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Laurus macrocarpa Lesquereux from the mid-Cretaceous (Cenomanian) Dakota Formation, USA, is a chlamydospermous seed, not an angiosperm fruit

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ABSTRACT. The fossil seed, *Decaturospermum macrocarpum* (Lesquereux) gen. nov. et comb. nov., is described based on specimens of latest Albian to mid-Cenomanian age (mid-Cretaceous) from the Dakota Formation of Nebraska, and Kansas, USA, which were previously named *Laurus macrocarpa* Lesquereux; and from the Woodbine Formation of Texas, USA, which were previously named *Laurocarpum tetragonale* MacNeal. All specimens are molds and casts lacking cellular details, but light microscopy and micro-CT scanning reveal key structural features. Combined information from eight specimens indicates that *D. macrocarpum* is a seed with an outer covering comprised of four valves. The four valves are reflected in the cast of the seed cavity, which has a quadrangular transverse section with four rounded edges. Each valve has a smooth outer surface covering a decay-susceptible outer layer that was replaced by sediment early during fossilization. Sediment filling the space left by the decay-susceptible outer layer preserves an impression of a distinctive dendritic reticulate system of longitudinal and transverse ribs on its inner surface, which reflects the outer surface of a decay-resistant inner layer, now seen only as a cavity. The inner surface of the decay-resistant inner layer is smooth, as is the outer surface of the cast filling the seed cavity. Below the seed cavity a downward extension of the decay-resistant layer forms a prominent swollen-cylindrical flange around the seed base. Decay-susceptible tissues inside the swollen flange are replaced by sediment but preserve the distinctive sinuous course of four vascular bundles. The position of each bundle suggests that it entered a valve in a near median position. Comparison of *Decaturospermum macrocarpum* with other seeds of Cretaceous age indicates that the two-layered, four-valved outer covering is the envelope of a chlamydospermous seed, which was most likely produced by plants closely related to extant Gnetales.

KEYWORDS: chlamydospermous seed, extinct gnetalean, Cretaceous, Kansas, Texas, Nebraska

INTRODUCTION

The flora of the Dakota Formation, known colloquially as the ‘Dakota Sandstone’, is a classic assemblage of fossil plants from the mid-Cretaceous of North America. Extensive collections in many North American and European museums consist mainly of angiosperm leaf impressions in a fine to medium-grained yellow-ochre sandstone matrix. These fossils are from sandstone facies of the Dakota Formation and while fossil plants also occur in coeval clays and silts (Dilcher, 1979) most ‘Dakota Sandstone’ specimens were collected in the mid- and late nineteenth century by C.A. Sternberg, R.D. Lacoe, and others (Andrews,

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1980), principally from Kansas and Nebraska. Similar material was also collected somewhat later from approximately contemporaneous deposits in northeast Texas (Knowlton, 1901; Berry, 1912, 1917, 1922; Winton, 1925; MacNeal, 1958) and western Minnesota (Berry, 1939). Descriptions of the Dakota Sandstone flora include more than 400 species (Lesquereux, 1868, 1874, 1883, 1891; Newberry, 1868; Gress, 1922), mostly based on impressions of angiosperm leaves with a much smaller fern and conifer component. The flora of the Dakota Formation unequivocally reflects the dominance of angiosperms in at least some habitats, approximately 90 million years before present, at a relatively early stage of angiosperm evolution.

Classic descriptions of plant fossils from the Dakota Formation focus almost entirely on angiosperm leaves, but early studies also described and illustrated specimens of a few reproductive structures (e.g. Lesquereux, 1868, 1874, 1891; Hollick, 1903; MacNeal, 1958) that are scattered among different museum collections. Dilcher (1979) highlighted some of these specimens in his review of early angiosperm reproductive structures, but the challenge of extracting sufficient detail from such material to enable useful results discouraged detailed study. Subsequent research focused instead on more informative compression fossils of angiosperm flowers and leaves from Dakota Formation clays and silts (Retallack and Dilcher, 1981; Basinger and Dilcher, 1984; Dilcher and Crane, 1984; Dilcher and Kovach, 1986; Upchurch and Dilcher, 1990; Wang and Dilcher, 2006a, b, 2009, 2018; Wang et al., 2011; Manchester et al., 2018).

In the mid-1980s, one of us (PRC), began a study of the angiosperm reproductive structures from the Dakota Sandstone, which resulted in the description of the enigmatic multifolliculate angiosperm fruit *Lesqueria* (Crane and Dilcher, 1984). Research on other reproductive structures from the Dakota Sandstone flora was set aside forty years ago but has now been revitalized by the availability of micro-CT techniques and the discovery of additional specimens during recent fieldwork (SRM). In this paper we reassess the structure and relationships of the disseminules originally interpreted as lauraceous fruits and named *Laurus macrocarpa* Lesquereux (1868, 1874). Reanalysis of material collected in the nineteenth century, and of the newly collected specimens, shows that "*Laurus*" *macrocarpa* is a chlamydospermous seed rather than an angiosperm fruit.

MATERIALS AND METHODS

The eight specimens analyzed in this paper originate from localities in three states (Fig. 1). All are preserved as three-dimensional casts and molds in a fine to medium grained ferruginous sandstone. As in the case of many fossil leaves from the Dakota Sandstone, the surface of the mold is formed by an iron encrustation that is finer than the surrounding matrix (Spicer, 1977). Two specimens are in the collections of the United States National Museum (USNM); one from Delphos, Kansas (USNM 50401) and the other from Decatur, Nebraska (USNM 42600). Four additional specimens from Decatur, Nebraska, collected in 2003, 2008, and 2021 from an overgrown roadside exposure immediately north of Decatur (UF locality 19025, 42°00.921′N; 96°15.223′W), are in the collections of the Florida Museum of Natural History at the University of Florida (UF 53136, 53138, 85533, 85553). Two specimens from Denton, Texas (ANSP 3485, 3486) are in the collections of the Academy of Natural Sciences, Philadelphia (ANSP). Both were collected by D.L. MacNeal from localities east of Denton along Fish-trap Road and the Texas-Pacific railroad. MacNeal (1958) provides detailed locality information. All of these sites were situated near the eastern margin of the mid-Cretaceous epicontinental seaway (Fig. 1 in Manchester et al., 2018).

In broad terms, the Dakota Formation appears to straddle the Early Cretaceous-Late Cretaceous boundary extending up into the Middle and perhaps Late Cenomanian. However, the ages of specific localities in the Dakota Formation of Kansas and Nebraska are often not well constrained. Radiometric dates from the Dakota Formation in Utah, on the western side

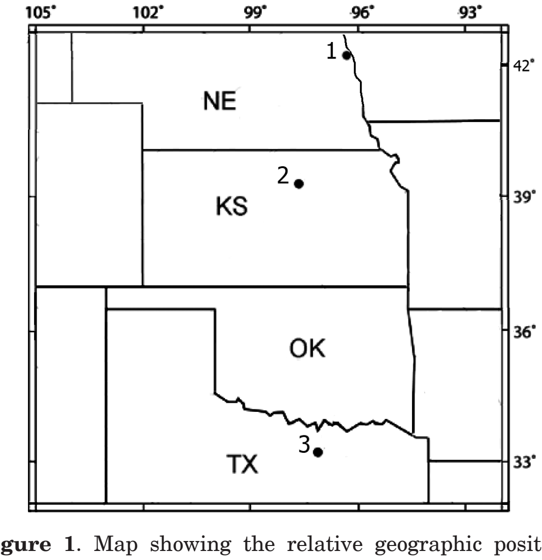

Figure 1. Map showing the relative geographic positions of the three localities from which *Decaturospermum macrocarpum* is known relative to the states of Nebraska (NE), Kansas (KS), Oklahoma (OK) and Texas (TX). 1 – Decatur, Nebraska; 2 – Delphos, Kansas; 3 – Denton, Texas. See text for additional details

of the mid-Cretaceous epicontinental seaway, suggest a Middle to Late Cenomanian age (Barclay et al., 2015). Floras on the eastern side of the seaway are mainly considered younger than Late Albian (Scott, 1970a, b; Ward, 1986), based on biostratigraphic correlations, and perhaps extend into the Middle Cenomanian (Brenner et al., 2000; Ludvigson et al., 2010). However, based on palynology and carbon isotopes, Gröcke et al. (2006) propose that the Rose Creek megafossil plant locality (Basinger and Dilcher, 1984; Upchurch and Dilcher, 1990; Manchester et al., 2018) in shales of the Dakota Formation south of Fairbury, southeastern Nebraska, straddles the Albian-Cenomanian boundary, with the plant-bearing beds of Late Albian age. Further south, the Woodbine Formation, which yields the fossils from Denton, Texas, is considered to be of Cenomanian age based on its stratigraphic position between the Late Albian-Early Cenomanian marine Grayson Marl and the Late Cenomanian-Early Turonian marine Eagle Ford Shale (Winton, 1925; MacNeal, 1958). Therefore, while the specimens considered in this paper cannot be precisely dated they are no older than the latest Albian and no younger than Late Cenomanian, and are from sediments probably equivalent to Subzone IIC or III in the palynological zonation of the mid-Cretaceous of the Atlantic coastal plain (Brenner, 1963; Doyle, 1969, 1978, 2012; Doyle and Hickey, 1976; Hickey and Doyle, 1977; Doyle and Robbins, 1977).

All of the specimens are preserved as molds and casts that lack anatomical preservation, but surface detail is preserved faithfully, and micro-CT scans also differentiate between the original encasing matrix, and the matrix that filled voids created when the original tissues rotted away (e.g. Fig. 3A–F). Micro-CT scans were performed at the University of Florida College of Engineering Nanoscale Research Facility with a GE Phoenix V|tome|xm240 CT Scanner, using a Tungsten reflection target with a voltage of 80 kV and current of 180 µA with a voxel size of 17.6 µm. We obtained 1800 images through a 360 degree rotation with 2 second exposures. The resulting datasets were processed with VG Studio Max 3.1, Avizo 9.0 Lite and Meshlab 2016.12 to obtain successive virtual sections, surface renderings and depth maps (Cignoni et al., 2008). Tiff stacks and interactive 3D meshes generated from the µCT data are archived at Morphosource (search *Decaturospermum* at morphosource.org).

SYSTEMATICS

Order: GNETALES?

Genus: ***Decaturospermum*** Manchester et P.R.Crane **gen. nov.**

Type: ***Decaturospermum macrocarpum*** (Lesquereux) Manchester et P.R.Crane **comb. nov.**

Genus diagnosis. Seed orthotropous, ellipsoidal, with an outer covering (envelope) that is four-angled in transverse section, with a smooth inner and outer surface that is formed by four equal-sized valves. Seed with a distinct apical micropyle. Seed base with a swollen-cylindrical flange surrounding a swollen pad of tissue that is traversed by four vascular bundles. From the base of the seed the vascular bundles curve gently outwards, gradually becoming more widely separated, before curving inwards and becoming more closely spaced as they approach the central seed cavity. Vascular bundles alternating with the four angles of the seed, aligned with the center of each flat face. Outer covering (envelope) of the seed consisting of a decay-susceptible outer layer, and a decay-resistant inner layer. Inner layer with a well-developed intricate system of anastomosing longitudinal and transverse ridges toward the outside, smooth toward the inside.

Etymology. *Decaturospermum* refers to the type locality of Decatur, Nebraska, USA with the suffix *spermum* (L = seed).

Plant Fossil Names registry. PFN 000799381 (for the new genus).

Species: ***Decaturospermum macrocarpum*** Manchester et P.R.Crane **comb. nov.**

Figs 2–7, 8A

Basionym. *Laurus “macrocarpus”* Lesquereux 1868, Amer. J. Sci. Arts, second series, vol. XLVI, p. 98.

Lectotype, designated here. *Laurus macrocarpa* Lesquereux 1874. Contrib. Fossil Flora Western Terr., Part I. Cret. Flora, p. 74, 75; pl. X, fig. 2, 2a. USNM 42600. (Figs 2A, 5).

Synonym.

1958 *Laurocarpum tetragonale* MacNeal; Monogr. Acad. Nat. Sci., Philadelphia 10, 119–120. Type: ANSP 2491 and 2491a.

Other specimens studied. USNM 50401A, B, Aa, Delphos Kansas; UF 19025-53136, 53138, 85533, 85553, Decatur, Nebraska; ANSP 3485 and 3486 (part and counterpart), ANSP 3526 and 3647 (part and counterpart), Denton Texas.

Preservation of seed structure. The seeds are preserved in three-dimensions, reflecting their inherent rigidity, but also the low compressibility of the sandstone matrix and early lithification given that other more delicate structures (e.g. petals, Hollick, 1903) in the Dakota Sandstone flora are also preserved

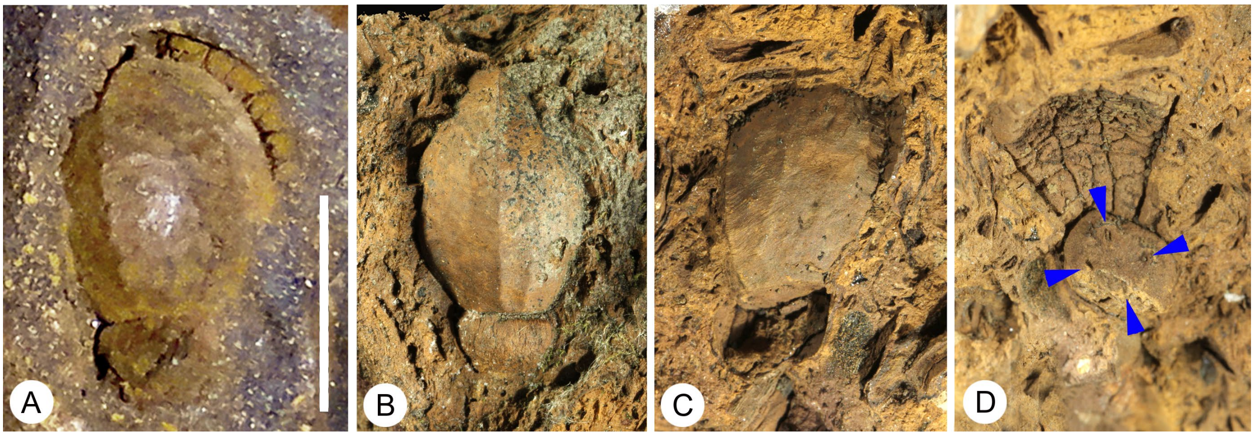

Figure 2. *Decaturospermum macrocarpum* gen. et comb. nov. from the Dakota Formation, Decatur, Nebraska, USA. Reflected light. **A**. Seed cast in lateral view showing part of the thick outer covering (envelope, upper right) that surrounds the ellipsoidal infilling of the seed body, a faint longitudinal rib and the swollen seed base. Note the two layers of the outer covering, the inner seen as a void from which the decay-resistant tissues have been lost, the outer seen as a filling of sandstone matrix into the space created by the early diagenetic loss of decay-susceptible tissues. The sandstone of this early diagenetic fill is slightly finer than that encasing the entire seed. USNM 42600 (Lectotype); **B**. Seed cast in lateral view showing ellipsoidal seed body and the swollen seed base. Note one prominent primary longitudinal rib and faint secondary longitudinal ribs on the cast of the seed body. UF 19025-85533; **C**, **D**. Part and counterpart (cast, C, and mold, D) of the ellipsoidal seed body and the swollen seed base. Note the smoothly faceted inner surface of seed (C) and two primary and two secondary longitudinal grooves linked by transverse grooves (D) that reflect the sculptured outer surface of the decay-resistant inner layer of the outer covering (envelope). Four symmetrically placed indentations in the cast of the swollen pad of tissue inside the decay-resistant basal flange indicate the positions of the four vascular bundles that enter the base of the seed (arrows) each on a radius equidistant between the two primary longitudinal grooves. UF 19025-53138. Scale bar = 10 mm (bar in A applies to all)

with minimal compression. We interpret the original seed structure in terms of the differential preservation of two kinds of tissues. Decay-susceptible tissues rotted away early in the processes of preservation and the resulting cavities were filled by sediment that is often somewhat finer than the sandstone in which the seed is embedded (Fig. 4A–F). Decay-resistant tissues persisted until after the matrix had lithified and the cavities created by rotting of the decay-susceptible tissues had been filled by sediment. Eventually, however, the decay-resistant tissues also rotted away leaving a second generation of cavities that were never filled by sediment and that remain in the specimens (Figs 2A, B, 4A, E, F, 5A, B, 6B, C, G). Decay-susceptible tissues include the presumed soft outer layer of the outer covering (envelope) (e.g. Fig. 4A, F), the outer layer of the swollen base (e.g. Fig. 4B, C, D), and the swollen pad of tissue inside it (e.g. Fig. 4B, C). Decay-resistant tissues include the presumed hard inner layer of the outer covering (envelope) (e.g. Figs 4A, E, F, 5C, D, 6C, G), the core of the swollen-cylindrical base (e.g. Fig. 4A–D) and the four vascular bundles (e.g. Figs 2D, 3I–M, 4A, B, D, 7D, E, J, K) noted in the original descriptions and illustrations of Lesquereux (1868, 1874).

Description. Seed orthotropous, consisting of an ellipsoidal seed body borne upon a swollen base (Figs 2A, B, 3A, K, 4A–C, 5A, B, E, 6A, 7A). Seed body about one and a half times longer than broad, ~15.5–18.4 mm long, 10.0–13.0 mm wide. Swollen seed base about one quarter the length of the seed body, ~3.0–3.8 mm long, 5.3–6.3 mm wide (Figs 2A, B, 3K, 4A, 5A, B, E, 6A, 7A, B). There is no indication of how the seeds were borne on the plant, but the axis must have been more robust that the slender axis associated with specimen USNM 42600 (Fig. 8A, B). The base of the seed is ~4 mm in diameter compared to the maximum diameter of the axis, which is ~1 mm.

The cast of the seed cavity has a distinct hollow apical projection ~0.5 mm long and ~0.2 mm wide, which is aligned with a channel ~0.45 mm diameter through the outer covering (Figs 5B, C, D, F–I, 7F, H, I). Cast of the seed cavity tetragonal, with a distinct rounded edge at each of the four angles (Figs 2A, B, 4E, 5A, B, 6A, 7B). Outer covering (envelope) of the seed composed of four equal valves (Figs 3G, J, 4E), the edges of which (Fig. 3C, D, G, H) correspond to the edges seen on the cast of the seed cavity (Figs 2A, B, 4E, 5A, B, 6A, 7B).

Outer covering (envelope) of the seed smooth externally (Figs 2A, 3F, 4A, C, E, F). Outer covering (envelope) ~1.3–1.7 mm thick, two-layered, with a decay-susceptible, presumed soft, outer layer up to ~1.2 mm thick, and a decay-resistant, presumed harder, inner

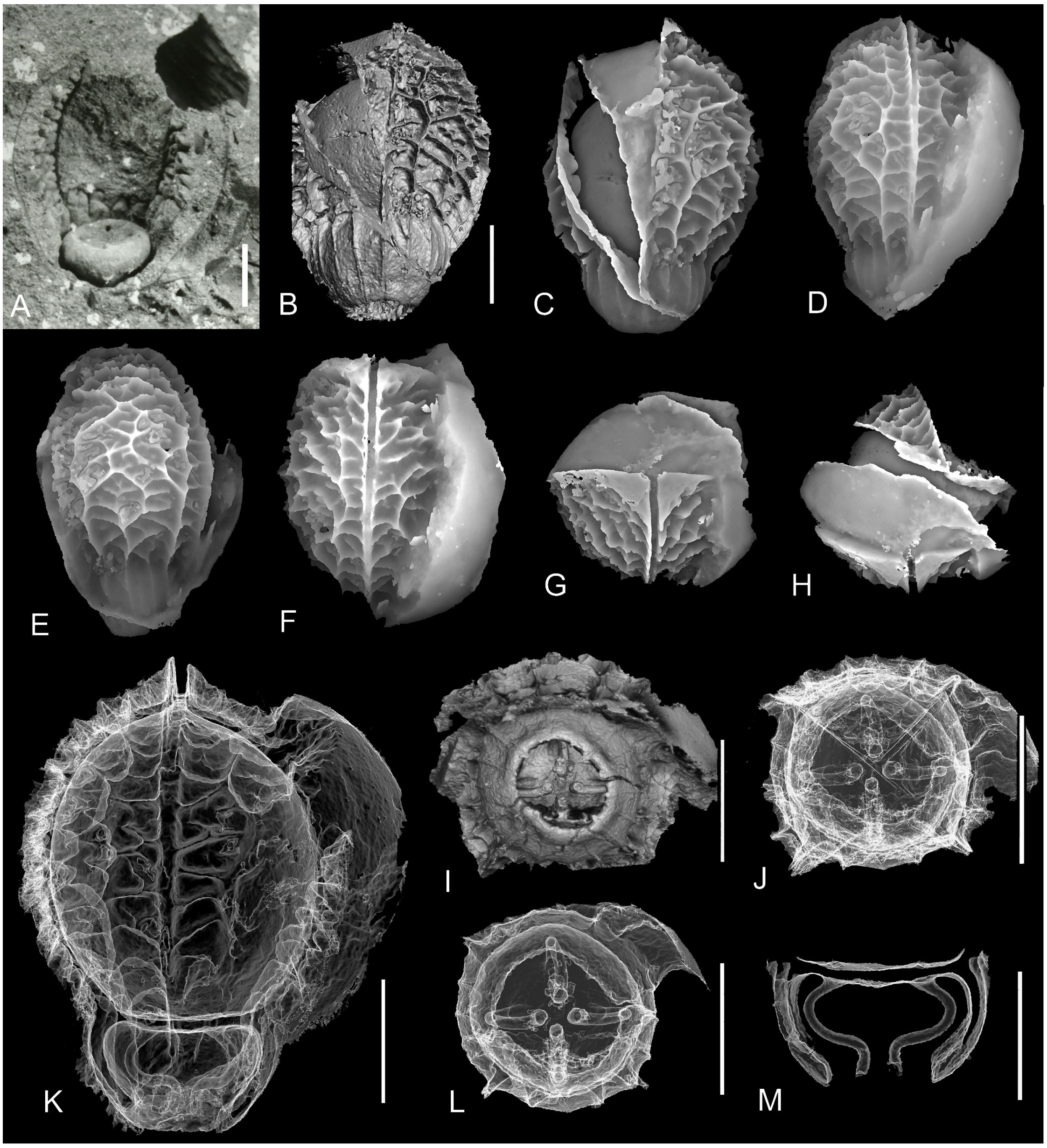

Figure 3. *Decaturospermum macrocarpum* gen. et comb. nov. from the Dakota Formation, Delphos, Kansas, USA. USNM 50401. Reflected light (**A**) and micro-CT scan images (**B–M**); depth maps (**C–H**), reflective surface rendering (**B**, **I**), translucent surface renderings (**K**, **J–M**). **A**. Exposed surface of the mold created by the tissue of the seed showing the protruding cast of the swollen pad of tissue inside the decay-resistant basal flange and the clearly defined smooth outline of the outer covering (envelope) at left and right; **B–E**. Seed rotated through different orientations on its longitudinal axis (tilted slightly in B and F) showing the sculpted surface of the decay-resistant inner layer of the outer covering (envelope) and its connection to the longitudinally ribbed outer surface of the swollen-cylindrical flange around the seed base. Note the well-developed primary longitudinal ribs separating adjacent valves (D, F), the ridges that form an irregular dendritic reticulate pattern and the smooth tips of the valves (F). There is a circular opening in the basal flange (B) and the cast of the ellipsoidal seed body is smooth (B, F); **G**, **H**. Seed in apical (G) and oblique apical (H) view showing two adjacent valves of the four valved outer covering (envelope) with well-developed primary longitudinal ribs along the groove that separates the two adjacent valves. Note the triangular unsculptured apex of each lobe around the micropyle, the smooth surface of the layer internal to the sculpted layer (G, H), and the smooth cast of the ellipsoidal seed body (H); **I**. Seed in basal view showing the ribbed outer surface of the swollen-cylindrical flange at the seed base that surrounds the four vascular bundles each of which is positioned on radii that alternate with the radii of the primary ribs seen on the outer surface of the flange and the inner decay-resistant inner layer of the outer covering (envelope); **J**, **L**. Seed in basal view with the detail of the main seed body included (J), and removed for clarity (L), showing the sinuous course of the four vascular bundles that first diverge widely before converging toward the central axis of the seed. Note the thickened rim at the base of the swollen-cylindrical flange and the lines of dehiscence between three of the four valves on radii alternate with the radii on which the vascular bundles are positioned (L); **K**. Seed in lateral view showing the sculpted surface of the inner decay-resistant inner layer of the outer covering (envelope) and the sinuous course of the vascular bundles inside the flange of the swollen seed base. Note the well-developed primary longitudinal ribs on either side of the groove separating two adjacent valves that also are slightly extended apically. Irregular secondary longitudinal and transverse ribs between the primary ribs form a dendritic reticulate pattern in which the areoles occasionally have free-ending minor ridges; **M**. Longitudinal thick section through the seed base showing the swollen-cylindrical flange and the sinuous course of two of the four vascular bundles. Scale bars = 5 mm (bar in B applies to B–H)

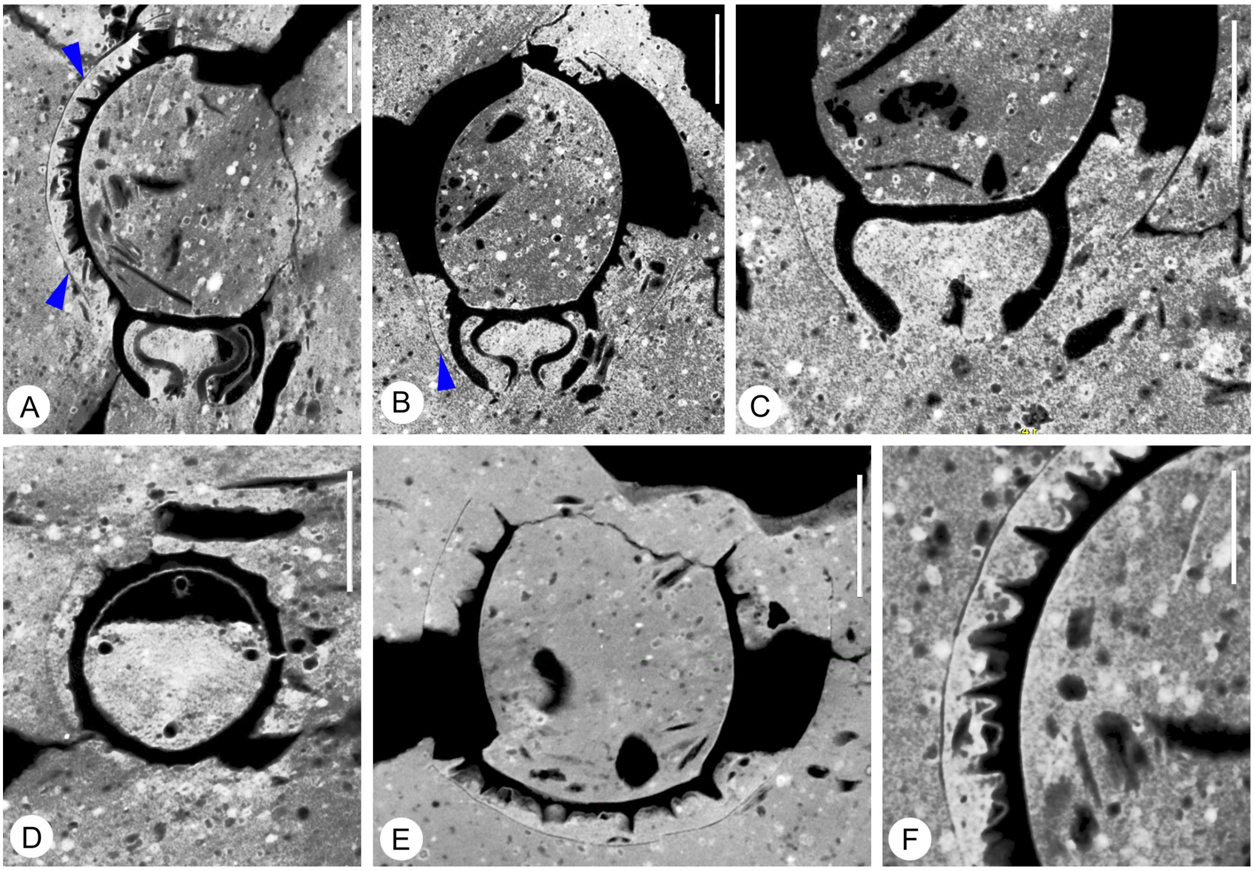

Figure 4. *Decaturospermum macrocarpum* gen. et comb. nov. from the Dakota Formation, Delphos, Kansas, USA. USNM 50401, same specimen as Fig. 3. Micro-CT scan images; virtual sections. **A**–**C**. Sections showing the cavities left by the decay-resistant inner tissues of the outer covering and the downward-directed, swollen-cylindrical flange around the seed base; **A**, **B**. Median longitudinal sections perpendicular to each other showing a portion of the smooth external surface of outer covering (envelope) defined by a thin smooth line probably reflecting its former epidermis (arrows), the sculptured inner layer of the outer covering with a smooth surface toward the inside, and the sinuous basal cavities that indicate the course of thick vascular bundles in the sandstone infilling of the basal flange. Finer sandstone matrix fills the interior of the swollen seed base and the lowermost outer part of the seed body; **C**. Detail of median longitudinal section rotated 30 degrees from B showing the horizontal septum separating the swollen seed base from the seed body, the convex wall of the basal flange and the sinuous course of the vascular bundles. The thin line indicating the external surface and probable epidermis of the outer covering extends to the base of the seed showing that it enclosed the decay-resistant basal flange; **D**. Transverse section through the swollen seed base showing the external ribs of the decay-resistant tissue and the position of four terete cavities reflecting the former position of the vascular bundles. Note also the smooth inner outline of the swollen-cylindrical flange, the smooth epidermis of the outer covering (envelope, left) and the finer sandstone matrix filling most of the seed cavity, except for occasional cavities seen as black areas; **E**. Transverse section through the body of the seed showing rounded quadrangular outline, and partial preservation of the two layers of the outer covering (envelope) with its smooth external surface; **F**. Detail of a transverse section showing smooth outer and inner surfaces of the outer covering (envelope) with the outer surface indicated by a fine line. The decay-resistant inner layer of the outer covering (envelope) is seen as an empty space, not filled by sediment, which is surrounded by a sediment-filled layer bounded externally by fine line reflecting the former position of the epidermis. Scale bars = 5 mm in A–E, 2.5 mm in F

layer up to ~1.3 mm thick (Figs 4A, E, F, 6C, G). Outer surface of the decay-resistant inner layer with an intricate and well-developed system of anastomosing longitudinal and transverse ridges forming a dendritic reticulate pattern (Figs 2D, 3A–K, 5A–G, I, 5D, E, 7L, M). Inner surface of decay-resistant inner layer smooth, as seen on the cast of the seed cavity (Figs 2A–C, 3C, H, 4A–C, E, F, 5A–E, 6A, F, 7B).

At the seed apex surrounding the apical projection the anastomosing longitudinal and transverse ridges of the decay-resistant inner layer are replaced by a solid block of decay-resistant tissue from which four ribs, which delimit the four valves in the fruit wall, diverge and extend downwards (Figs 2G, 5D, F). These four ribs continue into the well-developed swollen-cylindrical flange of decay-resistant tissue that forms the core of the swollen seed base. Outer surface of the flange with about 12 to 15 longitudinal ribs (Figs 3I, 4D, 7B). Four are continuations of the four primary ribs at the angles of the seed body (Fig. 3L), but between each pair are two or three subsidiary longitudinal ribs (Figs 3I, L, 4D, 7B). Inner surface of the flange smooth with an upper transverse septum that separates the seed cavity from the seed base (Figs 3K, M, 4A, C, 6C, 7C, D).

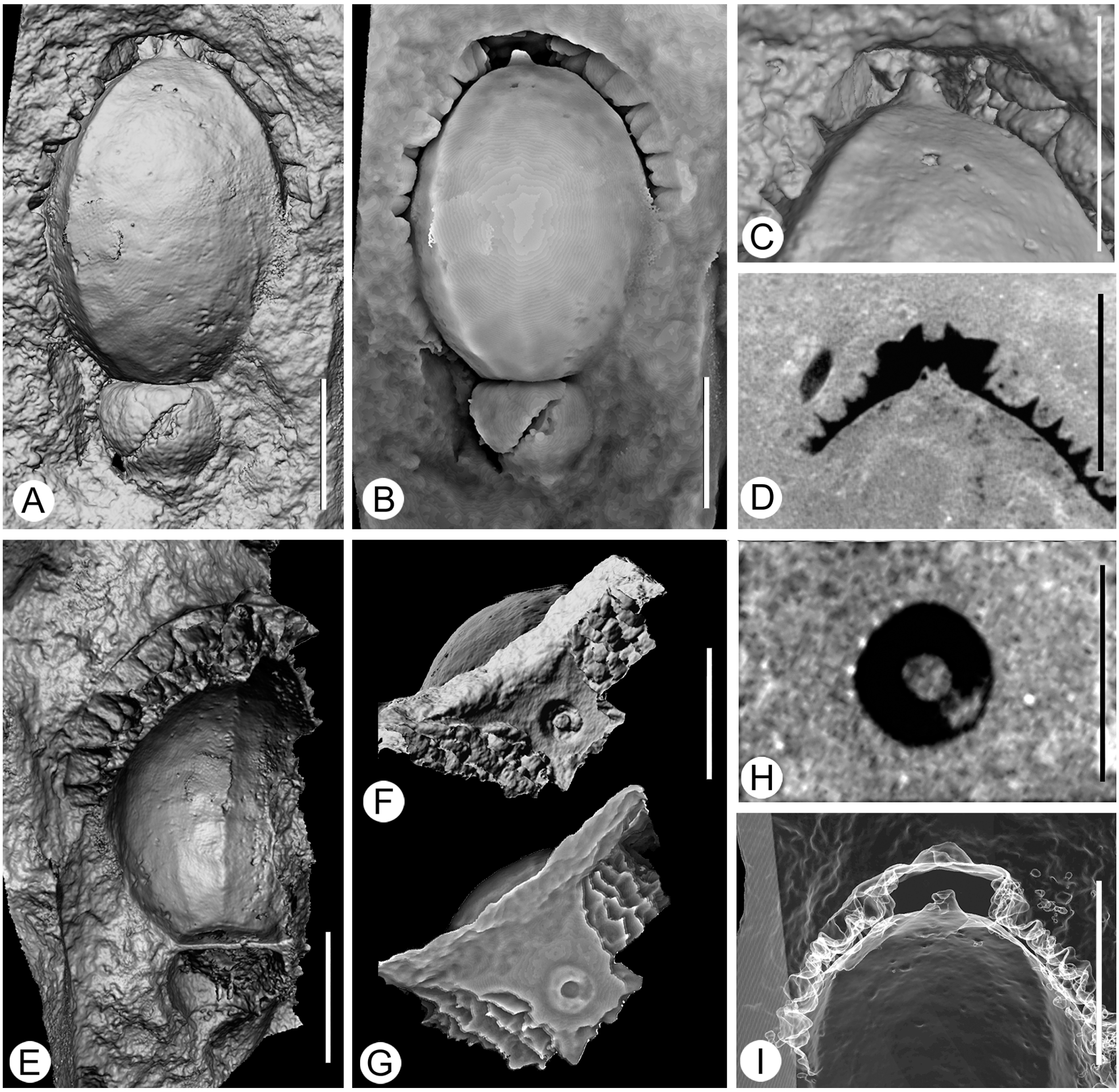

Figure 5. *Decaturospermum macrocarpum* gen. et comb. nov. from the Dakota Formation, Decatur, Nebraska, USA. USNM 42600 (Lectotype). Micro-CT scan images; reflective surface renderings (**A**, **C**, **E**, **F**), translucent surface renderings (**I**), virtual sections (**D**, **H**), and depth map (**B**, **G**). **A**. Seed in lateral view showing the cast of the seed cavity with infilling of the micropylar canal at the apex and the cast of the swollen seed base. Note the longitudinal rib on the cast of the seed cavity reflecting one edge of the quadrangular internal cross section; **B**. Seed in same orientation as A, showing the faint impressions of the dendritic reticulate pattern of thickenings in the inner part of the outer covering (envelope) and cast of the lower portion of the micropylar canal; **C**. Detail of the apical region in B showing the infilling of the proximal portion of the micropylar canal and the two layers of the outer covering (envelope), the inner seen as cavities from which the decay-resistant tissues have been lost, the outer seen as a fill of sandstone matrix; **D**. Virtual longitudinal section through the seed apex in the same orientation as C, showing the cavities (black) left by the loss of the decay-resistant tissue. Note the flattened surface of the seed apex and the solid raised area of decay-resistant tissue surrounding the fill of the micropylar tube; **E**. Seed in lateral view rotated 180 degrees from **A**, showing the distinct horizontal septum that delimits the base of the seed cavity separating it from the swollen seed base. Note the remains of the outer covering (envelope) at upper left; **F**, **G**. Apical views of seed showing one of the four sides of the angular seed apex with the smooth surface of the cast of the seed cavity (upper left) and the sculptured surface of the inner layer of the outer covering (envelope, lower left, upper right). Note the raised circular area around the infilling of the micropylar tube; **H**. Virtual transverse section through the seed apex showing the fill of the micropylar tube surrounded by a cavity created by the decay-resistant tissue of the outer covering (envelope); **I**. Transparent longitudinal section through the seed apex showing the two layers of the outer covering (envelope), the projection into the proximal part of the micropylar canal from the seed cavity, and the void left by the solid block of decay-resistant tissue around the micropyle. Scale bars = 5 mm in A, B, E–G; 1.5 mm in C, D, H, I

Swollen-cylindrical flange of harder decay-resistant tissue surrounding a swollen pad of softer, decay-susceptible tissue, which consists of a short stalk and an expanded head (Figs 2A, B, 3K, M, 4A–C, 5A, B, 6A, 7A). Four vascular bundles ~0.44 mm thick pass through the pad before entering the base of the seed cavity through the transverse septum (Figs 2D, 3I, J,

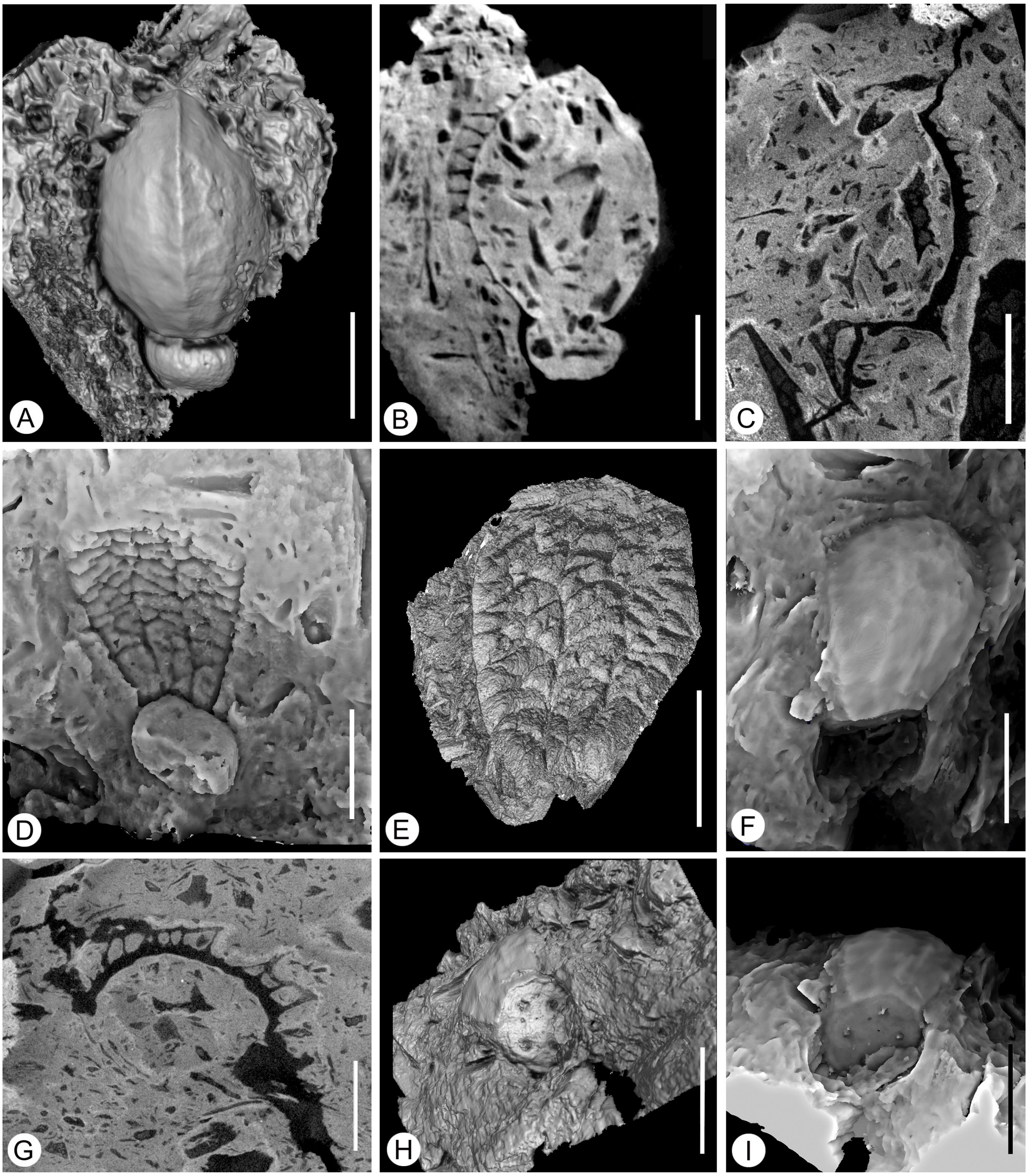

Figure 6. *Decaturospermum macrocarpum* gen. et comb. nov. from the Dakota Formation, Decatur, Nebraska, USA. **A**–**B**. UF 19025-85533. **C**–**I**. UF 19025-53138. Micro-CT scan images; reflective surface renderings (**A**, **E**, **H**), depth map (**D**, **F**, **I**), virtual sections (**B**, **C**, **G**). **A**. Lateral view showing casts of the seed cavity and of the swollen-cylindrical flange around the seed base; **B**. Longitudinal section in same orientation as A, showing casts of the seed cavity and the interior of the swollen basal flange. Note the two layers of the outer covering (envelope), the outer layer of decay-susceptible tissue that has been infilled by the sandstone matrix and the inner layer of decay-resistant tissue with ribs that are preserved as cavities; **C**. Longitudinal section of broken seed showing the cavities reflecting the remains of the decay-resistant tissue of part of the outer covering (envelope) and part of the basal flange; **D**, **E**. Oblique lateral view of a broken seed showing the position of the four vascular bundles on the cast of the decay-susceptible tissues inside the basal flange (D) and the impression of the ribbed inner layer of the outer covering (envelope) from one of the four seed valves (D, E). Note the two primary longitudinal ribs along the margins of the valve, the less clearly defined secondary longitudinal ribs and the irregular dendritic reticulate pattern. Note also that the vascular bundle scar corresponding to the remaining valve is in a median position (D); **F**. Oblique lateral view of a broken seed showing the cast of the seed cavity and the cavity from which the cast of the swollen decay-susceptible tissues inside the basal flange of the seed base has fallen away; **G**. Transverse section through a broken seed showing the cavities left by part of the decay-resistant inner layer of the seed envelope; **H**, **I**. Basal views of the cast of the decay-susceptible tissues inside the basal flange showing the four vascular bundles and the smooth inner surface of one of the four valves of the envelope. Note that the vascular bundle scar corresponding to the remaining valve is in a median position. Scale bars = 5 mm

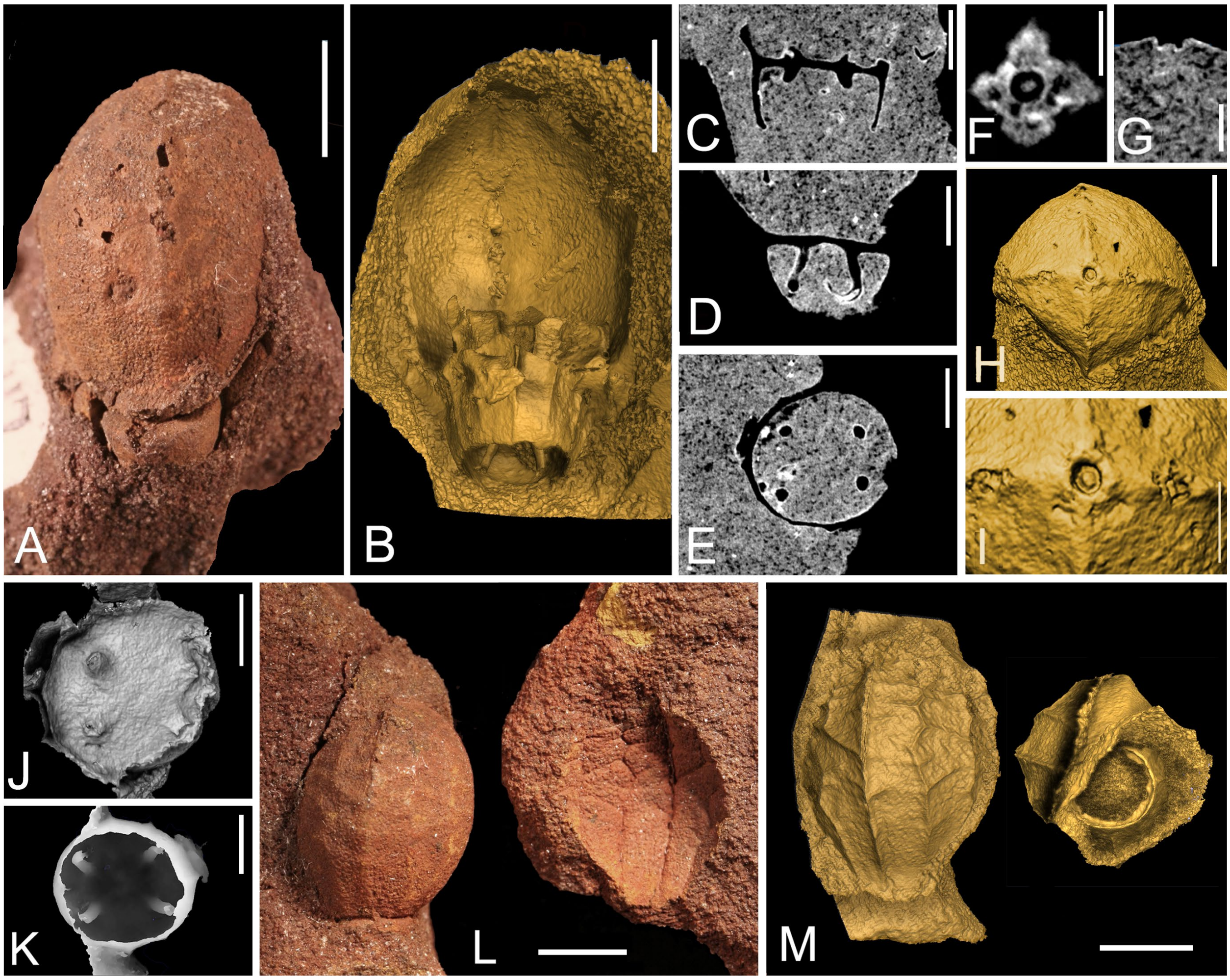

Figure 7. *Decaturospermum macrocarpum* gen. et comb. nov. from the Woodbine Sandstone, Denton, Texas, USA. **A–K**. ANSP 3647. **L**, **M**. ANSP 3485 and ANSP 3486. Reflected Light (**A**, **L**); Micro-CT scan images; reflective surface renderings (**B**, **H**, **I**, **J**, **M**), virtual sections (**C–G**), depth maps (**K**). **A**. Lateral view showing casts of the seed cavity and of the decay-susceptible tissues inside the basal flange of the seed base. Note the weakly-developed longitudinal rib on the cast of the seed cavity; **B**. Oblique lateral view showing the cast of the seed cavity with a weakly-developed longitudinal rib and the cast of the decay-resistant tissues that form the swollen-cylindrical flange around the seed base with primary and secondary ribs. Note the vascular bundles inside the basal flange; **C**, **D**. Longitudinal sections through the basal flange inside the swollen seed base showing the upper part of the vascular bundles inclined toward the center of the seed (D) but thinning and slightly inclined outward in the base of the seed cavity (C); **E**. Transverse section through the basal flange of the seed base showing the circular outline and four vascular bundles; **F**. Transverse section of apical region showing the filling of the micropylar tube; **G**. Longitudinal section showing outline of the sedimentary infilling of the micropylar region; **H**. Apical view of the cast of the seed cavity showing quadrangular outline; **I**. Detail of H, showing the infilling of the micropylar canal, surrounded by a raised ring in the position of the integument, which is separated by a circular furrow from the position of the outer covering (envelope); **J**. Septum separating the base of the seed cavity from the basal flange, viewed from below, showing the four vascular bundles entering from the periphery of the seed; **K**. Detail through the center of the decay-resistant tissues that form the swollen-cylindrical flange inside the seed base, viewed from below, showing the course of the vascular bundles within the skirt inclined toward the center of the seed; **L**. Part and counterpart of seed (ANSP 3485 left, ANSP 3486 right) showing cast of the seed body and the impression of the ribbed surface of the inner decay-resistant layer of the outer covering (envelope); **M**. Lateral (ANSP 3486 left) and basal (ANSP 3485 right) showing the ribbed outer surface of the decay-resistant inner layer of the outer covering (envelope), and the circular outline of the seed base above the level of the basal flange. Scale bars = 5 mm in A, B, H, L, M; 2 mm in C–E, J, K; 1 mm in F, G, I

L, 4D, 6D, H, I, 7E, J, K). The course of each of the four vascular bundles as it passes through the pad of softer tissue before entering the base of the seed is distinctively sinuous (Figs 3K, L, M, 4A, B). Proximally, near the seed base, each bundle is positioned about midway between the edge of the flange and the central axis of the seed (Figs 3M, 4A, B). Distally, each bundle first arcs gently inward bringing the four bundles closer together before gently curving outwards, which separates the bundles more widely and brings them closer to the perimeter of the pad (Figs 3M, 4A, B). Each bundle then curves back inwards toward the center of the pad. As they enter the seed cavity about 1.5 mm from the circumference of the pad they once again reverse course and are reflexed slightly outward (Figs 3M, 7C). Each

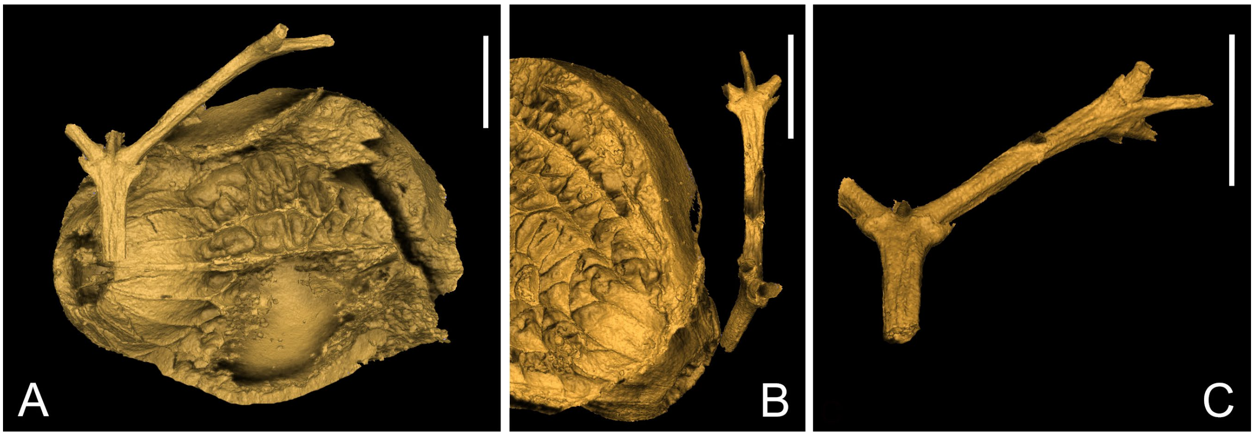

Figure 8. Decussately branched axis preserved within the same specimen as the lectotype of *Decaturospermum macrocarpum* gen. et comb. nov., but not visible externally. Dakota Formation, Decatur, Nebraska, USA (USNM 42600a). Reflective surface renderings. **A**, **B**. Seed in oblique lateral views showing adjacent axis with opposite and decussate branching; **C**. Axis digitally extracted and vertically oriented, showing opposite and decussate branching. Note the two small bracts subtending the two major branches. Scale bars = 5 mm

bundle alternates with the primary ribs on the outer surface of the decay-resistant flange and the ribs of the seed coat (Fig. 3I, J, L). Each bundle is positioned opposite one of the four flat faces of the seed body (Figs 2D, 3I, J, L, 4D, 6D, H, I), and most likely supplies one of the four valves.

DISCUSSION

ORIGINAL MATERIAL AND DESIGNATION OF LECTOTYPE

The name *Laurus macrocarpus* was first used by Lesquereux (1868: p. 98) in a paper describing more than 50 species based mainly on collections by F.V. Hayden from "north of Fort Ellsworth, Nebraska, or its vicinity," but also incorporating material from elsewhere in the "same formation, belonging to the Smithsonian Institution" (Lesquereux, 1868: p. 91). Lesquereux (1868) gave no locality data for *Laurus macrocarpus*. He also cited no specimens and provided no illustrations, but neither were required for valid publication at that time. Hence the 1868 account is the validating publication for the species name. Lesquereux (1874) provided a more detailed treatment of this species in which he corrected spelling of the epithet to *Laurus macrocarpa* Lesquereux, perhaps to be consistent with the gender of the genus name under the interpretation that it was a tree and conforming to the treatment of trees, such as *Laurus* and *Quercus* as feminine in botanical Latin. Lesquereux (1891) later cited the taxon as *Laurus macrocarpa*, which confirms that he intended to adopt this spelling.

In his 1874 treatment, using the name *Laurus macrocarpa*, Lesquereux again cites no specimens, but provides illustrations (Lesquereux, 1874: p. 74, 75; pl. 10, fig. 2, 2a). One of the two specimens in the Smithsonian (USNM) collections (USNM 42600), which is labelled as the holotype, is from Decatur, Nebraska consistent with what accompanies Lesquereux's description (Lesquereux, 1874: p. 75; "*Habitat*. – Near Decatur, Nebraska, *Hayden*"). The other specimen, USNM 50401, is in three pieces (USNM 50401A, B, Aa) and has a label affixed to it inscribed 'Lacoe 4053, NE of Delphos, Kansas'. Lesquereux (1868: p. 98) refers to the swollen seed base as 'club-shaped, smooth, marked upon its top, or on the surface where it joins the nut, by four vascular dots.' His later illustrations (Lesquereux, 1874: pl. 10, figs 2 and 2a) are small but clearly show these features. We cannot conclusively identify either of the two USNM specimens as the material that Lesquereux used to establish his species in 1868 because he cited no specimens. However, we infer that Lesquereux's 1868 description was based on both USNM specimens because the 'four vascular dots,' are only visible in USNM 50401. We think it likely that this specimen from Delphos was the basis for Lesquereux's 1874 illustration. However, Delphos is not mentioned, and the only locality referred to explicitly is Decatur, Nebraska (Lesquereux, 1874). Therefore, in the absence of explicit citations of specimens, we recognize USNM 42600 as the lectotype for the species.

OTHER SPECIMENS AND NOMENCLATURE

Conclusively attributable to *Decaturospermum macrocarpum* are specimens from the Woodbine Formation of Texas, for which MacNeal (1958) created the name *Laurocarpum tetragonale*. MacNeal (1958) described and figured the specimens, which he placed in a new species *Laurocarpum tetragonale* MacNeal. ANSP 3485 and ANSP 3486 are part and counterpart of the lectotype and were given the numbers 2491 and 2491a (MacNeal, 1958: p. 120, pl. 21, figs 3, 4). ANSP 3647 is specimen "no. 502" referenced and illustrated by MacNeal (1958: p. 120, pl. 21, fig. 5), for which the counterpart is now known (ANSP 3526). MacNeal (1958) recognized the strong resemblance of his specimens to *Laurus macrocarpa* and he also noted the characteristic features highlighted by Lesquereux, but he suggested that the 'Woodbine fruits are uniformly larger and differ in their 4-angled character from *L. macrocarpa.'* MacNeal suggested that this 'warrants specific differentiation.' Our comparison of the eight specimens available, including the four recently collected specimens from Decatur, Nebraska, suggests that there is no clear distinction between the two species, which we therefore place in synonymy. We also reject MacNeal's assignment of the Woodbine material, to the genus *Laurocarpum* Reid and Chandler along with his proposal (not formally implemented) to treat *Laurus macrocarpa* similarly. The genus *Laurocarpum* was established by Reid and Chandler (1933) to accommodate one-loculed, one-seeded angiosperm fruits from the Eocene London Clay flora that are thought to be related to the extant angiosperm family Lauraceae. We interpret the fossils from the Dakota Sandstone very differently and assign them to *Decaturospermum* gen. nov.

In addition to specimens referred to *Laurus macrocarpa* Lesquereux (1891) named a further specimen, cited as 'No. 530 of the museum of the University of Kansas. Collected by E.P. West,' *Laurus microcarpa* (Lesquereux, 1891: p. 93, 94; pl. 16, fig. 8). This specimen (now missing) has not been seen by us. According to Lesquereux (1891) this specimen resembles *D. macrocarpum*, but differs in having five, rather than four, vascular scars, as well as its smaller size. We therefore exclude it from our concept of the species. Also excluded is a single poorly preserved specimen from Barnes High, Brightstone Bay, Isle of Wight in the Wessex Formation (Aptian) of the Wealden of southern England (Austen and Batten, 2011: text-fig. 32.12G), which closely resembles *D. macrocarpum* in shape and size. We think that this specimen is probably attributable to *Decaturospermum*, but because it is poorly preserved and lacks critical details we cannot link it securely to the material from North America.

COMPARISON WITH SEEDS OF LIVING AND FOSSIL SEED PLANTS

Given the overwhelming abundance of angiosperm leaves in the Dakota Sandstone it is not surprising that Lesquereux (1868, 1874, 1891) interpreted the limited fossil material of this species as a fruit. However, his comparison with the drupes of Lauraceae is ruled out by the four valved construction. The apical projection is also hard to interpret as a style, and the swollen base, which might appear to represent a receptacle, is also strange, with four distinct, regularly-spaced, vascular bundles and a solid septum separating the basal flange from the main body. *Laurus macrocarpa* was recognized as interesting in the late 1970s (Dilcher, 1979) but the combination of features was puzzling when these specimens were studied by one of us (PRC) in the mid-1980s. However, since then, the expanded fossil record of Gnetales (Friis et al., 2011) and the numerous chlamydospermous seeds described from mesofossil floras of Early Cretaceous age from eastern North America and Portugal (Friis et al., 2007, 2009, 2013, 2014, 2019) have broadened the scope for potential comparisons.

The key features for interpreting the structure of the fossils and their relationships to living and fossil plants include their symmetrical four-angled form, the structure of the two-layered outer covering, the internal features of the swollen seed base, and the four vascular bundles that enter the base of the central seed cavity, each of which is opposite the center of one of the four seed faces and appears to supply one of the four valves. The symmetrical four-angled form implies that the seed did not mature in a tightly packed cone, which is also emphasized by the symmetrical position of the four vascular bundles. These bundles could be interpreted as the vascular supply to the nucellus and integument of the seed, but this is difficult to reconcile with the situation in

Ginkgo, cycads and conifers. There are no vascular bundles in the two-angled, or occasionally three-angled, seeds of *Ginkgo*, and while seeds of cycads vary in shape, they are never regularly four-angled and have a more complex, less symmetrical, vascular supply with an inner and outer set of vascular bundles (Zumajo-Cardona et al., 2021). Seeds of conifers vary in shape but are also not regularly four-angled and are generally have very different vasculature. Comparison to seeds of extant *Ephedra*, is more straightforward, but carries with it the implication that the outer covering of the seed is an envelope, rather than the integument, and hence that the seed is chlamydospermous, in which case the four vascular bundles are readily interpreted as supplying the envelope rather than the integument.

Seeds of *Ephedra* are generally either three-angled with three vascular bundles supplying a tripartite envelope, or bifacial with two vascular bundles supplying a bipartite envelope (Rydin et al., 2010). However, in several species, for example *Ephedra trifurca* Torrey ex S. Watson and *Ephedra californica* S. Watson, the seed is four-angled and the envelope is supplied by four symmetrically placed vascular bundles (Rydin et al., 2010: fig. 5) very comparable to the situation in *Decaturospermum* (see also *Ephedra fragilis* Desf., Rydin et al., 2010: fig. 2). Also significant is that in all species of *Ephedra* where the envelope supplied by four vascular bundles the seed is borne in a single-seeded cone (Rydin et al., 2010), which is also consistent with the symmetrical form of *Decaturospermum*. The envelope in most species of *Ephedra* also has an outer fleshy layer of parenchyma and an inner, harder, protective layer of fibers (Rydin et al., 2010), which can be readily compared with the outer decay-susceptible layer and inner decay-resistant layer inferred for the outer covering of the seed in *Decaturospermum*. The interpretation of the outer covering of the fossils as an envelope, rather than a fruit wall or integument, is also more consistent with its four-valved construction and the compound structure of the micropylar region in which the micropylar tube is separate from the four valves of the outer covering (Fig. 7H, I).

A gnetalean relationship is also supported by comparison of *Decaturospermum* with fossil of cones of *Bassitheca hoodiorum* Manchester et Crane from the Late Jurassic Morrison Formation of Utah and Colorado (Manchester et al., 2022). Cones of *Bassitheca* resemble those of extant species of *Ephedra* with two-seeded cones in which the seed envelope is supplied by three vascular bundles (e.g. *Ephedra foliata* Boiss et C.A.Mey, *Ephedra viridis* Coville, *Ephedra americana* Humb. et Bonpl. Ex Willd.). Especially informative is a specimen of *Bassitheca* (Manchester et al., 2022: fig. 5U, V) that shows an arrangement of three vascular bundles, which clearly resembles the symmetrical placement of the four vascular bundles in *Decaturospermum*. In this specimen of *Bassitheca* the three bundles alternate with the pair of bundles that supply the adjacent bract, exactly as seen in *Ephedra aphylla* Forssk. (Rydin et al., 2010: fig. 2A).

Recognition of the resemblances between the seeds of *Decaturospermum* and those of *Ephedra* implies that the fossil seeds are chlamydospermous, which in turn invites comparison with the diverse gymnosperm seeds from Early Cretaceous mesofossil floras that have been grouped together informally, as seeds of the BEG group (Bennettitales, Erdtmanithecales, Gnetales). All of these seeds have an envelope that encloses the integument and nucellus (Pedersen et al., 1989; Rydin et al., 2006a; Friis et al., 2007, 2009, 2013, 2014, 2019; Mendes et al., 2020) and 20 of the 27 species of BEG seeds reviewed by Friis et al. (2019) are four-angled. Where associated pollen is known for those seeds that are more-or-less square in cross section, the grains are ephedroid (Friis et al., 2019: table 1).

A further characteristic of *Decaturospermum* and other chlamydospermous seeds known from mesofossils is that the envelope usually has a soft outer layer that is often not well preserved, exposing the variously sculpted outer surface of the hard inner layer. The anastomosing ridges inferred for this layer in *Decaturospermum* are similar to the patterns on the sculpted outer surface of the hard inner layer of the envelope in many of these chlamydospermous seeds, for example, *Acanthocatia virginiensis* E.M.Friis, K.R.Pedersen et P.R.Crane, *Quadrispermum parvum* E.M.Friis, K.R.Pedersen et P.R.Crane and *Lobospermum rugosum* E.M.Friis, K.R.Pedersen et P.R.Crane, all from the early to middle Albian Puddledock mesofossil flora of Virginia. Similarly, in the slightly older, Aptian-early Albian, Catefica mesofossil flora from

Portugal, *Quadrispermum parvum* E.M.Friis, K.R.Pedersen et P.R.Crane and *Lobospermum* sp. have a hard inner layer of the envelope in which the outer surface is sculpted (Friis et al., 2019). None of these seeds have a pattern of sculpting as robust as that seen in *D. macrocarpum*, but the fundamental resemblance is clear.

Cattomia trapezoides E.M.Friis, K.R.Pedersen et P.R.Crane, a chlamydospermous seed from the Puddledock locality of the Potomac Group, is especially relevant for comparison with *Decaturospermum*. In *Cattomia* the envelope consists of an outer epidermis, an outer zone of nonlignified cells and an inner sclerenchymatous zone with an irregular sculpted surface (Friis et al., 2013). *Cattomia* differs from *Decaturospermum* in having four apical projections that extend from the corners of the four-angled seed, but it is the only chlamydospermous seed described so far that has a flange of decay-resistant tissue at the base comparable to that in *Decaturospermum* (Friis et al., 2013: fig. 9A–D). Inside this extended flange, *Cattomia* also shows fragmentary remains of the tissue to which the seed is attached (Friis et al., 2013: fig. 10G), but none of the mesofossil seeds described so far show the vascular bundles seen in *Decaturospermum.*

Taken together, the presence of a tetragonal envelope comprised of four valves, combined with the unusual vascular supply, the *Cattomia*-like flange around the seed base and other anatomical similarities, indicate that *Decaturospermum* is a chlamydospermous seed rather than an angiosperm fruit. However, *Decaturospermum* differs from all previously described fossil chlamydospermous seeds in its much larger size. Other chlamydospermous seeds described so far are typically less than 3 mm long and only exceptionally reach 5 mm long (Friis et al., 2019). At ~20 mm or more long, including the swollen seed base, *Decaturospermum* is significantly larger. It is also more than twice the size of seeds of extant *Ephedra*. Nevertheless, given the fundamental similarities between *Decaturospermum* and other chlamydospermous seeds, as well as the specific similarities to extant *Ephedra*, the closest living relatives of *Decaturospermum* are most likely among Gnetales. The presence of Gnetales in the sandstone facies of the Dakota Formation is also supported by a small shoot fragment present in the same hand specimen as the lectotype of *Decaturospermum* (USNM 42600). As in extant *Ephedra*, and as also in compression/impression specimens of gnetalean stems from the Early Cretaceous (Crane and Upchurch, 1987; Rydin et al., 2006b; Yang, 2010; Friis et al., 2011; Yang and Wang, 2013; Yang and Ferguson, 2015), the specimen shows opposite branching with each branch subtended by a bract (Fig. 8). We cannot assume that *Decaturospermum* and the axis are parts of the same species, but the shared relationship to Gnetales is intriguing.

CONCLUSIONS

Occasional conifer cones occur in the Dakota Sandstone flora, but *Decaturospermum* is the first gymnosperm reproductive structure from the flora to be described in detail. It highlights the opportunities for informative studies of such seemingly unpromising, but three-dimensionally preserved, fossil material. Micro-CT scanning, combined with reflected light observations, can provide high quality structural data that is of value for determining systematic relationships. The difference in size between *Decaturospermum* and the diverse chlamydospermous seeds recovered from mesofossil floras also illustrates the new perspectives that can emerge from exploring the plant fossil record preserved in a broad range of taphonomic settings using whatever techniques are appropriate.

The presence of a robust envelope in *Decaturospermum*, as in the seeds of extant *Ephedra* and *Gnetum*, as well as the seeds of extinct Bennettitales, Erdtmanithecales and related plants, means that protection of the embryo is transferred from a hard layer in the integument to a hard layer in the surrounding envelope, which then becomes an integral part of the dispersal unit. The integument itself was evidently thinner and less robust. However, the size of *Decaturospermum* establishes a new search image for future work on fossil chlamydospermous seeds and indicates that chlamydospermous seed structure can be recognized in diverse preservation states.

Decaturospermum establishes that plants related to Gnetales grew among the angiosperm-dominated mid-Cretaceous vegetation preserved in the sandstone facies of the Dakota Formation. Although unanticipated based on common perceptions of the Dakota Sandstone flora, the presence of a putative gnetalean is consistent with the ubiquity of ephedroid pollen in the Dakota Formation (Ludvigson et al., 2010). The macrofossil record of Gnetales and their allies has expanded dramatically in the past 40 years (e.g. Krassilov, 1986; Crane and Upchurch, 1987; Rydin et al., 2006b; Friis et al., 2011; Rothwell and Stockey, 2013; Yang and Ferguson, 2015; Manchester et al., 2021, 2022). *Decaturospermum* adds to that record, highlighting the continuing opportunities to expand what we know about the history of a key group of living seed plants, toward the goal of placing the three extant genera of Gnetales in context among their once abundant and diverse extinct relatives.

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