflora* to have narrower and more oblanceolate leaves than *N. sylvatica*. He observed that fruits were borne singly or in pairs on *N. biflora* and in clusters on *N. sylvatica*. Also, he recognized that *N. biflora* occurred only in wet sites, whereas *N. sylvatica* occurred from lowland to upland sites, but never in inundated locations. Applequist's most novel observation was that the flowers of *N. biflora* appear after the leaves are fully developed, whereas the flowers of *N. sylvatica* appear before full leaf development.

A brief study of oxygen requirements for germination of *Nyssa aquatica* seeds, showed that seeds would not germinate in continually flooded habitats (Shunk 1939). Further research on germination rates of tupelo seeds compared four different soil/water regimes (DeBell & Naylor 1972). In the second study, it was found that germination was most rapid in moist, then drained regimes, and that no germination occurred in soil that remained continually under water. However, germination did occur under water in the absence of soil.

A recent study of germination, regeneration, and growth rates of *Nyssa aquatica* compared three microhabitat substrate types and analyzed species establishment on the various substrates (Huenneke & Sharitz 1990). Germination occurred only rarely in completely submerged substrates. On emergent substrates, germination had the highest rate, but seed predation and erosional scour counteracted the germination rate and greatly lowered survivability. Although germination rates were lower on microhabitats of adjoining flooded and emergent substrates, seed predation was very low, erosional scour was ineffective, and the accumulation of a true soil demonstrated the greatest overall survivability of tupelo seedlings.

Another recent study compared successional effects between floodplain sites disturbed by thermal discharge and undisturbed sites (Muzika et al. 1987). Above-ground biomass and primary production were found to be greater in both the undisturbed riverine (floodplain) and stream habitats. Dominant taxa in the undisturbed habitats were *Taxodium distichum* and *Nyssa aquatica*. In the disturbed (or "recovering") habitats, *Salix caroliniana* and *Acer rubrum* were the dominant species. Biomass accumulation ratios were five to twenty times greater in the undisturbed habitats than in the disturbed habitats. The effects of thermal discharge were elimination of the floodplain vegetation and, even after 15 years of recovery, low biomass productivity that implied a general lack of habitat recovery.

A significant study of net biomass and population differentiation showed consistently variant physiological adaptations between upland, floodplain, and swamp populations of *Nyssa sylvatica* and *N. sylvatica* var. *biflora* (Keeley 1977; 1979). Keeley found that upland plants (*N. sylvatica*) were very intolerant of flooded soils. Much physiological deterioration occurred and survival rates were very poor after a year of flooded conditions. In comparison, the swamp plants [*N. biflora*] were very tolerant of flooded conditions reflected by high survival rates. Adaptations included the production of new roots which exhibited an increased capacity for alcohol fermentation. In contrast, floodplain plants [*N. sylvatica*] in drained conditions allocated more biomass to the shoots than to the roots, along with other traits similar to upland plants. However, under flooded conditions, the floodplain plants increased oxygen transport to the roots and had higher survival rates than the upland plants under flooded conditions.

Keeley concluded that the intermediate floodplain plants produced two ecologically induced phenotypes which were adaptable to, and had high survival rates for, either the upland or swamp conditions. Yet the similarities between upland and floodplain populations appeared to be greater than the similarities between floodplain and swamp populations. In recent research that examined the flavonoids and phylogenetics of the North American *Nyssa* (Burckhalter 1990), one of the conclusions was that upland and floodplain populations constitute *N. sylvatica* while swamp populations constitute *N. biflora*.

Flavonoids and Phylogenetics

Chromatographic extraction and UV spectral analysis of the flavonoids from North American *Nyssa* revealed a total of 10 different flavonoid compounds. The compounds were isolated from 114 specimens of *Nyssa* and seven specimens of *Cornus* (Burckhalter 1990). All compounds, that were isolated from three different species of *Cornus*, also occurred in *Nyssa*. In addition, six flavonoid compounds were isolated from one specimen of *Garrya*. With only one exception, all compounds from *Garrya* were more distantly related biochemically to the flavonoids isolated in both *Nyssa* and *Cornus* (Burckhalter 1990).

A multistate database was established using traditional morphological characters from 1290 specimens of *Nyssa*, 459 specimens of *Cornus*, and 24 specimens of *Garrya lindheimeri*. In addition, presence/absence of the flavonoids from all 122 specimens of *Nyssa*, *Cornus*, and *Garrya* were added to the database. Regardless of various adjustments of the data, all cladograms always revealed that *Nyssa* and *Cornus* were sister groups, that all five taxa of *Nyssa* were distinct taxa, and that all five taxa always displayed the same phylogenetic relationships within the genus (Burckhalter 1990).

The four types of flavonoid compounds isolated from *Nyssa* and *Cornus* were quercetin, quercetin glycosides, kaempferol, and kaempferol glycosides. Most compounds isolated from *Garrya* were apigenin and apigenin glycosides. Perhaps the single most outstanding characteristic among the flavonoids of *Nyssa* was a consistent occurrence of a quercetin glycoside in all 37 populations of *N. sylvatica*. In contrast, that glycoside never occurred in the 28 populations examined of *N. biflora*. Further, a kaempferol glycoside occurred in all populations of *N. biflora* that never occurred in *N. sylvatica* (Burckhalter 1990). Details of the flavonoids and phylogenetics will appear in a separate paper.

DISCUSSION

Status of *Nyssa sylvatica* and *Nyssa biflora*

Since the question of species separation between *Nyssa sylvatica* and *N. biflora* may be considered to be the greatest problem during the bibliographic history of the genus *Nyssa*, additional effort was pursued in examining species status for those two taxa. That effort was coordinated by reviewing characteristics of *N. sylvatica* that had been collected in moist lowland sites.

Variation in response to habitat or species hybridization long have been suggested as the reasons for similarity between *Nyssa biflora* and *N. sylvatica*. Frequently, it has been suggested that *N. biflora* is an aquatic or moist lowland variety of *N. sylvatica* (Eyde 1963; 1966; Little 1979; Godfrey & Wooton 1981; Godfrey 1988).

Nyssa sylvatica occurs in a much wider range of habitats than *N. biflora*. *Nyssa sylvatica* may be found from upland xeric localities to moist lowlands occasionally under water inundation. *Nyssa biflora* is restricted to truly aquatic habitats and occasionally marginally aquatic environments. Rarely, the habitats of the two species overlap. Usually the leaves of lowland *N. sylvatica* will be more narrow than leaves of nearby upland individuals. However, populations have been found where there is no apparent difference in leaf morphology between habitats. This may lead to confusion when collecting sterile specimens, since *N. biflora* normally has more narrow leaves.

In its northern extremes, for example Maine, Ontario, and Michigan, the habitat of *Nyssa sylvatica* tends to be low moist ground near swamps or lake margins (Otis 1931; Fernald 1950). Regardless, the leaves usually are wide and large, and the fruits normally are in multiples of three or more. Of many carpellate specimens examined, most appeared to have a reduced spikate-like peduncle. In review of 65 herbarium specimens from extreme northern locations, in Maine, Michigan, and Ontario, it was found that most were from low moist areas. The one collection from Canada used in the flavonoid and phylogenetics research (Burckhalter 1990) was made in a woodlot in moist rich flatwoods on sandy soil.

Flavonoid results from eight moist lowland site populations of *Nyssa sylvatica* demonstrated that this species may become established in extremely stressful and undesirable habitats, to which the species may, or may not, well adjust. The more similar leaf morphologies to *N. biflora*, combined with the occasional unhealthy appearance of the tree, gives support to genotypic plasticity resistance regardless of environmental limitations.

The flavonoid evidence from all of the lowland site *Nyssa sylvatica* collections indicated that *N. sylvatica* and *N. biflora* unquestionably are separate species (Burckhalter 1990). Without biochemical knowledge of the speciation between *N. sylvatica* and *N. biflora*, both Applequist (1959) and Keeley (1977, 1979) supported separate speciation for the two taxa in their research involving growth and development, and flooding tolerances.

Evolutionary relationships within *Nyssa*

Flavonoid, mophological, and cladistic analyses clearly delineate five taxa of *Nyssa* in North America (Burckhalter 1990). With *Cornus* as the outgroup, *Nyssa* was found to be the sister group to *Cornus*. As a result of the cladistic analyses, it may be speculated that *N. sylvatica* shares a lineage with an unknown ancestor that gave rise to the other four species of North American *Nyssa*. That unknown ancestor then gave rise to the two lineages which separate the *N. biflora* - *N. ursina* complex and the *N. aquatica* - *N. ogeche* complex (Fig. 1).

As may be compared with the characteristics of fossil nyssoids (Eyde & Barghoorn 1963), *Nyssa sylvatica* appears to be more similar to the fossil record of the Tertiary than the other four North American taxa of *Nyssa*. Eyde (1963) was led to the conclusion that *N. sylvatica* was the most similar extant North American *Nyssa* to the ancestral nyssoids.

Exomorphic characteristics represent closer relationships between *Nyssa biflora*, *N. ursina*, and *N. sylvatica* than between *N. aquatica*, *N ogeche*, and *N. sylvatica*. Both *N. aquatica* and *N. ogeche* exhibit many more derived characters,

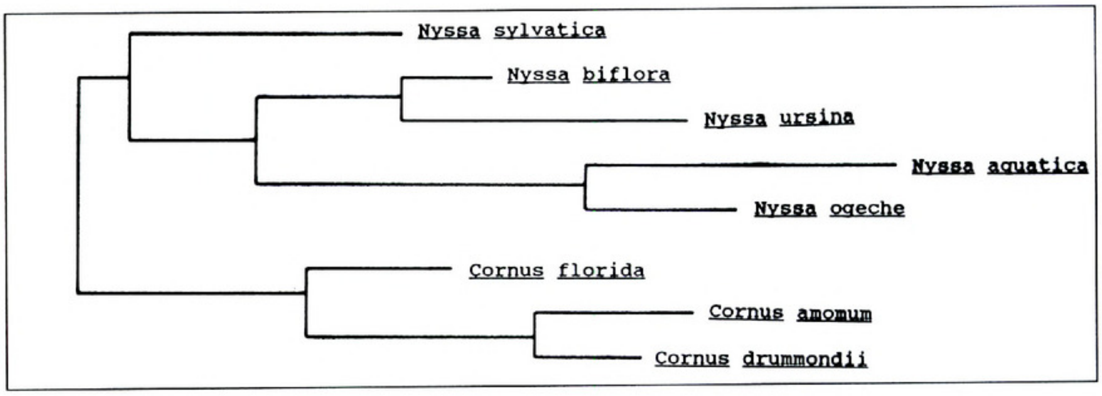

FIG. 1. Cladogram of North American *Nyssa* with *Cornus* as the Outgroup.

such as large fruits, single fruits per peduncle, and large leaves, than the more plesiomorphic *N. sylvatica*, *N. biflora*, and *N. ursina* (Burckhalter 1990).

Although the occurrence of specific flavonoid compounds was highly consistent within all populations of a given taxon, the presence and/or absence of specific compounds varied greatly between taxa. Efforts at determining evolutionary relationships from only the flavonoids, excluding exomorphic characteristics, were not significant. Those efforts included examining evolutionary biochemical pathways and presence/absence applied to phylogenetic analysis. Further discussion will appear in a separate paper.

Specimens for distribution maps

This research includes new distribution maps of the five species of *Nyssa* in Anglo-America. The maps have been compiled by a review of nearly 7100 specimens from herbaria throughout the central, eastern, and southern United States. Figures 2 through 6 represent county locations of specimens from naturally occurring populations for all five North American *Nyssa* taxa. The county representations were taken from the herbarium collections. Some specimen information was correlated with county collections cited in four publications covering certain geographical regions. Those publications include citations for specimen locations in Arkansas (Smith 1988), Georgia (Jones & Coile 1988), Missouri (Steyermark 1963), and North Carolina and South Carolina (Radford et al. 1968). Most of those specimen locations were repetitious with locations observed in the various herbarium specimens.

Only three sources are known that have published distribution maps for the entire range of the North American and/or Anglo-American species of *Nyssa* (Fernald 1935; Eyde 1963; Little 1971). Since the time of those publications, much additional distribution information has been accumulating in the form of herbarium specimens. Unfortunately, there are specimens which have not been viewed for inclusion into the new distribution maps. Nearly 400 specimens from GA were unavailable for review due to an extended loan to another institution.

Key to the Species

1. Trees; lowland to upland habitats; fruits in clusters usually 4 or 5 .... *Nyssa sylvatica*
1. Trees or shrubs; very moist habitats, swamps, usually inundated; fruits 1 or 2 per peduncle 2
   2. Leaves narrowly lanceolate, entire, usually 3 – 14 cm long; fruits usually 2 per peduncle; mature fruit blue-black, 0.6 – 1.4 cm long 3
   2. Leaves widely ovate to obovate, often dentate toward apex, usually 8 – 25 c long; fruits usually 1 per peduncle; mature fruit olive green to orange to light brown, 2 – 4 cm long 4
      3. Trees; leaves 5 – 14 cm long; fruit oblong, peduncle 1 – 4 cm long .... *Nyssa biflora*
      3. Shrubs; leaves 3 – 6 cm long; fruit globose, peduncle 0.5 – 2 cm long .... *Nyssa ursina*
         4. Leaves widely obovate, often dentate toward apex, 10 – 25 cm long, petiole 2 – 5 cm long; mature fruit olive green to brown .... *Nyssa aquatica*
         4. Leaves narrowly to widely ovate, occasionally dentate throughout, 8 – 18 cm long, petiole 0.5 – 1.5 cm long; mature fruit dull yellow to orange .... *Nyssa ogeche*

Species Descriptions and Distributions

Nyssa aquatica L., Sp. Pl. 1053. 1753; pro parte.

Nyssa uniflora Wangenh., Betyr. Teutsch. Fortstwiss. Nordam. Holz. 83, pl. 27, fig. 57. 1787.
Nyssa denticulata Aiton, Hort. Kew. 3:446. 1789.
Nyssa palustris Salisb., Prodr. Stirp. Chap. Allerton 175. 1796.
Nyssa angulisans Michx., Fl. Bor.-Amer. 2:259. 1803.
Nyssa tomentosa Michx., Fl. Bor.-Amer. 2:259. 1803.
Nyssa grandidentata Michx. f., Hist. Arbr. Forest. 2:252. 1813.
Nyssa denticulata Pursh, Fl. Amer. Sept. 1:178. 1814.
Nyssa candicans var. *grandidentata* D.J. Browne, Trees America 426. 1857.

Description: Trees aquatic, dioecious, seldom-branching, to 35 m tall; trunks usually buttressed. Leaves widely ovate to obovate, 10 – 25 cm long, 5 – 10 cm wide, the margins often dentate toward apex; petiole 2 – 5 cm long. Carpellate inflorescence usually imperfect, occasionally with sterile stamens, flower solitary and sessile, peduncle 2 – 5 cm long. Staminate inflorescence, imperfect, racemose to compact spikate to head-like to umbellate. Fruit dull yellow to olive green to light brown, oblong, 2 – 3 cm long.

Distribution: Occurrence of *Nyssa aquatica* (Fig. 2) is occasional to common throughout the Coastal Plain from southeastern Virginia, through the eastern Carolinas, central and southern Georgia, the western Florida panhandle, into southern and western Alabama. It is common throughout Mississippi, Louisiana, and eastern Arkansas. It is common also in localized portions of eastern Texas, southeastern Missouri, extreme southern Illinois, and western Tennessee. Being out of the typical Coastal Plain province, *N. aquatica* also may be found along upper reaches of the Tennessee River, in northeastern Alabama and south central Tennessee, and into the Arkansas River valley of west central Arkansas.

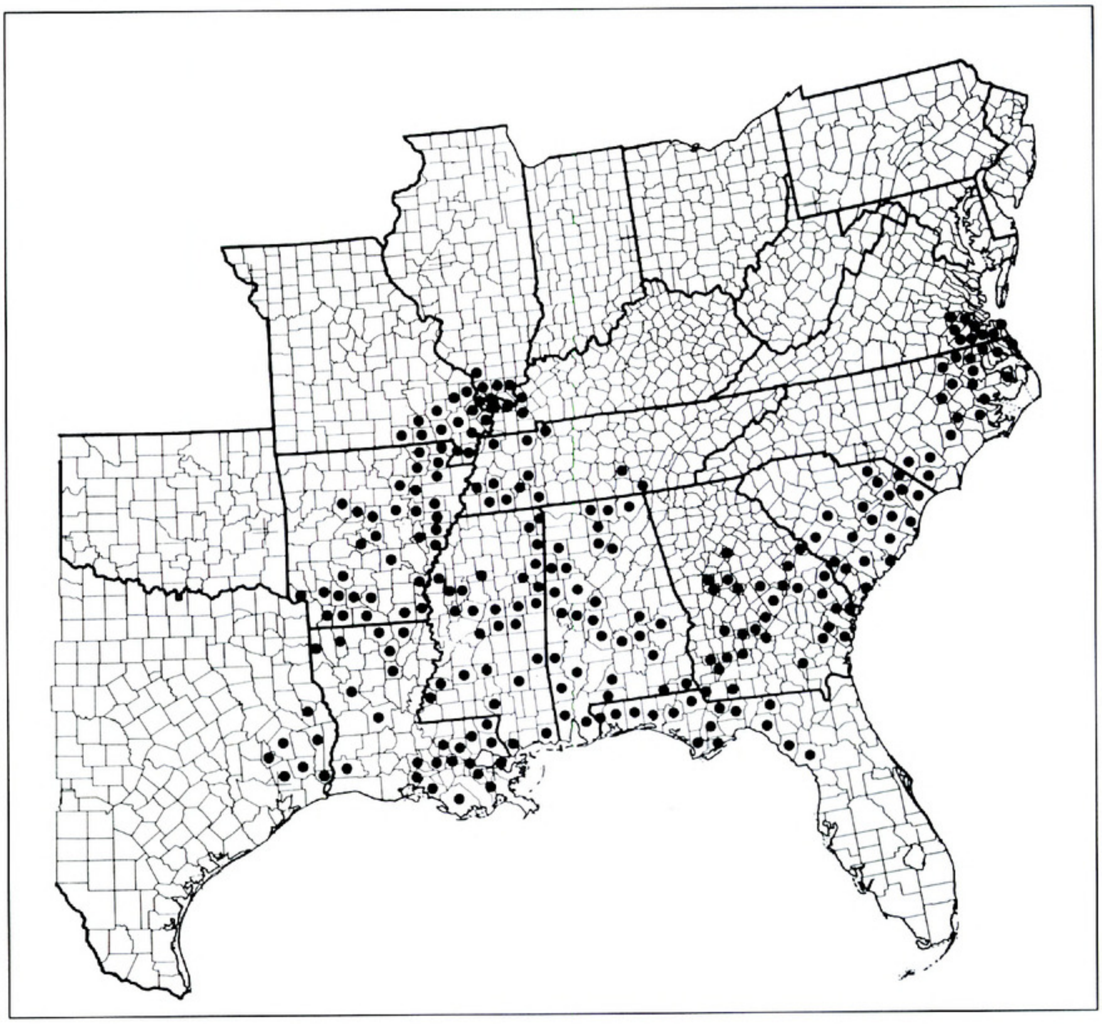

FIG. 2. *Nyssa aquatica*. Documented distribution by county in the United States.

Nyssa aquatica occurs primarily in swamps, along riverbanks, and occasionally in low moist floodplains. It may be found commonly in nearly monospecific colonies of very large trees in inundated swamps. *Nyssa biflora* or *Taxodium distichum* frequently are found growing with *N. aquatica*. One specimen collected in Duval County, Florida (Little 1971), has been redetermined to be *N. ogeche*. The occurrence of *N. aquatica* in east central Illinois is doubtful.

Nyssa biflora Walter, Fl. Carol. 253. 1788. *Nyssa sylvatica* var. *biflora* (Walter) Sarg., Sylva 5:76, pl. 218. 1893. *Nyssa sylvatica* ssp. *biflora* (Walter) E. Murray.

Nyssa servatilis E.H.L. Krause, Beih. Bot. Centr. 32:333. 1914.

Description: Trees aquatic, dioecious, seldom-branching, to 25 m tall, trunks usually buttressed. Leaves usually narrowly lanceolate, 5 – 14 cm long, 1.5 – 4 cm wide, often somewhat coriaceous with recurved margins, apex often rounded; petiole 0.5 – 1.5 cm long. Carpellate inflorescence usually imperfect, occasionally with sterile stamens, flowers usually in pairs, occasionally 1 or 3, sessile or

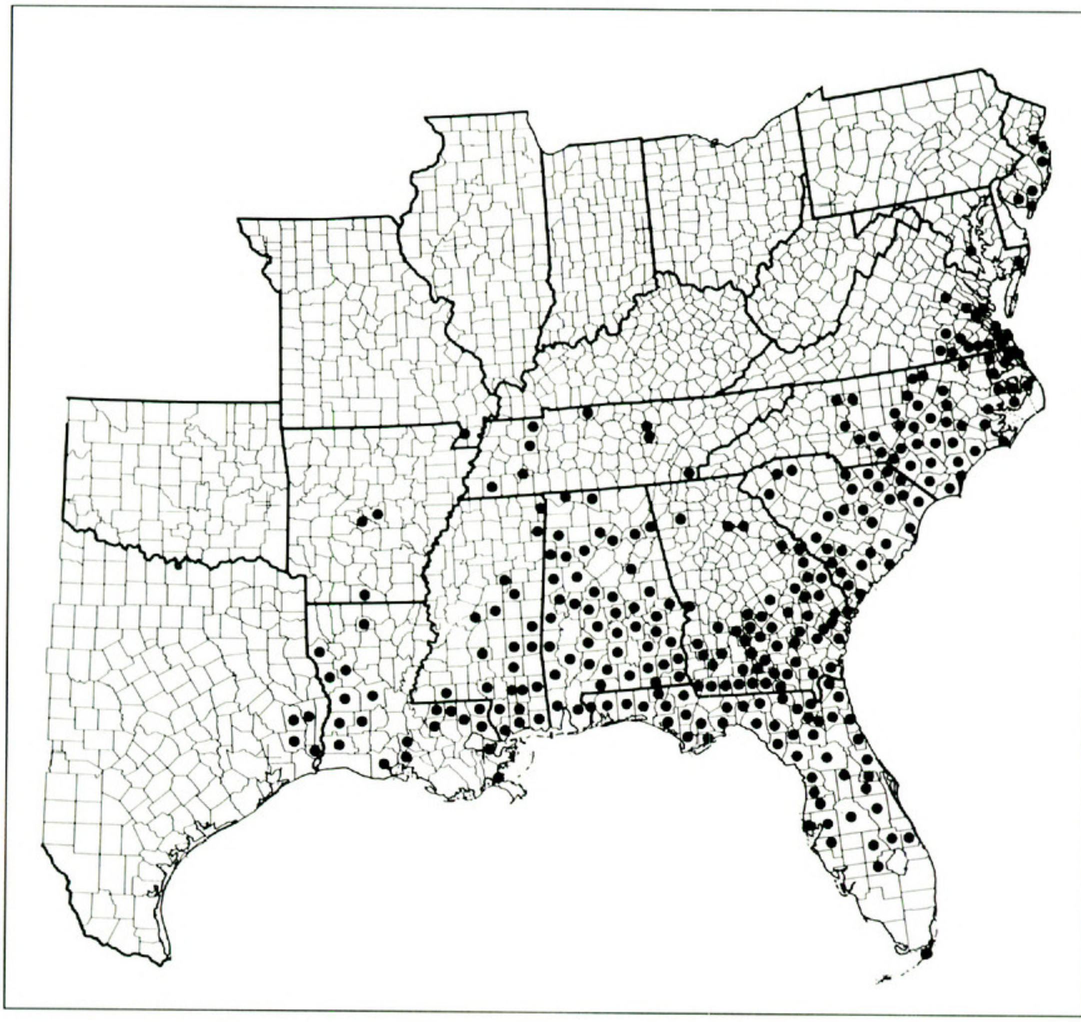

FIG. 3. *Nyssa biflora*. Documented distribution by county in the United States.

pedicellate, peduncle 1 – 4 cm long. Staminate inflorescence imperfect, racemose to compact spikate to umbellate. Stamens arising from margins of numerous, often pedicellate, circular pads. Fruit dark blue to black, ovoid, 0.7 – 1.4 cm long.

Distribution: Occurrence of *Nyssa biflora* (Fig. 3) is occasional to common throughout the Coastal Plain from central New Jersey to southeastern Texas. It is very common in inundated acidic swamps, and occasionally along low moist riverbanks or pond margins, from east central North Carolina to central Mississippi. Occurrence in northern Georgia, northern Alabama, central Tennessee, and southeastern Arkansas is very sporadic, but again, associated with inundated acidic swamps. *Nyssa biflora* often occurs in monospecific colonies or associated with *N. aquatica* or *Taxodium distichum*.

One collection originally identified as *Nyssa ursina*, attributed to J.K. Small from Lignumvitae Key, Monroe County, Florida (Long & Lakela 1971), has been redetermined to be *N. biflora*. Despite numerous attempts by various people to

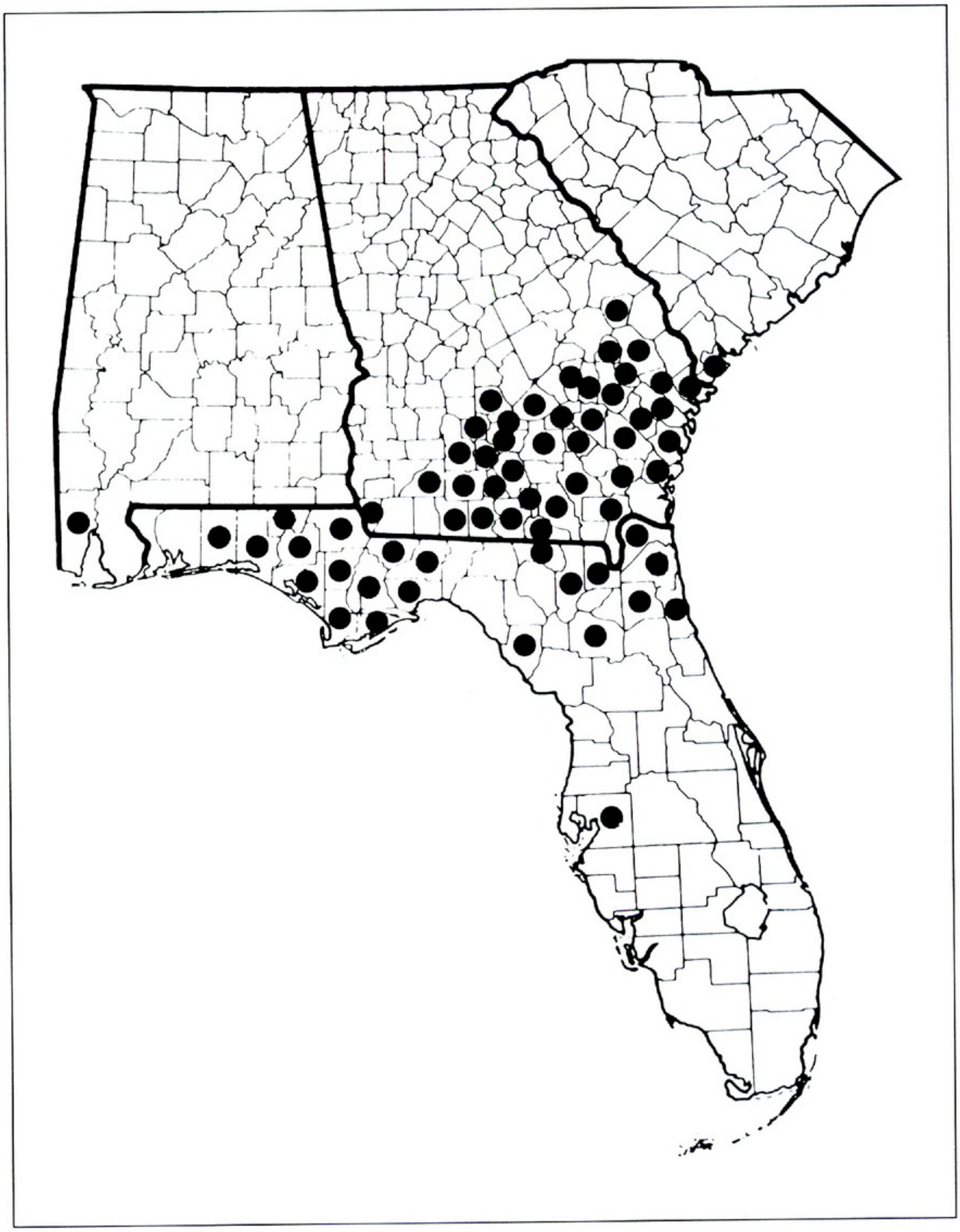

FIG. 4. *Nyssa ogeche*. Documented distribution by county in the United States.

relocate the occurrence of *N. biflora* in the Florida Keys, no recent collections have been made. It is questionable that *N. biflora* was collected in the Florida Keys due to a mis-labelling of Small's collection (Ward & Craighead 1990). Previously unknown populations of *N. biflora* were found in February and March 1992 in southern Okeechobee County, Florida.

Nyssa ogeche Bartram ex Marshall, Arbust. Amer. 97. 1785.

Nyssa coccinea Bartram, nom. nud.
Nyssa captiata Walter, Fl. Carol. 253. 1788.
Nyssa tomentosa Poir. in Lam., Encycl. 4:508. 1797.
Nyssa candicans Michx., Fl. Bor.-Amer. 2:259. 1803.
Nyssa oye-chee Steud., Nomencl. Bot. 558. 1821.
Nyssa acuminata Small, Fl. S.E. U.S. 852. 1903. *Nyssa ogeche* var. *acuminata* (Small) Eyles, Castanea 6:35. 1941.

Description: Large shrubs to small trees, aquatic, dioecious, usually 5 – 8 m tall, rarely to 12 m; numerous trunks arising from swollen base. Leaves usually widely lanceolate to ovate or with rounded tips, often with recurved margins and pubescent on underside, 8 – 18 cm long, 3 – 8 cm wide; petiole 0.5 – 1.5 cm long. Carpellate inflorescence occasionally imperfect, frequently with stamens, solitary and sessile, peduncle 0.5 – 2 cm long. Staminate inflorescence, imperfect, racemose to compact spikate to head-like to umbellate. Fruit dull yellow to olive brown to orange, oblong, 2 – 4 cm long.

Distribution: *Nyssa ogeche* (Fig. 4) occurs almost entirely in southeastern Georgia and northern Florida. It is known also from Beaufort County, South Carolina. Although this species is restricted to a relatively small geographical area, it is very common throughout much of its range. It commonly occurs in sandy-bottom swamps, bogs, along low riverbanks, and in deep-water swamps, where it may be associated with *N. biflora*. In many river swamps of southeastern Georgia and west central Florida, especially along the Apalachicola River, this species may be nearly monospecific.

One report of *Nyssa ogeche* was made from a Charles Mohr specimen collected in Mobile County, Alabama in 1890 (Eyde 1963), but in review of that specimen, it has been redetermined as *N. aquatica*. However, Mohr did not recognize this species to occur in Alabama (Mohr 1901). A second specimen collected by Mohr in Mobile County in 1892; was identified by Mohr as *N. uniflora*, but it was recently annotated as *N. ogeche* (Eyde pers. comm.). This is the only known specimen of *N. ogeche* from Alabama.

Nyssa ogeche has been expected to occur in extreme southeast Alabama, but no known collection exists. It occurs in adjacent counties in both Georgia and Florida. Extensive field work in Houston County, Alabama in 1988 and 1989 failed in locating *N. ogeche*.

Cultivated specimens of *Nyssa ogeche* are known from Hillsborough Co. Florida, Lake Co. Florida, and Orange Co. North Carolina. A second population of *N. ogeche* in Hillsborough County appears to be a naturally occurring spontaneous population.

Nyssa ogeche is the species from which honey is gathered, along the Apalachicola River in Florida, to produce the very high quality tupelo honey of legend and literature (Eyde 1963).

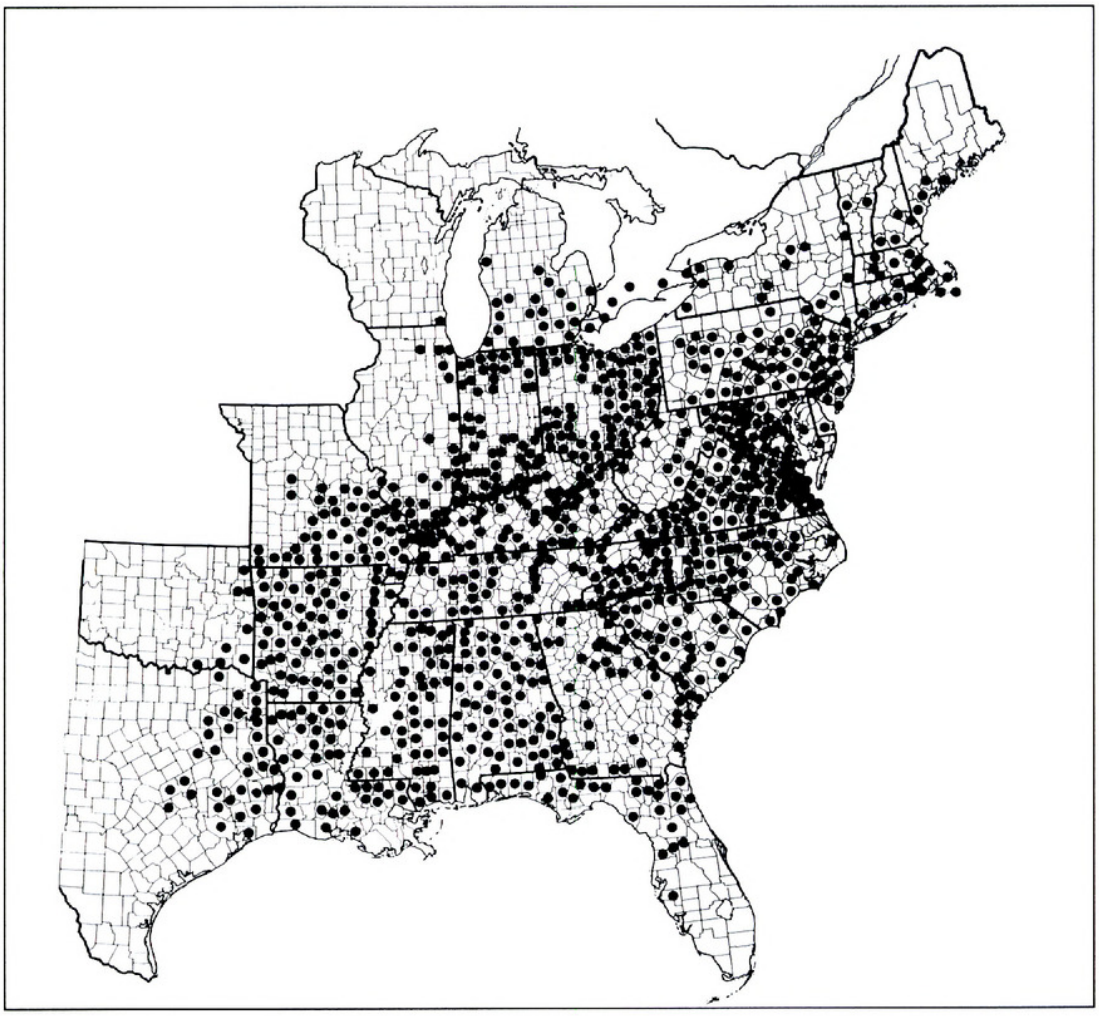

FIG. 5. *Nyssa sylvatica*. Documented distribution by county in the United States.

Nyssa sylvatica Marshall, Arbust. Amer. 97. 1785. *Nyssa multiflora* var. *sylvatica* (Marshall) S. Wats., Bibl. Index N. Amer. Bot. 442. 1878.

(*Nyssa aquatica* L. Sp. Pl. 1058. 1753; pro parte.)
Nyssa multiflora Wangenh., Beytr. Nordam. Holz. 46. 1787.
Nyssa integrifolia Aiton, Hortus Kew. 3:446. 1789.
Nyssa angulosa Poir. in Lam., Encycl. 4:507. 1797.
Nyssa canadensis Poir. in Lam., Encycl. 4:507. 1797.
Nyssa caroliniana Poir. in Lam., Encycl. 4:507. 1797. *Nyssa sylvatica* var. *caroliniana* (Poir.) Fern. Rhodora 37:436. 1935.
Nyssa villosa Michx., Fl. Bor.-Amer. 2:258. 1803.
Nyssa montana Hort., Michx., Fl. Bor.-Amer. 2:258. 1803.
Nyssa integrifolia glauca Hort., Pers., Syn. Pl. 2:614. 1807.
Nyssa ciliata Raf., Atlantic J. 176. 1833.
Nyssa sylvatica var. *aquatica* Sarg., Gard. & Forest 2:435. 1889.
Nyssa sylvatica var. *typica* Fern., Rhodora 37:434. 1935.
Nyssa sylvatica var. *dilatata* Fern., Rhodora 37:436. 1935.

Description: Trees terrestrial, dioecious, frequent-branching, to 30 m tall; trunks never buttressed, occasionally slightly expanded; limbs often arising from trunk at right angles. Leaves greatly variable from narrowly lanceolate to widely ovate to widely obovate, 6 – 18 cm long, 3 – 8 cm wide, narrow leaves never dentate, wide leaves often dentate toward apex; petiole 0.5 – 3 cm long. Carpellate inflorescence usually imperfect, occasionally with sterile stamens, usually 3 – 9 flowers, occasionally 2 in upland habitats, sessile or pedicellate, racemose to compact spikate to head-like, peduncle 1.5 – 4 cm long. Staminate inflorescence imperfect, racemose to compact spikate to head-like to umbellate. Stamens arising from margins of numerous, often pedicellate, circular pads. Fruit dark blue to black, ovoid, 0.8 – 1.8 cm long.

Distribution: *Nyssa sylvatica* (Fig. 5) occurs from southern Maine, across New York and southern Ontario, to central Michigan. It occurs sporadically across Illinois, and commonly across central Missouri to eastern Oklahoma and east central Texas. This species may be found near the Gulf Coast from eastern Texas to northern Florida, yet uncommon in the lower Mississippi River delta. It occurs occasionally into central Florida, but very commonly along the Eastern Seaboard to southern Maine. Although not included on the distribution map, disjunct populations of *N. sylvatica* are known from the Mexican states of Chiapas, Hidalgo, Puebla, and Veracruz (Miranda 1945; Eyde 1963; 1966).

An interesting coincidence is the great similarity between the geographical distributions of *Nyssa sylvatica* and *Cornus florida* (Little 1971). It may be uncommon to find two arborescent taxa within the same family with such a wide ranging geographical similarity.

The habitat of *Nyssa sylvatica* varies greatly from low moist woods to mesophytic or xerophytic upland woods. *Nyssa sylvatica* appears to prefer acidic soils rather than alkaline limestones. As a result, the species is not very common across central Kentucky or the Black Belt of Mississippi and Alabama. It is very common in well-drained upland habitats with poor soils. It may be found as a very common component of oak-hickory-pine woods. *Nyssa sylvatica* is considered to be a dominant tree species in the southern Appalachian Mountains (Whittaker 1956).

Nyssa sylvatica also occurs in lowland habitats, and this distribution often has been determined erroneously as indicating *N. sylvatica* var. *biflora*. Lowland *N. sylvatica* may have narrow leaves nearly identical with *N. biflora*, but a combination of other characters (multiple inflorescence, non-buttressed trunk, non-inundated habitat) is virtual assurance that the species is lowland *N. sylvatica*.

The few specimens of *Nyssa sylvatica* (at US) that were collected in eastern Kansas during the 1880s and 1890s are considered to have been made from cultivated trees.

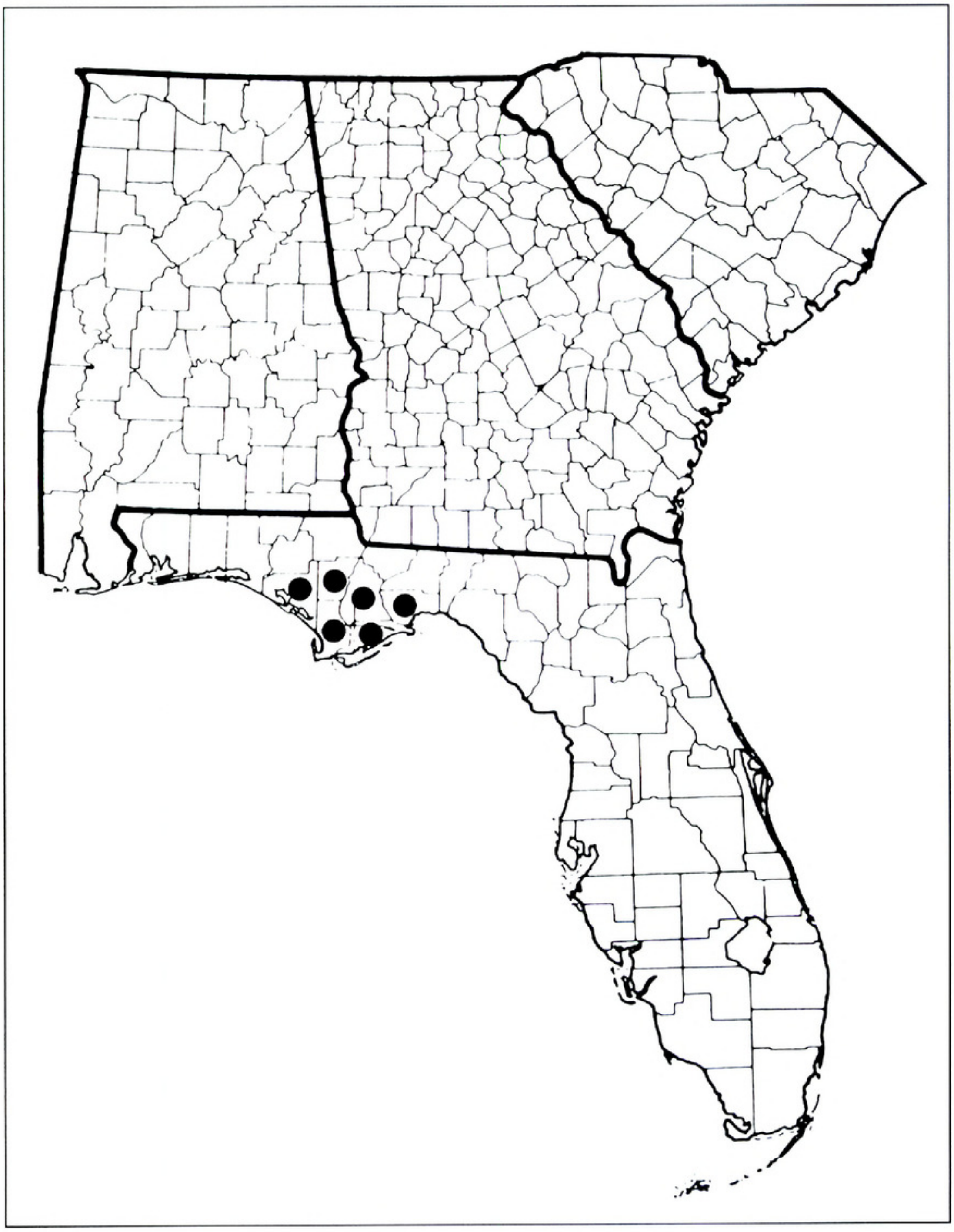

FIG. 6. *Nyssa ursina*. Documented distribution by county in the United States.

Nyssa ursina Small, Torreya 27:92. 1927.

Description: Shrubs or small trees, aquatic, usually to 3 m tall, occasionally to 5 m; trunks expanded to buttressed. Leaves narrowly lanceolate, 3 – 6 cm long, 1 – 2 cm wide; petiole 0.3 – 1 cm long. Carpellate inflorescence usually imperfect, occasionally with sterile stamens, flowers usually in pairs, rarely 1 or 3, sessile or pedicellate, peduncle 0.5 – 2 cm long. Staminate inflorescence imperfect, racemose to compact spikate to head-like to umbellate. Stamen clusters arising from margins of numerous, often pedicellate, circular pads. Fruit dark blue to black, globose, 0.6 – 1 cm long.

Distribution: *Nyssa ursina* (Fig. 6) appears to occur in only six counties in west central Florida associated with the Apalachicola and Ochlockonee Rivers. At least one author has considered *N. ursina* to be a component of the remnant refugium of the Apalachicola River area (Clewell 1977). Three specimens from southeastern Georgia (at NCU) identified as *N. ursina* have been redetermined to be *N. biflora*. The specimens from Lignumvitae Key, Florida, collected by J. K. Small and believed to be *N. ursina* (Eyde 1963), also have been redetermined to be *N. biflora*.

The typical habitat for *Nyssa ursina* is very low moist ground where it is uncommon to abundant in low moist flatwoods but common in inundated swamps and sloughs. The entire region of its habitat is very low in elevation above sea level. Many authors consider this species to be a variety of *N. biflora*, but locations have been seen where both species occur within one half kilometer of each other, and both species exhibit their own specific characteristics.

A 1991 specimen collected by J.R. Burkhalter in Escambia County, Florida appears to be *Nyssa ursina* and may represent a new disjunct location for the species. Further research into this population is anticipated.

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