



FIRST OCCURRENCE OF NYSSA ENDOCARPS AND ASSOCIATED FUNGI IN THE OLIGOCENE OF SOUTH CHINA: PALAEOGEOGRAPHICAL AND PALAEOECOLOGICAL SIGNIFICANCE

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Abstract: Co-evolutionary relationships of plants and fungi are of great importance for the phylogeny of both groups. *Nyssa* was widely distributed in the northern hemisphere during the Cenozoic. Extant species of *Nyssa* exhibit a disjunct distribution between eastern North America, Central America and East Asia. Here, a new species, *Nyssa nanningensis* Xu & Jin, is described based on fruit endocarps from the upper Oligocene Yongning Formation of the Nanning Basin, South China. This new fossil record of *Nyssa* expands the known palaeogeographical distribution of the genus to the low latitudes of East Asia. Associated fossil fungal fruiting bodies on *Nyssa* endocarps are assigned to the

new fossil genus and species, *Yongnicta nyssae* Tobias & Maslova. This new genus is similar to some members of extant wood destructor taxa Coronophorales and Amphisphaerales (Sordariomycetes, Ascomycota). About 3% of the *Nyssa* endocarps studied were affected by *Yongnicta nyssae*. Low frequency of fruit damage indicates that endocarps could be released from mesocarps by animals eating fleshy parts of fruits, making them potentially available to wood-destroying fungi.

Key words: *Nyssa*, endocarp, *Yongnicta nyssae*, fossil fungi, late Oligocene, South China.

PHYLOGENETIC relationships within the order Cornales have long been controversial (Magallón *et al.* 1999; Albach *et al.* 2001). Current molecular phylogenetic studies recognized the monophyly of each cornalean family and support five major clades comprising ten families: Cornaceae and Alangiaceae; Nyssaceae, Mastixiaceae and Davidiaceae; Grubbiaceae and Curtisiaceae; Hydrangeaceae and Loasaceae; Hydrostachyaceae (Fan & Xiang 2003; Xiang *et al.* 2011). The latest update of the Angiosperm Phylogeny Group (APG) classification recognized seven families in Cornales: Nyssaceae, Hydrostachyaceae, Hydrangeaceae, Loasaceae, Curtisiaceae, Grubbiaceae and Cornaceae (APG 2016).

The genus *Nyssa* Gronov. ex L., previously considered to represent the family Cornaceae (Eyde 1988, 1997; Kubitzki 2004), is now placed in Nyssaceae along with *Campthoeca* Decne., *Davidia* Baill., *Mastixia* Blume, and

Diplopanax Hand.-Mazz. (APG 2016). Seven extant species of *Nyssa* (Wang *et al.* 2012; Zhou *et al.* 2018) have a disjunct distribution in East Asia, eastern North America and Central America (Fig. 1). *Nyssa sylvatica* Marshall, *N. ogeche* Bartram ex Marshall, and *N. aquatica* L. occur in North America (Eyde 1997). All of these species commonly inhabit swamps, stream banks and floodplains at low elevations in humid, warm temperate climates (Tucker 2016). An additional species, *Nyssa talamancana* Hammel & N. Zamora, was recently described from Costa Rica and Panama (Hammel & Zamora 1990). Although seven species of *Nyssa* have been recognized by Fang *et al.* (1983) and accepted by Qin & Phengklai (2007) in the Flora of China, only three species are confirmed in eastern Asia based on morphological and molecular data: *N. javanica* (Blume) Wangerin, *N. yunnanensis* W.Q. Yin ex H.N. Qin & Phengklai, and *N. sinensis* Oliv. Four

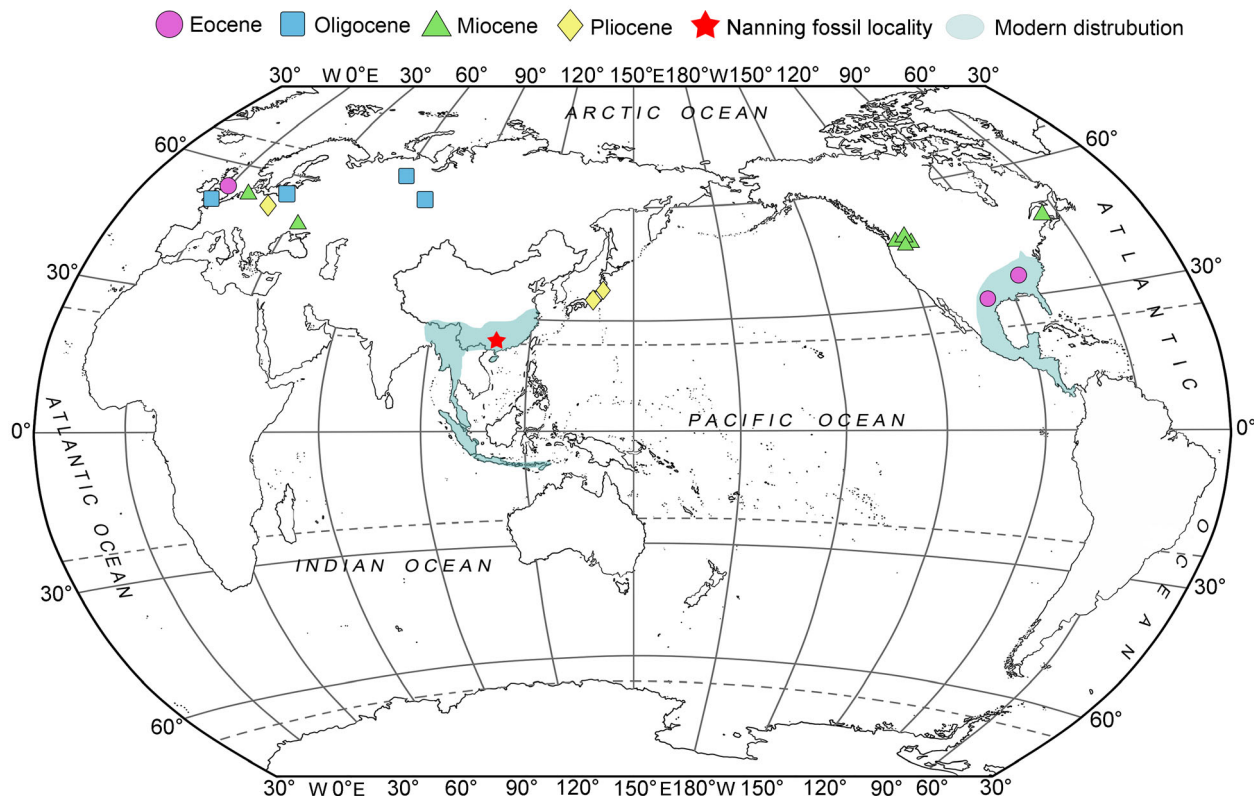


FIG. 1. Modern distribution and fossil records of *Nyssa*.

other described species, *N. shangszeensis* Fang & Soong, *N. wenshanensis* Fang & Soong, *N. leptophylla* Fang & T.P. Chen and *N. shweliensis* (W.W. Sm.) Airy-Shaw, are barely differentiated from *N. sinensis* (Airy-Shaw 1969; Fang & Soong 1975; Wang *et al.* 2012). *Nyssa yunnanensis* is a canopy tree species confined to mountainous bogs and marshes in southern Yunnan Province, China (Fu 1989; Tan & Deng 2016), and is an endemic and critically endangered Chinese species (Sun 1998; Sun *et al.* 2009). The native distribution range of *Nyssa javanica* includes southern China, India, Myanmar, Vietnam, Laos, Indonesia and Malaysia, extending just south of the equator in Java (Eyde 1963). *Nyssa sinensis* is widely distributed in central and south-western China, Myanmar and Vietnam (Wen & Stuessy 1993).

Nyssa is one of the plant genera with abundant fossil records in the Cenozoic of the northern hemisphere. Many fossil localities are outside the range of its modern distribution, for example, in Europe, western North America, western Siberia, and Japan (Manchester 1994; Eyde 1997). The rapid diversification of *Nyssa* was correlated with the global warmth of the early Eocene (Tiffney 1985a, b; Zhou *et al.* 2020). Subsequently, this genus suffered widespread extinctions on a global scale which were most likely linked to climatic changes in the early Oligocene and at the end of the Neogene (Wolfe 1985; Zhou *et al.* 2020).

The earliest cornalean fruits are known from the uppermost Turonian of eastern North America, and the lowermost Coniacian of eastern Asia and western North America (Takahashi *et al.* 2002; Atkinson *et al.* 2018, 2019). Several extinct cornalean taxa, *Hironoia* Takahashi, Crane & Manchester from the Coniacian of Japan (Takahashi *et al.* 2002), an undescribed Drumheller fruit from the Campanian of Alberta, Canada (Manchester *et al.* 2015; Atkinson 2018), and *Amersinia* Manchester, Crane & Golovneva from the Paleocene of North America and eastern Asia (Manchester *et al.* 1999) were originally assigned to the nyssoids due to the presence of fibres in the endocarps. However, subsequent phylogenetic analysis showed that the *Hironoia-Amersinia* clade is sister to Curtisiaceae (Atkinson 2018).

Fossil fruits assigned to *Nyssa* were reported for the first time by Heer (1869) from the Paleocene Atanekerd-luk Formation, west Greenland. However, these follicular fruits, widespread in the Cretaceous and the Palaeogene of the northern hemisphere, were subsequently assigned to the family Cercidiphyllaceae Engl. (Crane & Stockey 1985, 1986). The oldest confirmed fossil endocarps of *Nyssa* have been reported from the lower Eocene London Clay Formation, southern England (Reid & Chandler 1933; Chandler 1961) and the middle Eocene Clarno Formation of Oregon (Scott 1954; Manchester 1994). Three endocarp sculpture types (ridged with sunken bundles,

ridged with raised bundles, and smooth) are distinguished in the fossil endocarps of *Nyssa* in Europe and North America, indicating that significant diversification of this genus had already occurred by the Eocene (Eyde 1997). Many of the fossil fruits are three or four-carpellate, the traces of major vascular bundles indicate the greater number of petals and stamens in extinct forms, and the sizes of some fossil fruits are much larger than in extant species (Eyde 1966).

Fungi are an essential component of modern and ancient ecosystems with a fundamental role in biosphere function. They act as mediators between organic and inorganic matter and are responsible for decay of the substrate they utilize. Therefore, fungi are palaeoenvironmentally and phylogenetically significant. Ascomycetes comprise the largest and most diverse group of extant fungi with the best known evolutionary history (e.g. Kalgutkar & Jansonius 2000; Tripathi 2009; Saxena & Tripathi 2011; Taylor *et al.* 2015). The Cenozoic records of Ascomycota show that they became conspicuously diverse by this time, but finds of fungi associated with angiosperms are rare compared to the number of similar extant associations (e.g. Dilcher 1965; Phipps & Rember 2004; Ding *et al.* 2011; Klymiuk *et al.* 2013; Ma *et al.* 2015; Conran *et al.* 2016; Wang *et al.* 2017; Xu *et al.* 2021).

Since fossil fungi are often fragmentary, characteristic morphological features of extant taxa are not always available, hampering their classification in terms of extant fungi (e.g. asci are not usually preserved), and identification becomes problematic. The incompleteness of the fossil record, and thus the impossibility of reconstructing the whole fungal organism and all stages of its life cycle, also hinder fossil fungal identification. In Ascomycota, the teleomorphic and anamorphic stages of different taxa can be morphologically more or less similar, so in the absence of significant morphological data, and the impossibility of routinely applying molecular methods to fossils, their determination is difficult. In the case presented here, the identification of the fossil fungus is based on all the available morphological features which allows direct comparison with extant analogues and host plant–fungus relationships.

The majority of fossil fungal records consist of isolated fruiting bodies, dispersed hyphae and spores (Taylor *et al.* 2015). Fungal fruiting bodies with *in situ* spores and associated with plants are rare. In that context, our record of fungal fruiting bodies with spores inside *Nyssa* endocarps is significant. The identification of extant fungi is not limited to their external morphology but requires detailed cytological examination, study of the teleomorph–anamorph connections, physiological–biochemical characters and molecular analysis; therefore it is not possible to assign fossil fungi to extant genera.

In this paper, we describe a new species, *Nyssa nanninensis* sp. nov. based on mummified endocarps from the

upper Oligocene Yongning Formation of the Nanning Basin, South China, as well as a new genus and species of fungal fruiting bodies, *Yongnicta nyssae* gen. et sp. nov. that affected several *Nyssa* endocarps. Based on the morphological similarity between Oligocene fungal bodies with *in situ* spores and some extant members of two orders of Sordariomycetes, we erect here a new extinct genus: *Yongnicta*. This new fossil records expand the known palaeogeographical distribution of *Nyssa* to South China, provide important data for the investigation of the possible migration paths and diversification of the genus, as well as illustrate the co-evolutionary relationships between plants and fungi.

MATERIAL AND METHOD

Geological setting

A total of 113 mummified endocarps of *Nyssa* were collected from the upper part of the Yongning Formation, which was exposed at a construction site (22°52'50"N, 108°25'2"E) in Santang Town, Nanning City (Fig. 2). The Yongning Formation covers the majority of the Nanning Basin (Zhao 1993). The upper part of the Yongning Formation is mainly composed of bluish-grey clayey mudstones, interspersed with a few coal seams and thin sandstones. The age of the formation is considered to be late Oligocene based on mammal fossils (Zhao 1983, 1993; Quan *et al.* 2016). The plant-bearing deposits document a low-latitude Oligocene mummified fossil flora in East Asia for the first time (Quan *et al.* 2016). All specimens and slides are housed at the Museum of Biology, Sun Yat-sen University, Guangzhou, China.

Specimen preparation

The mummified endocarps were washed using ultrasonic cleaners (JP-020S, 120W; Jiemeng, Shenzhen, China) and then air dried. The specimens were photographed and measured using a Zeiss Stereo Discovery V20 stereo microscope equipped with an AxioCam HRc digital camera (Zeiss, Jena, Germany) and Nikon SMZ25 stereo microscope (Nikon, Tokyo, Japan) at the Museum of Biology, Sun Yat-sen University, Guangzhou, China. Specifically, the fruit specimens were scanned using a Zeiss Xradia 520 Versa x-ray microscope at the University of Science and Technology of China, Hefei, China. The image data was processed with Dragonfly v.4.1 (<https://www.theobjects.com/dragonfly>). For scanning electron microscope (SEM) study, endocarps were transversely cut across the middle half, mounted on standard copper plates, coated with gold, and examined using a JSM-6330F SEM (JEOL Ltd., Tokyo, Japan). Terminology for



FIG. 2. The geographical location of Nanning Basin, China.

the fruit description follows detailed monograph of Kirchheimer (1938) on fossil Nyssaceae.

The samples with fungi were sectioned using a freezing microtome Leica CM1950 (Leica, Wetzlar, Germany) at a thickness of 8 μm , and then photographed using a light microscope (LM) Olympus BX53 (Olympus, Tokyo, Japan) equipped with an UPlanFLN 60 \times digital camera.

SYSTEMATIC PALAEOLOGY

Fruit

By Sheng-Lan Xu and Jian-Hua Jin

Order CORNALES Dumort., 1829

Family NYSSACEAE Juss. ex Dumort., 1829

Genus NYSSA Linné, 1753

Nyssa nanningensis sp. nov.

Figures 3, 4

Derivation of name. The epithet refers to the Nanning Basin, where the collections were made.

Holotype. NNF650, endocarp, designated here (Fig. 3A, B)

Paratypes. NNF624 (Fig. 3C, D). NNF115 (Fig. 3E, F). NNF695 (Fig. 3G, H). NNF117 (Fig. 3I, J). NNF199 (Fig. 3K, L). NNF599 (Fig. 3M, N). NNF116 (Fig. 3O–R).

Diagnosis. Endocarp woody, obovoid, rarely elliptical in outline, with the widest point above the midline, dorsally flattened, unilocular. Endocarp exterior surface with five to seven longitudinal narrow grooves and as many rounded wide ridges. Broadly triangular germination valve with rounded lateral edges and acute apex confined to the apical third of endocarp on the dorsal side. Peripheral vascular bundles sunken in the grooves. Locule roughly W-shaped in transverse section. Fibrous endocarp walls 0.5–0.9 mm thick.

Locality. Santang Town, Nanning, Guangxi, South China.

Stratigraphical position. Yongning Formation, Nanning Basin, upper Oligocene.

Repository. The Museum of Biology, Sun Yat-sen University, Guangzhou, China.

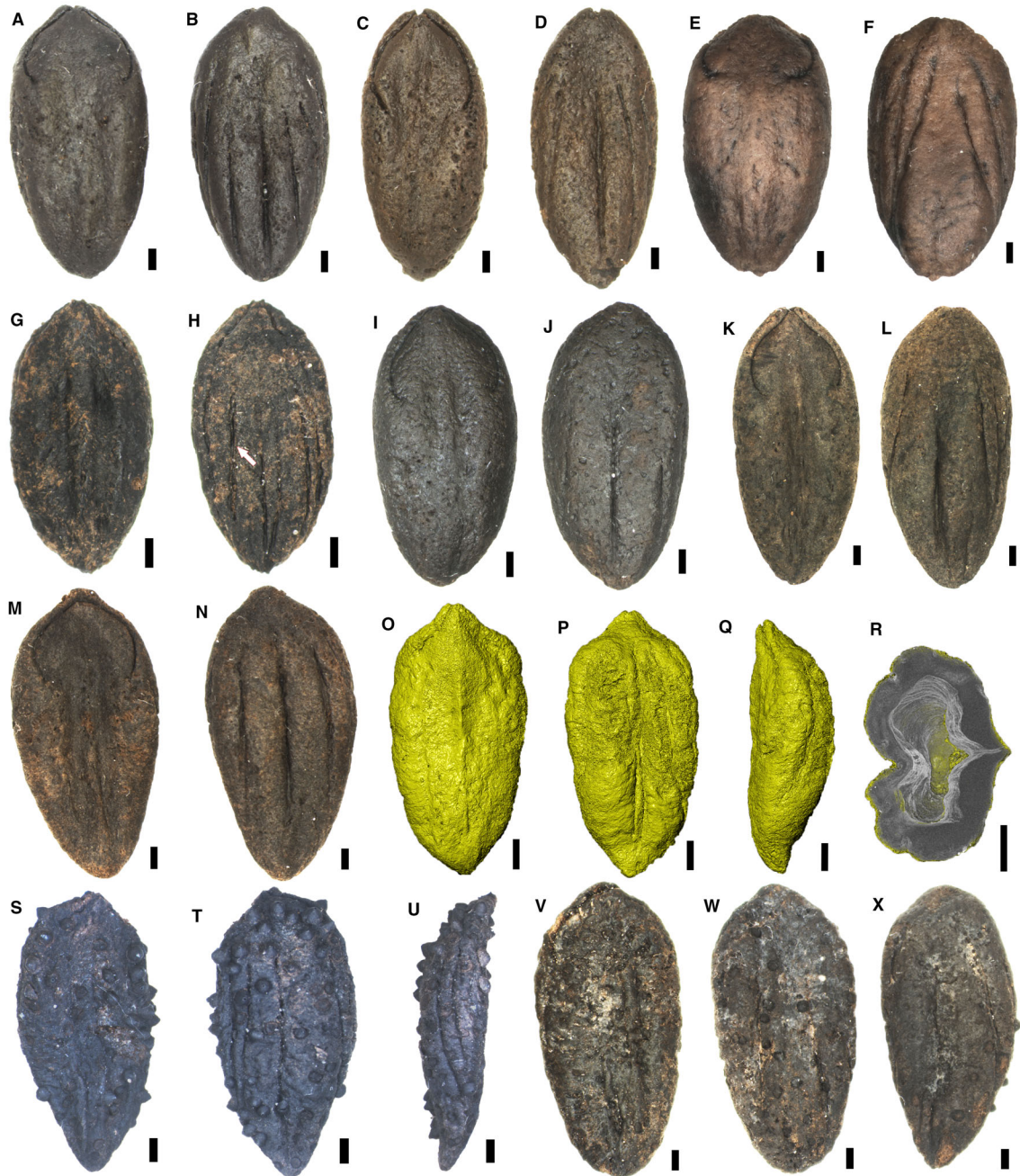


FIG. 3. Endocarps of *Nyssa nanningensis* sp. nov. A–B, holotype NNF650: A, dorsal surface showing broad germination valve; B, ventral surface. C–D, paratype NNF624: C, dorsal surface; D, ventral surface with rounded ridges of unequal width. E–F, paratype NNF115: E, dorsal surface showing low median ridge and short germination valve; F, ventral surface showing bifurcated vascular bundles. G–H, paratype NNF695: G, dorsal surface with median longitudinal ridge; H, ventral surface with vascular bundles grouped in pair within the groove (arrow). I–J, paratype NNF117: I, dorsal surface showing conspicuous median longitudinal ridge; J, ventral surface. K–L, paratype NNF199: K, dorsal surface showing broadly triangular germination valve with rounded acute apex; L, ventral surface showing bifurcated vascular bundles. M–N, paratype NNF599: M, dorsal surface showing median longitudinal groove with two adjacent narrow ridges; N, ventral surface. O–R, paratype NNF116: O, isosurface rendering of endocarp, dorsal view; note clearly convex middle rib; P, isosurface rendering of endocarp, ventral view; Q, isosurface rendering of dorsoventrally compressed endocarp in lateral view; R, isosurface rendering of endocarp with roughly W-shaped locule in transverse section. S–U, endocarp with numerous fungal ascomata in: S, dorsal; T, ventral; U, lateral view; holotype of *Yongnieta nyssae* gen. et sp. nov., NNF294. V–W, endocarp with fungal ascomata in: V, dorsal; W, ventral view, NNF676. X, endocarp with fungal ascomata, ventral view, NNF626. Scale bars represent 1 mm.

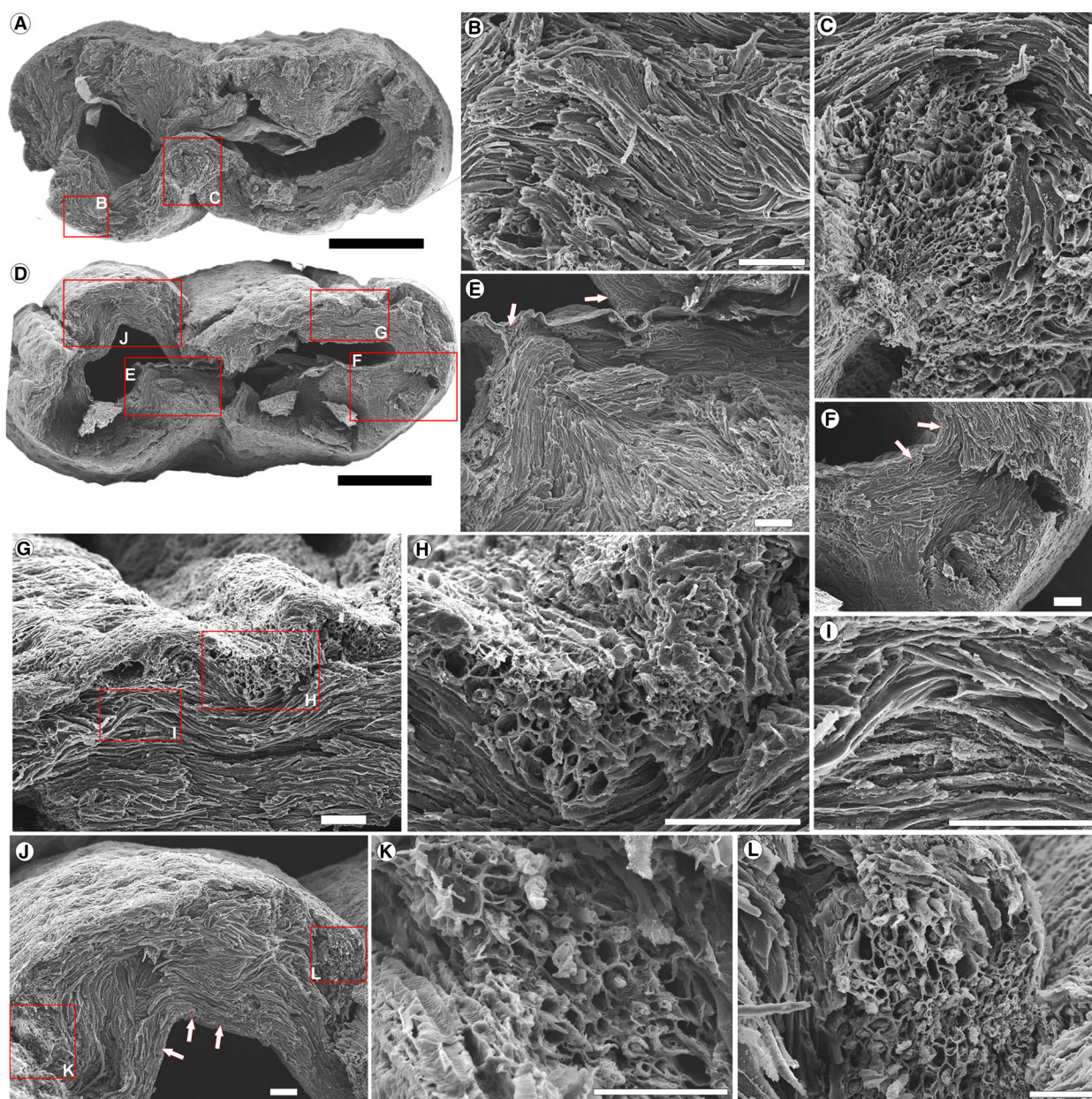


FIG. 4. The transverse section of the endocarp of *Nyssa nanningensis* sp. nov., NNF-117. A–C, apical part of the endocarp; ventral surface at the bottom of image; B, enlargement of fibres; C, enlargement of vascular bundle. D–F, basal part of the endocarp; ventral surface at the top of image; E–F, enlargements of endocarp wall showing several layers of the inner longitudinal fibres (arrows). G–I, enlargement of vascular bundle in D, sunken in the groove; H, enlargement of vascular bundle and fibres; I, transverse fibres from the outer portion of endocarp wall. J, enlargement of fibres and vascular system in D showing the peripheral vascular bundles in the grooves, transverse fibres and inner longitudinal fibres (arrows). K–L, enlargement of vascular bundles in J. Scale bars represent: 1 mm (A, D); 100 μm (B, C, E, F, G–I, J); 50 μm (K, L).

Description. Woody endocarps are obovoid, rarely elliptical in outline, dorsally flattened (Fig. 3Q, R, U), generally with the widest point above the midline, apex oval lacking a sharp protrusion. Endocarps are 7.4–15.9 mm long and 4.2–8.0 mm wide, mean length of complete endocarps are 12.5 mm and mean width 6.5 mm. Five to seven longitudinal narrow grooves, and as many rounded ridges, commonly of unequal width, appear on external

endocarp surfaces, mostly on the ventral side (Fig. 3B, D, F, H, J, L, N, R). The dorsal midline is marked by a conspicuous longitudinal ridge (Fig. 3A, E, G, I, K, O, R), rarely by a deep groove with two adjacent longitudinal narrow ridges (Fig. 3M). Endocarps are unilocular (Figs 3R, 4A), locule is roughly W-shaped in transverse section because of two internal ridges on the dorsal wall, and a deep nearly median groove on the ventral endocarp

surface corresponding to a ridge within the locule (Figs 3R, 4A). The germination valve is located on the dorsal side, usually confined to the apical third of the endocarp, broadly triangular, with rounded lateral edges and an acute apex (Fig. 3A, C, E, G, I, K, M, O, Q). Peripheral vascular bundles are sunken in the grooves (Fig. 4C, G, H, J–L), some of the bundles bifurcate and anastomose (Fig. 3F, L), and occasionally vascular bundles are grouped in pairs within the grooves (Fig. 3H); minor bundles are also visible in the innermost layer of the endocarp (Fig. 4E). Fibrous endocarp walls are 0.5–0.9 mm thick (Fig. 4A, B, D, I); one or several layers of the inner longitudinal fibres are surrounded by a layer of circumlocular fibres, followed by thick layer of randomly oriented fibres within the central part of the endocarp wall, while a layer of transverse fibres form the outer portion of the endocarp wall (Fig. 4E, F, J).

Fungi

By Anna V. Tobias and Natalia P. Maslova

Phylum ASCOMYCOTA Cavalier-Smith, 1998

Genus YONGNICTA nov.

Mycobank LSID. 839905

Derivation of name. From Yongning Formation of the Nanning Basin, South China.

Type and only species. *Yongnicta nyssae* sp. nov.

Generic diagnosis. Fossil dome-shaped dark fruiting bodies, with rounded or oval bases. Fruiting body ostiolate, with papillate central pore. Peridium pseudoparenchymatic, wall cells with munk pores. Spores uni-septate, ellipsoid, fusoid.

Yongnicta nyssae sp. nov.

Figures 3S–X, 5, 6, 7

Mycobank LSID. 839908

Derivation of name. From host plant *Nyssa*.

Holotype. NNF294, endocarp with numerous fruiting bodies, designated here (Fig. 3S–U).

Paratypes. NNF626 (Fig. 3X), NNF676 (Fig. 3V, W).

Specific diagnosis. Fossil fruiting bodies on *Nyssa* endocarp. Fruiting bodies solitary or in groups, flask-shaped, with rounded or oval bases up to 0.8 mm in diameter, and up to 0.6 mm high. Fruiting body ostiolate with

papillate central pore. Peridium pseudoparenchymatous, up to 50 µm, cells with munk pores. Spores approximately 33–35 × 16–19 µm, uni-septate, ellipsoid, fusoid, slightly constricted at the septum, with germ pore at the end.

Type locality. Santang Town, Nanning, Guangxi, South China.

Stratigraphical position. Yongning Formation, Nanning Basin, upper Oligocene.

Repository. The Museum of Biology, Sun Yat-sen University, Guangzhou, China.

Description. Fruiting bodies are irregularly distributed, solitary or in groups, visible as flask-shaped structures on the endocarp surface (Fig. 5A–F), with the base diameter ranging from 0.5 to 0.8 mm. The base of the fruiting body is rounded or slightly oval, slightly immersed in endocarp tissues (Fig. 5C–F). The fruiting body height in vertical section is up to 0.6 mm (Figs 5A, 6A, C, D). The fruiting body has a single central protruding ostiolar canal with a papillate central pore up to 100 µm in diameter (Figs 5A–E, 7A). The peridium is up to 25 µm thick, and composed of irregular, tightly packed, isodiametric in shape (Fig. 6B, E, F), short-celled hyphae forming a pseudoparenchyma (Fig. 7B, D, H). Some pseudoparenchymatous cells bear a rounded munk pores (Fig. 7D, H). A few hyphae fragments are visible inside the fruiting bodies (Fig. 7A–D). Asci are not preserved. Spores are 33.8–35.4 × 16.7–19.5 µm in size, uni-septate, ellipsoid fusoid, slightly constricted at the septum (Fig. 7C–F, H), with a germ pore at the end (Fig. 7E). The spore surface is mostly finely granulate, with flattened sculpture elements; occasional regions with papilla-like elements up to 1 µm high were observed for some spores (Fig. 7F–H).

Host plant. Endocarps of fossil species *Nyssa nanningensis*.

DISCUSSION

Generic assignment

The extant genera of Nyssaceae are characterized by fruits with endocarps composed of fibres, a germination valve on each one-seeded locule opening from the apical end of the locule, the absence of an axial vascular bundle in the ovary, and the presence of grooves and ridges on the surface of the endocarp (Wen & Stuessy 1993; Eyde 1997;

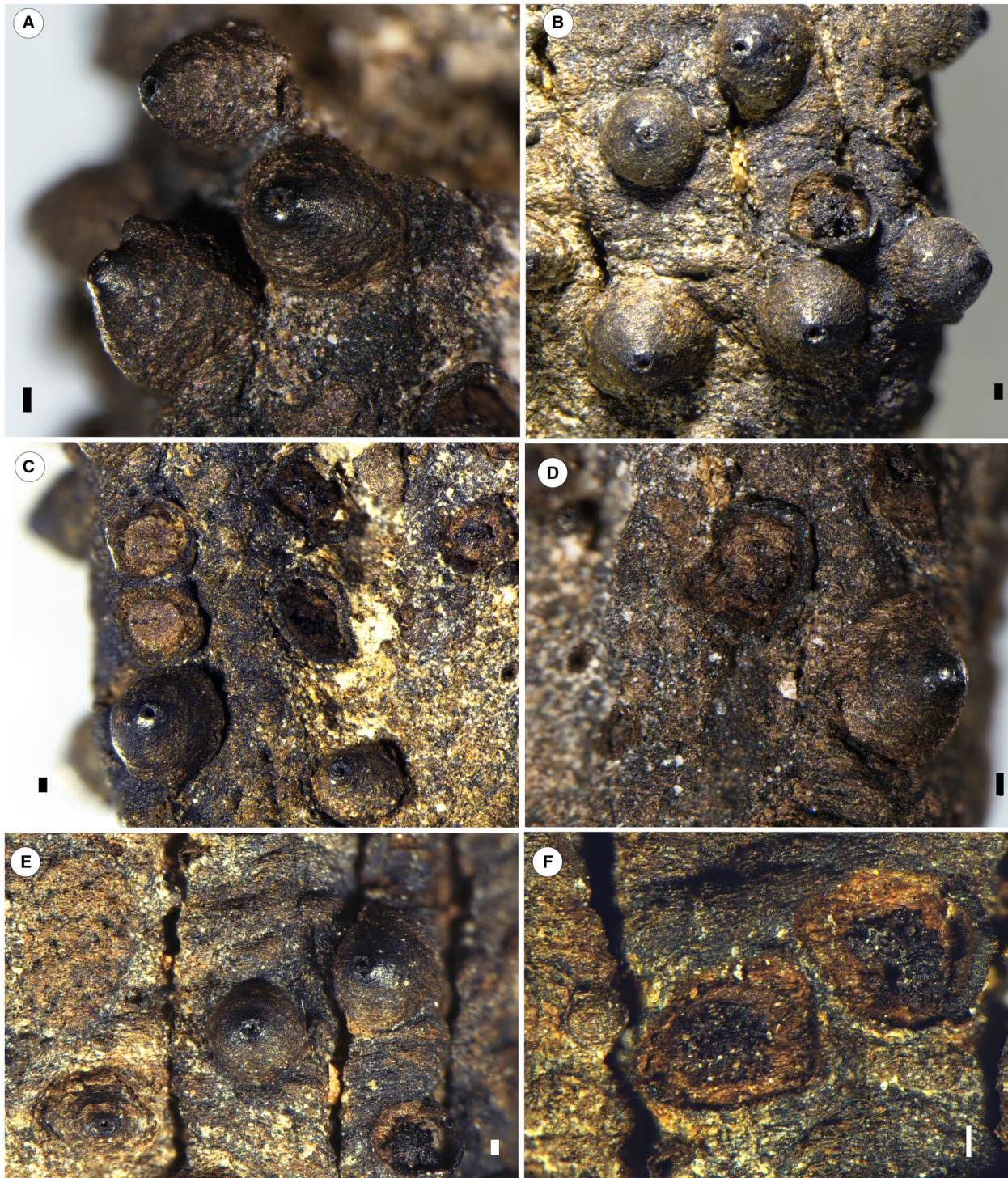


FIG. 5. Macromorphology of fruiting bodies of *Yongnicta nyssae* gen. et sp. nov., holotype NNF294. Irregularly distributed dome-shaped fruiting bodies have a single central protruding ostiolar canal with a central pore; note circular or slightly oval scars after fruiting body abscission. Scale bars represent 0.1 mm.

Manchester *et al.* 2007). The fossil fruits reported in this study display unilocular woody endocarps consisting of fibres, triangular germination valves restricted to the

apical third of the endocarp, and peripheral vascular bundles that extend the length of the endocarp causing grooves and ridges on the surface. This suite of characters

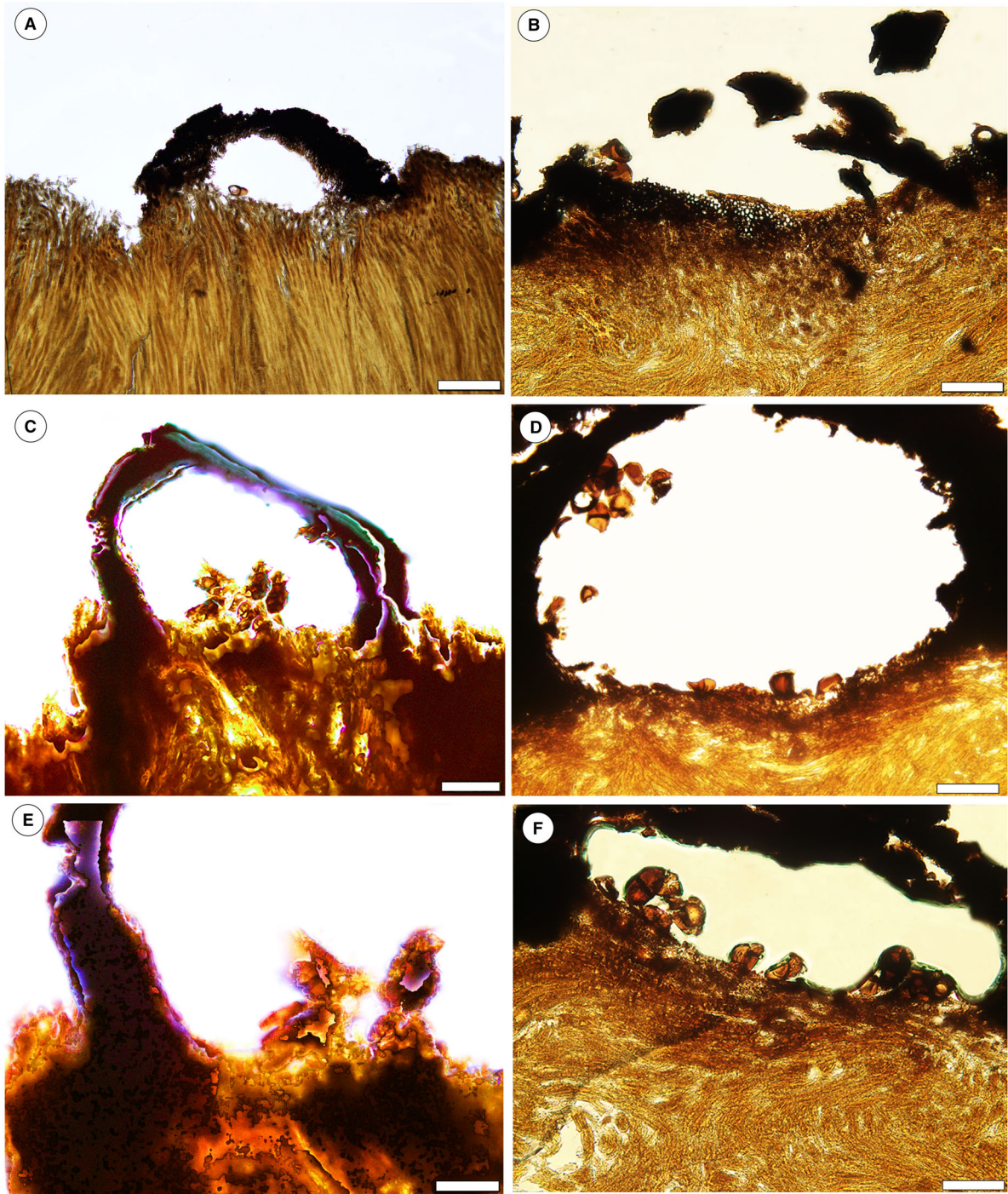


FIG. 6. Fruiting body of *Yongnicta nyssae* gen. et sp. nov. in longitudinal section, holotype NNF294. A, D, F, dome-shaped fruiting body with spores inside. B, pseudoparenchyma slightly immersed in endocarp tissues. C, E, fragments of probable asci inside the fruiting body. Scale bars represent: 50 μm (B, D, E, F); 100 μm (A, C).

is known for the genus *Nyssa* (Eyde & Barghoorn 1963; Eyde 1997).

The fossil genus assigned to the Nyssaceae, *Browniea* Manchester & Hickey, and recognized from the Paleocene of North America, is distinguished from *Nyssa* in having

globose infructescences composed of numerous elongate fruits with five persistent epigynous sepals and a single style with two stigmatic arms (Manchester & Hickey 2007). *Browniea* fruits are unilocular and single-seeded, and with fruit walls that are relatively thin compared to

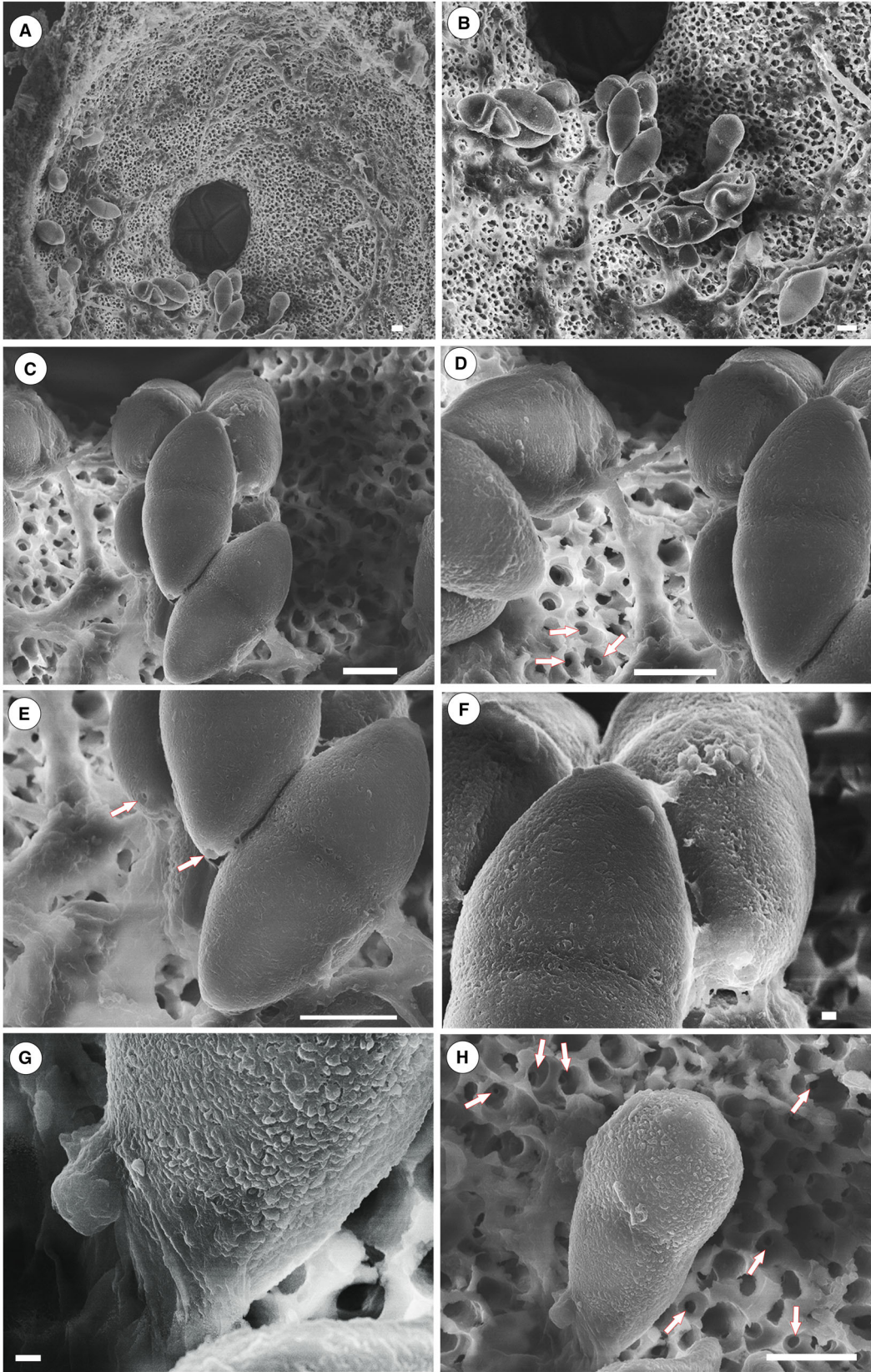


FIG. 7. Fruiting body inner surface of *Yongnicta nyssae* gen. et sp. nov., holotype NNF294, SEM. A, peridium of short-celled hyphae forming the pseudoparenchyma; spores and hyphae inside fruiting body are visible; note central rounded pore of the ostiolar canal. B, enlargement of fruiting body wall and spores in A. C, uni-septate spores. D, enlargement of hyphae and spores in C; porate cells (munk pores) of fruiting body wall are visible (arrows). E, enlargement of spores in C with a germ pore at the end (arrows). F, spore slightly constricted at the septum. G, finely granulate spore surface. H, spore and fruiting body wall composed of short-celled hyphae with rounded munk pores (arrows). Scale bars represent 10 μm (A–E, H); 1 μm (F, G).

thick-walled *Nyssa* endocarps. *Browniea* infructescences and fruits strikingly resemble those of extant *Camptotheca*, but the presence of prominent bract scars at the inflorescence base, thicker fruit walls, and distinct calyx lobes are important characters to distinguish *Browniea*. The endocarps of *Browniea* have elongate germination valves extending from the basal one-fourth to the apex of the fruit and contrast strongly with the short apical germination valve in *Nyssa*, *Camptotheca* and *Amersinia*.

Based on fruit morphology and anatomy, *Amersinia* was originally defined as an extinct nyssoid genus (Manchester *et al.* 1999; Manchester & Hickey 2007). As in *Browniea* and *Camptotheca*, *Amersinia* infructescences are heads bearing numerous closely packed fruits. The fruits are trilocular (rarely tetralocular), one-seeded per locule, with an epigynous disk and a calyx without free tips. The inner endocarp layer is composed of fibres that are mostly oriented transversely, whereas the peripheral part of the endocarp walls is composed of sclereids (Manchester *et al.* 1999). Although vascularization in Nyssaceae endocarps is confined to the septum periphery (Eyde 1963), the endocarps of *Amersinia* have both trans-septal vascular bundles and bundles in the central axis (Manchester *et al.* 1999). Among extant Cornales, axial vascular bundles occur only in Hydrangeaceae, Loasaceae, Curtisiaceae and Grubbiaceae (Eyde 1967; Manchester *et al.* 2007; Yembaturova *et al.* 2009; Atkinson *et al.* 2017, 2018).

The extant genus *Camptotheca* is distinguished from *Nyssa* by having a very thin endocarp surrounded by parenchymatous mesocarp, a higher endocarp length to width ratio, a roughly triangular endocarp in cross section, and large numbers of fruits clustered in globose heads (Manchester *et al.* 1999; Noll 2013). The fruits of *Camptotheca* are only unilocular and bilocular, and tricarpeolate, as indicated by the presence of three styles (Eyde 1963; Gong *et al.* 2018).

In contrast to the 1–4-locular endocarps of *Nyssa*, fruits of extant *Davidia* species have 6–10 single-seeded locules, each of them bearing a dorsal germination valve that extends nearly the full length of the endocarp (Hill 1933; Eyde 1997; Manchester 2002). Numerous fossil records of this genus are reported from the Paleocene of North America and eastern Asia (Manchester 2002), and from the Pliocene and Pleistocene of Japan (Kokawa 1965; Tsukagoshi *et al.* 1997). The Paleocene species, *Davidia antiqua* (Newberry) Manchester, differs from the

extant *D. involucrata* Baill. only in the smaller size of the fruit and the lack of a median rib over each locule (Manchester 2002).

Mastixia and *Diplopanax* are closely related to *Nyssa*. Unilocular single-seeded fruits of *Mastixia* with a stony endocarp can be distinguished from those of *Nyssa* in having the fruit stone with a smooth, finely creased, or knobby surface (Kirchheimer 1936; Eyde 1963), and a prominent longitudinal inward fold along the dorsal side of the endocarp intruding the locule and forming a U-shape in cross section (Eyde & Xiang 1990; Manchester *et al.* 2007; Manchester & Collinson 2019). The germination valve of *Mastixia* extends down the entire length of the endocarp (Manchester & Collinson 2019). Fruits of *Diplopanax* are also unilocular with a thick corky mesocarp, a fibrous endocarp, an elongate dorsal germination valve that runs the full length of the fruit; and a prominent infold that intrudes the locule resulting in C or U-shaped locule outline in cross section. Compared to *Mastixia*, the fruits of *Diplopanax* have multiple vascular bundles extending longitudinally through the stone, rather than being concentrated in a pair of ovular bundles (Manchester & Collinson 2019).

Comparison with fruits of extant and fossil species of Nyssa

The endocarp shape, size, surface sculpture and type of germination valve are diagnostic characters of *Nyssa* species (Manchester 1994). Surface ribbing patterns and vascular strands are constant among modern species, which means that they can be used as key characters for species classification (Eyde 1997). Several longitudinal grooves arching from endocarp sides to the placental region indicate the former position of the ovular supply (Eyde 1963).

The fossil endocarps of *Nyssa nanningensis* reported in this study bear 5–7 prominent grooves on the surface, alternating with rounded ridges, with peripheral vascular bundles sunken in the grooves (Fig. 4A, C, G, H). The endocarps of extant species *N. aquatica* (Table 1) differ in being larger (length range 14.0–28.3 mm in *N. aquatica* versus 7.4–15.9 mm in studied fossil species), having about 10 sharp ridges, vascular bundles situated on the endocarp ridges, and an acuminate germination valve apex (Eyde 1963; Noll 2013). *Nyssa javanica* endocarps are similar to those of the fossil species in size, locule

TABLE 1. Endocarp comparison of extant species of *Nyssa*.

Species	Distribution	Endocarp outline	Length (mm)	Width (mm)	Endocarp surface	Surface ridge number	Germination valve shape	Locule number	Type of vascular bundle	References
<i>Nyssa javanica</i> (Blume) Wangerin	South-eastern China, north-east India, Myanmar, Thailand, Vietnam, Laos, Indonesia & Malaysia	Ellipsoid	14.0–26.0	11.0–15.2	Relatively smooth	1–3	Rounded	1	Smooth-surfaced	Eyde (1963); Wang <i>et al.</i> (2012)
<i>Nyssa sinensis</i> Oliv.	Central and south-western China	Oblong or obovoid	7.1–14.4	4.3–8.5	Rounded ridges	7–10	Rounded	1–2	Sunken	Wen & Stuessy (1993)
<i>Nyssa yunnanensis</i> W.Q. Yin ex H.N.Qin & Phengkhai	South-western China	Ellipsoid	15.2–17.2	12.5	Rounded ridges	3–5	Rounded	1	Sunken	Wang <i>et al.</i> (2012); Noll (2013)
<i>Nyssa sylvatica</i> Marshall	North America	Ellipsoid	7.5–12.8	5.4	Rounded ridges	7–12	Rounded	1	Sunken	Eyde (1963); Wang <i>et al.</i> (2012)
<i>Nyssa aquatica</i> L.	North America	Obovoid	14.0–28.3	11.2	Sharp ridges	9–10	Acuminate	1	Raised	Eyde 1963; Noll (2013)
<i>Nyssa ogeche</i> Bartram ex Marshall	North America	Round	14.7–29.3	10.2	Sharp ridges	10–15	Triangular	(1)–2	Sunken	Dilcher & McQuade (1967)
<i>Nyssa talamancana</i> Hammel & N. Zamora	Costa Rica & Panama	Ellipsoid	37.0–52.0	16.0–22.0	Rounded ridges	9–12	Triangular	2–3	Sunken	Hammel & Zamora (1990); Noll (2013)

number, having a distinct median ridge on the dorsal surface, and in having several internal ridges resulting in a roughly W-shaped locule outlines, but differ in having a relatively smooth endocarp surface and vascular bundles above the ridges (Eyde 1963; Noll 2013).

The endocarps of *N. sylvatica*, *N. ogeche*, *N. talamancana*, *N. yunnanensis* and *N. sinensis* are ribbed, with vascular bundles sunken between broad ribs. *Nyssa talamancana* is reported to have very hard, woody endocarps with vascular bundles running in 9–12 grooves alternating with low, rounded ridges; the endocarps are 37–52 mm long, 16–22 mm wide, and so significantly larger than endocarp sizes observed in other modern species and fossil *Nyssa nanningensis* (Hammel & Zamora 1990). Mostly unilocular elongated endocarps of *N. ogeche* have about a dozen sharp ridges, with their crests extended radially as papery wings, and 10–15 thick vascular bundles in the grooves between these ridges; the germination valve is acute (Eyde 1963). *Nyssa yunnanensis* differs from all other species in having broadly oblong endocarps with an average length of 16.2 mm and a width of 12.5 mm (Noll 2013). Strictly one-seeded endocarps of *N. yunnanensis* have a low number of endocarp ribs, reported as 3–5 by Wang *et al.* (2012). *Nyssa sylvatica* and *N. sinensis* are reported to have 7–12 vascular grooves on the surface, share a similar size and have rounded ribs, but endocarps of *N. sinensis* are usually both unilocular and bilocular, in contrast to *N. sylvatica* which very rarely has bilocular endocarps (Eyde 1963; Wen & Stuessy 1993; Noll 2013). Ventral walls of the endocarps of both extant species are up to twice as thick as the dorsal side, which is not typical for the fossil endocarps from Nanning.

As with the extant species, the size and shape of the endocarp and germination valve, the position of vascular bundles relative to the surface grooves and ridges, and locule number are important characters by which extinct species of *Nyssa* can be distinguished (Table 2). The species *Nyssa disseminata* (R. Ludw.) Kirchh., which extends from the Oligocene to the Pliocene in Europe, and *N. sibirica* P.I. Dorof. ex Zhilin from the Oligocene–Miocene of western Siberia are most similar to *N. nanningensis*. *Nyssa disseminata* endocarps are elliptical in outline, widest at the midpoint, unilocular or very rarely bilocular, 5–14 mm long and 4–7 mm wide, with 6–9 grooves and wide rounded ridges on the surface; vascular strands are sunken within grooves; germination valves are broad triangular with more or less rounded lateral edges (Ludwig 1857; Mai 1973; Mai & Walther 1978; Eyde 1997; Noll 2013). *Nyssa nanningensis* differs from *N. disseminata* in endocarp outline, dorsoventral flattening, and its W-shaped locule outline, whereas endocarps of *N. disseminata*, if they are not secondarily (post mortem) flattened, have a rounded outline in cross section and smooth locule surfaces lacking internal ridges (Ludwig 1857,

pl. 20 fig. 2f). Endocarps of *N. sibirica* differ from those of *N. nanningensis* in being of smaller size, having an endocarp apex frequently tapered to a point, and in possessing 5–6 vascular bundles on the dorsal surface (Dorofeev 1963; Noll 2013).

Nyssa ornithobroma Unger, a widespread species in the Oligocene to the Pliocene of Europe, western Siberia and Kazakhstan (Unger 1861; Mai & Walther 1978; Eyde 1997) differs distinctly from *N. nanningensis* in having larger endocarps (7–24 mm long and 4–12 mm wide), which are usually broad obovoid in shape, 1–4 locular, and have germination valves with acuminate apices. The endocarp surface has about 10 rounded ridges getting high and sharp in the apical part; vascular bundles are mostly sunken within narrow grooves but are usually raised on ridges near the endocarp apex (Mai & Gregor 1982; Eyde 1997; Noll 2013).

The Eocene *N. oviformis* E.M. Reid from St Tudy, Brittany, France, has unilocular thick walled (up to 3 mm) endocarps with 10–12 shallow longitudinal grooves on the surface carrying vascular bundles (Reid 1927).

Nyssa bilocularis (Reid & Chandler) Chandler from the lower Eocene London Clay Formation is reported to have ovoid bilocular endocarps that are up to 18.5 mm long by 10 mm wide, with 8–10 broad ribs and vascular bundles between them. Germination valves are confined to the apical half of the endocarp (Reid & Chandler 1933; Chandler 1961; Eyde 1997).

Nyssa cooperi Chandler is known from the Herne Bay site of the London Clay (Chandler 1961). This species possesses small trilocular endocarps, 9.5 mm long and 6.25 mm wide, with broad triangular germination valves restricted to the apical third of the endocarp. A few vascular bundles are sunken in grooves, the endocarp walls are thick, woody and fibrous (Chandler 1961; Eyde 1997). Endocarps of *N. bilocularis* and *N. cooperi* show affinities with modern Asian species *N. sinensis* and *N. sylvatica* from North America (Wen & Stuessy 1993). Zhou *et al.* (2020) considered that these fossils could not be assigned to any living lineage of *Nyssa*, based on their morphology.

Early Miocene *N. brandoniana* (Lesq.) Eyde & Barghoorn from Brandon, Vermont, USA, with a relatively smooth endocarp surface and few vascular bundles on that surface is similar to the extant *N. javanica* (Hitchcock 1853; Lesquereux 1861; Eyde & Barghoorn 1963; Noll 2013). *Nyssa brandoniana* has much larger endocarps than *N. nanningensis* (25–45 mm long and 18–30 mm wide); they have a germination valve extending at least half of the endocarp length, with an acuminate or mucronate apex. The locule internal surface lacks ridges (Noll 2013).

Type specimens of *N. complanata* Lesq. have also been obtained from the lower Miocene of Brandon, Vermont (Hitchcock 1853; Lesquereux 1861). Endocarps of *N. complanata* (5.6–11.8 mm long and 3.2–8.8 mm wide)

TABLE 2. Comparison of *Nyssa* fossil species endocarps with those of *Nyssa nanningensis* sp. nov.

Species	Age	Localities	Endocarp outline	Endocarp length (mm)	Endocarp width (mm)	Number of surface ridges	Germination valve shape	Germination valve position*	Locule number	Type of vascular bundle	References
<i>Nyssa nanningensis</i> sp. nov.	Oligocene	Guangxi, China	Elliptical to obovoid	7.4–15.9	4.2–8.0	5–7	Broad	1/3	1	Sunken	This study
<i>Nyssa disseminata</i> (R. Ludw.) Kirchh.	Oligocene to Pliocene	Central Europe	Elliptical	5.0–14.0	4.0–7.0	6–9	Broad triangular	1/3	1–(2)	Sunken	Ludwig (1857); Mai (1973); Mai & Walther (1978)
<i>Nyssa sibirica</i> P.I. Dorof. ex Zhilin	Oligocene to Miocene	Western Siberia	Elliptical, rare obovoid	4.7–9.9	2.0–5.0	8–11	Broad triangular	1/3	1	Sunken	Dorofeev (1963)
<i>Nyssa ornithobroma</i> Unger	Oligocene to Pliocene	Europe, western Siberia, Kazakhstan	Broad obovoid	7.0–24.0	4.0–12.0	~10	Oval to triangular	1/3	1–4	Sunken, raised on ridges near the endocarp apex	Unger (1861); Mai & Walther (1978); Mai & Gregor (1982); Eyde (1997)
<i>Nyssa oviformis</i> E.M. Reid	Late Eocene	Brittany, France	Ovoid	15.5	9.0	10–12	Horse-shoe shape	1/3	1	Sunken	Reid (1927)
<i>Nyssa bilocularis</i> (E.M. Reid & Chandler) Chandler	Early Eocene	London Clay, England	Ovoid	18.5	10.0	8–10	Broad sub-triangular	1/2	2	Sunken	Reid & Chandler (1933); Chandler (1961)
<i>Nyssa cooperi</i> Chandler	Early Eocene	London Clay, England	Obovoid	9.5	6.3	a few	Broad triangular	1/3	3	Sunken	Chandler (1961)
<i>Nyssa brandoniana</i> (Lesq.) Eyde & Barghoorn	Early Miocene	Brandon, Vermont, USA	Rounded, elliptical, or obovoid	25.0–45.0	18.0–30.0	a few	Tapering to acuminate apex	1/2	1	Sunken, surface nearly smooth	Lesquereux (1861); Eyde & Barghoorn (1963)
<i>Nyssa complanata</i> Lesq.	Early Miocene	Brandon, Vermont, USA	Ovoid or elliptical	5.6–11.8	3.2–8.8	10–15	Triangular	1/2	2–4	Sunken	Eyde & Barghoorn (1963)
<i>Nyssa lescurii</i> (Hitchc.) Perkins	Early Miocene	Brandon, Vermont, USA	Elliptical or ovoid	13.5–24.0	7.0–13.5	10–15	Usually not visible externally	1/2	1–2	Sunken	Hitchcock (1862); Eyde & Barghoorn (1963)

(continued)

TABLE 2. (Continued)

Species	Age	Localities	Endocarp outline	Endocarp length (mm)	Endocarp width (mm)	Endocarp Number of surface ridges	Germination valve shape	Germination valve position*	Locule number	Type of vascular bundle	References
<i>Nyssa eolignitica</i> Berry	Middle Eocene	Western Tennessee, USA	Elliptical to ovoid	14.0–26.0	4.5–12.0	10–15	Usually not visible externally	1/2	2–(3)	Sunken	Berry (1916); Dilcher & McQuade (1967)
<i>Nyssa grayensis</i>	Miocene to Pliocene	North-eastern Tennessee, USA	Fusiform	(21.5–) 25.0–33.3	11.0–15.0	17–20 (-23)	Triangular	1/3–1/2	2–(3)	Sunken	Noll (2013)
<i>Nyssa spatulata</i> (Scott) Manchester	Middle Eocene	Clarno Nut Beds, Oregon, USA	Oblong, ovoid or elliptical	20.1–30.0	12.0–21.5	9	Elliptical	1/2	3	Sunken	Scott (1954); Manchester (1994)
<i>Nyssa scoffii</i> Manchester	Middle Eocene	Clarno Nut Beds, Oregon, USA	Fusiform in lateral view	12.6–16.5	6.1–9.5	~10	Inverted U-shape	1/3	3	Sunken	Manchester (1994)
<i>Nyssa pachycarpa</i> Miki	Pliocene	Honshu, Japan	Ovoid or oblong	10.0–20.0	10.0–20.0	~10	Triangular	~1/2	2	Sunken	Miki (1956)

*The proportion of germination valve relative to total length of endocarp.

are similar to those of *N. nanningensis* in size range, but differ in having mostly ovoid or elliptical outlines, 10–15 rounded longitudinal external ridges with remains of vascular bundles in grooves, and 2–4 locules with triangular valves confined to the apical half of the endocarp (Eyde & Barghoorn 1963). Endocarp walls in *N. complanata* are composed of a single inner layer of longitudinal fibres surrounded by a narrow layer of circumlocular fibres, and an outer region of aggregated fibres running in different directions (Eyde & Barghoorn 1963). Another species, *N. curta* Perkins, from the Miocene of Vermont (Perkins 1904) and the Eocene of Tennessee (Berry 1930) was later included in *N. complanata* (Eyde & Barghoorn 1963; Eyde 1997). It should be noted that both of these species from the Miocene of Vermont and the Eocene of Tennessee were recently transferred to the fossil genus *Carpolithus* L. as *C. complanata* (Lesq.) Wang, Blanchard & Dilcher, based on an impression specimen from the middle Eocene Claiborne Group in western Tennessee (Wang *et al.* 2013).

Endocarps of *N. lescurii* (Hitchc.) Perkins are the only *Nyssa* endocarps collected from the silt deposits overlying the Brandon lignites, whereas those of all other fossil *Nyssa* species from the Miocene of Vermont were found within the lignite layers (Eyde & Barghoorn 1963). *Nyssa lescurii* differs from *N. nanningensis* in having elliptical endocarps, 13.5–24.0 mm long by 7.0–13.5 mm wide, usually circular in cross section, with 10–15 rounded regular ridges. The external endocarp surface is horizontally wrinkled (Hitchcock 1862). Both unilocular and bilocular forms are common in this species. The germination valves are not usually visible externally. The characteristic feature of this species is a conical projection in the apical region interpreted as a styler remnant and a calyx rim. Endocarp walls are thick (often up to 3 mm); several layers of longitudinal fibres line the locules and the fibrous tissue has a very dense appearance (Hitchcock 1862; Eyde & Barghoorn 1963; Noll 2013).

The calyx rim at the apex is also a diagnostic feature of another North American species, the middle Eocene *N. eolignitica* Berry from Puryear and Lawrence clay pits in western Tennessee (Berry 1916; Dilcher & McQuade 1967; Eyde 1997). *Nyssa eolignitica* appears to be closely related to *N. lescurii*, but differs in the larger number of locules (2–3) and their endocarp wall thickness (1–2 mm). Dilcher & McQuade (1967) provided the amended description of *N. eolignitica* and included fossil species *N. wilcoxiana* Berry from the Eocene of Tennessee (Berry 1916, 1930) in the synonymy of *N. eolignitica*. The endocarp impressions of *N. eolignitica* and *N. wilcoxiana* from the Puryear clay pit have recently been assigned to *Palmocarpus wilcoxiana* (Berry) Wang, Blanchard & Dilcher (Wang *et al.* 2013).

'*Nyssa grayensis*' from the Miocene Gray Fossil Site, USA was informally described by Noll (2013) in his

Master's thesis. *Nyssa nanningensis* is readily distinguished from this species in terms of endocarp shape, size, and number of locules. Endocarps of '*Nyssa grayensis*' are fusiform tapering at the apical and basal ends, (21.5–) 25.0–33.3 mm long and 11–15 mm wide, with 17–20 (–23) vascular grooves on the surface. Endocarps possess 2 (–3) locules, each with a triangular valve confined to the apical half of the endocarp. The innermost part of the endocarp wall is composed of many layers of longitudinal fibres, the outer wall layer consists of tangentially arranged fibres, while the wall portion between these layers is composed of randomly arranged fibres (Noll 2013).

Endocarps of *N. scottii* Manchester from the middle Eocene of Clarno, Oregon, USA, is fusiform, roughly circular in cross section, 12.6–16.5 mm long and 6.1–9.5 mm wide, consistently trilobular, and with three inverted U-shaped germination valves restricted to the apical third of the endocarp. Surface ribs are coarse and about the same size as the alternating grooves with sunken vascular bundles. Endocarp walls, 1.2 mm thick, are composed of fibres arranged in swirling groups (Manchester 1994).

Another species from the Eocene of Clarno with trilobular endocarps, *N. spatulata* (Scott) Manchester, possesses larger endocarps, 20.1–30.0 mm long and 12.0–21.5 mm wide, that are oblong, ovoid or ellipsoidal in shape, roughly circular to rounded-triangular in cross section, with nine rounded longitudinal ridges. Germination valves in the apical half of the endocarp are large and elliptical in outline. Locules are C-shaped in cross section (Scott 1954; Manchester 1994).

In contrast to *N. nanningensis*, *N. pachycarpa* Miki from the Pliocene of Japan has ovoid or oblong bilobular endocarps pointed at the apex, are 10–20 mm long by 10–20 mm wide, and with typically 10 ribs on the surface (Miki 1956). The endocarps have an outer layer of transverse fibres and vascular bundles that tend to be grouped in clusters (Noll 2013). The endocarp wall is thicker (often up to 3 mm) than the wall of *N. nanningensis* (0.5–0.9 mm).

Chelebaeva described as *N. lescurii* some endocarps from the upper Eocene of southern Koryak Upland, north-eastern Russia (Gladenkov *et al.* 2005). The impressions of endocarps are large (up to 26–28 mm long and 11–16 mm wide), oblong to elliptical, rounded on both ends or broadly pointed towards the base, with 8–10 vascular bundles running the length of the endocarps from base to apex. The germination valves are not distinctly visible. Anatomical details of the endocarps are unknown due to preservation conditions.

Palaephytogeography of Nyssa

The fossil endocarps described in this study are the first fossil record of *Nyssa* in China, and the first fossil

occurrence of the genus in its current distribution area in Asia. These fossils provide convincing evidence of the presence of *Nyssa* in the low latitudes of East Asia from at least the late Oligocene, and contribute to understanding the potential migration routes of the genus.

As mentioned above, the earliest fossil record of Cornales is from the late Turonian of eastern North America and the early Coniacian of western North America and eastern Asia (Takahashi *et al.* 2002; Atkinson 2016; Atkinson *et al.* 2018, 2019). Phylogenetic analysis places these fossils within the grade of extinct taxa leading to the clade of extant nyssoids in core Cornales (Atkinson 2018). One of the oldest known extinct members of Nyssaceae, *Browniea*, is recorded from the Paleocene of North America. Its morphological similarities with Chinese endemic *Camptotheca* suggests an early vicariance or dispersal event between North America and eastern Asia across Beringia (Manchester & Hickey 2007). This dispersal history of Nyssaceae is also supported by the occurrence of an extinct species of another genus endemic to China, *Davidia antiqua* (Newb.) Manchester, in the Paleocene of both western North America and eastern Asia (Manchester 2002).

The oldest fossil endocarps of *Nyssa* are known from the lower Eocene of Europe (Reid & Chandler 1933; Chandler 1961; Manchester & Collinson 2019) and the middle Eocene of North America (Berry 1930; Scott 1954; Manchester 1994). All these species possess bi- or trilobular endocarps. Zhou *et al.* (2020) considered it likely that the oldest *Nyssa* species from Europe represented the stem lineage of the genus. The fossil record supports the importance of the North Atlantic land bridge for *Nyssa* dispersal during the Eocene. Edible berry-like fruits of *Nyssa* could also have been distributed over long distances by migratory birds and other animals. In Asia, *Nyssa* endocarps do not appear until the Oligocene (Dorofeev 1963). *Nyssa sibirica* from the Oligocene of western Siberia is similar to the Oligocene–Miocene European species *N. disseminata*, which may be evidence of *Nyssa* dispersals within the Eurasian continent. However, the possible occurrence of *Nyssa* endocarps in the upper Eocene of the Koryak Upland (Gladenkov *et al.* 2005) may also indicate a migration of Nyssaceae between Asia and North America during the Eocene. These fossils appear to be related to extant *N. talamancana* based on the external morphology and large size.

Several phylogenetic studies have been conducted to explore the biogeographical history of *Nyssa* and its species relationships (Wen & Stuessy 1993; Wang *et al.* 2012; Zhou *et al.* 2018, 2020). Wen & Stuessy (1993) proposed a European origin for *Nyssa* based on fossil data and cladistic analysis of two disjunct clades, the *N. javanica*–*N. talamancana* clade and the *N. sinensis*–*N. sylvatica* clade. These authors also assumed migration

of the genus from Europe to North America in the early Cenozoic via the North Atlantic land bridge, as well as from Europe to Asia. The species *N. talamancana* from Central America was considered to be an endemic of a formerly widely distributed northern lineage. A recent study by Zhou *et al.* (2020) integrated data from gene sequences, plant morphology, fossils and climate to resolve the phylogeny, biogeography and evolution of ecological niches and morphology of *Nyssa*. This confirmed an early separation of *N. talamancana* from the other living *Nyssa* species supported by its restricted geographical distribution and distinctive reproductive morphology. Based on molecular data, the remaining *Nyssa* species were separated into three lineages: a *N. javanica*–*N. yunnanensis* clade in eastern Asia; a *N. aquatica*–*N. ogeche* clade in eastern North America; and a *N. sinensis*–*N. sylvatica* clade disjunct in eastern Asia and eastern North America. A close relationship between *N. sinensis* and *N. sylvatica* has been recognized in several molecular phylogenetic studies (Wang *et al.* 2012; Zhou *et al.* 2018, 2020), and this is supported by anatomical and morphological evidence (Titman 1949; Eyde 1963; Wen & Stuessy 1993).

The newly established species *N. nanningensis* is morphologically most similar to the fossil species *N. disseminata* and *N. sibirica*. Both these fossil species are related to the extant clade of *N. sinensis*–*N. sylvatica* based on the morphological similarity of their endocarps. The similarity of the Palaeogene species of *Nyssa* from South China to European and Asian fossil species related to the *N. sinensis*–*N. sylvatica* clade is also confirmed by their pollen resemblances. *Nyssa*-type pollen grains described from the middle–upper Eocene of the Changchang Basin, Hainan Island, closely resemble the pollen of extant *N. sinensis* and *Nyssa* pollen from the middle Eocene of Germany, but differ distinctly from the pollen of *Nyssa* sp. obtained from the middle Eocene Princeton Chert in Canada. Younger taxa from the Miocene of Germany and Austria show few similarities in ectexine ornamentation (Hofmann *et al.* 2019). Hence, our fossils and other palaeontological data support the phylogenetic estimates of Zhou *et al.* (2020) that the ancestral range of one of the major Nyssaceae clades, the *N. sinensis*–*N. sylvatica* complex, was most likely to have been widespread across Eurasia in the Palaeogene.

Marked extinctions in the early Oligocene and the late Neogene correlate with global climatic cooling (Zachos *et al.* 2001; Westerhold *et al.* 2020) and the disappearance of the Bering land bridge in the Pliocene (Graham 2018) may have resulted in the East Asia – east North America disjunct distribution of *Nyssa*. The disjunction between *N. sinensis* and *N. sylvatica* complex occurred at approximately 18 Ma, in the Miocene, based on fossil and molecular biological evidence (Zhou *et al.* 2020).

Systematics and comparative morphology of examined fossil fungi and extant taxa

The identification of fossil fungal fruiting bodies is complicated and often controversial. The main difficulty lies in the morphological similarity of some fungal sexual and asexual states, which cannot always be distinguished when presented with incomplete morphology as is often the case for fossil remains. Because no molecular data could be applied to the fossil fungi identification, our approach is based on the analysis of the whole range of available morphological features of *Yongnicta* and comparison with extant taxa that which exhibit similar characteristics.

The new genus *Yongnicta*, established here for the fossil fruiting bodies, is most similar to those of members of the living Sordariomycetes. The fossil fungal remains appear to represent perithecia. Perithecia are flask-shaped structures with a well-defined cavity and peridium, opened by an ostiole. Asci are not preserved well in *Yongnicta*, but some structures interpreted here as a fragment of the asci are visible (Fig. 6C, E). This interpretation is also supported by similarities in the complex of morphological features displayed by *Yongnicta* fruiting bodies and the ascomata of some extant representatives of Sordariomycetes. Somewhat similar fruiting bodies are inherent in Dothideomycetes and some pycnidial anamorphic Ascomycetes, but some features (such as the absence of a stroma, the presence of a peridium with munk pores, as well as the size of fruiting bodies and spores) make the *Yongnicta* fruiting bodies more similar to the perithecia of Sordariomycetes.

One striking feature of *Yongnicta* is the presence of peridial pores, which are known as munk pores (Munk 1953; Carroll & Munk 1964). Munk pores are found between adjacent cells of the ascomata wall. Although the function of munk pores is still unknown, Bianchinotti (2004) suggested that they might serve to transport moisture to the interior of the ascoma and in promoting ascospore release.

Among extant Sordariomycetes, the order Coronophorales is characterized by solitary or grouped superficial ascomata with munk pores on the peridium cell walls (e.g. Nannfeldt 1975; Cannon 1995; Bianchinotti 2004; Huhndorf *et al.* 2004; Mugambi & Huhndorf 2010; Maharachchikumbura *et al.* 2016). Coronophorales includes families Bertiaceae, Ceratostomataceae, Chaetosphaerellaceae, Coronophoraceae, Nitschkiaceae and Scortechiniaceae (Maharachchikumbura *et al.* 2016; Wijayawardene *et al.* 2020). Among them, four families (Bertiaceae, Scortechiniaceae, Nitschkiaceae and Chaetosphaerellaceae) are defined as bearing peridium cells with munk pores. Like *Yongnicta*, Nitschkiaceae and Chaetosphaerellaceae are characterized by uni-septate ascospores, while Scortechiniaceae possess aseptate spores, and among Bertiaceae spores vary from aseptate to multiseptate

(Maharachchikumbura *et al.* 2016). In Nitschkiaceae, *Nitschkia floridana* Fitzp. possesses munk pores on the ascoma wall cells and uni-septate ascospores (Vasilyeva *et al.* 2010). This species originally was described from the eastern USA, but later it was documented from China, Korea, southern India and eastern regions of Russia (Teng 1934; Subramanian & Sekar 1990; Vasilyeva *et al.* 2010).

Originally, munk pores were considered unique to representatives of Coronophorales but they were later also found to occur in a few ascomycete taxa outside this order (e.g. Jensen 1985; Cannon 1995; Bianchinotti 2004; Zhang *et al.* 2006). Munk pores are known in the extant genus *Vialaea* Sacc. of the monotypic family Vialaeaceae (Cannon 1995). Vialaeaceae used to be placed in the order Xylariales, Sordariomycetes (Senanayake *et al.* 2014), but based on molecular data joined the Amphisphaeriales (Wijayawardene *et al.* 2018; Hyde *et al.* 2020). Globose perithecial ascomata with munk pores and uni-septate ascospores are observed in extant *Vialaea mangiferae* Senan. & K.D. Hyde, which is known from northern Thailand (Senanayake *et al.* 2014). One of the principal features delimiting *Vialaea* from *Yongnickta* is the shape of the *Vialaea* ascospores, which are elongated, with two widest points situated towards the apices and an extended central attenuation.

We compared the complex of *Yongnickta* morphological features with those in other extant members of the Amphisphaeriales. The most closely related genus is *Amphisphaeria* Ces. & De Not. (Amphisphaeriaceae). The family Amphisphaeriaceae was originally placed within the order Xylariales (Kang *et al.* 1998; Smith *et al.* 2003; Maharachchikumbura *et al.* 2015) but is now re-assigned to the Amphisphaeriales based on molecular data and divergence time estimations (Senanayake *et al.* 2015; Samarakoon *et al.* 2016; Hongsananan *et al.* 2017; Wijayawardene *et al.* 2018, 2020; Hyde *et al.* 2020). Wang *et al.* (2004) recognized only 12 species within *Amphisphaeria*, but now the genus encompasses 19 species based on morphological and genetic data (Dissanayake *et al.* 2020; Hyde *et al.* 2020). The generic scope has been expanded by synonymizing *Lepteutypa* Petr. under *Amphisphaeria* (Samarakoon *et al.* 2020).

The new genus *Yongnickta* exhibits several morphological characters specific to the extant genus *Amphisphaeria*: dome-shaped ostiolate ascomata with pseudoparenchymatous walls and ellipsoid, fusoid, slightly constricted at the septum, uni-septate ascospores. Among *Amphisphaeria* species, *A. polymorphoides* Teng & S.H. Ou, described from Hainan, China (Wang *et al.* 2004), shows the closest morphological similarity to *Yongnickta nyssae*. This extant species possesses scattered, erumpent to superficial, globose ascomata with a conic-papillate relatively large ostiole, deliquescent asci, and relatively large oblong-fusoid, slightly constricted at the central septum, ascospores that measure 72–80 × 20–24 µm (Wang *et al.* 2004).

Amphisphaeria polymorphoides differs morphologically from *Yongnickta nyssae* only in that it has larger ascospores and has no munk pores on the ascomata walls. Other members of the Amphisphaeriaceae with some morphological peculiarities differing from *A. polymorphoides* are also common in China (Dissanayake *et al.* 2020).

Morphologically, the new genus *Yongnickta* combines features of some Coronophorales and Amphisphaeriales. It is worth mentioning that the most similar extant taxa which have been compared with *Yongnickta* come from the south-east of Asia (*Nitschkia floridana*: China, Korea; *Vialaea mangiferae*: Thailand; *Amphisphaeria polymorphoides*: Hainan, China). A mosaic combination of morphological characters that characterized the new Oligocene genus could testify to a possible affinity for these taxa.

Recently, Wijayawardene *et al.* (2020) provided an outline of the classification of the kingdom Fungi. Since this analysis includes fossil fungi, updated with recent findings and published data, we used it for the comparing the new genus with other fossils. None of the listed fossils exhibit similarity with *Yongnickta*.

Host plants and ecological interpretation of fungi

The fungus *Yongnickta nyssae* was detected on woody *Nyssa* endocarps. Most members of Coronophorales and Amphisphaeriales are saprobic on bark and dead branches being mostly terrestrial wood degraders, and are widespread in temperate, subtropical, and tropical regions (e.g. Hyde *et al.* 1996; Wang *et al.* 2004; Liu *et al.* 2015; Maharachchikumbura *et al.* 2016; Samarakoon *et al.* 2019; Senanayake *et al.* 2019). Many hosts of fungi belonging to these orders are various woody angiosperms and conifers.

According to the Mycoportal (<https://mycoportal.org/portal>) database, more than one hundred species of fungi are associated with the different organs of *Nyssa*. The majority of them are members of the Basidiomycota. Among Ascomycota, fungi that use the different organs of *Nyssa* as a substrate belong to the Sordariomycetes, specifically the orders Xylariales (e.g. *Diatrypella favacea* (Fr.) Ces. & De Not., *Eutypa ludibunda* Sacc., *Biscogniauxia weldenii* (J.D. Rogers) Whalley & Læssøe, *Nemania atropurpurea* (Fr.) Pouzar, *Rosellinia aquila* (Fr.) Ces. & De Not., *Daldinia fissa* Lloyd, *Hypoxylon* spp., *Xylaria* spp.), Boliniales (*Endoxyla avocetta* (Cooke & Ellis) A.I. Romero & Samuels; *Lentomitella cirrhosa* (Pers.) Réblová), Diaporthales (*Cryptodiaporthe paulula* (Cooke & Ellis) Wehm.; *Massariovalsa sudans* (Berk. & M.A. Curtis) Sacc., syn. *Melanconis nyssogena* Ellis & Everh.; *Valsa* spp.), Microascales (*Hunttiella moniliformis* (Hedgc.) Z.W. de Beer, T.A. Duong & M.J. Wingf.), Hypocreales (*Thyronectria cucurbitula* (Tode) Jaklitsch & Voglmayr, syn. *Nectria*

cucurbitula (Tode) Fr.; *Dialonectria episphaeria* (Tode) Cooke, syn. *Cosmospora episphaeria* (Tode) Rossman & Samuels), Coniochaetales (*Coniochaeta sordaria* (Fr.) Petr.), Coronophorales (*Fracchiæa heterogenea* Sacc.), Sordariales (*Lasiosphaeria ovina* (Pers.) Ces. & De Not.), Chaetosphaeriales (*Menispora cobaltina* Sacc, anamorpha), and Amphisphaeriales (*Pestalotia* sp., anamorpha). All of these Sordariomycetes taxa are substantially different from *Yongnickta nyssae*. The main differences are based on the ascomata and ascospore morphology (e.g. presence of a well-developed basal stroma, ascomata with a long neck, aseptate or multiseptate ascospores). Additionally, neither of these taxa are characterized by monk pores on the ascomata cell walls. The anamorpha stages (*Menispora cobaltina* and *Pestalotia* sp.) mentioned above are critically different: the first belongs to the hyphomycetes and the second one possesses an acervula and conidia with bristles.

The association of some Dothideomycetes with different *Nyssa* organs is also evident from Mycoportal (<https://mycoportal.org/portal>). The class Dothideomycetes encompasses a highly diverse group of fungi that has been reviewed comprehensively (e.g. Hyde *et al.* 2013; Maharachchikumbura *et al.* 2016; Dong *et al.* 2020; Hongsanan *et al.* 2020a, b; Hyde *et al.* 2020). Many members of Dothideomycetes are saprobic in various habitats worldwide, being the important decomposers of woody plant organs. According to Mycoportal, members of the orders Asterinales (*Asterotomella erysiphoides* (Kalchbr. & Cooke) Bat. & Cif.), Botryosphaeriales (*Botryosphaeria stevensii* Shoemaker, *Phyllosticta* spp., anamorpha), Capnodiales (*Mycosphaerella* spp.), Dothideales (*Otthia* sp.), Patellariales (*Rhizodiscina lignyota* (Fr.) Hafellner), Pleosporales (*Herpotrichia diffusa* (Cooke) Ellis & Everh.), Tubeufiales (*Berkleasmiium concinnum* (Berk.) S. Hughes) and Kirschsteinietheliales (*Kirschsteiniethelia atra* (Corda) D. Hawksw.) prefer *Nyssa* as substrates. Only *Kirschsteiniethelia atra*, *Herpotrichia diffusa*, *Mycosphaerella* and *Otthia* species possess uni-loculate ascostromata, in some details similar to perithecia, and two-celled ascospores. Nevertheless, all these fungi differ morphologically from *Yongnickta* in detail, for example, in having ascomata with appanate bases (*Kirschsteiniethelia atra*), ascomata with long flexuous hyphae (*Herpotrichia diffusa*) and less prominent ostioles (*Mycosphaerella* and *Otthia*). Moreover, these species lack monk pores on the peridium cells.

A few features (e.g. superficial fruiting bodies, uni-septate spores) occur in some Dothideomycetes taxa, while the combined characteristic morphological features of the new genus *Yongnickta* (superficial ostiolate fruiting bodies with a papillate central pore, monk pores on the wall cells, and uni-septate spores) do not occur in any of them. Additionally, many of them prefer other ecological niches.

Of the 113 endocarps of *Nyssa* examined, only 3 (about 3%) were affected by *Yongnickta nyssae*. Such low frequency of fruit damage probably indicates only occasional fungal attack on fruits lacking mesocarps. The juicy mesocarps of *Nyssa* are not a favourable substrate for saprobic fungi, which tend to invade woody surfaces. The fleshy drupes of *Nyssa* are eaten by birds, bears and small mammals (Les 2018), and thus endocarps may be released from the mesocarps through feeding activities and then become available to wood-destroying fungi. Fruits falling after maturation, and subsequently rotting, also promote endocarp release, but this seems less likely here as only a few fruits of *N. nanningensis* bear fungal damage.

CONCLUSION

The late Oligocene fruits described in this study are assigned to the new species *Nyssa nanningensis* sp. nov., which is related to the *N. sinensis*–*N. sylvatica* clade based on the morphology and anatomy of endocarps. This species is the first fossil evidence of *Nyssa* in the present distribution area of the genus in Asia, and the first fossil record in China. The discovery of this new taxon expands the palaeogeographical distribution of *Nyssa* to the low-latitude regions of East Asia and provides a new datum for tracing the diversification of this genus in the past. Fossil fungal fruiting bodies found on some *Nyssa* endocarps are recognized as a new genus and species, *Yongnickta nyssae* gen. et sp. nov., which is most similar to the extant members of the Coronophorales and Amphisphaeriales (Sordariomycetes, Ascomycota). Taxa with which the new genus is compared are saprobes on decaying wood. We infer that *Yongnickta nyssae*, inhabiting woody endocarps, possessed a similar life strategy.

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DATA ARCHIVING STATEMENT

Data for this study are available in MorphoSource (<https://www.morphosource.org/projects/000366359>) including the x-ray CT image series for specimen NNF116: <https://doi.org/10.17602/M2/M366949>

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