

Early Eudicot flower and fruit: *Dakotanthus* gen. nov. from the Cretaceous Dakota Formation of Kansas and Nebraska, USA

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ABSTRACT. An extinct plant that populated the eastern margin of the Cretaceous Midcontinental Seaway of North America about 100 million years ago has attracted interest as one of the earliest known bisexual flowers in the fossil record. Reexamination of the type specimen of *Carpites cordiformis* Lesq., and corresponding specimens from sandstones and clays of the Dakota Formation of Kansas and Nebraska and the correlative Woodbine Sandstone of Texas, with both light microscopy and micro CT scanning, leads to a revised concept of the morphology and affinities of the “Rose Creek flower”. The moderately large flowers (22–30 mm diameter) have two perianth whorls: five basally fused sepals and five free spatulate petals. The gynoecium is pentacarpellate with five styles. A crescent-shaped nectariferous pad occurs at the base of the gynoecium aligned with each sepal. Ten stamens are inserted at the level of the nectaries, one whorl organized opposite the sepals and another opposite the petals. *In situ* pollen is oblate, brevitrilocporate and finely verrucate. The fruits are loculicidal capsules with persistent calyx and disk. Comparing the full suite of observed characters with those of extant angiosperms indicates particularly close similarity to the monogeneric fabalean family Quillajaceae, with shared features of perianth number and morphology, nectary position and morphology, stamen number and morphology, and gynoecium merosity, although the fossil differs from extant *Quillaja* in fruit type (capsule vs basally syncarpous follicles) and especially in pollen morphology (10 µm oblate, microverrucate, vs 30–40 µm prolate, striate).

KEYWORDS: fossil, angiosperm, Quillajaceae, flower, fruit, pollen, Rose Creek flower, Albian, Cenomanian

INTRODUCTION

In the late 1800s when the leaf flora of the Cretaceous Dakota Sandstone was initially monographed, Lesquereux (1874, 1892) recognized various co-occurring fruits preserved 3-dimensionally within the sandstone. One of those fruit types is a pentalocular capsule that has been attributed to different species based on different specimens, for which the binomial *Carpites cordiformis* Lesquereux (1892) retains priority. A century later,

Basinger & Dilcher (1984) recognized an unnamed flower from shales of the Dakota Formation in Nebraska. These flowers, informally dubbed the “Rose Creek flower” (Dilcher & Crane 1984a), were shown to be bisexual and actinomorphic, representing the earliest well-documented example of this condition in the diversification of angiosperms (Basinger & Dilcher 1984, Schönenberger & von Baltazar 2006, Friis et al. 2011).

In addition to the specimens illustrated by Basinger & Dilcher (1984), a large number of “Rose Creek flowers” collected by Dilcher and students were deposited in the University of Florida (UF) paleobotanical collection, including a range of preservational quality and ontogenetic states from flowers in anthesis to mature fruits. The mature fruits correspond to those known as *Carpites cordiformis* that Lesquereux (1892) described from the Dakota Sandstone. However, the generic name *Carpites*, commonly used as a catchall for fossil fruits of uncertain affinity, and based on type material unlike that of these Dakota fruits, is inappropriate. Here, we recognize these fossil flowers and their fruits with a new generic name and combination, *Dakotanthus cordiformis* (Lesq.) Manchester, Dilcher, Judd & Basinger comb. nov., and provide more complete documentation of the morphology.

The combination of optical, scanning electron microscopy (SEM) and microcomputed tomography (μ CT scanning) observations provided substantial new information on this species and have led us to conclude that there were ten stamens rather than the five originally interpreted (Basinger & Dilcher 1984). The new observations corroborate the assignment to the Eudicots and lead us to a new view of systematic relationships.

Some authors had argued for rhamnalean affinities of the “Rose Creek flower” (Richardson et al. 2000, 2004) because the stamens were thought to be only five and opposite the petals.

Our recognition that the flowers were instead diplostemonous, with ten stamens, indicates that these flowers belong elsewhere within the Rosid Clade. Here we compile the morphological characters of this extinct plant, and we infer its possible position with reference to current concepts of the phylogeny of angiosperms.

MATERIALS AND METHODS

Specimens have been recovered from multiple sites in Nebraska, Kansas, and Texas representing deposition along the eastern margin of the North American Cretaceous Epicontinental Seaway (Fig. 1, Tab. 1). These compressions, impressions, and sandstone casts and molds of fruits were studied from collections including these: the Smithsonian, Washington, D.C. (USNM), Division of Paleobotany collections; the University of Kansas, (KUPB); and the Florida Museum of Natural History, Gainesville (UF).

The Dakota Formation is considered to be late Albian to Cenomanian in age, ca 100 Ma (Upchurch & Dilcher 1990, Brenner et al. 2000, Ludvigson et al. 2010). Although radiometric dates from zircon are available from Dakota Formation sites along the western side of the Epicontinental Seaway in Utah, indicating Middle to Late Cenomanian age (Barclay et al. 2015), the dating of floras on the eastern side of the seaway relies mainly on biostratigraphic correlation. Numerous specimens were collected by David Dilcher and colleagues and students from shales of the Dakota Formation from a quarry 6 miles south of Fairbury, southeastern Nebraska; they are deposited at the Florida Museum of Natural History. Referred to as the Rose Creek locality (Rose Creek pit sensu Gröcke et al. 2006), this site includes a diverse leaf flora and was considered by Upchurch & Dilcher (1990) to be early to middle Cenomanian. However, Gröcke et al. (2006)

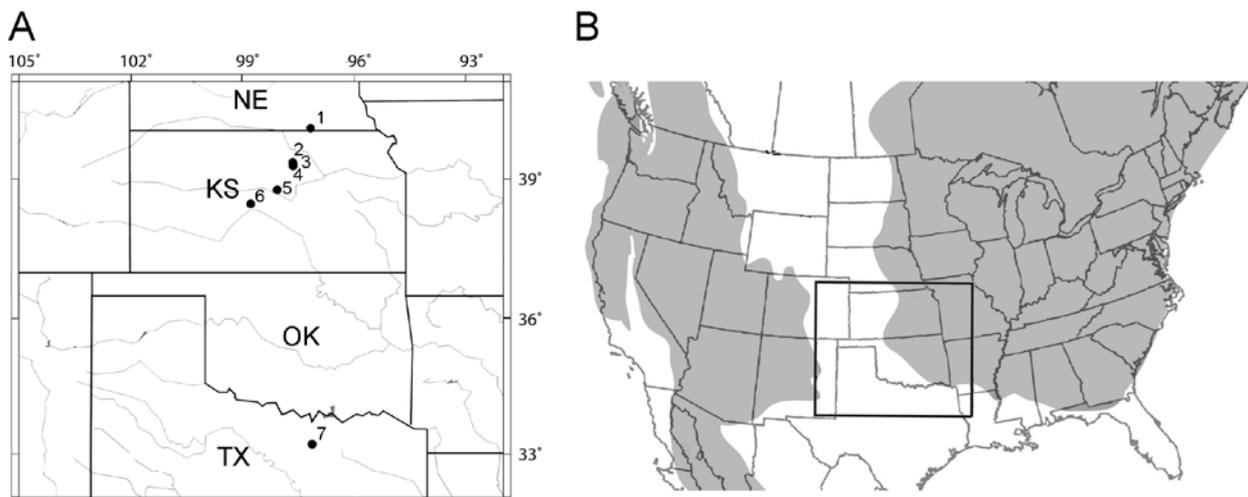


Fig. 1. Distribution of *Dakotanthus* with respect to the Early Cretaceous Epicontinental Seaway. **A.** Map showing localities from which *D. cordiformis* is known, from Nebraska (NE), Kansas (KS) and Texas (TX), plotted from the data in Table 1, using <https://coastalmap.marine.usgs.gov/mapit/> **B.** Paleogeographic reconstruction of North America during the late Albian, ca 101 million years ago, with rectangle denoting the area of the locality map in A. Land shaded, oceans unshaded, following Slattery et al. 2015

Table 1. Localities from which *Dakotanthus cordiformis* is known. These data were used for plotting on the map in Figure 1

Number on map, Fig. 1	Geographic source	Original coordinates	Latitude and Longitude	Geologic horizon (and lithology)	Exemplary specimens
1	Rose Creek, Jefferson Co., Nebraska	Sec.14, T 1N, R 2 E	40°03.01' N 97°10.12' W	Dakota Formation (shale)	UF15713-3427
2	Ottawa Co., Kansas	SW ¼ sec 15, T 9 S, R 3 W	39°16.212' N 97°38.377' W	Dakota Formation (sandstone)	<i>Carpites cordiformis</i> Holotype: USNM 50016
3	Cloud or Ottawa Co., Kansas	T 8 S or T 9 S, R 3 W	39°20.583' N 97°38.885' W (approximation)	Dakota Formation (sandstone)	" <i>Carpites tiliaceus?</i> (Heer) Lesquereux" (Lesquereux 1892): USNM 50025
4	Delphos, Kansas	ca 10 miles NE of Delphos	39°18.433' N 97°38.669' W	Dakota Formation (sandstone)	" <i>Nordenskioldia borealis</i> Heer" (Lesquereux 1992); USNM 50023
5	Ellsworth Co., Kansas	NE 1/4 sec 11, T15S, R 7W 5	38°45.947' N 98°03.770' W	Dakota Formation (sandstone)	KUPB-C 2053
6	Hoisington, Barton Co., Kansas	Ctr E1/2, sec. 20 T18 S, R 13 W	38°28.310' N 98°46.918' W	Dakota Formation (shale, clay)	UF 15706-3072
7	Denton, Denton Co., Texas	?	33°12.891' N 97°07.984' W (approximation)	Woodbine Formation (sandstone)	UF 18881-49955

have proposed, based on palynology and carbon isotope investigations through the local 10-m-thick section, that the Rose Creek pit straddles the Albian-Cenomanian boundary, with the leaf and flower megafossils occurring below the boundary.

A few impression specimens were recovered at Hoisington, Kansas from the Janssen Clay Member of the Dakota Formation (Tab. 1). This member was deposited after the J sequence boundary (Retallack & Dilcher 2012) and considered to be Cenomanian based on palynological data (Ludvigson et al. 2010).

Detailed stratigraphic controls are lacking for some of the localities collected in the 1800s, and it is likely that the position of individual sandstone localities may range from late Albian to early Cenomanian (Brenner et al. 2000), thus traversing the Early Cretaceous-Late Cretaceous boundary. As the Cretaceous has no formally recognized "Middle", we can say informally that these represent "mid-Cretaceous" plants.

Other specimens were recovered from the Woodbine Formation from a site in or near Denton, Texas. The Woodbine flora has been considered to be Cenomanian based on its stratigraphic position between the Late Albian–Early Cenomanian marine Grayson Marl and the Late Cenomanian–Early Turonian marine Eagle Ford Shale (MacNeal 1958, Friis et al. 2011).

Fossils were photographed by reflected light with a Canon Rebel 450 digital SLR with a 60 mm macrolens. MicroCT Scanning (μ CT) was done initially at Duke University's Shared Materials Instrumentation Facility, using a Nikon XTH 225 ST at 145 kV, with 1800 projections over 360° with a voxel size of 61 μ m. Subsequently, specimens were μ CT-scanned at the University of Florida, College of Engineering Nanoscale Research Facility, with GE Phoenix V|tome|xm240 CT Scanner, using a Tungsten reflection target and 0.5 mm copper filter, with a voltage of 120 kV and current of 100 μ A with 2100 images for voxel size of 42 μ m. The resulting datasets were processed with Avizo and Meshlab to obtain successive virtual sections, translucent volumes, and surface renderings. Example 3D meshes generated from the μ CT data have been archived under

the designation *Dakotanthus cordiformis*, at www.morphosource.org.

Pollen was preserved in only a few of the specimens and was retrieved by macerating small bits of carbonaceous material removed directly from anthers. Scanning electron microscopy was done initially with an ETEC Autoscan model U-1 in the former Department of Plant Sciences, Indiana University, during the 1980s, and more recently the original stubs were viewed again with a Hitachi SU5000 field-emission scanning electron microscope at the Interdisciplinary Center for Biotechnology Research at the University of Florida.

SYSTEMATICS

Dakotanthus gen. nov.

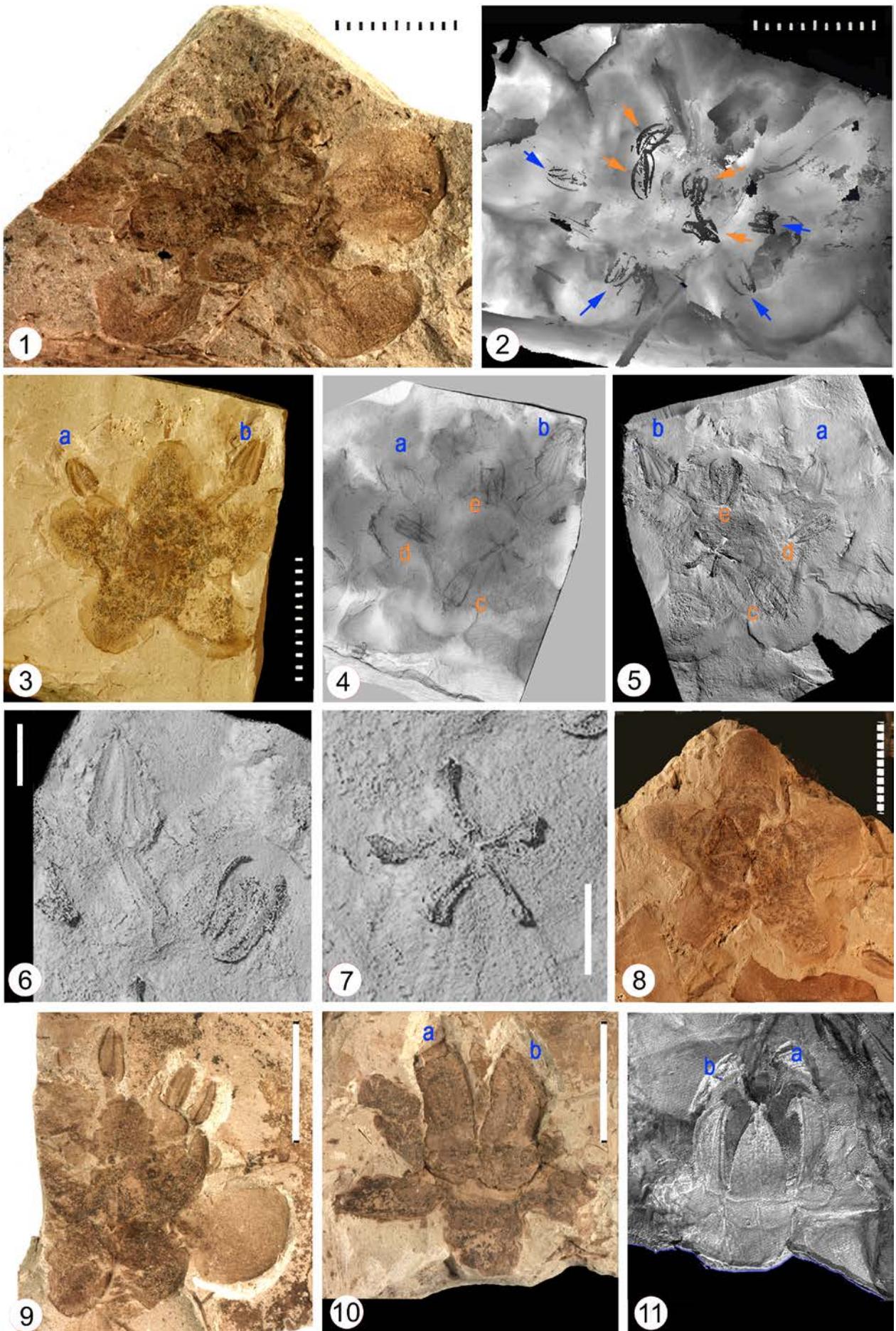
Pl. 1–4

Etymology. The generic name refers to the Dakota Formation, within which these fossils occur, and *anthos* (Gr) = flower.

Type species: *Dakotanthus cordiformis* (Lesq.) Manchester, Dilcher, Judd & Basinger comb. nov.

Basionym. *Carpites cordiformis* Lesquereux 1892, Monogr. U.S. Geol. Surv. 17: 220, pl. 22, fig. 9.

Other names applied. *Carpites tiliaceus?* (Heer) Lesquereux (Lesquereux 1892, p. 221, pl. 22, fig. 6). USNM 50025. Differs from *Carpolithus tiliaceus* Heer type material of Heer (1869). Specimen re-illustrated photographically by Dilcher 1979, p. 309, fig. 32. *Nordenskioldia borealis* Heer (Lesquereux 1892,



p. 219, pl. 44, fig. 3). Differs from *N. borealis* type material of Heer (1870).

Holotype. USNM 50016 (Lesquereux 1892, pl. 22, fig. 9; refigured here pl. 3, fig. 11).

Epitypes. We here designate the following specimens as epitypes: KUPB-C 2053 (Pl. 3, figs 1–10), USNM 50023 (Pl. 4, figs 4–9). UF 18881-49955 (Pl. 3, figs 13–17); UF15713-3427 (Pl. 1, figs 1, 2), UF3429 (Pl. 1, figs 3–7). UF5742 (Pl. 1, figs 10, 11), UF3423 (Pl. 2, figs 8–12), UF12958 (Pl. 1, fig. 8; Pl. 3, fig. 12).

Additional informative specimens. Fruits in sandstone: UF 18881-49955, USNM 50025 (Pl. 4, figs 10–12). Fruits in shale: UF 15713-5742, 6051, 70018. Flowers with intact anthers in shale: UF 15713-3521, 3522 (Pl. 1, fig. 9), 3532, 3533, 3538, 5252, 5253, 5259, 5268, 5287, 5609, 5965, 12939. Flowers in shale: UF 15713-3369, 3370, 3381, 3382, 3424, 3517, 3519, 3524, 3525, 3527, 3528, 3529, 3531, 3534, 3535, 3536, 4027, 5246, 5247, 5249, 5250, 5251, 5254, 5255, 5256, 5257, 5258, 5261, 5263, 5296, 5317, 5607, 5687, 5691, 5692, 5769, 5776, 5897, 5899, 6052, 6060, 6062, 6065, 6066, 6069, 6081, 12941, 12942, 12964, 13010, 13011, 13021, 13034, 32462, 32474, 32476, 32477, 70831, 70832, 70833, 70835, 70838, 70840, 70846, 70848, 70849. Isolated stamens in shale: UF 15713-3426, 5270 (Pl. 2, fig. 7), 5283 (Pl. 2, fig. 6), 5285, 5288 (Pl. 2, fig. 5), 5290 (Pl. 2, fig. 4), 32447. From Hoisington, Kansas: tattered flowers in shale: UF 15706-3073, 3074, 3080.

Nomenclature. The oldest binomial for this taxon is *Carpites cordiformis* Lesquereux 1892, based on a single capsular valve. This

valve, with its median septum, clearly was from a loculicidal capsule and it matches in size and shape those seen in more complete specimens from the same sedimentary horizon. However, the name *Carpites* Schimper 1874, often used as a taxonomic bin for indeterminate fossil fruits, was founded on an unrelated fruit from the Miocene of Oeningen, Switzerland (Andrews 1970). Because of its distinctive set of features, the Dakota species warrants recognition as a distinct genus. The attribution to Heer's genus *Nordenskioldia* was a case of mistaken identity; that genus, properly spelled *Nordenskioldia*, has schizocarpic fruits rather than capsules, and lacks the large persistent sepals and nectary disk seen on the Dakota fruits (Crane et al. 1991). While the single capsular valve of Lesquereux appears to belong to the same taxon as the many additional specimens attributed to the species, we consider the holotype to be ambiguous for the purposes of full description of the species. We therefore have recognized additional specimens as epitypes (ICN, Article 9.8; McNeill et al. 2012). "ICN Article 9.8. An epitype is a specimen or illustration selected to serve as an interpretative type when the holotype, lectotype, or previously designated neotype, or all original material associated with a validly published name, is demonstrably ambiguous and cannot be critically identified for purposes of the precise application of the name to a taxon."

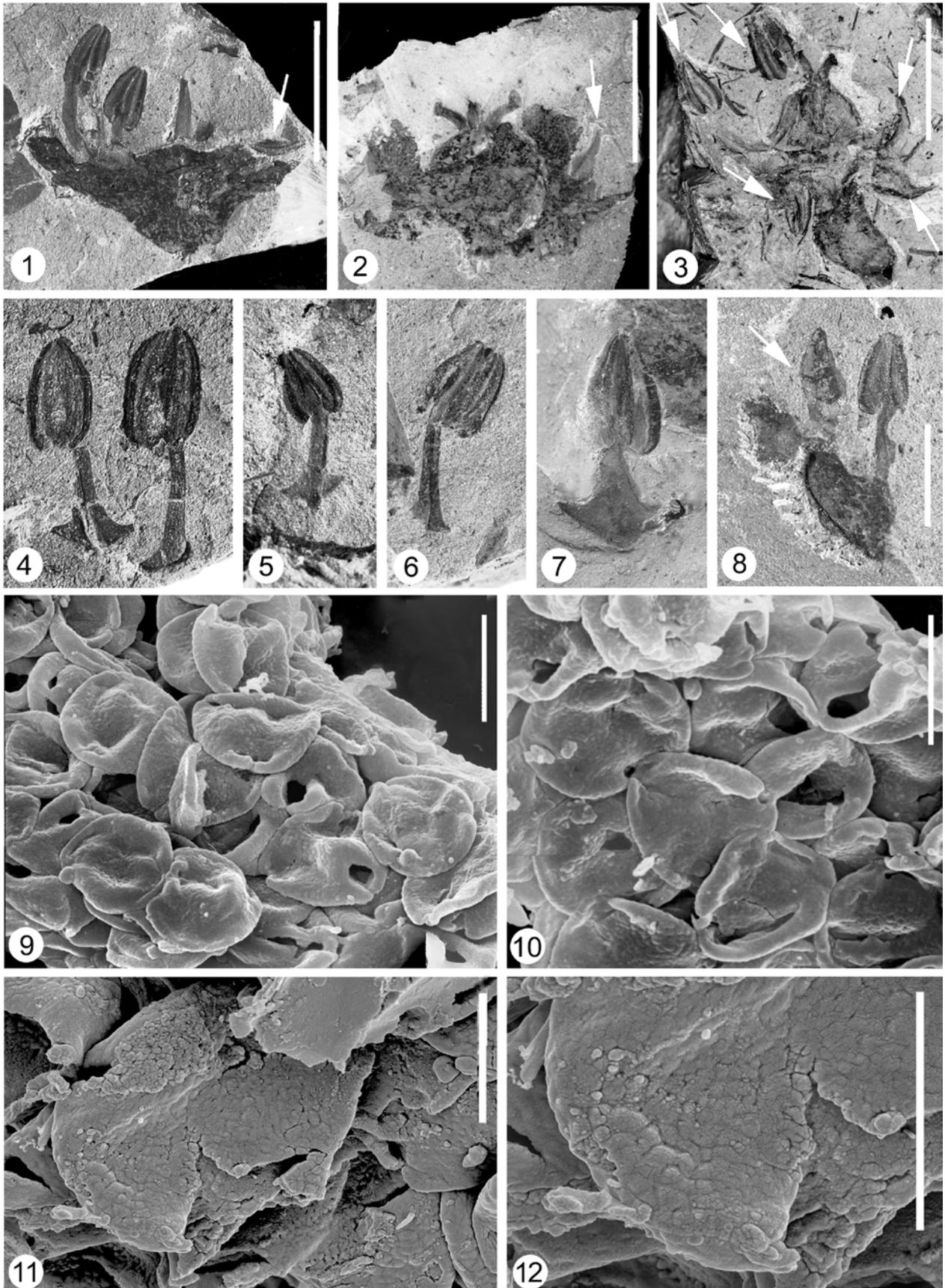
Original Species Description. "Fruit deeply impressed into the stone, cordiform, separated in the middle by a deep, linear furrow, as though composed of two narrowly obovate ovules, which are straight and confluent

←

Plate 1. *Dakotanthus cordiformis* (Lesq.) comb. nov. flowers in shale from Rose Creek, Nebraska; **1.** Vertically compressed specimen showing actinomorphic perianth including five-lobed calyx and four free petals, with a fifth petal inferred from symmetry. Reflected light, UF15713-3427. Previously figured (Basinger & Dilcher 1984, fig. 1a); **2.** Same specimen rendered translucent (depth mapping from μ CT data), revealing anthers (arrows) hidden beneath sediment surface and therefore not visible in fig. 1. Orange arrows indicate inner whorl of antisepalous anthers; blue arrows indicate outer whorl of antipetalous anthers; **3–7.** Single specimen viewed by various methods. Counterpart of specimen previously figured (Basinger & Dilcher 1984, fig. 1d), UF15713-3429; **3.** Flower by reflected light showing five sepals, compressed central gynoecium and two attached antipetalous stamens (labeled a, b) alternating with sepals; **4.** Same specimen in same orientation, with sediment rendered translucent by μ CT, revealing five style arms in center and three additional anthers labeled c, d, e; **5.** Same specimen flipped over, surface rendering of flower with anthers labeled as in fig. 4, μ CT; **6.** Detail of stamens, the one at left corresponding to "b" in figs 3–5, the one at right hidden within sediment, visible only by x-ray, corresponding to "e" in figs 4, 5; **7.** Detail of the five styles, μ CT surface rendering enlarged from fig. 5; **8.** Vertically compressed mature flower with pentagonal gynoecium, surrounded by crescent-shaped nectaries aligned with sepals. Reflected light, UF15713-12958 (same specimen figured by μ CT in Pl. 3, fig. 12); **9.** Flower with calyx and some petals and anthers visible. Reflected light, UF15713-3522; **10.** Specimen in fruiting condition with four persistent sepals visible and two valves of fruiting capsule (labeled, a, b), viewed from front by reflected light. UF15713-5742; **11.** Same specimen, isosurface from μ CT, showing the five loculicidal capsule valves mostly hidden within sediment (those labeled a and b corresponding to those seen at surface in fig. 10). Also note the nectary pads at junction of sepal and capsule. Scale bar = 1 cm in 1–3. Scale bar in 3, applies to 3–5. Scale bar = 2 mm in 6, applies to 6, 7. Scale bar = 1 cm in 8–10, scale bar in 10 applies to 10, 11

in the middle, rounded above, curved on the sides, pointed at the upper end, convex on the surface.” (Lesquereux 1892, p. 220).

Revised Generic and Species Description. Flowers 22–30 mm diameter, 14–19 mm high, with two five-merous, hypogynous



perianth whorls. Calyx thick, persistent; calyx lobes ovate, 10–13 mm long (from center of flower to apex of calyx lobe), 4.7–8.7 mm wide. Petals spathulate, membranous, 12–15 mm long, 10–15 mm wide, attached near base of gynoecium. Ovary dome-shaped, 8–10 mm wide, pentacarpellate with five locules. Five styles diverging from common point at apex of ovary, each with capitate stigma. Five crescent-shaped nectariferous pads situated at base of gynoecium and opposite and adnate to each sepal. Ten stamens inserted at level of the nectaries, one whorl organized opposite sepals (each at apex of a nectary lobe) and the other whorl opposite petals (and in sinus between adjacent nectary lobes). Stamens consisting of filament 5–7 mm long with flared base and dorsifixed ovate-ellipsoidal anther 3–6 mm long, 2.7–3.5 mm wide. *In situ* pollen oblate, triaperturate, grains oblate to spheroidal, 8–12 μm in equatorial diameter; apertures appear porate at surface but frequently somewhat torn meridionally, possibly along short colpi; ornamentation finely verrucate. Fruits globose to ovoid, five-valved loculicidal capsules, 10–12 mm wide and high, borne on thick, short pedicels (2 mm wide, 3 mm long) and with persistent sepals and persistent nectaries; capsules with thin septa, opening without central column.

DETAILED DESCRIPTION

More than 70 flowers and fruits from the Rose Creek locality were examined, plus several specimens from other sites in Kansas and Texas (Fig. 1, Tab. 1). Our revised reconstruction of the flowers is presented, along with a floral diagram in Figure 2. These pentamerous flowers are actinomorphic with the perianth clearly differentiated into calyx and corolla. They are relatively large, 22–30 mm

wide, but the calyces are relatively shallow (10–15 mm deep), such that most specimens are preserved in vertical, rather than lateral compression. The Rose Creek specimens represent a range of maturation states from young flowers with intact petals and stamens, probably at anthesis, to mature dehiscent fruits with persistent sepals from which the petals and stamens have fallen away. Some specimens reveal a short, thick pedicel (Pl. 4, figs 2, 5).

The calyx consists of five connate, ovate sepals. The sepals decrease in thickness abruptly ca 1–1.8 mm from the margin, resulting in a thin marginal flange that is frequently torn or cracked (Pl. 1, fig. 1). This cracking is consistently present in the flowers and is not considered an artifact of preservation, but rather a developmental occurrence as the flowers opened. This marginal tissue is eroded or decayed in mature and fruiting specimens. The calyces persist after other floral organs have been lost, facilitating the recognition of specimens preserved in both sandstone and clay.

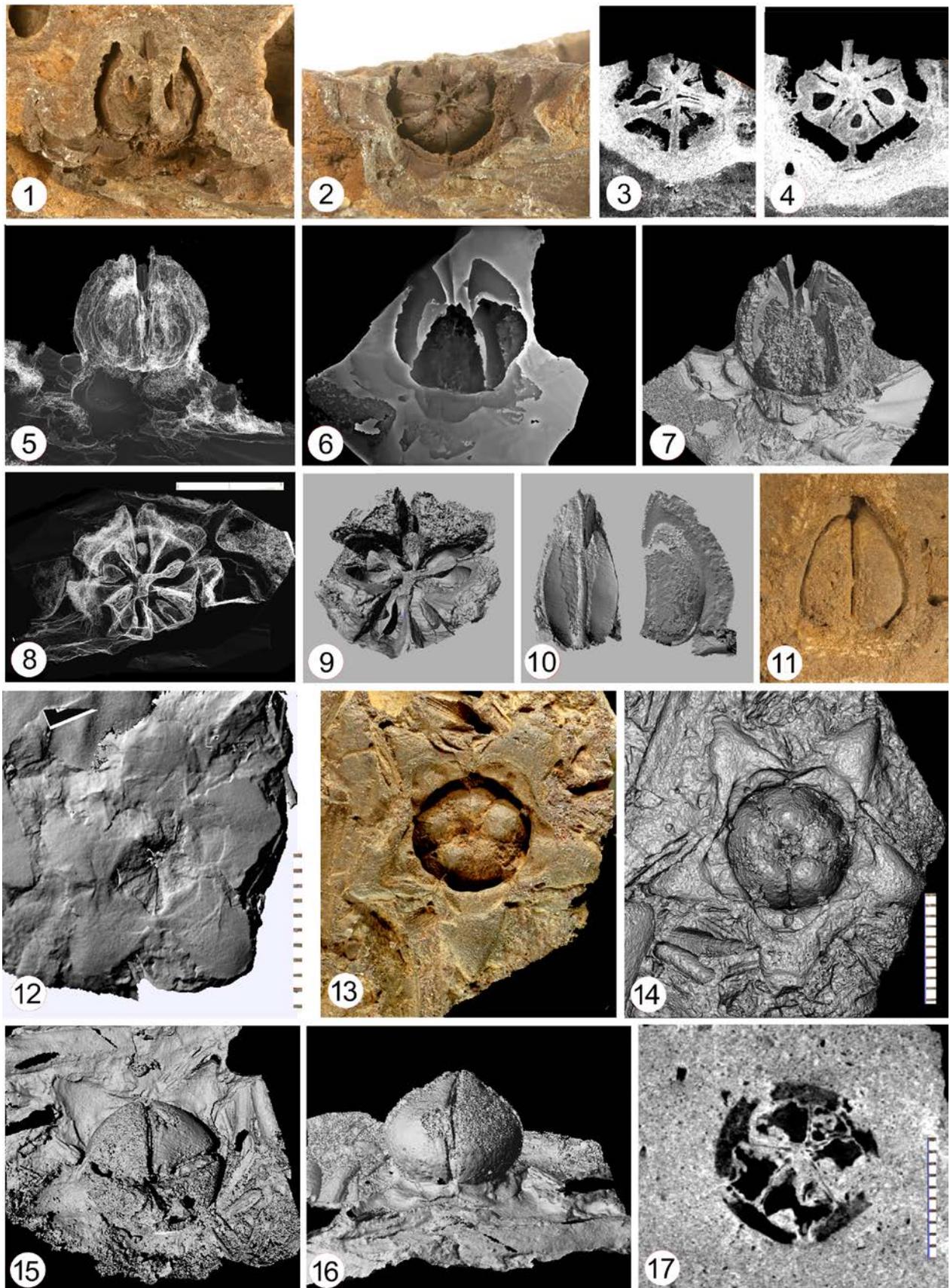
The petals are widely obovate, with a rounded to slightly retuse or cleft apex and an attenuate base, and are about twice as long as the sepals. They are thin, lack distinct venation, and probably were quite delicate during life. The petals more commonly occur isolated than in attachment to the flowers, indicating that they probably were abscised as the flowers matured.

Many features of the Rose Creek flower were already described from compression and impression specimens by Basinger & Dilcher (1984). A peculiar feature deduced from the specimens and techniques available then was the observation of only five stamens, positioned opposite the petals. This unusual arrangement led to later interpretation that these flowers might be related to Rhamnaceae (Crepet et al. 2004, Richardson et al. 2000, 2004). However,

Plate 2. Flowers, stamens and *in situ* pollen of *Dakotanthus cordiformis* (Lesq.) comb. nov. from Rose Creek, Nebraska, UF locality 15713. 1–3. Laterally compressed flowers; 1. Flower showing calyx in profile view with four visible stamens, two with complete anthers (left), one incomplete anther (arrow) and one filament (center), UF3428; 2. Tattered flower with three styles visible at apex, and two stamen filaments (arrows), UF 5266; 3. Specimen showing dome-shaped gynoecium terminated by styles with expanded tips, with parts of five stamens exposed (arrows) including anthers and filaments. UF4026; 4–8. Detached stamens showing variation in size, and distinctive flared filament base; 4. Two adjacent isolated stamens, UF5290; 5. Smaller stamen with typical triangular, flared filament base, UF5288; 6. UF5283; 7. Stamen with broader than usual filament, UF5270; 8. Floral fragment with two attached stamens. Pollen was macerated from anther at arrow UF3423; 9–12. Clumps of pollen isolated from specimen in fig. 8, SEM; 9. Clump showing rounded oblate grains; 10. Same clump positioned to show triaperturate grains; 11. Grains under higher magnification showing microverrucate ornamentation. Central grain shows intact colpus (upper left) but has ruptured along the right-front aperture; 12. Same as in fig. 8, enlargement of ornamentation. Scale bar = 10 mm in 1–3. Scale bar = 5 mm in 8, same scale in 4–8. Scale bar = 10 μm in 9, 10. Scale bar 5 μm in 11, 12

reexamination of the same specimens by x-ray using μ CT scan technology has revealed an additional whorl of stamens, hidden within the sediment (Pl. 1, figs 2, 4, 5). Although we did

not find any compression specimens with all ten stamens in place, the symmetry of anther placement in the most complete compression specimens (Pl. 1, figs 2, 4) is consistent with



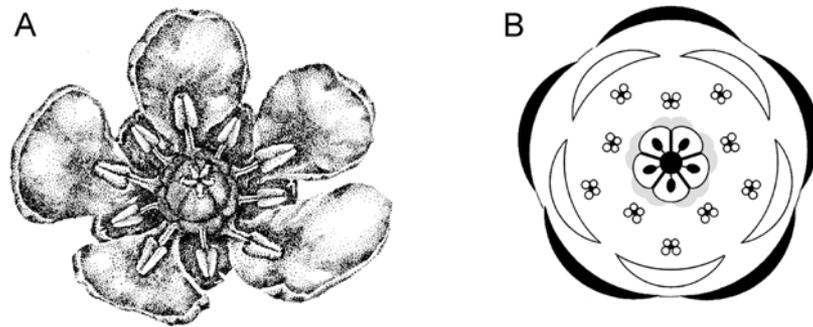


Fig. 2. A. Artistic reconstruction of *Dakotanthus cordiformis*, popularly known as the “Rose Creek flower”, modified from Basinger & Dilcher (1984) by the insertion of antiseipalous stamens. B. Floral diagram with conventions of Ronsse De Craene (2010)

the position of filament scars on the complete sandstone molds (e.g., Pl. 3, fig. 14). The sandstone specimens show ten circular filament scars at the level of the nectaries, one at the center point of each pad, opposite a sepal, and one at each of the junctions between adjacent nectary pads (Pl. 3, figs 13, 14). Thus, there were ten stamens in diplostemonous arrangement. This, along with the fruit morphology, excludes affinity with Rhamnaceae. The outer whorl of stamens appears to have been opposite the petals (Pl. 1, figs 2–5).

As with the petals, stamens are rarely found attached to the flowers (Pl. 1, figs 2–6, Pl. 2, figs 1–3) but are commonly found isolated in the sediment (Pl. 2, figs 4–8), indicating that they abscised. They are readily recognized by the distinctively flared filament bases, which reflect the geometry of their insertion on and adjacent to the nectaries. The filaments are 5–6 mm long, 0.6–0.8 mm thick, expanded at base to 2–3 (rarely 5) mm wide. The anthers are ovate to ellipsoidal, 3–6 mm long, 2.7–3.5 mm

wide, and are dorsifixed and tetralocular with longitudinal dehiscence slits. The connective does not extend beyond the pollen sacs. The axis of symmetry of the anther is commonly bent relative to the axis of the filament (Pl. 2, figs 4–6), suggesting that the anthers were versatile.

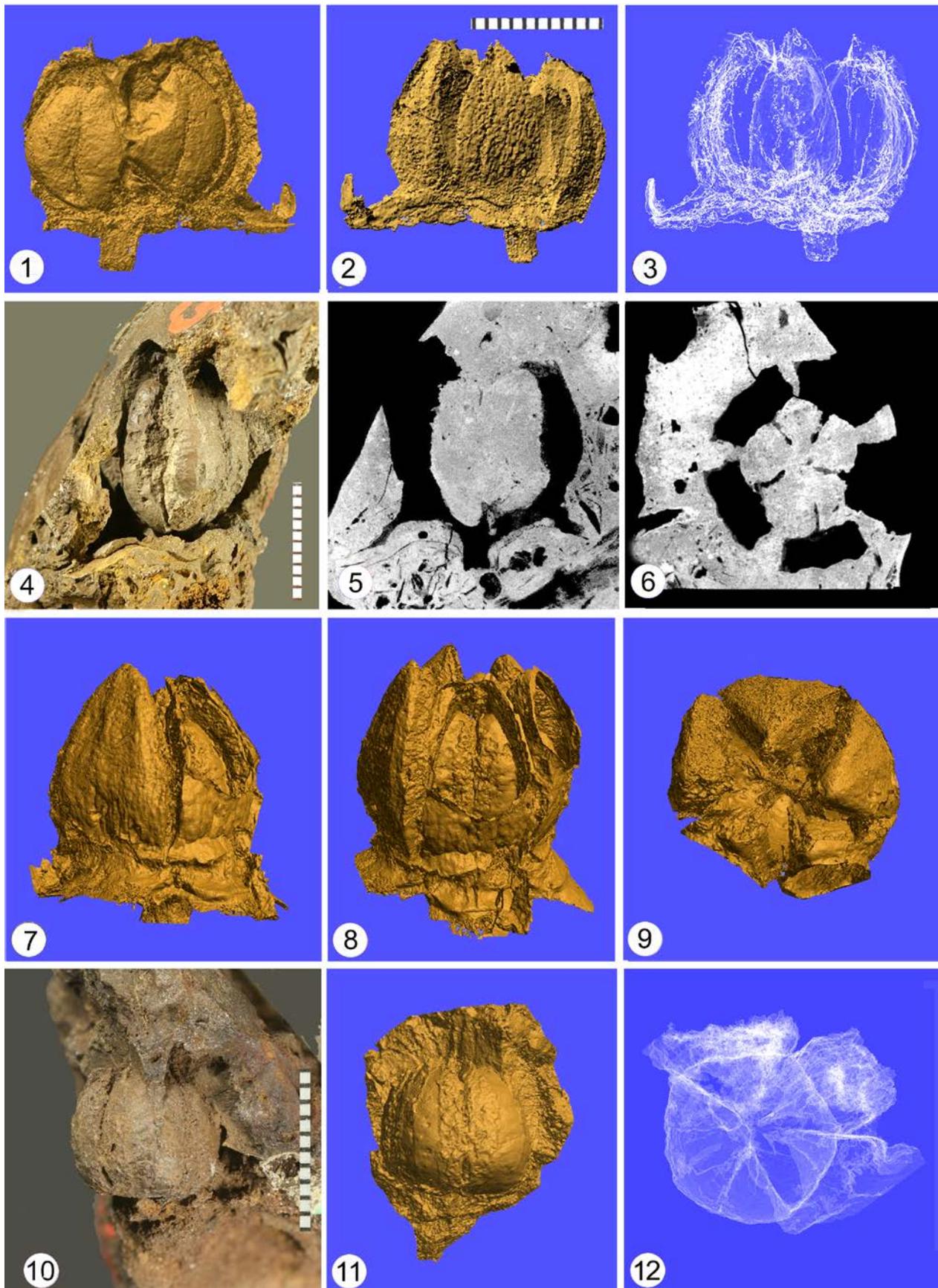
Pollen was found in only three anthers. The grains illustrated here (Pl. 2, figs 9–12) are from a stamen connected with other remnant floral parts (Pl. 2, fig. 8). The grains are flattened, adherent in clumps, and impossible to isolate. The grains are quite delicate and tend to shatter when an effort is made to separate them. We infer the grains to have originally been oblate rather than prolate, because the orientation of the apertures indicates that most grains have been flattened equatorially rather than laterally. The grains appear psilate by transmitted light microscopy, but SEM reveals microverrucate ornamentation (Pl. 2, figs 11, 12). The grains are relatively thick-walled, and despite their small size it seems likely that they were



Plate 3. *Dakotanthus cordiformis* (Lesq.) comb. nov. fruits preserved in sandstone from Late Early Cenomanian localities in Kansas, Nebraska, and Texas. **1–10.** Fruit preserved as empty mold in sandstone, Ellsworth County, Kansas, KUPB-C 2053; **1.** Lateral view, showing outline of capsule, wall thickness, and remains of hypogynous, persistent calyx. Reflected light; **2.** Transverse view from base looking upward into cavity remaining where fruit wall disintegrated, leaving only locule casts. Reflected light; **3, 4.** Digital sections showing pericarp, thin septa and five cavities that might represent seeds in axile placentation. Note sedimentary infilling of loculicidal dehiscence fissures. Fig. 3 is near apex, and fig. 4 is near the equator; **5.** Lateral view of same specimen, Meshlab X-ray reconstruction from μ CT data; **6.** Same fruit in oblique apical view showing five opened capsule valves. Meshlab Depth map from μ CT data; **7.** Isosurface rendering of same specimen with simulated reflected illumination from μ CT data; **8.** Same rendering as fig. 5, viewed apically, showing loculicidal dehiscence with five valves and what appears to be one seed in each locule; **9.** Same rendering as 7, viewed apically, showing opened valves; **10.** One valve from fig. 9 digitally removed, viewed ventrally and laterally for comparison with holotype shown in fig. 11; **11.** Holotype, isolated fruit valve, with median septum indicating that it is from loculicidally dehiscent capsule. Reflected light, USNM 50016; **12.** Immature fruit from Rose Creek, Nebraska, viewed apically, showing pentagonal gynoeceium surrounded by nectary pads and sepals, μ CT of same specimen shown in Pl. 1 fig. 8, UF15713-12958; **13–17.** Transversely oriented specimen from Woodbine Sandstone near Denton, Texas. UF 18881-49955; **13.** Fruit viewed basally, showing impression of sepals, nectaries, and bases of locule casts, reflected light; **14.** Same view as 13, surface rendering from μ CT data, clearly showing crescent-shaped nectary aligned with each sepal, with circular staminal scars at midpoint and margins of each nectary; **15.** Apical view of fruit reconstructed as a surface rendering of the negative space within the sedimentary mold seen in figs 13, 14, simulating the fruit as it appeared when deposited. The five valves and pointed persistent sepals are clearly seen; **16.** Same, lateral view showing smooth outer surface of capsule and crescent-shaped facets at base of capsule, representing the persistent nectaries; **17.** Digital transverse section. Black regions are empty spaces remaining after fruit wall, septa and locule content disintegrated. Scale bars = 1 cm. Bar in 8 applies to 1–11. Bar in 14 applies to 13–16

mature. The grains are clearly triaperturate, but details of the apertures are often obscured by compaction and fracturing as seen by SEM.

Some apertures appear porate, while others are more slit-like. We interpret the pollen to be tricolporate with relatively short colpi.



The gynoecium is superior and consists of a whorl of five connate carpels forming a central dome in the flower, with five styles diverging from a common point at the apex. Basinger and Dilcher (1984) inferred this stylar arrangement from longitudinally fractured specimens (e.g. Pl. 2, figs 2, 3); their inference is now confirmed by μ CT scanning of intact specimens (e.g. Pl. 1, figs 3–5, 7). Each style is terminated by a subglobose capitate stigma (Pl. 1, fig. 7; Pl. 2, figs 2, 3). Compressed fruits preserved in shale (e.g., Pl. 1, figs 10, 11, Pl. 4, figs 1–3) can be matched to the uncompressed, three-dimensionally preserved specimens in sandstone, such as those of Lesquereux (1892; see listing above) and Dilcher (1979, p. 309, figs 31, 33). For example, the μ CT scans of fruits preserved in shale in lateral view (e.g. Pl. 1, fig. 11, Pl. 4, figs 1–3) match precisely the fruit morphology seen in the sandstone specimens (Pl. 3, figs 5–7, 12–16), including the morphology of the valves, the persistent sepals, and nectary lobes.

The fruits include relatively large, five-valved capsules that have opened (Pl. 1, fig. 11, Pl. 3, figs 6, 7, Pl. 4, figs 2, 3, 9), indicating that they were probably mature. The mature fruit is a globose to ovoid capsule ca 10–12 mm wide and high, subtended by persistent remains of the calyx and nectaries. Dehiscence is loculicidal and proceeds from the fruit apex down the center of the dorsal wall of each carpel. The pericarp is 1–1.5 mm thick and the septa are only ca 0.3 mm thick. A thickening or rib, which may have contained a vascular strand, runs along the ventral margin of each septum (Pl. 3, figs 3, 4, 17). None of the fruits that have been recovered retain seeds. One Dakota Sandstone specimen shows a single ellipsoidal cavity within each locule cast (Pl. 3, fig 4) which might represent the position formerly occupied by a seed enveloped by sediment and later decomposed. The positive-relief μ CT

reconstruction of these seed spaces indicates axile placentation (Pl. 3, figs 8, 9). However, there are other cavities scattered through the same sandstone pieces, suggesting an alternative interpretation that the seed-shaped spaces within the fossil fruits may have resulted from sediment that concentrically lined the locules.

DISCUSSION

AFFINITIES

The collective features of the *Dakotanthus* flower and fruit are consistent with the Rosid Clade, and specifically the five-merous flowers with distinct petals. Among the extant orders of Rosidae, similarities with the modern fabalean family Quillajaceae are particularly striking. The single modern genus of that family, *Quillaja* Molina, has five-merous flowers with five triangular sepals, five spatulate petals, a strongly lobed nectary disk, ten stamens, five fused carpels, and axile placentation. This matches many of the characteristics of *Dakotanthus*. The nectary morphology, with crescent-shaped lobes aligned to the sepals, is very similar, as is the unusual positioning of the two staminal whorls: the five antesealous and five antepetalous stamens are positioned at the nectary pads and sinuses, respectively (Bello et al. 2008). These two features may be synapomorphies, indicating a phylogenetic relationship of *Dakotanthus* with *Quillaja*. Inflorescences of *Quillaja* are polygamomonoecious, bearing three to five flowers, with lateral male flowers and a central hermaphrodite flower; the flowers are 15 mm in diameter with white petals. We have not confirmed the inflorescence type for *Dakotanthus*, but note that we have seen no evidence of this type of floral dimorphism.

Plate 4. *Dakotanthus cordiformis* (Lesq.) comb. nov. fruits from shale and sandstone. **1–3.** Fruit digitally isolated from Rose Creek, Nebraska, shale showing thick short pedicel, hypogynous calyx, μ CT images. UF 15713-6051. Scale bar = 1 cm; **1.** Surface rendering of specimen viewed as exposed at surface of shale, showing ventral surface of two capsule valves, each with median septal crease; **2.** Same specimen viewed through shale from behind, showing three opened capsule valves and remains of persistent stamen (projecting left); **3.** Same, rendered translucent to show attachment of pedicel and remnant anther; **4–9.** Specimen from NE of Delphos, Kansas, referred to *Nordenskioldia borealis* Heer by Lesquereux 1892, USNM 50023; **4.** Lateral view of fruit represented by smooth locule casts surrounded by empty crevices left by disintegration of fruit wall and calyx. Reflected light; **5.** Virtual longitudinal section showing thick wall, thin longitudinal septa, persistent calyx and short thick pedicel; **6.** Virtual transverse section near equator, showing five valves, thin septa and five sediment-filled locules and loculicidal dehiscence fissures; **7–9.** Same specimen, surface renderings of fruit in lateral and apical views, μ CT scan showing five valves, hypogynous nectary pads and fragmentary calyx; **10–12.** Specimen called *Carpites tiliaceus* by Lesquereux 1892, from Cloud or Ottawa County, Kansas. USNM 50025; **10.** Viewed laterally, showing locule casts, each with median septal crease. Reflected light; **11.** Same view, isosurface reconstructed from μ CT scan data; **12.** Apical view rendered translucent to show complete locule casts and thick, fragmentary capsule wall. Scale bars = 1 cm. Bar in 2 applies to 1–3. Bar in 4 applies to 4–9. Bar in 10 applies to 10–12

Given the age of this fossil, which is very early with respect to the occurrence of extant Rosid families, we would not expect *Dakotanthus* to fall neatly within a modern family. Notable differences between *Dakotanthus* and *Quillaja* include the fruit type and pollen morphology. Whereas the fossil taxon has a syncarpous capsule (but with five free styles) that opens loculicidally, such that each valve reveals the septum ventrally along its midline, in *Quillaja* the fruits are only basally syncarpous and are usually described as follicles which dehisce separately, releasing numerous winged seeds. These differences in fruit morphology reflect quite different degrees of carpel fusion. Whereas extant *Quillaja* is nearly apocarpous, with carpels fused only near the base, each dehiscing independently, *Dakotanthus* gynoecia are syncarpous except apically where the five styles diverge, and they dehisce as a distally opening loculicidal capsule. Interestingly, the ovaries of *Quillaja* appear to be more strongly fused in flowering condition, and seemingly become more distinct as the lobed fruits develop (likely a derived feature). *Quillaja* produces distinctive unilaterally winged seeds. No such seeds have been observed in the Dakota Formation.

The oblate, microverrucate pollen of *Dakotanthus* is readily distinguished from the prolate, striate pollen of *Quillaja*. Oblate to suboblate grains occur in the related fabalean family Surianaceae, in which ornamentation ranges from striate to verrucate (Claxton et al. 2005). However, pollen of *Dakotanthus* (ca 10 μm equatorial diameter) is considerably smaller than that of *Quillaja* (ca 22–30 μm) and Surianaceae (15–65 μm) (Claxton et al. 2005). The pollen of *Dakotanthus* certainly seems to have been adaptive for insect dispersal because it is too small to have been effective for wind dispersal due to physical limitations summarized by Whitehead (1983).

The large and distinctive crescent-shaped nectaries in *Dakotanthus*, closely similar to the receptacular nectaries fused to the sepals in mature flowers of *Quillaja* (Bello et al. 2008), apparently functioned as an attractant for insect pollination. *Quillaja saponaria* Molina is important today in honey production in Chile and its flowers are known to attract a diversity of insect visitors. Díaz-Forestier et al. (2009) observed 14 species of Coleoptera, 6 of Diptera, 14 of Hymenoptera and 5 of

Lepidoptera as visitors of *Quillaja saponaria* flowers, with Hymenoptera and Coleoptera showing the highest frequency of visitation.

Another clade of Rosids relevant for comparison with *Dakotanthus* is the Rosales as currently circumscribed (Soltis et al. 2018). This relationship would be supported by the presence of the nectary disk, if this structure in the fossil is interpreted to represent a modified hypanthium. *Dakotanthus*, however, does not possess obvious synapomorphies with particular subclades of Rosales, such as a reduction to a single staminal whorl (in the clade containing Rhamnaceae, Ulmaceae, Moraceae, etc.) or distinct carpels and numerous stamens (in the clade comprising Rosaceae itself); therefore, if related to Rosales, it would likely be in an extreme basal position within the order. Thus, morphological support for a position within Rosales (which has often been suggested; see Richardson et al. 2000, 2004) is not as strong as the support for a position close to Quillajaceae of the Fabales. Although we have not conducted a formal phylogenetic analysis, we hypothesize that *Dakotanthus* represents a basal lineage within the Fabales.

Recently, another genus of flower with Rosid Clade affinities, *Caliciflora*, was recognized from sediments of slightly younger age from the Potomac Group of northeastern Maryland (Friis et al. 2016). Like *Dakotanthus*, *Caliciflora* has five sepals and five petals, but it has only eight anthers and three free carpels. They differ markedly in size. The single specimen of *Caliciflora* is 0.75 mm in diameter and has numerous stellate hairs; based upon numerous specimens, *Dakotanthus* is 22 to 30 mm in diameter and lacks such hairs. There appears to be little relationship between these two fossil taxa, but together they demonstrate early diversification within the Rosid Clade.

The Rose Creek flora of Nebraska has yielded a large number of *Dakotanthus* specimens, as well as the diverse leaf compression flora described by Upchurch & Dilcher (1990). We do not know which, if any, of the leaves recognized from the Dakota flora were borne by the same plant as *Dakotanthus*. However, based on the rosid affinities, we can rule out its close relationship to the leaves that Upchurch & Dilcher (1990) recognized as of Magnoliales, Laurales, Illiciales and unknown magnoliid-grade foliage types. Those leaf fossils are often preserved with

intact cuticle and we would expect the flower sepals to preserve cuticle as well if they were related; also, the floral features of *Dakotanthus* fit with Eudicots rather than Magnoliids. More likely candidates for the foliage would be the Rose Creek leaves attributed to “Rosidae order unknown” (*Anisodromum wolfei* Upchurch & Dilcher or *Citrophylllum doylei* Upchurch & Dilcher). Other leaves that might be considered include those identified more generally as Magnoliopsida subclass unknown (*Dicotylophyllum myrtophylloides* Upchurch & Dilcher, *D. rosafluviatilis* Upchurch & Dilcher, *D. aliquantuliserratum* Upchurch & Dilcher, *D. expansolobum* Upchurch & Dilcher).

PALEOECOLOGY

Dakotanthus occupied coastal areas on the eastern margin of the Cretaceous Midcontinental Seaway (Fig. 1), probably growing in coastal wetlands. The Rose Creek beds in Nebraska, where these flowers were found in abundance, were deposited in brackish water conditions, inferred based on sedimentological features and the occurrence of *Brachidontes* bivalves in life position within the same mudstones and shales that contain the plant fossils (Upchurch & Dilcher 1990). The presence of fruits as far south as Denton, Texas, indicates that the range of *Dakotanthus cordiformis* extended more than 800 km from north to south in these coastal environments. It has been proposed that these kinds of coastal wetlands were pivotal in the early radiation of angiosperms (Retallack & Dilcher 1981a, 1986). Other elements of the community known from fruits and seeds in the Dakota flora include the Magnoliids *Lesqueria* (Crane & Dilcher 1984), *Archaeanthus* (Dilcher & Crane 1984b) and *Prisca* (Retallack & Dilcher 1981b), and the eudicot families Platanaceae (Wang et al. 2011) and Combretaceae (*Dilcherocarpon combretoides* Manchester & O’Leary 2010).

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