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Symplocos Fruits from the Pliocene of Colombia

Steven R. Manchester,[1,5] Terry A. Lott,[1] Fabiany Herrera,[2] Henry Hooghiemstra,[3] Vincent M. Wijninga,[3] and Peter W. Fritsch[4]

[1]Florida Museum of Natural History, University of Florida, Gainesville, Florida 32611, USA; steven@flmnh.ufl.edu; lott@flmnh.ufl.edu
[2]Chicago Botanic Garden, Glencoe, Illinois 60022, USA; fherrera@chicagobotanic.org
[3]Institute for Biodiversity and Ecosystem Dynamics (IBED), Department of Ecosystem and Landscape Dynamics (ELD), University of Amsterdam, Science Park 904, 1098XH Amsterdam, The Netherlands; H.Hooghiemstra@uva.nl; vmwijninga@gmail.com
[4]Botanical Research Institute of Texas, 1700 University Drive, Fort Worth, Texas 76107, USA; pfritsch@brit.org
[5]Author for covrrespondence (steven@flmnh.ufl.edu)

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Abstract—Fossil fruits of *Symplocos* (Ericales: Symplocaceae) are here recognized from the Pliocene of Guasca, Colombia, based on specimens formerly attributed to *Cordia* (Cordiaceae, Boraginales). *Symplocos vera* (Berry) comb. nov. is represented by 19 lignitized fruits. The fossils are recognized as belonging to *Symplocos* primarily by their woody endocarps that are apically truncate and that possess 3 to 5 apical germination pores and locules, and a central vascular canal extending the length of the endocarp. In several key characters they are highly congruent with the endocarps of the extant Neotropical clade *S.* ser. *Symplocos*. Some of the extant species in the series are variably 3- to 5-locular; 4-locular endocarps are otherwise rare in *Symplocos*, and 5-locular endocarps appear to be unique to this series. *Symplocos vera* is the only specifically named record of fossil *Symplocos* fruits with accessible voucher specimens from South America. The younger Neogene age of the fossils relative to those attributed to *S.* ser. *Symplocos* from the late Eocene of Texas, along with a report of Colombian fossil endocarps from the middle Miocene, supports the North America to South America migration inferred for this clade from molecular phylogenetic data.

Keywords—Biogeography, endocarps, fossils, Symplocaceae, South America.

The ericalean genus Symplocos Jacq., with about 350-400 living species of trees and shrubs distributed in warm areas of the Americas, Asia, and Malesia to northeastern Australia, is one of two genera recognized within Symplocaceae (Fritsch et al. 2008; Plants of the World Online 2019). Both genera, *Cordyloblaste* Henschel ex Moritzi and *Symplocos*, have a fossil record in Europe, with that of *Symplocos* being particularly rich (e.g. Kirchheimer 1950; Mai and Martinetto 2006; Manchester and Fritsch 2014). *Symplocos* also has a few records in North America (e.g. Tiffney et al. 2018; Huegele and Manchester 2019).

Despite the diversity of modern species of *Symplocos* in the Neotropics, the fossil record of the genus there remains poorly known. Fossil endocarps have previously been identified to the genus, illustrated, and briefly described from three localities in the Guasca Region at 2650 m elevation in Department of Cundinamarca, Colombia (Fig. 1) by Wijninga and Kuhry (1990, 1993) and Wijninga (1996) but no binomials were established. These fossils, ranging in age from Miocene to late Pliocene (~17–3 Ma), occur in floodplain, lake, and swamp deposits (Hooghiemstra et al. 2006). Fossil pollen grains have also been attributed to *Symplocos* from the same sections in Colombia (Wijninga and Kuhry 1990, 1993; Wijninga 1996; Hooghiemstra et al. 2006) but without description or photographic documentation, so we are unable to comment further on them. Graham (1991) described and illustrated two kinds of *Symplocos* pollen from the Pliocene of Panama and noted that his Type 1 was comparable to *S. chiriquensis* Pittier, and Type 2 similar to extant *S. pycnantha* Hemsley.

The Colombian fossil fruits treated here were previously identified to the genus *Cordia* L. (Boraginales: Cordiaceae; Berry 1924). We provide formal nomenclatural revision, transferring these fossils to *Symplocos*, with establishment of a new combination at the species level. We justify the basis for their placement in *Symplocos* and in particular one clade (series) within the genus, and discuss the paleobotanical and biogeographical significance of the transfer.

Materials and Methods

Studied Material—Nineteen specimens of the original material described by Berry (1924) were reexamined. The endocarp specimens are lignitized and three-dimensionally preserved. The material is deposited at the Smithsonian National Natural History Museum paleobotanical collections, Washington, DC (USNM). In addition, the specimens previously cited by Wijninga and Kuhry (1990, 1993) and Wijninga (1996), now housed at the University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics, were studied in comparison with Berry's material.

Imaging and Tomography—Fossils were photographed under reflected light by using a Canon Rebel 450 digital SLR with a 60 mm macrolens. Micro CT scanning (μCT) of 19 specimens was performed in a single batch at the University of Florida, College of Engineering Nanoscale Research Facility by using a GE Phoenix V | tome | xm240 CT Scanner with a Tungsten reflection target and 0.5 mm copper filter, a voltage of 120 kV and current of 100 μA, and 2100 images for voxel size of 42 μm. The resulting datasets were processed with Avizo 9 Lite and Meshlab (2016.12 version) to obtain successive virtual sections, translucent volumes, and surface renderings.

Location, Stratigraphy, and Age—Berry (1924) specified that the fossils studied here were collected by Brother H. Ariste-Josephare from the lignite deposit at "Paramo de Guasca" in the Department of Cundinamarca, Colombia but did not include any other locality information. More recently, Wijninga and Kuhry (1993) illustrated fossil *Symplocos* fruits that we consider to be conspecific from the lower part of their Guasca 103 section exposed in a gully 1.5 km northeast of the village of Guasca. The lower 10 m of their section, composed of clays with intercalations of lignite and some sands, yielded pollen, lignitized fruits and seeds including fruits of *Symplocos*. These strata belong to the upper part of the Tilatá Formation, which is inferred to be late Pliocene (~3.6–2.5 Ma; Andriessen et al. 1993; Wijninga and Kuhry 1993; Helmens 2004; Corredor et al. 2015). The Guasca area at 2650 m elevation (Fig. 1) is currently part of the high plain of Bogotá which is located in the upper montane forest belt. Under natural conditions the Guasca study area is covered by high plain forest (Cleef and Hooghiemstra 1984), swamps, and open herbaceous vegetation. Other localities of the Tilatá Formation yielding *Symplocos* fruits include site Subachoque 39 at

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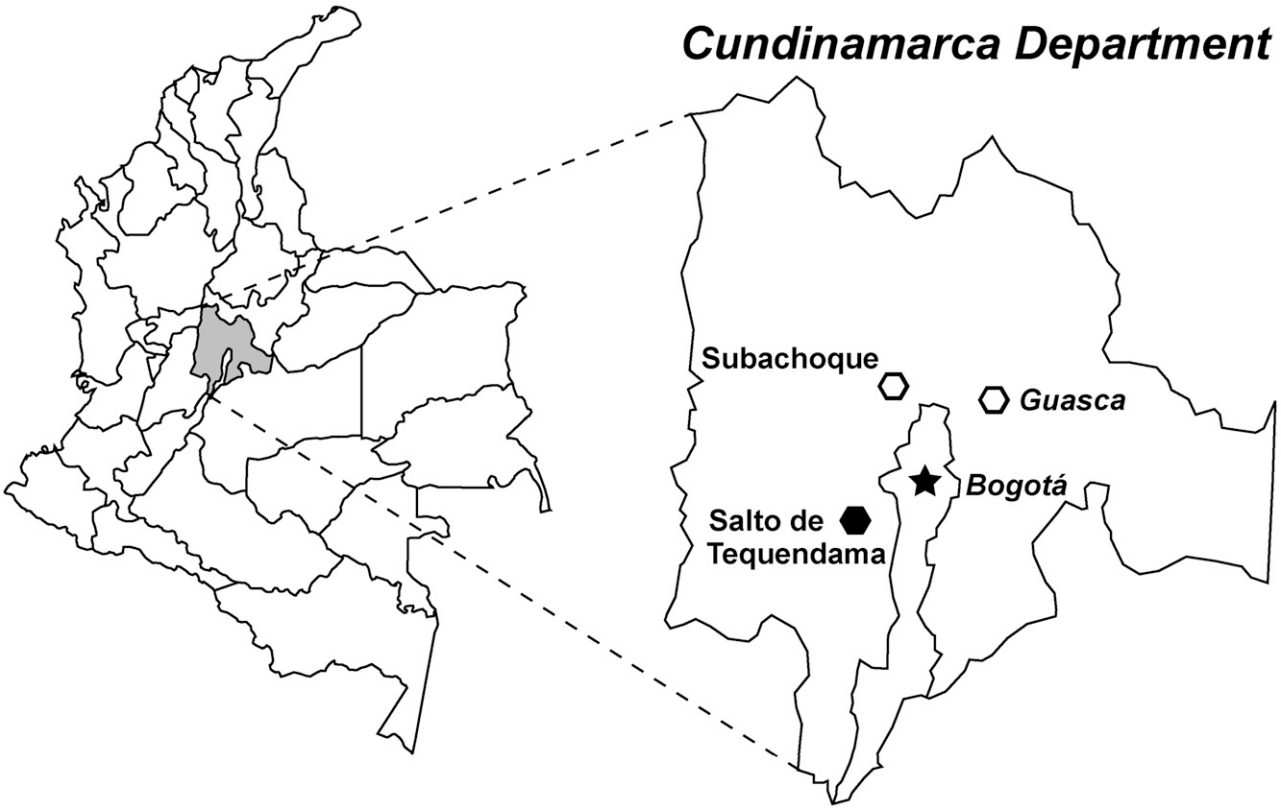


FIG. 1. Map showing paleobotanical sites in the Tilatá Formation of Cundinamarca Department, Colombia, including Guasca, the source of *Symplocos vera* (Berry 1924; Wijninga and Kuhry 1993). Adjacent sites with previously illustrated *Symplocos* fossils are Subachoque (Wijninga and Kuhry 1990) and Salto de Tequendama (Wijninga 1996). White hexagons = Pliocene sites; black hexagon = Miocene site.

2820 m elevation (Wijninga and Kuhry 1990) and Salto de Tequendama I site at 2475 m elevation (Wijninga 1996). The voucher specimens described by Wijninga and Kuhry (1990, 1993) are deposited at the University of Amsterdam, Institute for Biodiversity and Ecosystem Dynamics.

TAXONOMIC TREATMENT

Symplocos vera (Berry) Manchester, P.W. Fritsch & F. Herrera comb. nov. BASIONYM: *Cordia vera* Berry, Bull. Torrey Bot. Club 51: 66, figs. 1–19. 1924. TYPE: COLOMBIA. Cundinamarca: Guasca Region, *Brother H. Ariste-Joseph s.n.* (lectotype, here designated: USNM 320736).

Berry (1924) did not indicate a holotype. Among the syntypes that he illustrated, we designate the specimen depicted in his Fig. 5 (USNM 320736; refigured here, Fig. 2B–I), which is 5-locular, as the lectotype. Among the 19 fossils recognized here as *Symplocos*, there is variation from 3 to 5 locules, with more specimens that are 3-locular. The specimens of Berry's original collection that we examined are USNM 320721–320739, 320721–320739.

Emended Diagnosis—Fruit drupaceous, broadly ellipsoidal to cylindrical-obovoid with widest diameter at or above the equator in lateral view, slightly curved, often slightly tapering to base, broadly ellipsoid (likely from compression) to circular in cross section, 7–12 (average 9.8) mm long × 4–5 (average 4.4) mm in equatorial diameter, length/diameter ratio 1.8:1 to 3.0:1; base rounded, apex truncate. Remnants of external tissue (exocarp + mesocarp) possibly crushed, 0.083–0.153 mm thick. (Figs. 2T, U, Y, 3E, O, X).

Endocarp sclerotic, most commonly 3-locular (Figs. 2T, 3H, V, DD, GG, HH, II), but also 4- (Fig. 3O, W, X) and 5-locular (Figs. 2I, U, 3N), locules radially arranged; surface striate with shallow grooves running from apex to base (e.g., Figs. 2B–D, W, X, 3I–K, AA), but unribbed; base with small central pit coinciding with a longitudinal central vascular canal extending from base to apex (e.g. Figs. 2G, R, S, 3D, E, CC); apex truncate, lacking marginal lip, containing 3 to 5 apical pores, commonly occluded with clay in the fossils (e.g. Figs. 2R, S, Y, 3E, L, N); pores nearly circular in outline and separated by 3 to 5 shallow radially arranged septa, each pore leading to a locule.

Endocarp wall composed of sclerenchyma, 0.7 to 0.9 mm thick (measured near greatest equatorial diameter from dorsal side of locule to endocarp periphery), thicker than septa; fertile locules 1-seeded (Figs. 2U, 3X), longitudinally elongate, nearly circular to elliptic, subcuneiform, or subangled in medial cross section, some locules smaller than others and often one predominantly large, sterile locule occasionally collapsed; septa often thicker toward the wall associated with the rounded outer edges of locules; septal walls from adjacent carpels completely fused, i.e. without suturing.

DISCUSSION

Wijninga (1996) was the first to recognize that Berry's fossils actually represent *Symplocos* but he did not make any nomenclatural revision to transfer them out of *Cordia*. The *S. vera* type material closely resembles the endocarps illustrated and described as *Symplocos* Type A, from a silty layer within the

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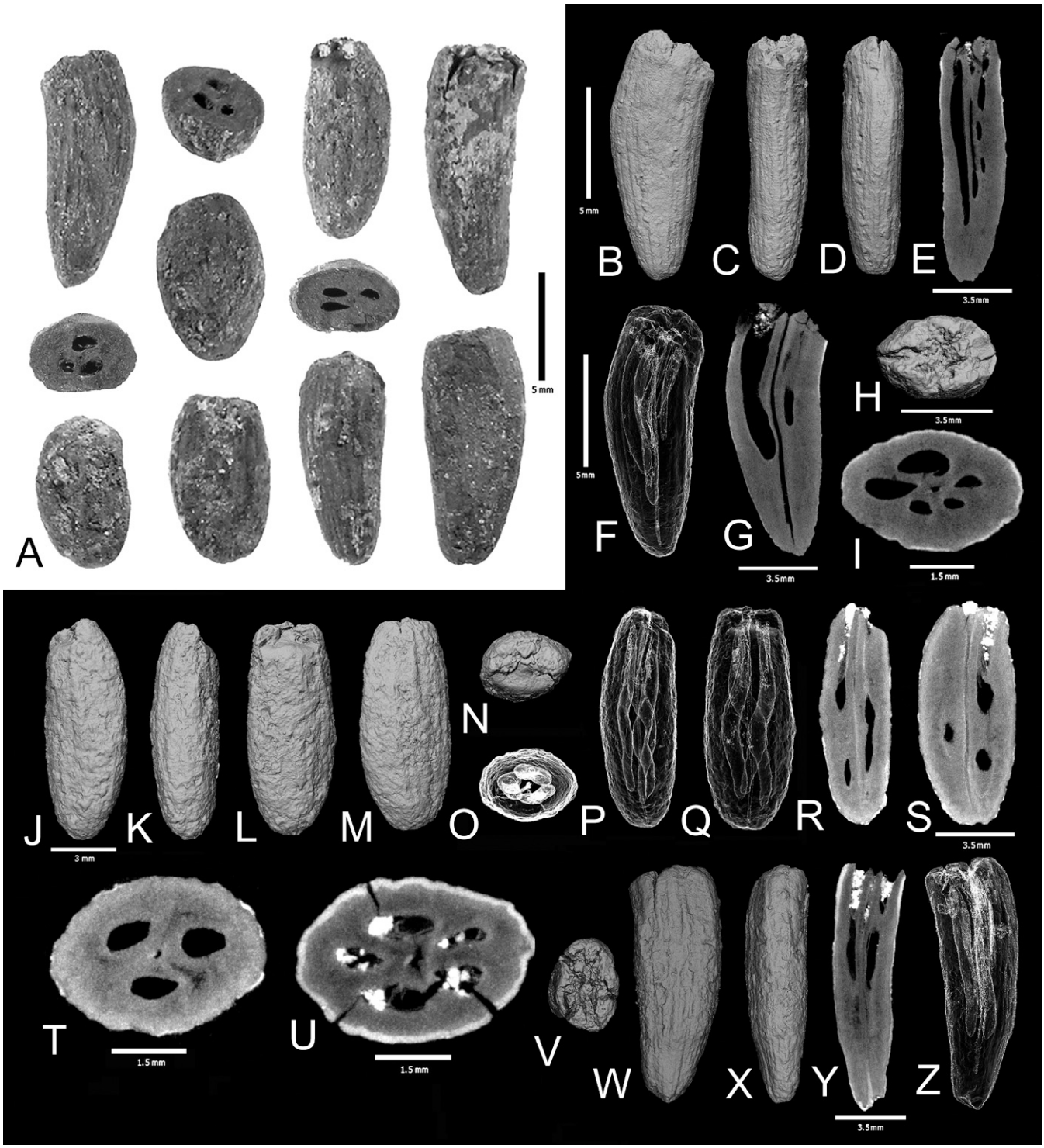


FIG. 2. Fossil fruits of *Symplocos vera* (Berry) comb. nov. A. Eleven examples from the syntype collection of Berry (1924), including lectotype at upper left, by reflected light. B–I. Multiple views and virtual sections of the lectotype, USNM 320736, from micro-CT scanning. B–D. Surface in three longitudinal views. E. Longitudinal section in plane parallel to the views of C, D, intercepting central canal and two elongate locules. F. Surface rendering with translucency to show positions of locules within the endocarp. G. Longitudinal section in plane parallel to the views in B, F. H. Apical view. I. Transverse section showing thick wall and 5 locules. J–T. Multiple views and virtual sections of USNM 320727 from micro-CT scanning. J–M. Lateral views. N. Apical view, opaque surface rendering. O, Apical view with translucency, showing position of locules. P, Q. Longitudinal views with translucency in same orientations as K, L. R, S. Virtual longitudinal sections. T. Virtual transverse section. U–Z. Multiple views and virtual sections of USNM 320731. U. Transverse section showing five locules. V. Apical view. W, X. Longitudinal views. Y, Z. Virtual longitudinal sections.

lignites at a site 1.5 km northeast of the town of Guasca (Fig. 1) by Wijninga and Kuhry (1993). We consider the material of Berry (1924) and Wijninga and Kuhry (1993) to be conspecific, corresponding in shape, size, and surface ornamentation. The endocarps of Wijninga and Kuhry (1993) are 2-locular (two specimens), 3-locular (70 specimens), and 4-locular (11 specimens); those of Berry's collection are 3-locular (13 specimens, 4-locular (three specimens), and 5-locular (three specimens).

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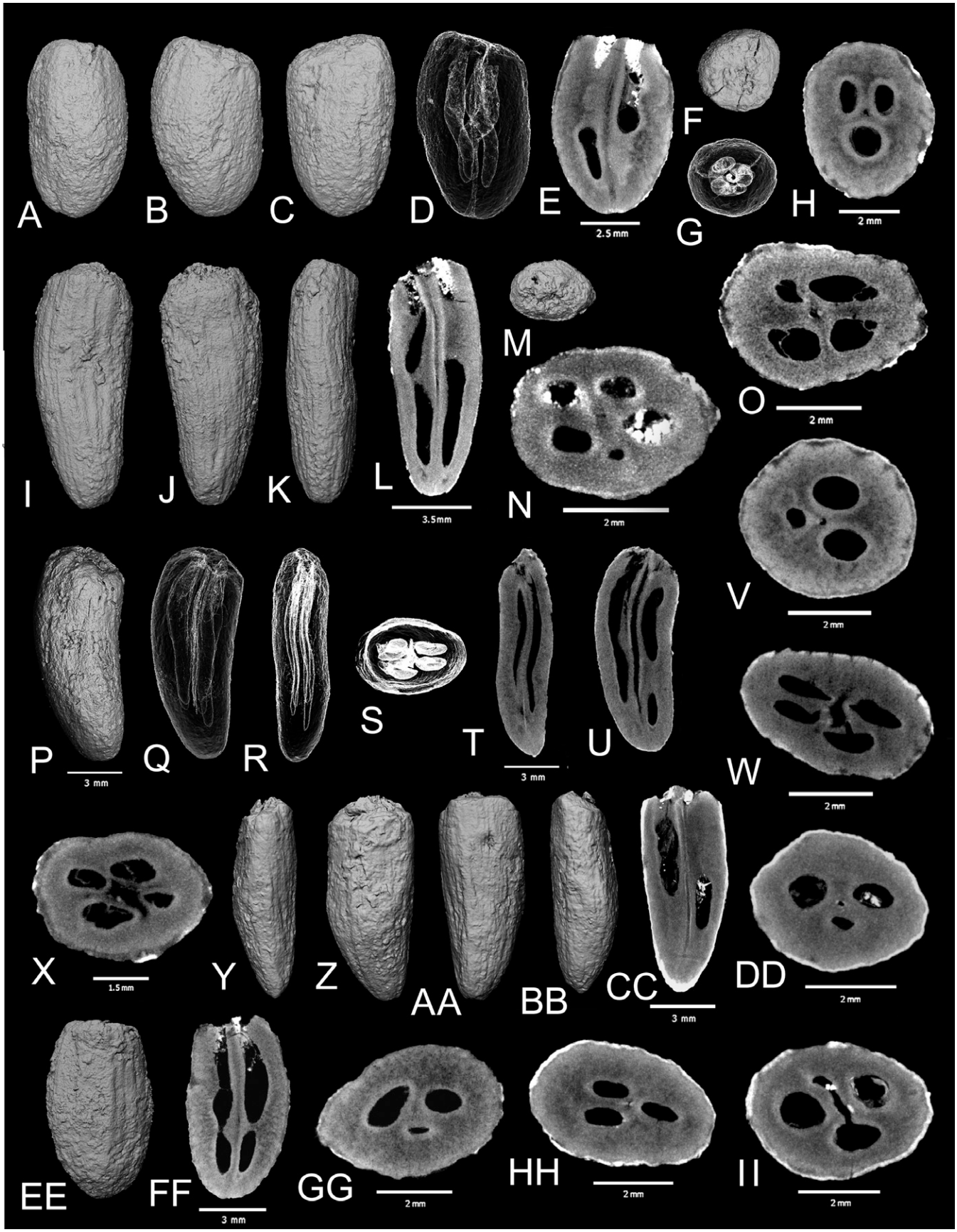


FIG. 3. Fossil fruits of *Symplocos vera* (Berry) comb. nov. micro-CT scan images. A–H. Multiple views and virtual sections of USNM 320728. I–N. Multiple views and virtual sections of USNM 320730. O. Virtual transverse section showing 4 locules, USNM 320725. P–U, W. Multiple views and digital sections of USNM 320735 showing 4 locules. V. Virtual transverse section showing 3 locules, USNM 320721. X. Virtual transverse section with 4 locules, USNM 320734. Y–DD. Trilocular fruit, USNM 320723. EE–GG. Trilocular fruit in lateral view, longitudinal section, and transverse section, USNM 320729. HH, II. Trilocular fruits in virtual transverse section, USNM 320724, USNM 320726.

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A second morphotype, *Symplocos* Type B, reported by Wijninga and Kuhry (1993), from lignite at the same site as their Type A, was distinguished by a somewhat less elongate form and tendency for shorter length (7.0–10.2, average 8.3 vs. 5.6–15.6, average 10.3 mm). This might represent a distinct species.

The paleoenvironmental reconstructions by Wijninga and Kuhry (1993) indicated that the *Symplocos* fruits were part of a subandean forest (i.e. lower montane; ~1000–2300 m altitude), which contrasts with the present elevation of ca. 2650 of the Guasca region. The *Symplocos* specimens used in Wijninga and Kuhry's interpretation of late Pliocene paleoecology of the Guasca Valley are missing and thus not available for further study.

Berry (1924, p. 61), stated that "The fossils [of this species] are exceedingly abundant and I have some hundreds of specimens." He assigned this species to the boraginaceous genus *Cordia*. Although the endocarps bear a superficial resemblance to those of *Cordia*, the locules of *Cordia* do not enter to an apical truncation, and a central fruit axial canal is not observed in its endocarp (De Souza 2008), as it is in the fossils. Moreover, *Cordia* ovaries typically are bicarpellate and falsely 4-locular by intrusion of the placenta to form partitions demarcating four locules, each with an ovule. In most species, only one ovule matures, resulting in a single-seeded fruit. A transverse section of the indurated endocarp typically shows the three abortive locules pushed to one side along the outer endocarp wall (James Miller pers. comm., April 2020).

The fossils are strongly concordant with fruits of extant and fossil Symplocaceae. Endocarps can be identified as members of the Symplocaceae primarily by a wall composed of sclereids, an apical truncation with germination pores, and a central vascular canal extending the length of the endocarp (Mai and Martinetto 2006; Manchester and Fritsch 2014; Tiffney et al. 2018). As in the fossils, both genera of the Symplocaceae have species with endocarps that can be variably 3- to 5-locular. Among the extant members of the Symplocaceae, both species of *Cordyloblaste* Hensch. ex Moritzi and many species of *S.* [subg. *Symplocos* sect. *Symplocos*] ser. *Symplocos* exhibit this variation. However, endocarps of *Cordyloblaste,* unlike the fossils, have a conical apex with apical pores that are narrowly elliptic or slit-like in outline, whereas those of *Symplocos* have a more or less flat apex with apical pores that are more or less cuneiform to occasionally nearly circular in outline.

Symplocos vera fossils exhibit a combination of other features that provide an unequivocal assignment to *Symplocos* ser. *Symplocos*: the outer wall is unribbed but finely and irregularly grooved; in cross section at about the middle axially, the endocarp wall is relatively thick and notably thicker than the septa; the septa themselves are relatively thick, especially near their outer edges, and completely fused, i.e. without medial suturing. The endocarp tissue exhibits a distinctive mottled pattern (Tiffney et al. 2018; SRM and PWF pers. obs.). Furthermore, *S.* ser. *Symplocos* is the only clade of the genus that has species with endocarps that can be variably 3- to 5-locular. Most species in the clade have consistently 3-locular endocarps, but species such as *S. fuliginosa* B.Ståhl, *S. jurgensenii* Hemsl., *S. limoncillo* Bonpl., and *S. martinicensis* Jacq. regularly vary from 3- to 5-locular (Ståhl 1996, 2010; Kelly et al. 2016). Four-loculed endocarps are otherwise rare in *Symplocos* (e.g. occasionally *S. racemosa* Roxb. and *S. theifolia* D.Don sensu Nooteboom (1975), and 5-locular endocarps are apparently restricted within *Symplocos* to *S.* ser. *Symplocos* (Fritsch et al. 2008; SRM and PWF pers. obs.).

Symplocos ser. *Symplocos* ranges from southern North America (one species) through Central America and the Antilles to central South America. *Symplocos fuliginosa* is an example of a species with this condition from the northern Andes and thus generally overlaps in geographic range with the location of the fossils, but it has fruits that are much larger (often > 20 mm). In contrast, *S. martinicensis*, another species with the 3- to 5-locular condition distributed in the Antilles and non-Andean northern South America, exemplifies a species with fruits that possess a similar size range as that of the fossils. Phylogenetic sampling and resolution is still too poor to ascertain whether all species of *S.* ser. *Symplocos* with endocarps that have the 3- to 5-locular condition form a clade (see Fritsch et al. 2008).

Symplocos vera is the only specifically named record of fossil *Symplocos* fruits from South America, but it is not the only fossil record of the genus from the continent. Besides the Guasca Pliocene specimens of Berry (1924) and Wijninga and Kuhry (1993) with an age of ca. 3 Ma, two other occurrences of *Symplocos* endocarps have been recognized from Colombia (Fig. 1). Wijninga and Kuhry (1990) illustrated and described an unnamed species from the Pliocene of Subachoque Valley ca. 5–4 Ma. It has urn-shaped endocarps 5.5–9.0 mm long and 3–4.5 mm wide with a slight constriction below the apical truncation and three locules; two kinds were recognized varying in prominence of surface ribs. An older occurrence, estimated to be of middle Miocene age, ca. 17–11 Ma, is the Salto de Tequendama I site (Wijninga 1996). The four endocarps studied from that site were illustrated and described as trilocular, laterally deformed, elliptic or ovate, sometimes narrowly elliptic or obovate, with a rounded base and truncate apex and with anastomosing longitudinal grooves and ridges. With dimensions of 5–7 (avg. 6.3) mm long and 2.5–3.8 (avg. 3.3) mm wide, these are smaller than *S. vera* and tend to be elliptical rather than obovate, and not as wide at the apical truncation. The specimens of Wijninga and Kuhry (1990) and Wijninga (1996) will be reevaluated in a separate treatment when CT-scanning information becomes available.

Fossil fruits similar to those of *Symplocos vera* were recently described as *S. fritschii* Huegele from the Late Paleogene of Trinity County in eastern Texas (Huegele and Manchester 2019). These fossils were also assigned by the authors to *S.* ser. *Symplocos* because their endocarps have five locules, five apical pores, and a relatively thick wall and septa. Other fossils that appear to belong to *S.* ser. *Symplocos* are *S. tetraporina* Mai from the early and middle Miocene in the Lusatia region of Germany (Mai and Martinetto 2006). These fossil fruits have a truncate apex, four locules, a relatively thick wall and septa, and an outer wall with furrows, as in some *S.* ser. *Symplocos*. Another possible representative of *S.* ser. *Symplocos* is *S. pseudogregaria* Kirchheimer from the late Eocene to middle Miocene of central Europe. The endocarps of this species have a truncate apex, 3 to 5 locules [only those with 3 were depicted in Kirchheimer (1950) and Mai and Martinetto (2006)] and a thick wall. The endocarp of *S. pseudogregaria* depicted in Kirchheimer (1950: Fig. 184, as *S. poppeana* Kirchheimer), however, has some incomplete septal suturing that may agree more with the endocarps of *S.* sect. *Lodhra* G.Don (see Tiffney et al. 2018).

Although only two regions of the Americas (Colombia and Texas) have fossil fruits that can be identified as belonging to *Symplocos* ser. *Symplocos*, the location and age of these fossils are consistent with the historical biogeography of the genus based on clade divergence times (Fritsch et al. 2015). The earliest dispersal between North America and South America in *S.*

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ser. *Symplocos* is hypothesized to have occurred between 7.5 and 8.9 Ma from North America to South America, with two additional later dispersals in the same direction. Although they constitute only two data points, the American fossils are considered to belong to *S.* ser. *Symplocos*, consistent with the direction of migration based on molecular divergence times, with the Eocene Texas *S. fritschii* occurring earlier than the Colombian *S. vera*. The Texas fossils were published after the divergence time analysis of Fritsch et al. (2015). If they had been used as a fossil calibration in the divergence time analysis, it is likely that the earliest dispersal estimated from North America to South America would have been dated much earlier than 7.5–8.9 Ma. This suggests that the arrival in Colombia occurred much earlier than the Pliocene age of *S. vera*, but could be in line with the Colombian fossils dated from the middle Miocene ca. 17–11 Ma. On this basis, a reanalysis of divergence times that includes these American fossils appears to be warranted.

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Author Contributions

SRM accessed and CT scanned the fossil specimens and helped with emended diagnosis and compiled the images. TAL processed CT datasets and edited the initial manuscript. FH updated geologic occurrence data, prepared Fig. 1, and contributed to the writing. HH and VMW provided information on geologic occurrence of the fossils including those they studied previously now in collections of University of Amsterdam and helped with final editing. PWF conducted comparative work on extant Symplocaceae and contributed to the writing.

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