Two new species of *Symplocos* based on endocarps from the early Miocene Brandon Lignite of Vermont, USA

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ABSTRACT. We describe two new species of *Symplocos* (Symplocaceae) from the early Miocene Brandon Lignite Flora of Vermont, USA. The endocarps of *Symplocos laevigata* (Lesq.) comb. nov. are most similar in morphology and anatomy to those of the extant species *S. tinctoria* of southeastern North America and *S. wikstroemiifolia* of eastern Asia, both of *S.* sect. *Hopea*, and to those of several species of *S.* sect. *Lodhra*, endemic to eastern Asia; they are also somewhat similar to those of *S. minutula* of the Tertiary of Europe. The endocarps of *Symplocos hitchcockii* sp. nov. are most similar in morphology and anatomy to those of living members of *S.* sect. *Lodhra*, and are also somewhat similar to fossil *S. incurva* of the Tertiary of Europe. This report extends the fossil record of *Symplocos* endocarps to eastern North America and underscores the mixed mesophytic to subtropical nature of the Brandon flora.

KEYWORDS: *Symplocos*, Symplocaceae, endocarps, early Miocene, Brandon Lignite, Vermont, USA

INTRODUCTION

The Brandon Lignite flora of Forestdale, Rutland County, Vermont (43°50′N, 73°03′W) provides one of the few windows into the Neogene vegetation of northeastern North America (Graham 1999, Ochoa et al. 2012, Baumgartner 2014). It was first noted by Edward Hitchcock (1853), and the fruits and seeds were initially described by Leo Lesquereux (1861a, b). They were again studied in the early 1900s by the state geologist of Vermont, George Perkins (1904, 1906), resulting in a proliferation of new genera and species, now recognized to represent variations within a far more limited diversity of taxa. A detailed re-investigation of the flora was initiated by Elso Barghoorn in the late 1940s, resulting in descriptions of the woods (Spackman 1949) and

palynoflora (Traverse 1955), as well as examinations of fruits and seeds of the Nyssaceae (Eyde & Barghoorn 1963) and Alangiaceae (Eyde et al. 1969). In subsequent research, fruits and seeds were described representing the Alismataceae, Illiciaceae, Lythraceae, Magnoliaceae, Rutaceae, Sargentodoxaceae, Staphyleaceae and Vitaceae (Tiffney & Barghoorn 1976, 1979, Tiffney 1977a, b, 1979, 1980, 1981, 1993, Haggard & Tiffney 1997). The known flora is dominated by mixed mesophytic forest elements, several of which have been extirpated from North America but persist in eastern Asia.

Symplocos Jacq. (Ericales: Symplocaceae) was first recognized in the Brandon flora from pollen (Traverse 1955). Tiffney (1977a) identified two separate fruit morphologies as belonging to the genus, but these were

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neither described in detail nor formally named, although Mai (1986) illustrated and commented on them. The nomenclature of these and other Brandon fossils was complicated because the pioneering investigators applied multiple specific and generic names to what was ultimately the same species. Further, the Brandon fossils were illustrated by drawings (Lesquereux 1861b), and their descriptions often involved only the external morphology, with no information on internal structure or anatomy. Additionally, many of the type specimens were difficult to locate.

Extant *Symplocos* comprises about 350 living species of trees and shrubs, distributed from India through Southeast Asia and Malesia to northeastern Australia, as well as in the Americas, where they are mostly restricted to the Neotropics (Nooteboom 1975, Fritsch et al. 2008). During the Tertiary, *Symplocos* was common and widely distributed in Europe (e.g. Mai & Martinetto 2006). Endocarps of the genus have been reported from Tertiary sites in North America (Tiffney 1977a, Doyle et al. 1988, Manchester 1994). Reports of fossil leaves (e.g. Chaney & Sanborn 1933, MacGinitie 1969) are difficult to confirm because of their similarity to those of other ericalean genera.

The classification of extant Symplocaceae has been updated through phylogenetic analyses based on morphological characters and DNA sequence data (Fritsch et al. 2008). This classification, accommodating the genera *Symplocos* and *Cordyloblaste* Henschel ex Moritzi, and including two subgenera, three sections, and two series within *Symplocos*, has provided a framework for the evaluation of fossil representatives of the family. Fruit morphology and anatomy provide additional characters that help to circumscribe clades resolved by DNA. Hence, fossil fruits can provide information relevant for the phylogenetic placement of extinct species and facilitate the study of biogeographic patterns through time.

The Brandon fossil fruits are well preserved, with anatomical features of endocarp, mesocarp and exocarp intact, facilitating detailed comparison with extant members of the Symplocaceae. On this basis, we describe two species of *Symplocos* from the Brandon Lignite, evaluate their phylogenetic position in relation to extant species, and consider their biogeographic implications. Of particular interest is whether these fossils are more closely related to extant North American, South American, or Old World species.

STRATIGRAPHY

The Brandon flora occurs within lignite and associated variegated clays situated in an elongate, narrow, kaolin-filled cleft between two resistant Cambrian rocks: the Dunham Dolomite and Cheshire Quartzite. The full extent of the deposit is uncertain, but underground mining in the late 19th and early 20th centuries suggests that it is ca 60 m deep, ca 100 m across and ca 1–2 km long. During the Pleistocene glaciation, much of the fossil-bearing deposit was eroded away, but portions of the lignite and associated clays were forced into the kaolin by the overriding ice, protecting the fossils. No other rocks of Cenozoic age occur in proximity, and there is no basis for radiometric dating; thus, the age of the sediments is based entirely on biostratigraphy. Tiffney (1994), reviewing the carpological flora, and Traverse (1994), reviewing the palynological evidence, both independently and jointly (Tiffney & Traverse 1994) suggested an early Miocene age for the flora, with Traverse (1994) suggesting more specifically a middle early Miocene age: ca 18 to 20 Ma.

MATERIALS AND METHODS

The deposit is generally covered by Pleistocene and Holocene sediments, and was mined locally for coal in the middle 1800s. The mining revealed the material described by Lesquereux (1861a, b). It was again mined for paper clay and pigmented clays in the late 1800s through 1920s, providing Perkins with material. The precise derivation of these early fossils within the deposit is unclear, as many came from underground workings. A small area of sediment near the surface was uncovered with the use of heavy equipment in the late 1940s and again in the early 1970s. This revealed a narrow band of lignite and associated dark gray plastic clay. Both were distorted and clearly not in the original position, presumably having been deformed by the passage of Pleistocene ice. The two separate units reflect distinct environments and have yielded slightly different floras, although with elements in common. Collection involved taking large masses of the lignite and the clay and breaking them by hand to seek fossils; the clay was also broken down in a mild base and sieved for smaller specimens (Tiffney 1990).

The sectioned fossil materials were prepared by Richard Eyde and Bruce Tiffney by dehydrating in

ethanol and embedding in celloidin (Johansen 1940) prior to sectioning with a Bausch & Lomb sliding microtome (# 10164) in sections 20 to 40 μm thick, and were visualized by transmitted light. Several fossils, including the type material, were examined with x-ray microCT scanning technology, using a GE Phoenix V|tome|xm240 CT Scanner at the University of Florida College of Engineering Nanoscale Research Facility, with a tungsten reflection target. Reconstructed tiff stacks were processed with Avizo 9.0 lite software to obtain isosurface renderings and virtual slices.

We examined fruits of 198 living species represented by more than 420 collections of the herbaria of Naturalis Biodiversity Centre-Leiden (L), the Field Museum (F), the California Academy of Sciences (CAS and DS) and Harvard University (A and GH). They were sectioned transversely with a diamond-bladed annular saw and photographed to record internal morphology and anatomy by reflected light. Fruits from the same collections were boiled to soften them, and outer tissues removed to expose the endocarp surface features. For additional anatomical characters, fruits of selected specimens were then either sectioned with a sliding microtome or embedded in epoxy and ground to 30-μm thickness for transmitted light microscopy.

Fossil specimens cited are deposited in the Harvard University Museum Paleobotanical Collection (HUMP) and the Smithsonian National Museum of Natural History (USNM).

SYSTEMATIC DESCRIPTIONS

ERICALES Dumort.

SYMPLOCACEAE Desf.

Symplocos Jacq.

Symplocos laevigata (Lesq.) Tiffney, Manchester & P.W.Fritsch, **comb. nov.**

Fig. 1A–U

Basionym. *Nyssa laevigata* Lesq., Lesquereux 1861a, p. 361; Lesquereux 1861b, p. 717, fig. 156 (re-described and illustrated).

Additional prior reports.

1904 *Nyssa laevigata* Lesq., G.Perkins; p. 198, pl. 79, figs 99, 113, 114. (Perkins also identifies fig. 109 as *N. laevigata*, but the illustrated fruit does not appear to be the same as the others).

1977a *Symplocos* species A; Tiffney, pgs 212–213, pl. 16, figs A–C.

1986 *Symplocos* Type 1; Mai, Tafel I, figs 24, 25.

Nomenclatural note. Lesquereux (1861a) provided the first published description of this fossil, but without illustration. Instead, he cited the illustrations that were to be published in the upcoming volume *Report on the Geology of Vermont* (*RGV*; Lesquereux 1861b). The *RGV* was published in two volumes (Hitchcock 1861). The illustrations of several taxa of Brandon fossil fruits and seeds and their captions were published in the first volume (pgs 228–234), and the descriptions (repeated from Lesquereux 1861a) were published as an appendix in the second volume, pages 712–718. In initially describing *Nyssa laevigata*, Lesquereux (1861a, p. 361) cited the figure in which it was to be illustrated in *RGV* volume one as Fig. 156. In his description of *N. laevigata* in *RGV* volume two, page 717, however, he cites the accompanying illustration as Fig. 151. However, it is clear that the *RGV* illustration number should have been 156, as suggested in Lesquereux (1861a).

In the description of *Nyssa laevigata* in both Lesquereux (1861a) and *RGV*, Lesquereux compared this fossil to living *N. multiflora*. However, a detailed (by the standards of the time) description in *RGV* accompanying Fig. 156 (p. 231) accords more with *Symplocos* than with *Nyssa*. Further, in this "caption" Lesquereux specifically compared *N. laevigata* with *Carpolithus minutulus* Sternberg from the Miocene brown coal of Salzhauzen, Germany. Subsequent research by Kirchheimer resulted in the reassignment of *C. minutulus* to *Symplocos minutula* (Sternberg) Kirchh. (Kirchheimer 1949), anticipating the current paper.

Emended description. Fruit ovoid-ellipsoidal to narrowly ellipsoidal, circular to slightly triangular in cross section, 7.8–14.5 (average 10) mm long × 3.1–6.3 (average 4.8) mm in equatorial diameter, length/diameter ratio 2.3–2.5. Exocarp compressed, thin, probably fleshy. Mesocarp tissue (Figs 1L–N, U) 0.3 mm thick, composed of isodiametric to irregularly polygonal cells 25–67 μm in diameter not invading between locules. Endocarp sclerotic, 3-locular; surface finely and deeply striate, with a series of shallow grooves running from apex to base, but unribbed (Figs 1E, J); base with small central pit (Fig. 1I); apex truncate (Figs 1B, E, J, K), opening into a narrow concavity lacking marginal lip, containing three apical pores more or less cuneiform in outline arranged in a triangle, each leading to a locule and separated by 3 shallow to deeply recessed septa; apically exposed portion of septa rounded, lacking median groove; central vascular canal

Fig. 1. Fossil fruits of *Symplocos laevigata* (Lesq.) Tiffney, Manchester & P.W.Fritsch, comb. nov. **A–D**. Lectotype, USNM312122b; **A**. Lateral surface; **B**. Longitudinal section, showing apical aperture, two locules with remains of seed coat, and portions of central vascular canal; **C**, **D**. Transverse sections ca 1/3 (**C**) and 1/2 (**D**) of the distance from apex, showing three locules; **E–G**. Fruit with shorter dimensions, USNM312122c; **E**. Lateral surface; **F**. Longitudinal section, showing two locules and central vascular canal; **G**. Transverse section ca 1/4 of distance from apex; **H–K**. Larger specimen, HUMP65905; **H**, **I**. Apical (**H**) and basal (**I**) surface views; **J**. Lateral surface; **K**. Longitudinal section, showing two locules with remains of seed coat; **L–N**. Successive transverse sections from apex to near base of one fruit, HUMP65907, with portion of adhering mesocarp and exocarp remaining; **O**. Oblique, nearly transverse section in apical 1/3 of endocarp, HUMP65913, showing the three locules; **P–R**. Transverse sections, HUMP65914, in apical 1/3 (**P**, **R**) and basal 1/3 (**Q**); **S**. Longitudinal section of same specimen as O; **T**. Enlargement of seed coat from R, showing outer uniseriate layer of greatly thickened cells, and inner crushed layer; **U**. Pericarp in transverse section, showing endocarp (lower 2/3 of image) and mesocarp, HUMP65914. Scale bars: E, P = 5 mm (applies to A–Q); R, S = 2 mm; T = 50 µm; U = 300 µm. A–D, F–K from microCT scan; E, L–U from transmitted / reflected light

present; endocarp wall composed of sclerenchyma, 0.8–1.0 mm thick (measured near greatest equatorial diameter, from dorsal side of locule to endocarp periphery); fertile locules 1-seeded, longitudinally elongate, irregular in cross section but not consistently circular or cuneiform, one tending to be much larger than the other two at least toward base, the other two sometimes collapsed; septa of more or less equal thickness throughout; septa walls from adjacent carpels completely fused.

Endocarp tissue uniform (Fig. 1U), not mottled by intervening ductwork, composed of sclereids 22–30 μm in diameter close to locule, becoming larger (30–50 μm diameter) in outer portions of inner half of endocarp wall. Outer half of endocarp wall composed of horizontal, radially aligned, elongate sclereids 60–90 × 20–35 μm (Fig. 1U). Sclereid wall thickness 9–11 μm. Idioblasts with rhomboidal crystals rare or absent. Seed elongate, seed coat composed of inner layer of crushed cells and prominent uniseriate outer layer of peculiarly thickened sclereids 40–80 μm in diameter, each with thick inner and anticlinal walls but thin external walls, giving a U-shaped appearance in longitudinal section (Fig. 1T).

L e c t o t y p e. USNM312122b, Fig. 1A–D. The original Fig. 156 of Lesquereux (1861b) depicts three syntype specimens which were archived in a single container in the type collection of USNM under catalog number USNM312122. Clockwise from the top, the specimens in the original drawing are designated a, b and c.

A d d i t i o n a l   s p e c i m e n s. HUMP65907–65914 (thin-sectioned), 66902–65906, 65923–65928, 65941–65947.

R e m a r k s. Our description is based on 68 specimens from the silty facies and 41 from the lignite itself (Tiffney 1977a), in addition to three specimens from Lesquereux's (1861a, b) investigation that appear to be from a silty facies. The fruits from the lignite average 11.5 × 5.0 mm, whereas those from the silt average 10.5 × 4.7 mm, and the range of variation (7.8–14.5 mm long; 3.1–6.3 mm diameter) is similar in the specimens from the two facies.

The morphology and anatomy of the fossils, including the apically truncate endocarp with three germination pores, an endocarp composed of sclereids, and the presence of a central vascular canal, indicate that they belong to the Symplocaceae. *Symplocos laevigata* can be distinguished from *Cordyloblaste* by the carpel number (consistently 3, versus 2–5 within the same species), endocarp truncate at apex (versus conical), with apical pores that are more or less cuneiform in outline (versus narrowly elliptic in outline, or slit-like), and locules irregular in near-equatorial diameter, with septa of more or less equal width throughout (versus more or less regularly circular in cross section and the septa consequently becoming wider at their outer ends). Furthermore, in *Cordyloblaste* the endocarp tissue possesses a distinctive mottled pattern formed by a reticulate ductwork of narrow tubes with red contents intruding the endocarp, whereas the fossils lack such mottling. These characters exclude the fossils from *Cordyloblaste* and are consistent with the fruit characters of *Symplocos*. Kirchheimer (1949, 1957) recognized two extinct symplocaceous genera in the Tertiary of Europe: *Sphenotheca* Kirchh. and *Pallioporia* Kirchh. The former was subsequently merged with *Symplocos* (Manchester & Fritsch 2014). *Pallioporia* has many of the characters of *Symplocos* but is distinguished by pronounced surficial pitting and by having large lacunae in the endocarp wall, unknown in other Symplocaceae. This differs from *S. laevigata*, which lacks these features.

An additional combination of characters can be used to assess the major clade within *Symplocos* to which the *S. laevigata* fossils belong. *Symplocos* is divided into *S.* subg. *Palura* (G.Don) P.W.Fritsch and *S.* subg. *Symplocos*. The latter is divided into three sections: *S.* sect. *Hopea* Benth. & Hook.f. (as corrected nomenclaturally from *S.* sect. *Barberina* A.DC. in Aranha Filho et al. 2010), *S.* sect. *Lodhra* G.Don and *S.* sect. *Symplocos*. *Symplocos* sect. *Symplocos* is divided into two series: *S.* ser. *Urbaniocharis* (Brand) P.W.Fritsch and *S.* ser. *Symplocos* (Fritsch et al. 2008). The fossils can easily be excluded from *S.* subg. *Palura* by their symmetrical endocarps (versus asymmetrical) and completely fused septa (versus not fused, such that the endocarp is separable into pyrenes). The fossils can also be excluded from *S.* ser. *Symplocos* by their lack of endocarp tissue mottling of the same type present in *Cordyloblaste*, which appears to be present in all or most species of *S.* ser. *Symplocos* (e.g. Fig. 3I), and by their irregularly shaped locules in near-equatorial cross section (versus more consistently circular). *Symplocos laevigata* can also be

excluded from *S.* ser. *Urbaniocharis* because this series has smaller fruits with only one or two locules, and the locules are separated by a much thinner (hyaline) septum.

This leaves possible affinity with two sections: *Symplocos* sects. *Lodhra* and *Hopea*. The species of *S.* sect. *Lodhra* exhibit the highest diversity of fruit and endocarp characters of any section, so on the basis of macromorphology it is difficult to exclude the Brandon fossils from this section with certainty. Whereas most species of the section have endocarps with either ribbed endocarp walls or incompletely fused septa, some living species have completely fused septa, as in the fossils (e.g. *S. cerasifolia* Wall., *S. pyrifolia* Wall., *S. sulcata* Kurz; Fig. 3M), and others have unribbed endocarp walls (e.g. *S. celastrifolia* Griff. ex C.B.Clarke, *S. dryophila* C.B.Clarke, *S. macrocarpa* Wight ex C.B.Clarke; Fig. 3N). A few species exhibit the combination of unribbed endocarp walls and completely fused septa (*S. cylindracea* Noot., *S. megalocarpa* H.R.Fletcher), and several have both of these characters and also possess one locule larger than the other two (i.e. *S. glomerata* King ex C.B.Clarke, *S. racemosa* Roxb., *S. verticillifolia* Noot).

The fossils are also similar to two species of *Symplocos* sect. *Hopea*. The species of this section are mainly Neotropical, except for *S. tinctoria* (L.) L'Hér. (eastern United States) and *S. wikstroemiifolia* Hayata (China, Malaysia, Vietnam). Like *S. laevigata*, the species of the section have endocarps with completely fused septa (when visible) and almost always an unribbed wall (slightly ribbed in *S. culminicola* Standl. & Steyerm.). The endocarps of the Neotropical members in the section differ from *S. laevigata* in their consistently one-locular condition as seen in near-equatorial cross section (with the other two locules completely crushed) or, in species with more than one well developed locule, their hyaline septa. The Neotropical species also have an outer endocarp wall distinctly thinner than that of the fossils. In contrast, *S. tinctoria* and *S. wikstroemiifolia* are both similar to the fossils in their wall thickness (Fig. 3C, D, G, H) and, in *S. wikstroemiifolia*, moderately thick (versus hyaline) septa (Fig. 3G, H). However, neither species exhibits the 3-locular condition (i.e. with none of the locules crushed), as can occur in *S. laevigata*: *S. tinctoria* is consistently 1-locular (with the other two crushed),

and *S. wikstroemiifolia* is consistently 2-locular, with one large and one small locule. *Symplocos tinctoria* and *S. wikstroemiifolia* form a clade that is sister to a clade comprising the rest of the section (except for *S. longipes* Lundell, which forms a trichotomy with these two clades; Fritsch et al. 2008). As such, the 3-locular condition of *S. laevigata* could indicate that the fossils lie on the lineage leading to the living clade, because the ancestral states of locule number (i.e. well developed locules) have been reconstructed as either one or three (Fritsch et al. 2008).

Tiffney (1977a) suggested an affinity of these Brandon fossils to *Symplocos tinctoria*. The fossils are indeed similar to *S. tinctoria* in the characters above and also in their radially elongate sclereids in the outer half of the endocarp, an unusual feature in the genus (compare Fig. 1U with Fig. 3E). However, the septum in *S. tinctoria* has sclereids arranged in distinct rows parallel to the septal borders, whereas in *S. laevigata* they are arranged in a more random, nonaligned pattern within the septa. In this respect, the fossil is more similar to the other species of *S.* sect. *Hopea*, including *S. wikstroemiifolia*. *Symplocos tinctoria* endocarps consistently have only one well developed locule. *Symplocos laevigata* often possesses three well developed locules, but sometimes two are smaller than the third or crushed, especially toward the base of the fruit (Fig. 1B, C, D, N, Q, R). In contrast, *S. wikstroemiifolia* consistently has two locules with the third always crushed. The seeds are straight in both the fossil and *S. tinctoria*; they are curved in *S. wikstroemiifolia* (the only curved seeds in *S.* sect. *Hopea*; Nooteboom 1975, Fritsch et al. 2008).

In its general shape and size, surficial morphology (smooth to shallowly grooved), and tendency to have one locule dominant over the others, *Symplocos laevigata* is similar to *S. minutula* of the European late Oligocene to early Pliocene, which Mai and Martinetto (2006) compared to *S. tinctoria*. *Symplocos minutula* has no or only few crystalliferous idioblasts (Kirchheimer 1957, p. 594), as is the case in *S. laevigata*. Mai and Martinetto also compared *S. minutula* with extant *S. ramosissima* Wall. ex G. Don of East Asia (*S.* sect. *Lodhra*), where such idioblasts are also present. We CT-scanned a specimen of *S. minutula* (D.H. Mai 2001-1129 from the Fortuna 9b site, Germany) and found it to be composed entirely

of isodiametric sclereids without the anticlinally aligned cells observed in the peripheral zone of *S. laevigata* endocarps (not shown).

Symplocos hitchcockii Tiffney, Manchester & P.W.Fritsch, **sp. nov.**

Fig. 2A–L

Prior reports.

1977a *Symplocos* species B; Tiffney, pgs 213–215, pl. 16, figs D–F.
1986   *Symplocos* type 2; Mai, Tafel II, figs 14, 15.

Etymology. The epithet recognizes the pioneering work of E. Hitchcock on the Brandon Lignite.

Description. Fruit ellipsoidal to broadly ellipsoidal, circular to broadly ellipsoidal in cross section, 7.0–11.4 (average 9.2) mm long × 4.7–6.9 (average 5.7) mm in equatorial diameter. Exocarp thin. Mesocarp tissue 0.2–0.4 mm thick, composed of isodiametric to irregularly polygonal parenchyma cells 25–55 µm in diameter, invading endocarp in valleys of deeper folds (Fig. 2G), particularly at either end of fruit, and penetrating along middle region of each septum. Endocarp sclerotic, 3-locular, often with equatorial bulge (Fig. 2F) and with slight constriction in diameter just below a distinct, rather smooth, and often inflated apical collar (Fig. 2A–C); surface strongly and unevenly rugose (Fig. 2A, F), the rugosities trending parallel to long axis of fruit and becoming sharply subdued at apical constriction; base with prominent central pit (Fig. 2D); apex truncate, with three apical pores arranged in a triangle (Fig. 2B, C), each leading to a locule and separated by 3 septa; central vascular canal present; endocarp wall composed of sclerenchyma 0.3–0.5 mm thick (measured near equator of fruit); locules 1-seeded, longitudinally elongate, irregular in transverse outline but not consistently circular or cuneiform, all locules more or less well developed; septa of more or less equal width throughout, septa walls from adjacent carpels fused but partially separated by intruded mesocarp tissue.

Endocarp tissue uniform, not mottled by intervening ductwork, composed of isodiametric sclereids 12.5–30 µm in diameter randomly arranged in central part, but tending to be aligned in anticlinal rows near periphery. Idioblasts present, scattered, ca 15–20 µm in diameter, containing solitary rhomboidal crystals (Fig. 2L). Seed anatropous, seed coat composed of inner layer of crushed cells and uniseriate outer layer of peculiarly thickened sclereids 40–60 µm in diameter, each with thick inner and anticlinal walls but thin external walls, giving U-shaped appearance in longitudinal section (Fig. 2K).

Holotype. here designated. HUMP65916 (Fig. 2A–D, G).

Paratypes. HUMP65915, 65917–65921 (thin-sectioned), 65929–65940.

Remarks. This species is known from 28 specimens from the lignite, and possibly one from the silty facies. Again, the apically truncate endocarp with three germination pores, an endocarp composed of sclereids, and the presence of a central vascular canal are distinctive of the Symplocaceae. *Symplocos hitchcockii* can be assigned to *Symplocos* on the same reasoning as for *S. laevigata*. Although the septa are intruded by mesocarp as in *S.* subg. *Palura*, the endocarp is symmetrical, unlike endocarps of this section. The ribbing on the endocarp wall, as well as the consistent presence of three well developed locules, safely excludes these fossils from *S.* sect. *Hopea*. The intrusion of mesocarp into the septal area dividing the three carpels is consistent with *S.* sect. *Lodhra*, as illustrated by *S. anomala* Brand (Figs 3K, L) and *S. macrocarpa* Wight ex C.B.Clarke (Fig. 3N); *S.* subg. *Palura* appears to be the only other clade of the Symplocaceae containing species with intruded mesocarp. The presence of abundant idioblasts is also consistent with *S.* sect. *Lodhra* (Fig. 3P). Idioblasts can occur in *S.* ser. *Urbaniocharis* as well, but this series has fruits with only one or two locules, and the locules are separated by a much thinner (hyaline) septum. The endocarp tissue is formed of sclereids lacking mottling, which, among other characters such as the absence of 4- and 5-locular endocarps, excludes the fossils from *S.* ser. *Symplocos*. Thus, the endocarps of *S. hitchcockii* possess features that strongly favor placement within *S.* sect. *Lodhra*, which is now restricted to Asia but which was also well represented in the Tertiary of Europe (Mai & Martinetto 2006, Manchester & Fritsch 2014, Fritsch et al. 2015).

The inflated apical collar and sharply truncate apex of *Symplocos hitchcockii* are similar to those of *Symplocos incurva* (Kirchh.) Manchester & P.W.Fritsch (recently transferred from *Sphenotheca incurva* Kirchh.; Manchester
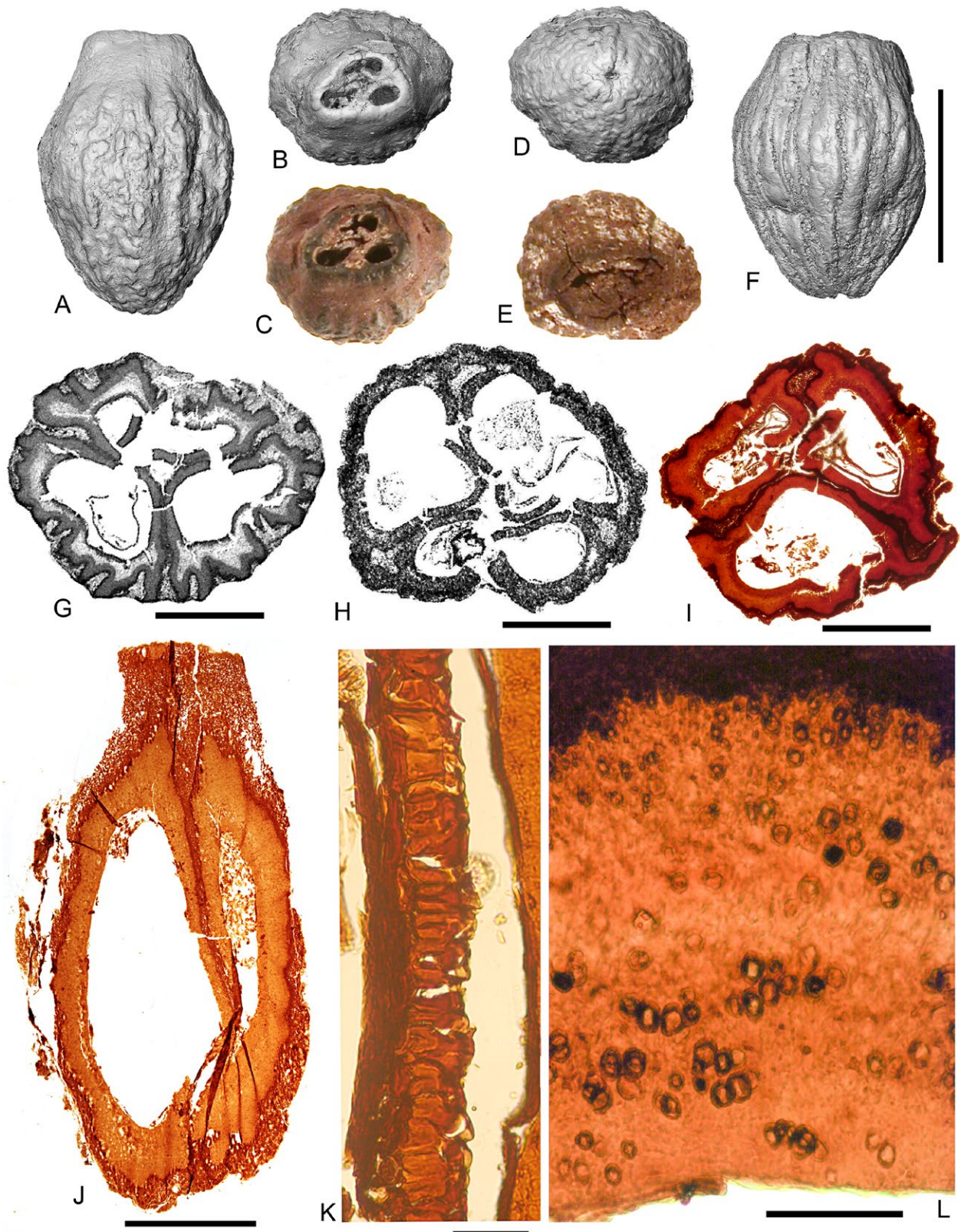
Fig. 2. Fossil fruits of *Symplocos hitchcockii* Tiffney, Manchester & P.W.Fritsch, sp. nov. **A–D**. Holotype, HUMP65916, external surface in lateral (**A**), apical (**B**, **C**) and basal (**D**) view; **E–F**. Another fruit, HUMP65917, in apical (**E**) and lateral (**F**) view; **G**. Transverse section (near middle of fruit) of holotype, HUMP65916; **H**. Transverse section of endocarp (near middle of fruit) from fruit in E–F; **I**. Transverse section of specimen near middle of fruit, showing mesocarp and endocarp, with remains of seeds within locules, and parenchymatous intrusions along midlines of septa, HUMP65921; **J**. Longitudinal section, showing distinction between mesocarp and endocarp, and two of the elongate locules, HUMP65918; **K**. Enlargement of seed coat from J; **L**. Enlargement from H, showing scattered crystalliferous idioblasts within endocarp. Scale bars: F = 5 mm (applies to A–F); G–J = 2 mm; K = 50 µm; L = 100 µm; A, B, D, F, G, H from microCT scan; C, E, I–L from transmitted / reflected light

& Fritsch 2014) from the Miocene of Germany. The endocarps of the latter, however, are larger and appear to lack the rough surface of the Brandon species. Among the fruits and seeds previously published from Brandon, none seem to be clearly representative of *S. hitchcockii*, although Perkins (1904) illustrated *Cinnamomum nova-angliae* Lesq. and *C. corrugatum* G.Perkins (Pl. 79, figs 105, 108), both of which somewhat approximate the shape but do not appear to match precisely. The web site of the Perkins Geology Museum of the University of Vermont illustrates three endocarps (Perkins Museum # 80022) conforming to *S. hitchcockii* (http://www.uvm.edu/perkins/DisplayW.php?fname=PGMFS80022_000). These may represent the specimens Perkins examined.

DISCUSSION

Of the endocarps described here, those of *Symplocos laevigata* occurred in both units and were predominantly from the silt, whereas those of *S. hitchcockii* were predominantly from the lignite but with one possible specimen from the silt. This could be inferred to reflect a difference in the ecology of the two parent plants, with *S. laevigata* perhaps growing adjacent to open water and *S. hitchcockii* having been transported farther, perhaps from a more shaded situation. *Symplocos laevigata* appears to be closest either to species in the extant *S.* sect. *Lodhra* or to the extant clade of *S. tinctoria* of the eastern United States and *S. wikstroemiifolia* of eastern and southeastern Asia (*S.* sect. *Hopea*), and *S. hitchcockii* is most similar to *S.* sect. *Lodhra* of eastern and southeastern Asia, Australia and Oceania.

Traverse (1955) recognized three species of *Symplocos* pollen from the Brandon deposit, which he subsequently transferred to the form genus *Porocolpopollenites* Pflug (Traverse 1994: Pl. 3, figs 12–14). Pollen was infrequent (1–3 grains per thousand) in all cases. *Symplocos scabripollinia* Traverse was compared with *S. tinctoria*, and *S. jacksoniana* Traverse with *S. paniculata* Wall. ex G.Don of the eastern Asian monotypic *S.* subg. *Palura*. Many species of *S.* subg. *Palura*, *S.* sect. *Lodhra* and *S.* sect. *Hopea* are similar in their pollen features, and the fossil pollen *S. jacksoniana* and *S. scabripollinia* both fall within the variation observed in these clades (van der Meijden 1970, Nagamasu 1989a, b, Aranha Filho et al. 2009, P.W. Fritsch, unpubl. data). If these pollen grains are from the same plants as the fossil fruits, then *S.* subg. *Palura* can be excluded, and this would reinforce the close affinity of *S. laevigata* with either *S.* sect. *Lodhra* or the *S. tinctoria*/*S. wikstroemiifolia* clade. The other fossil pollen ascribed to *Symplocos* in Traverse (1955), *S. novae-angliae* Traverse, was compared with *S. chiriquensis* Pittier (= *S. limoncillo* Bonpl.) of *S.* ser. *Symplocos*. These fossil pollen grains are similar to many pollen types in *S.* ser. *Symplocos* (Barth 1979, 1982, P.W. Fritsch, unpubl. data) and could have affinity with *S. limoncillo* or other species in *S.* ser. *Symplocos*. *Symplocos paniculata* is eastern Asian and *S. limoncillo* is Mexican/Central American. Regardless, the affinities of the modern counterparts underscore the mixed mesophytic to marginally subtropical nature of the flora, mixing elements still present in southeastern North America through Central America with lineages now absent from the New World.

Based on phylogenetic and ancestral area analysis from DNA sequence data, the biogeographic history of *Symplocos* (Manchester & Fritsch 2014) has been interpreted to reflect a European origin followed by westward migration to the New World in the Eocene via the North Atlantic Land Bridge (Tiffney 1985); subsequently, the genus spread southward in the New World into South America (Fritsch et al. 2015). Its arrival in Asia has been suggested to follow the closure of the Turgai Strait (Tiffney & Manchester 2001), with an eastward migration from Europe (Manchester & Fritsch 2014) to Asia. Although *Symplocos* is present at the Eocene-Oligocene border in the Pasekovo flora of eastern Russia (Vikulin 2014), it is currently not recognized in the Tertiary floras of China, and has its earliest appearance in Asia at the Mio-Pliocene border in Japan (Tanai & Onoe 1961), becoming common in Plio-Pleistocene floras (e.g. Miki 1937, Miki & Kokawa 1962, Nirei 1968).

On the basis of the same DNA data, it has also been inferred that the lineage comprising *Symplocos tinctoria* and *S. wikstroemiifolia* migrated back to Eurasia from North America ca 9.8–8 Ma (Fritsch et al. 2015). Although the pattern of disjunction is consistent with migration of the most recent common ancestor of *S. tinctoria* and *S. wikstroemiifolia*

across Beringia, the timing of the disjunction at ca 9.8–8 Ma appears to be too late for a Beringial crossing. *Symplocos* is not known from Alaskan Miocene pollen floras (Leopold & Liu 1994, White & Ager 1994, White et al. 1997) or leaf floras (Wolfe 1966, 1980). Further, the

paleobiogeographical context is not consonant with the presence of *Symplocos* (Tiffney 2008). The floras that were present ca 10–8 Ma from the Betulaceae zone/transitional subzone of White et al. (1999) are characterized by the loss of "thermophilous taxa" including, for example,
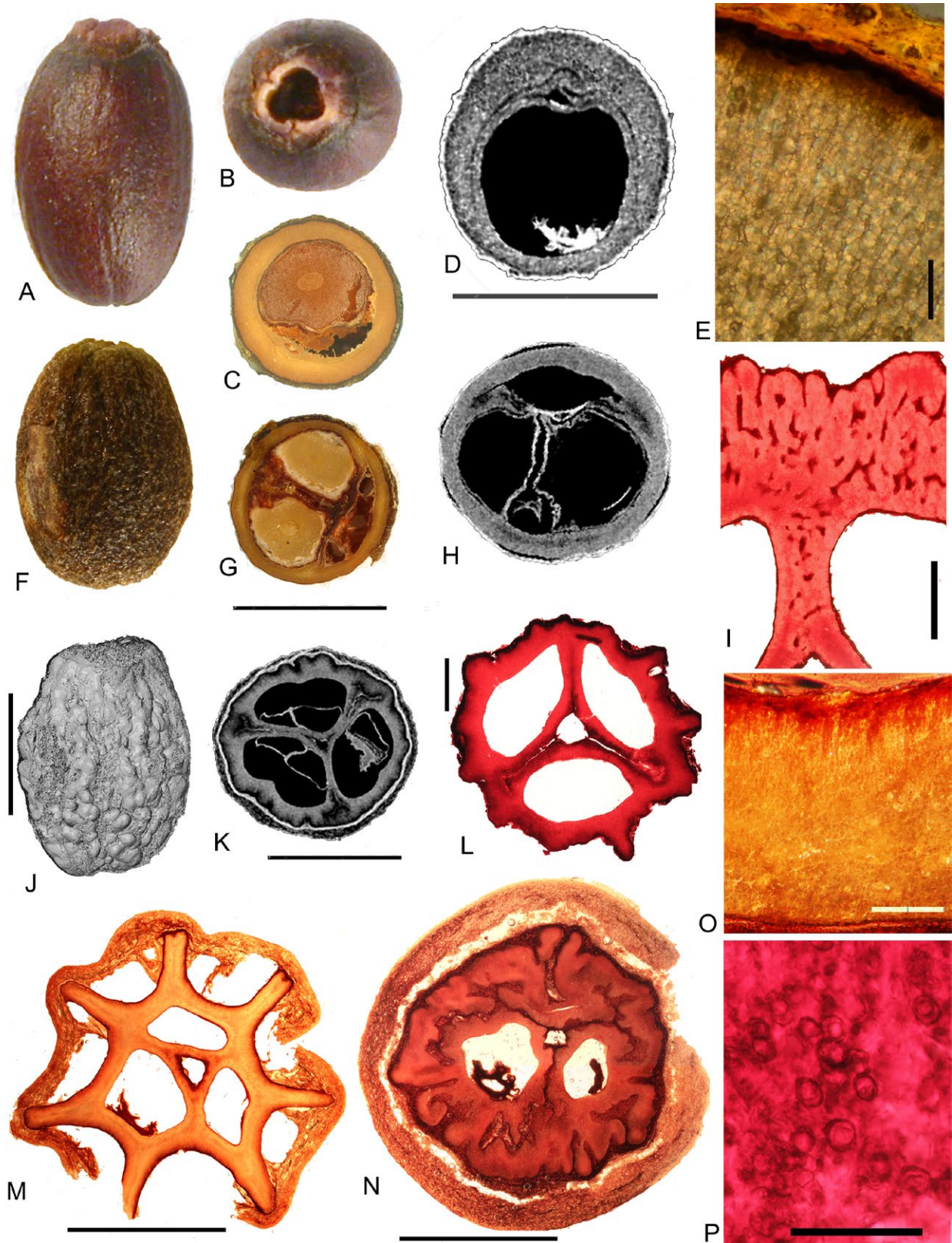
Carya Nutt., *Ilex* L., *Fagus* L., *Nyssa* L., *Liquidambar* L. and *Quercus* L. Whereas *S. paniculata* is deciduous and *S. tinctoria* is commonly so (Radford et al. 1968), the rest of the genus is evergreen and warm-temperate to subtropical in its physiological adaptations, and the Alaskan flora at the proposed time of migration seems inhospitable to *Symplocos*, given our current knowledge of its physiology. Similarly, migration back to Eurasia via Europe in the later Miocene does not seem reasonable, as neither pollen nor megafossils of *Symplocos* are present in the Miocene floras of Iceland (Denk et al. 2011). Hence, the current fossil record does not support the hypothesis that *S. tinctoria* and *S. wikstroemiifolia* returned to Eurasia from North America ca 9.8–8 Ma. via the North Atlantic or Bering land bridges.

However, because the sectional affinities of *Symplocos laevigata* were unclear until the present study, it could not be included as one of the fossils used in the calibration of Fritsch et al. (2015). A future re-analysis of divergence times with the inclusion of *S. laevigata* at the stem node of the *S. tinctoria*-*S. wikstroemiifolia* clade with a minimum calibration date of 18 million years would be expected to push back the divergence between the two species considerably. If *S. laevigata* instead belongs to *S.* sect. *Lodhra*, then its placement at the stem node of this latter section would not change the estimated divergence time because older Eocene and Oligocene fossils were used for calibration at the stem node of and within *S.* sect. *Lodhra*, respectively (Fritsch et al. 2015).

Symplocos fruits are present in the middle and late Eocene of the western United States. Those from the middle Eocene of Oregon (Manchester 1994) are casts lacking preservation of internal anatomy, preventing further determination. Specimens from the late Eocene La Porte and associated floras of California (Doyle et al. 1988, B.H. Tiffney, unpubl. data) are compressed and coalified, making it difficult to assess anatomical features. However, the surface sculpture of the endocarps is most similar to that of the Old World *S.* sect. *Lodhra*. Other western North American reports are confined to leaves from the early Eocene Green River Formation of Colorado (MacGinitie 1969) and the Oligocene Goshen flora (Chaney & Sanborn 1933) and possibly pollen from the Miocene Clarkia flora of Idaho (Gray 1985). However, the foliage-based identifications cannot be confirmed due to convergence in leaf architecture among various ericalean genera. Later megafossil records of the genus are not currently recognized from the west coast of North America.

In eastern North America, the earliest macrofossils of *Symplocos* were reported from the early Eocene of Maryland (Tiffney 1999), coeval with its first occurrence in England (Reid & Chandler 1933, Chandler 1961). However, subsequent reinvestigation of this material (Manchester, pers. obs.) has revealed anatomical and morphological features inconsistent with *Symplocos* (lack of an apical truncation and pores; smooth-surfaced rounded endocarp surrounded by a longitudinally ribbed mesocarp). Consequently, we are unaware of any other current eastern North American reports of endocarps of the genus other than this paper. However, pollen attributed to *Symplocos* is known from the late Paleocene of eastern North America (Frederiksen 1988) to the Miocene of Maryland and Massachusetts (Frederiksen 1984), suggesting that the genus was fairly

Fig. 3. Extant *Symplocos* species for comparison with the fossils. **A–E**. *S. tinctoria* of *S.* sect. *Hopea*; **A**, **B**. Endocarp in lateral (**A**) and apical (**B**) view. Field Museum 1335954: Correll & Correll 10470; **C**. Transverse section of fruit from near middle, showing large locule and two collapsed locules on either side of central canal, which is situated against inside of outer wall. Arnold Herbarium: G.W. Letterman Aug. 20, 1821; **D**. Transverse section of fruit from near middle, showing features similar to C. Arnold Herbarium: Fox 456; **E**. Detail of outer portion of endocarp wall, from same collection as D, showing radially aligned sclereids; **F**, **G**. Fruit of *S. wikstroemiifolia* of *S.* sect. *Hopea*, California Academy of Sciences Herbarium 10219100: Longxishan Exp. 2510; **F**. Lateral view; **G**. Transverse section from near middle, showing two locules, the larger showing section through the two arms of a U-shaped seed; **H**. Transverse section from near middle of *S. wikstroemiifolia*, showing features similar to those in G. Arnold Herbarium: H.H. Hu. 239; **I**. *S. austin-smithii* Standl. of *S.* ser. *Symplocos*, showing mottled pattern typical for endocarps of *S.* ser. *Symplocos*. Arnold Herbarium: M.E. Davidson 803; **J**, **K**. *S. anomala* of *S.* sect. *Lodhra*, endocarp surface in lateral view (**J**) and fruit in transverse section from near middle (**K**) Leiden Herbarium: SAN 56690; **L**. *S. anomala* in transverse section from near middle. Arnold Herbarium: Lau 26356; **M**. Transverse section from near middle of fruit of *S. cerasifolia* Wall. of *S.* sect. *Lodhra*, showing strongly developed ribs. Leiden Herbarium: Beusekom and Hengkahai 1029; **N**. Transverse section from near middle of fruit of *S. macrocarpa* subsp. *macrocarpa* of *S.* sect. *Lodhra*, showing weakly fused septa. Leiden Herbarium: Kostermans 26225; **O**. *S. cerasifolia*, detail of endocarp wall from section in M, showing anticlinally aligned sclereids near periphery; **P**. Endocarp tissue of *S. anomala* in transverse section, showing scattered crystalliferous idioblasts, from same collection as L. Scale bars: D = 5 mm (applies also to H); G = 5 mm (applies also to A–C, F); J, K, M, N = 5 mm; E, P = 100 μm; O = 200 μm; I, L = 1 mm; D, H, J, K from microCT scan; A–C, E–G, I, L–P from transmitted / reflected light

widespread in eastern North America prior to the middle Miocene climatic deterioration.

The only other fossil endocarps of *Symplocos* previously described from the New World are those that were called *Cordia vera* Berry (1924) from the Pliocene of Guasca, Colombia. Although a formal recombination is still needed, these are assignable to the extant Neotropical *S.* ser. *Symplocos* on the basis of their ellipsoidal to cylindrical shape, truncate apex, unribbed (but irregularly striate) surface, more or less cylindrical locules in equatorial cross section with the septa wider toward the wall, completely fused septa, and endocarp tissue with mottling. This locality is considered late Pliocene by Wijninga & Kuhry (1990). Manchester (pers. obs.) has noted at least two distinct morphologies of fruit casts of *Symplocos* from the Oligocene Catahoula Formation of Texas. These are in need of more detailed investigation.

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