Highlights

- *Cavilignum pratchettii* is a new Neogene angiosperm from eastern Tennessee, U.S.A.

- *Cavilignum* is based on four-chambered fossil endocarps with open germination pores.

- *Cavilignum* cannot be definitively classified within angiosperms.

- *Cavilignum* is the first extinct plant macrofossil genus from Gray Fossil Site.

A suite of fossil endocarps representing a new taxon from the early Pliocene Gray Fossil Site, Tennessee, U.S.A., is described as *Cavilignum pratchettii* gen. et sp. nov. *Cavilignum* is represented by circular to oblong endocarps that have a truncate apex, a mucronate base, and a smooth outer surface. The endocarp wall has three layers. The outermost layer is of uncertain composition. The inner wall structure is fibrous, with an outer layer of radially-oriented fibers and an inner layer of circumferentially-oriented fibers. The endocarps typically have four chambers (locules) divided by thick septa; two narrow canals penetrate the septa from the apex to the base of each endocarp. The locules are open apically. Because no evidence of structures that may have sealed the chambers was found, *Cavilignum* is interpreted as having open germination pores. Apically-oriented, open germination pores most obviously suggest an affinity with the angiosperm family Symplocaceae, but endocarps of Symplocaceae differ from *Cavilignum* in several critical characteristics (e.g., wall histology, presence of a basal pit). While several other groups (e.g., Anacardiaceae, Cornales) produce drupaceous fruits with endocarps comparable in some characteristics to those of *Cavilignum*, none is structurally congruent enough to suggest an affinity with the new fossil genus. Thus, *Cavilignum* cannot be conclusively assigned to a known extinct or extant angiosperm genus or family. *Cavilignum* is the first extinct plant genus described from the Gray Fossil Site macroflora.

Keywords: angiosperm, fossil, endocarp, Gray Fossil Site, Neogene, Pliocene

Cavilignum pratchettii gen. et sp. nov., a novel type of fossil endocarp with open locules from the Neogene Gray Fossil Site, Tennessee, USA

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1. Introduction

The Neogene is a time of transition, when the relatively warm world of the early to middle Miocene gave way to a world shaped by global cooling in the late Miocene to Pliocene, eventually culminating in the widespread northern hemisphere glaciations of the Pleistocene (e.g., Tiffney, 1985; Tiffney and Manchester, 2001; Zachos et al., 2001; Milne, 2006). These changes helped to shape the flora of eastern North America, with certain genera identified from Neogene macrofossil floras—such as *Paliurus* Mill. (Lott et al., 2019), *Pterocarya* Kunth (McCartan et al., 1990), *Sargentodoxa* Rehder & E.H.Wilson (Tiffney, 1993; McNair et al., 2019), and *Sinomenium* Diels (Liu and Jacques, 2010)—disappearing from the region prior to the present day. Our understanding of plant taxonomic richness and extinction in eastern North America from the Neogene to the present is hampered by the sparseness of the known plant macrofossil record (Fig. 1; Tiffney and Manchester, 2001; Corbett, 2004; Stults et al., 2010; Stults and Axsmith, 2011a, 2015; Lott et al., 2019). The distribution of Neogene floras in this region is also highly uneven, with the greatest concentration of material across space and time occurring in the Gulf Coast states, in a band of the Neogene formations extending from eastern Texas to the Florida panhandle. Among these floras, Alum Bluff, Citronelle, and Hattiesburg are the best documented (Fig. 1; Berry, 1916a, b, c; Corbett, 2004; Stults et al., 2010; Stults and Axsmith 2011a, b, 2015; Dockery and Thompson, 2016; Lott et al., 2019; McNair et al., 2019). Outside of the Gulf Coast region, the early Miocene Brandon Lignite flora of Vermont is the most thoroughly studied (see Tiffney, 1994, and references therein; Haggard and Tiffney 1997; Tiffney et al., 2018), whereas formal systematic treatments are lacking for many macrofossil taxa (e.g., *Potentilla* L., *Pterocarya*, *Trapa* L.) preliminarily identified from some other important floras (e.g., Brandywine, Pipe Creek Sinkhole: McCartan et al., 1990; Farlow et al., 2001).

The Pliocene Gray Fossil Site (GFS), eastern Tennessee, U.S.A., is an isolated Neogene paleobiota from the Appalachian region (Fig. 1) that provides data critical for understanding the evolution of eastern North American vegetation during this time of climatic and environmental transition. GFS is interpreted as an ancient sinkhole deposit preserving a paleobiota that is especially rich in fossil vertebrates, but that also includes abundant and diverse plant microfossil and macrofossil remains (e.g., Parmalee et al., 2002; Wallace and Wang, 2004; Mead et al., 2012; Bourque and Schubert 2015; Ochoa et al., 2016). The GFS macrofossil flora includes wood, fruits, seeds, and leaves. Over thirty genera of plants are thought to be represented in the GFS macroflora (Mead et al., 2012; Ochoa et al., 2016), although only a subset have been described (Gong et al., 2010; Liu and Jacques, 2010; Brandon, 2013; Noll, 2013; Huang et al., 2014, 2015). The described taxa have all been assigned to extant plant genera and show strongest affinities to taxa from Laurasian continents, especially those found in the modern and Cenozoic fossil floras of North America and Asia, as well as the Cenozoic flora of Europe (Gong et al., 2010; Liu and Jacques, 2010; Brandon, 2013; Noll, 2013; Huang et al., 2014, 2015). Angiosperms described from GFS fruit and seed fossils include extinct species of Chinese moonseed (*Sinomenium macrocarpum* Liu & Jacques: Liu and Jacques, 2010), bladdernut (*Staphylea levisemia* Huang et al.: Huang et al., 2015), hickory (*Carya tennesseensis* Huang et al.: Huang et al., 2014), tupelo (*Nyssa* L., sp. nov.: Noll, 2013), and grapes (*Vitis* L., 3 species: Gong et al., 2010).

In this study, we describe a new genus and species of angiosperm from GFS represented by fossil endocarps. These endocarps are unusual in having four, or less commonly three, open locules. While the endocarps share features with endocarps of some modern flowering plant groups, most notably Symplocaceae Desf. (Ericales) and certain Anacardiaceae R.Br. (Sapindales), they also differ in critical ways that exclude them from these families. Thus, their affinities are unclear, and we interpret them as representing an extinct Pliocene element of the flora.

2. Methods

2.1. Context of the flora

Gray Fossil Site was discovered during road construction in the year 2000 and covers up to about 3 ha of land (Parmalee et al., 2002). Although initially macrofossil-bearing sediments at the site were estimated to be late Miocene to early Pliocene in age (Hemphillian, 4.5–7 million years old) (Paramlee et al. 2002; Wallace and Wang, 2004), a more recent assessment by Samuels et al. (2018) has narrowed the age range of the sediments to the early Pliocene (Blancan, 4.5–4.9 million years old). Many vertebrate fossils have been uncovered at GFS, including a mixture of extinct animals, groups extirpated from eastern North America but still present elsewhere, and genera still native to the region; the fauna includes fish, amphibians, reptiles, birds, and mammals such as bats (*Eptesicus* Rafinesque), tapirs (*Tapirus* Brünnich), extinct North American camels (cf. *Megatylopus* Matthew & Cook), red pandas (*Pristinailurus bristoli* Wallace & Wang), wolverines (*Gulo sudorus* Samuels et al.), and mastodons (e.g., Parmalee et al., 2002; Wallace and Wang, 2004; Hulbert et al., 2009; Boardman and Schubert 2011; Mead et al., 2012; Bourque and Schubert, 2015; Czaplewski, 2017; Jasinski and Moscato, 2017; Doughty et al., 2018; Samuels et al., 2018, 2019).

The Pliocene climate at GFS is interpreted as somewhat warmer with less seasonal temperature variation than the modern climate of Gray, Tennessee (Shunk et al., 2006; Mead et al., 2012; Noll, 2013; Baumgartner, 2014; Simpson and Mickle, 2019). The site was inhabited by cold-intolerant vertebrates like *Alligator* Cuvier and beaded lizards (Shunk et al., 2006; Mead et al., 2012), as well as tropical to warm temperate plant genera such as *Taxodium* Rich. (Brandon, 2013; Noll, 2013), *Corylopsis* Siebold & Zucc. (Ochoa et al., 2016; Quirk and Hermsen, unpublished data), *Nyssa* (Noll, 2013), and *Sinomenium* (Liu and Jacques, 2010). Evidence from isotopes, palynomorphs, wood, the carpofossil flora, and the fauna suggests that the environment surrounding the GFS sinkhole was wooded (e.g., Wallace and Wang, 2004; Shunk et al., 2006, 2009; DeSantis and Wallace, 2008; Ochoa et al., 2012), although interpretations of tree density vary. DeSantis and Wallace (2008) interpreted the local habitat as a “moderately dense” forest based on carbon isotope data from grazing animals, whereas Ochoa et al. (2012, 2016) interpreted the environment as more open (woodland to savanna) and subject to disturbance based on the composition of the flora, the presence of large herbivores, and indicators of drought (wood with false growth rings, sedimentology) and fire (occurrence of charcoal, perylene, and the bamboo genus *Arundinaria* Michx.). The taxonomic composition and frequency distribution of the palynomorphs recovered from the GFS sediments indicates that the dominant tree types were oak (*Quercus* L.) and hickory (*Carya* Nutt.), with pine (*Pinus* L.) also common (Wallace and Wang, 2004; Ochoa et al., 2012; Worobiec et al., 2013).

2.2. *Fossil specimens*

Excavations at the site are ongoing. Fruits and seeds are collected from GFS as part of bulk sediment samples. To separate the fossils from the surrounding sediments, GFS staff and volunteers wet-screen the sediments, after which the screened material is dried; screened and dried fossils are then picked under dissecting microscopes.

Many specimens of the type of endocarp described for this study have been recovered from GFS. Of these, many exhibit various degrees of compression; some were also incomplete, brittle, cracked, or deteriorated at the time of study. The description herein is based on 35 specimens that were complete or nearly complete, although they may have experienced compression or cracking; three specimens that were sectioned transversely by previous investigators; and two additional specimens that appear to have broken longitudinally on their own (specimen numbers are given below in the “Systematic Paleontology” section). All fossil material examined for this study is permanently held at the East Tennessee State University Museum of Natural History (ETMNH) collections, Gray Fossil Site, Gray, Tennessee, U.S.A.

2.3. Imaging & measurements

Fossil endocarps were studied using a Nikon SMZ1500 stereomicroscope with a Nikon Digital Sight DS-Fi2 camera head and a Nikon SMZ18 stereomicroscope with a Nikon DS-Ri2 camera. Images were captured and measurements taken using NIS-Elements software (1991–2018, Laboratory Imaging); ImageJ was also used for measurements (Rasband 1997–2018). A micro-computed tomography (micro-CT) scan of three specimens (ETMNH 18139, 18148, and 19561) was performed at Ohio University using a TriFoil Imaging eXplore CT 120 Small Animal X-Ray CT Scanner (see associated Research Data). The specimens were placed in a row end-to-end and scanned in a single session. Micro-CT scans were examined using MicroView software (2011–2018, Parallax Innovations), and selected slices were saved as TIFF files to illustrate the internal structure of the endocarps. Adobe Photoshop CC (1990–2018, Adobe) was used to reorient (rotate or flip) saved slices and construct plates. The brightness or levels on some photomicrographs were adjusted in Photoshop.

3. Systematic Paleontology

Class: Magnoliopsida (angiosperms)
Order: Unknown
Family: Unknown
Genus: *Cavilignum* Siegert & Hermsen, gen. nov.

Generic diagnosis: Endocarp lignitic, circular to oblong in lateral view, apex truncate, base mucronate, outer surface smooth. Locules three to four, divided by septa oriented perpendicularly to one another; locules open at the endocarp apex and closed at the base. Two small, unbranched canals traversing the full length of the endocarp; canals open apically on the longer septum to either side of the intersection between the septa; canals open basally to either side of the basal mucro. Endocarp wall with an outer layer of unknown composition and two inner fibrous layers; outer layer of fibers radially oriented and inner layer of fibers circumferentially oriented.

Type: *Cavilignum pratchettii* Siegert & Hermsen, sp. nov. (Plates I, II)

Etymology: *Cavilignum* is a compound of the Latin *cavus* and *lignum* meaning "hollow stone" (or hollow fruit pit), referring to the four hollow locules of the endocarps.

Species: *Cavilignum pratchettii* Siegert & Hermsen, sp. nov.

Species diagnosis: As for the genus.

Holotype: ETMNH 18149 (Plate I, 1, 9). Held at the East Tennessee State University Museum of Natural History fossil collections, Gray Fossil Site, Gray, Tennessee, U.S.A.

Paratypes: ETMNH 18128–18132, 18134–18146, 18148, 18150 (broken longitudinally), 18151 (sectioned specimen), 18153 (sectioned specimen), 19566 (broken longitudinally), 19557 (sectioned specimen), 19560–19563, 19565, 19569, 19570, 19576, 19578, 19580, 22637–22640, 24514.

Type locality & stratigraphy: All specimens come from the Gray Fossil Site, Gray, Tennessee, USA (36.386° N, 82.498° W). Sediments at GFS are considered Blancan (early Pliocene), 4.5–4.9 Ma (Samuels et al., 2018).

Etymology: The species epithet is named after deceased author Sir Terry Pratchett, who wrote numerous books and plays throughout his career that inspired millions. He taught us how to understand the world and our place in it, which is really what science is about. He told us that, in order to really see the world, you have to "[o]pen your eyes and then open your eyes again" (Pratchett, 2003).

Description: The specimens represent lignitic endocarps that are circular to oblong in lateral view, with a truncate apex, a mucronate base, and a smooth outer surface (Plate I, 1–8). They are 9.4–15.5 mm in length and 8.0–14.2 mm in width, length/width ratio 0.9–1.5. The endocarps are somewhat flattened in cross-section (Plate I, 9–13; Plate II, 1, 2). We interpret the cross-sectional shape as naturally elliptical and greater in width than depth; the elliptical shape is exaggerated in some specimens that show evidence of compression (Plate II, 1). Specimens showing little or no distortion from compression (Plate I, 9–13) measure 5.7–7.6 mm in depth; the ratio of the longer radius (width) to the shorter radius (depth) is 1.5–1.9.

The endocarps typically have four locules (Plate I, 9–12), although sometimes only three fully develop (Plate I, 11, 13; Plate II, 2). The apex of each locule is open, and the openings of the locules are oval in shape (Plate I, 9–11). The locules measure about up to about 2.1 mm x 3.9 mm along the radii. In longitudinal view, the locules are oblong, rounded at the base, truncate apically, and extend nearly the full length of the endocarp (Plate II, 3–6, 11).

The locules are partitioned by two septa oriented perpendicularly to each other (Plate I, 9–13). The longer septum is 0.4–0.8 mm thick, whereas the shorter septum is 0.9–2.8 mm thick. Two narrow canals occur to either side of the intersection between the septa, measuring about 0.2–0.9 mm wide (Plate I, 9–13; Plate II, 2, 7). They extend the full length of the endocarp (Plate II, 10, 11). The canals are open at the apex of the endocarp on the longer septal wall, to either side of the junction between the septa (Plate I, 9–11). At the base, the openings of the canals can be observed on the outer surface of the endocarp on either side of the basal mucro, where they sometimes appear to be slit-like openings (Plate II, 8, 9). The canals may represent the former positions of vascular bundles, although no vascular tissue was observed within them.

The endocarp wall is 1.3–2.7 mm thick. The outermost layer of the endocarp wall has an indistinct composition (Plate II, 12, 14). The inner wall is fibrous, with two distinct fiber orientations in cross section. The outer fibers are radially oriented (Plate I, 12, 13; Plate II, 1, 2, 12–14). The inner fibers are oriented in a direction perpendicular to the outer fibers, roughly circumferential or tangential (Plate II, 12, 14). Amber-colored deposits are present in cracks in the wall of one specimen (Plate II, 14), which may indicate the presence of resin.

4. Discussion

4.1. Structural interpretation of Cavilignum

Cavilignum pratchettii is represented by stony, typically four-chambered structures, each chamber presumably representing a carpel. The chambers are open at one end, here interpreted as the apical end (Plate I, 9–11). The apical openings of the chambers appear to be intrinsic structural features of *Cavilignum* rather than, for example, holes created by foraging animals, because they are consistently present and uniform in appearance. No valves, opercula, or plugs that may once have sealed the chambers have been discovered attached to or in association with the *Cavilignum* structures; there are also no discernable dehiscence scars. Thus, the chambers were likely persistently open rather than pores revealed upon dehiscence, as in a capsule. Because the *Cavilignum pratchettii* structures are dry, stony, four-chambered, and open but lacking a dehiscence mechanism, we are interpreting them as endocarps with open germination pores; it is possible that the pores were once covered by additional layers of the pericarp (e.g., a fleshy mesocarp) that are not preserved.

4.2. Similar endocarps and potential affinities

The presence of three (rare) to four locules, lidless germination pores, and a fibrous endocarp wall are the most obvious characters that distinguish *Cavilignum* from endocarps of other angiosperm taxa and that may provide clues to the affinities of the genus. Specimens here assigned to *Cavilignum pratchettii* are likely the GFS plant macrofossils previously reported to have affinities to Symplocaceae (Noll, 2011; Y. Liu, pers. comm. in table 1 of Ochoa et al., 2016). Symplocaceae include two genera and about 320 species of trees and shrubs present in tropical to warm temperate climates;

extant species are distributed in eastern North America to the Caribbean, Central America, and northern South America in the Western Hemisphere and southern and eastern Asia to eastern Australia in the Eastern Hemisphere (Nooteboom, 1975; Fritsch et al., 2008, 2015; Liu and Qin, 2012). The vast majority of species in the family are included within *Symplocos* Jacq., whereas only two species are assigned to the East Asian genus *Cordyloblaste* Hensch. ex Moritzi (Fritsch et al., 2008). Plants in the family are trees or shrubs that produce drupes with hard or sometimes papery endocarps (see, e.g., Liu and Qin, 2012; Manchester and Fritsch, 2014; Tiffney et al., 2018). Endocarps may have one to five chambers and characteristically have open apical germination pores (Nooteboom, 1975; Mai and Martinetto, 2006; Fritsch et al., 2008; Liu and Qin, 2012). Fossil symplocaceous endocarps are widespread in Cenozoic deposits of the Northern Hemisphere (e.g., Chandler, 1961a, b; Nooteboom, 1975; Mai & Martinetto, 2006; Manchester and Fritsch, 2014; Fritsch et al., 2015; Tiffney et al., 2018).

While endocarps of *Cavilignum* are similar to endocarps of members of the family Symplocaceae in that they have locules that are open apically, they differ in other characteristics. *Symplocos* endocarps are often characterized by the presence of an apical depression in which the germination pores occur; the lip of this depression sometimes exhibits a thickened apical collar or "bulge" (Mai and Martinetto, 2006). *Cavilignum* endocarps show neither depression nor collar (Plate I, 1–11). The base of *Symplocos* endocarps is rounded to tapered with a small central pit (Mai and Martinetto, 2006), whereas *Cavilignum* endocarps are mucronate, i.e., have a short, extended basal point (Plate I, 1–8). *Symplocos* endocarps often have a central canal at the junction of the septa separating the locules (Mai and Martinetto, 2006); *Cavilignum*, in contrast, has dual canals that are offset from the intersection of the septa and that open to either side of the basal point on the outer surface of the endocarp (Plate I, 9–13; Plate II, 7, 8, 9). While the structure of the endocarp or drupe wall of *Symplocos* is somewhat varied (Liu and Qin, 2012; Manchester and Fritsch, 2014; fig. S2 of Fritsch et al., 2015; Tiffney et al., 2018), no illustrated sections of *Symplocos* show a fibrous wall structure similar to that observed in *Cavilignum* (Plate II, 12–14).

Cordyloblaste, with the species *C. henschelii* Mortizi and *C. pendula* (Wight) Alston (Fritsch et al. 2008), is sometimes included in *Symplocos* (Nooteboom, 1975; Wu and Nooteboom, 1996). *Cordyloblaste* endocarps are similar to those of *Cavilignum* in that they lack an apical bulge (Mai and Martinetto, 2006) and have two to five locules (Tiffney et al., 2018). However, *Cordyloblaste* endocarps are circular in cross section (see fig. S2b in Fritsch et al., 2015); the individual locules are small compared to the overall diameter of the endocarp (see fig. S2b in Fritsch et al., 2015) and circular to oval in transverse section (supporting information in Fritsch et al., 2015; Tiffney et al., 2018). Furthermore, the endocarp wall of *Cordyloblaste* is “mottled” and penetrated by a reticulum of “narrow tubes” (Manchester and Fritsch, 2014, p. 72; Fritsch et al., 2015, appendix S3, p. 15; Tiffney et al., 2018, p. 189), quite distinct from the fibrous wall of *Cavilignum* endocarps (Plate II, 12–14).

Another family known for drupaceous fruits with endocarps sharing some similarities with *Cavilignum* is Anacardiaceae R.Br. Anacardiaceae are a diverse group of woody plants found in tropical to temperate climates worldwide (Pell et al., 2011; Weeks et al., 2014); they are well represented in the fossil record, including on the basis of their endocarps (e.g., Chandler, 1961a, b; Tiffney et al., 1994; Herrera et al., 2012;

Rozefelds et al. 2015; Fu et al., 2017). Endocarps of Anacardiaceae can be multiloculate (Pell et al., 2011; Herrera et al., 2018, 2019), like *Cavilignum*. As in *Cavilignum*, anacardiaceous endocarps have fibrous walls, although the orientation of the fibers in anacardiaceous endocarps has been described as “tortuous” (Herrera et al., 2018, 2019). Germination pores in anacardiaceous endocarps, when present, are typically sealed by a plug, valve, or other structure (Herrera et al., 2018); no such structures have been found in the germination pores of *Cavilignum*. Furthermore, even when the germination pores of anacardiaceous endocarps are located near the apical end of the endocarp (as in, e.g., *Sclerocarya* Hochst. and *Choerospondias* B.L.Burtt & A.W.Hill), their apertures are still somewhat lateral in orientation (see Herrera et al., 2018). The germination pores of *Cavilignum* are truly apical with no lateral deflection (Plate I, 9–11). Finally, endocarps of Anacardiaceae often have pitted, textured, or sculptured surfaces and/or internal lacunae (Herrera et al., 2018, 2019), none of which are observed in *Cavilignum* (Plate I, 1–8, 12, 13; Plate II, 1–5, 6, 10, 11).

Other endocarps comparable to those of *Cavilignum* are found in Cornales, Humiriaceae A.Juss., and *Vitex* L. Cornalean endocarps are similar to *Cavilignum* endocarps in that they can have several locules and a smooth surface; however, cornalean endocarps open by germination valves (Atkinson et al., 2016, 2017; Manchester and Collinson, 2019). Endocarps of Humiriaceae, which may have apical foramina (depressions), have germination valves; some also have a lacunose wall that appears spongiform in transverse section (Herrera et al. 2010, 2014). *Vitex* (Verbenaceae J. St.-Hil.) has a four-chambered endocarp, although the endocarp is strongly obovoid, has operculate germination pores, and has a single, central channel for the vascular tissue (Godley, 1971). No other families of angiosperms produce endocarps that are particularly comparable to those assigned to *Cavilignum.*

4.3. Conclusions

The combination of smooth outer surface, four (sometimes three) locules, truncate apex, basal mucro, open and apical germination pores, two small canals penetrating the septa that are open apically and basally, and fibrous wall histology distinguish the new genus *Cavilignum* from endocarps of other angiosperm taxa, both living and extinct. While the locule number and open, apical germination pores are similar to those of members of Symplocaceae, the fibrous wall structure, two small canals that open to the outside of the endocarp basally, and the presence of a basal mucro rather than a basal pit preclude assignment to that family. Endocarps from other families investigated also show critical differences from *Cavilignum*. Thus, the affinities of the endocarps remain unresolved. Angiosperm taxa previously described from Gray Fossil Site have all been assigned to extant genera and support a biogeographic interpretation of a Pliocene flora with strong connections to fossil and modern Eurasian and North American floras. *Cavilignum* is the first report of a new genus of angiosperms from the Gray Fossil Site macroflora, and it suggests the presence of an extinct Pliocene element in the flora.

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Plate captions

Figure 1. Locations of major Neogene macrofossil floras in eastern North America discussed in the text. For a review of Miocene localities, see Lott et al. (2019). **Miocene**: 1. Brandon Lignite, early Miocene, Vermont (Tiffney, 1994); 2. Alum Bluff, middle Miocene, Florida (Berry, 1916a; Corbett, 2004; Jarzen et al., 2010; Lott et al., 2019); 3. Hattiesburg, middle Miocene, Mississippi (McNair et al., 2019); 4. Brandywine, late Miocene, Maryland (McCartan et al. 1990). **Pliocene:** 5. Gray Fossil Site, early Pliocene, Tennessee; 6. Pipe Creek Sinkhole, early Pliocene, Indiana (Farlow et al., 2001); 7. Citronelle, late Pliocene, Alabama and Florida (Berry, 1916b; Stults et al., 2010; Stults and Axsmith, 2011a, b; 2015). Point map created with SimpleMappr (Shorthouse, 2010).

Plate I. *Cavilignum pratchettii* C. Siegert & Hermsen, gen. et sp. nov. All scale bars = 2 mm.

1–8. Endocarps in lateral view, showing variation in size, shape, and prominence of the basal mucro. Longitudinal cracks or splits visible on some specimens are interpreted as artifacts rather than intrinsic structural features. 1. ETMNH 18149 (holotype). 2. ETMNH 18132. 3. ETMNH 18139 4. ETMNH 18128. 5. ETMNH 19562. 6. ETMNH 18143. 7. ETMNH 18142. 8. ETMNH 18148.

9–11. Apical view of endocarps, showing open locules. 9. ETMNH 18149 (holotype). 10. ETMNH 18151. 11. ETMNH 19561.

12–13. Transverse sections of endocarps, showing locules, fibrous wall structure, and central canals. 12. ETMNH 18151. 13. ETMNH 18153.

Plate II. *Cavilignum pratchettii* C. Siegert & Hermsen, gen. et sp. nov. Structural details of the endocarps. Figures 1–5, 11, are virtual slices from micro-CT scans. Scale bars: 6, 7, 12–14 = 1 mm; 8–10 = 2 mm.

1. Transverse section of endocarp showing collapsed locules. ETMNH 18148.

2. Transverse section of endocarp showing three well-developed locules (A, B, C), and a central canal (Ca, arrow); second canal obscured by crack in septum between locules A and B. ETMNH 19561.

3. Longitudinal section of endocarp showing two oblong locules with portions of the collapsed septa near their apices (upper two locules in 1). ETMNH 18148.

4. Longitudinal section of endocarp showing two locules corresponding to A and B in 2. ETMNH 19561.

5. Longitudinal section of endocarp perpendicular to section in 4, showing two locules corresponding to B and C in 2. ETMNH 19561.

6. Endocarp, broken longitudinally, showing two locules. ETMNH 19566.

7. Transverse section of an endocarp at the junction of the septa, showing two canals. ETMNH 18151.

8. Base of sectioned endocarp, showing two canals opening to the outside. ETMNH 18151.

9. Base of sectioned endocarp, showing two canals opening to the outside. ETMNH 19557.

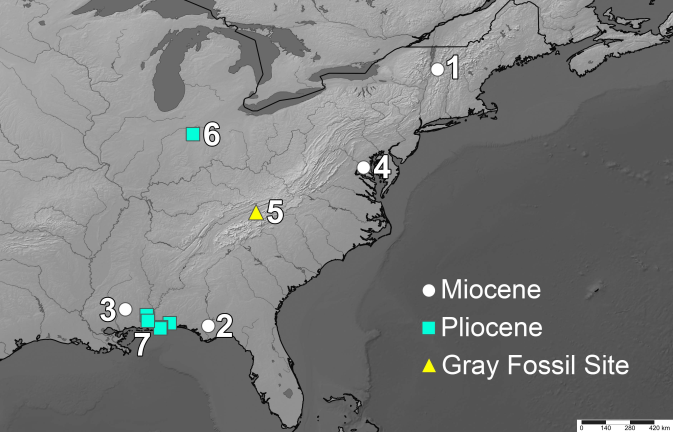
10. Endocarp, broken longitudinally, showing the length of one of the central canals. ETMNH 18150.

11. Longitudinal section of endocarp (perpendicular to section in 4, parallel to section in 5) showing one locule (corresponding to B in 2) and one central canal (corresponding to canal in 2). ETMNH 19561.

12. Transverse section of an endocarp showing the fibrous endocarp wall. ETMNH 18151.

13. Endocarp, broken longitudinally, showing fibrous wall. ETMNH 18150.

14. Transverse section showing cracks in the endocarp wall with amber-colored substance. ETMNH 18151.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● Miocene
■ Pliocene
▲ Gray Fossil Site
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280
420 km

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