

AN EARLY CRETACEOUS FRUIT WITH AFFINITIES TO CERATOPHYLLACEAE¹

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A new genus and species with affinities to Ceratophyllaceae from the Lower Cretaceous of Kansas, USA is reported. The fruits of *Donlesia dakotensis* gen. et sp. nov. are smooth achenes with two winged lateral spines, two winged facial spines, one stylar spine, and a long peduncle with a distinctive groove. The facial spines are arranged perpendicular to the lateral spines. The seed contains two cotyledons and a central plumule. Dichotomous leaves associated with *Donlesia dakotensis* fruits are whorled, petiolate, and lack denticles. The fruit morphology of *D. dakotensis* differs from extant and fossil members of Ceratophyllaceae in its tetra-radial symmetry, the presence of two winged facial spines, a long peduncle, and the lack of other appendages on the fruit surface. It seems to be more closely related to section *Ceratophyllum* of extant *Ceratophyllum*. This relationship suggests that section *Ceratophyllum* of extant *Ceratophyllum* may represent the ancestral members of the ancient *Ceratophyllum* lineage. The presence of this species in the Dakota Formation further confirms that there were diverse aquatic plants living in freshwater lakes along the eastern margin of the Western Interior Seaway during the Early Cretaceous.

Key words: aquatic plant; Ceratophyllaceae; Dakota Formation; *Donlesia*; Early Cretaceous; fossil fruit; Kansas.

Ceratophyllum, the only extant genus in the Ceratophyllaceae, possesses unique morphological and molecular characters that suggest it had an early divergence from all other angiosperms. Therefore, its fossil history is of particular interest to paleobotanists and neobotanists.

The relationship of *Ceratophyllum* to other angiosperms remains unresolved (Mathews, 2006). Earlier researchers (Dahlgren, 1980, 1989; Takhtajan, 1980, 1997; Cronquist, 1981) suggested that the genus was closely related to *Cabomba*. However, phenetic analyses (Les, 1986c, 1988c, 1991) and results based upon observations of floral development (Iwamoto et al., 2003) do not support this close relationship. Earlier molecular phylogenetic analyses (Les et al., 1991; Chase et al., 1993; Qiu et al., 1993) suggested that *Ceratophyllum* represented a sister group to the rest of angiosperms. Recent phylogenetic analyses place *Ceratophyllum* (Ceratophyllaceae) as sister to the eudicots (Qiu et al., 1999; Soltis et al., 1999, 2000; APG II, 2003; Borsch et al., 2003; Hilu et al., 2003; Jansen et al., 2007; Moore et al., 2007). Duvall et al. (2006) and Qiu et al. (2006) suggested that the Ceratophyllaceae are sister to Chloranthaceae. Other molecular analyses (Soltis et al., 1997; Qiu et al., 1999, 2000; Zanis et al., 2002; Davies et al., 2004) place *Ceratophyllum* as a sister group to the monocots.

Members of extant *Ceratophyllum* are submerged aquatic plants widely distributed in freshwater ponds, marshes, and quiet streams in tropical and temperate areas around the World. The plants are rootless and herbaceous with three to 11 whorled leaves at each node. The leaves have an inconspicuous petiole. The lamina is simple and linear or is dichotomously divided

into linear, filiform segments; each segment has two rows of thorn-like denticles (Les, 1993, 1997; Fu and Les, 2001).

The most useful taxonomic characters are the fruit size and the nature of the spines on the fruits (Les, 1993). The fruits are indehiscent, ellipsoid achenes with smooth, papillose, or tuberculate surfaces and prominent spines. The spines usually include an apical stylar spine (which in some species develops only into a short awliform structure) and a pair of basal spines, although these are lacking in some species. Some species may have additional marginal spines (often joined by a wing) or a pair of elongate facial spines. The seed is unitegmic with two fleshy cotyledons and a massive and highly developed plumule (Wilmot-Dear, 1985; Les, 1993; Fu and Les, 2001).

On the basis of observations of fruit and leaf variation, Wilmot-Dear (1985) recognized two living species, i.e., *Ceratophyllum demersum* L. and *C. submersum* L., each with four varieties. On the other hand, Les (1985; 1986a–c; 1988a–c; 1989) divided the genus into three sections, sect. *Ceratophyllum* L., sect. *Muricatum* Les, and sect. *Submersum* Les, each with two species.

Fossil *Ceratophyllum* fruits have been reported from the Cretaceous of Canada (Serbet et al., 2008) and Mexico (Estrada-Ruiz et al., 2009), the Tertiary of the United States (Axelrod, 1985; Herendeen et al., 1990; Manchester, 2000; Wilf, 2000; Johnson, 2002), the Middle Miocene of eastern China (Hu and Chaney, 1940; Wang et al., 2005), the Middle and Late Miocene of Europe (Dorofeev, 1963, 1974; Gregor, 1978; Mai and Walther, 1978; van der Burgh, 1983; Mai and Walther, 1988; Geissert et al., 1990; Dyjor et al., 1998; Mai, 2001; Gümbel and Mai, 2006), the Oligocene of Kazakhstan (Avakov, 1962), the Late Miocene of Austria (Knobloch, 1977), the Late Miocene and Pliocene of Japan (Ozaki, 1991), the Pliocene of Bulgaria (Palamarev, 1982; Mai and Wähnert, 2000) and Germany (van der Burgh, 1987; Gümbel and Mai, 2004), and the Holocene/Pleistocene of Canada (Terasmae and Craig, 1958; Ritchie and DeVries, 1964), Jordan (Ohlhorst et al., 1982), the Netherlands (Pals et al., 1980), northern Europe (Backman, 1943; Hessland, 1946; Griffin, 1980) and the United States (Watts and Bright, 1968; Gruger, 1973; Van Zant, 1979; Pierce and Tiffney, 1986). The purpose of this paper is to present a new genus within the

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family Ceratophyllaceae from the Lower Cretaceous of Kansas, USA based upon fruit and seed morphology.

MATERIALS AND METHODS

The specimens presented in this paper were collected from two localities of the Dakota Formation in Kansas, USA (Fig. 1; also see Text-figs. 6–8 in Retallick and Dilcher, 1981a for detailed locality information). Some specimens presented here were briefly reported by Dilcher (1989) but without a formal description and diagnosis. Each locality is assigned a unique number after the prefix “UF” (for University of Florida). The Acme Brick Co. I (UF15708) and II (UF18730) localities are in the same clay pit about 6 km east of Kanapolis, Ellsworth County, Kansas. The specimens were collected from interbedded siltstone and sandstone at the southern end of the clay pit. Site I (UF15708) is about 2.5 m stratigraphically lower than site II (UF18730).

All specimens are preserved as compression or impressions. The seed tegma was removed from the specimen using a needle, rather than through chemical processing. When necessary, the matrix was degaged to reveal the entire fruit. Both the part and counterpart of one specimen were broken in the plane of the fruit, resulting in four parts to reveal the two facial spines. All specimens were photographed using a Nikon D100 digital camera and only sharpness, brightness, and contrast of the images were manipulated using Adobe (San Jose, California, USA) Photoshop 10 software. All specimens are stored in the Paleobotany and Palynology Type and Figured Collection at the Florida Museum of Natural History, the University of Florida, Gainesville, Florida, USA. Fruits of modern *Ceratophyllum* were examined from the UF Modern Fruit and Seed reference collection at the Florida Museum of Natural History.

The age of the plant-fossil-bearing sequences is Late Albian (latest Early Cretaceous) based on palynostratigraphic and sedimentological analyses (Brenner et al., 2000; Gröcke et al., 2006). Interpretations of sedimentary environments for these localities are floodplain lake and overbank (the Acme Brick Co. I and II locality, Kansas; UF15708 and UF18730). The interpretation of predominantly freshwater environments has been confirmed by the presence of several other freshwater aquatic plants (Kovach and Dilcher, 1985; Skog and Dilcher, 1992, 1994; Skog et al., 1992; Wang and Dilcher, 2006; C. Martín-Closas (University of Barcelona) and D. Dilcher in press).

SYSTEMATIC PALEOBOTANY

Order—Ceratophyllales Bischoff

Family—Ceratophyllaceae Gray

Genus—*Donlesia* Dilcher and Wang gen. nov.

Type species—*Donlesia dakotensis* Dilcher and Wang sp. nov.

Generic diagnosis—Fruits achenes and the fruit body fusiform, tetra-radially symmetric with two winged lateral spines, two winged facial spines, one stylar spine, and a long peduncle; stylar spine tapering gradually toward the apex; peduncle very long with a distinctive groove that is absent from the stylar, facial, and lateral spines; fruit surface smooth; seed shape ovoid to obovate with two cotyledons and a distinct plumule.

Derivation of generic name—In honor of Donald H. Les in recognition of his contributions to the study of *Ceratophyllum*.

RESULTS

***Donlesia dakotensis* sp. nov. (Figs. 2–14)**—**Specific diagnosis**—Same as for the genus *Donlesia*.

Description—The fruits are indehiscent achenes with fusiform bodies (Figs. 2, 4, 6–9, 12). The achenes possess two winged lateral spines (Figs. 2, 4, 6, 8, 12), two winged facial spines (Figs. 3, 5, 6, 8), one stylar spine (Figs. 2, 6, 8), and a long peduncle (Figs. 6–9, 12). The average fruit size (fruit body excluding spines) is 4.0 mm long (range 3–5.5 mm, $N = 22$; Table 1) and 2.7 mm wide (range 1.6–4 mm, $N = 22$; Table 1). Except for the spines, the surface of the fruit body is smooth.

There are two planes of symmetry for the fruit, one with two winged lateral spines and one with two winged facial spines (Figs. 2–5). The two planes are oriented at 90° to each other. One specimen with both part (Fig. 2) and counterpart (Fig. 4) shows two lateral spines on one plane. When each part is split along the central axis, two facial spines are revealed perpendicular to the lateral spines (Figs. 3, 5). Most compression or impression specimens only show two lateral spines (Figs. 2, 4, 9, 12). Some specimens show three spines of which two are lateral spines and one is a facial spine (Figs. 6, 8). The base of

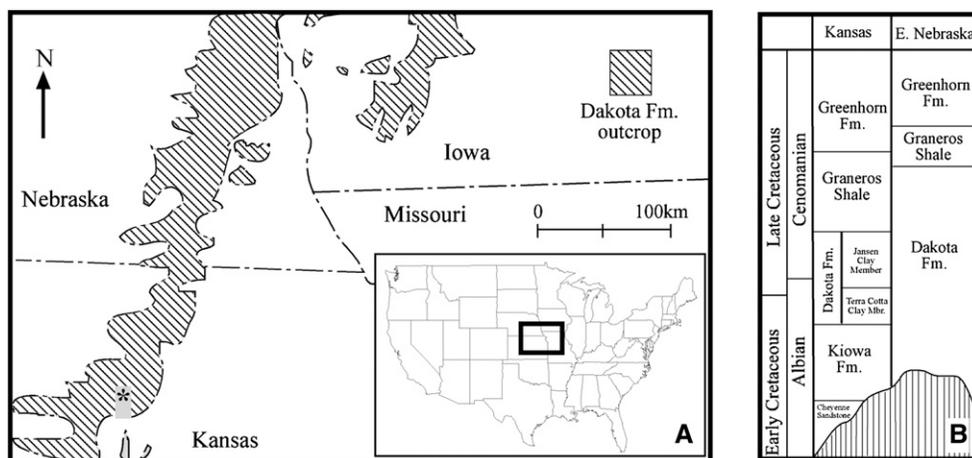
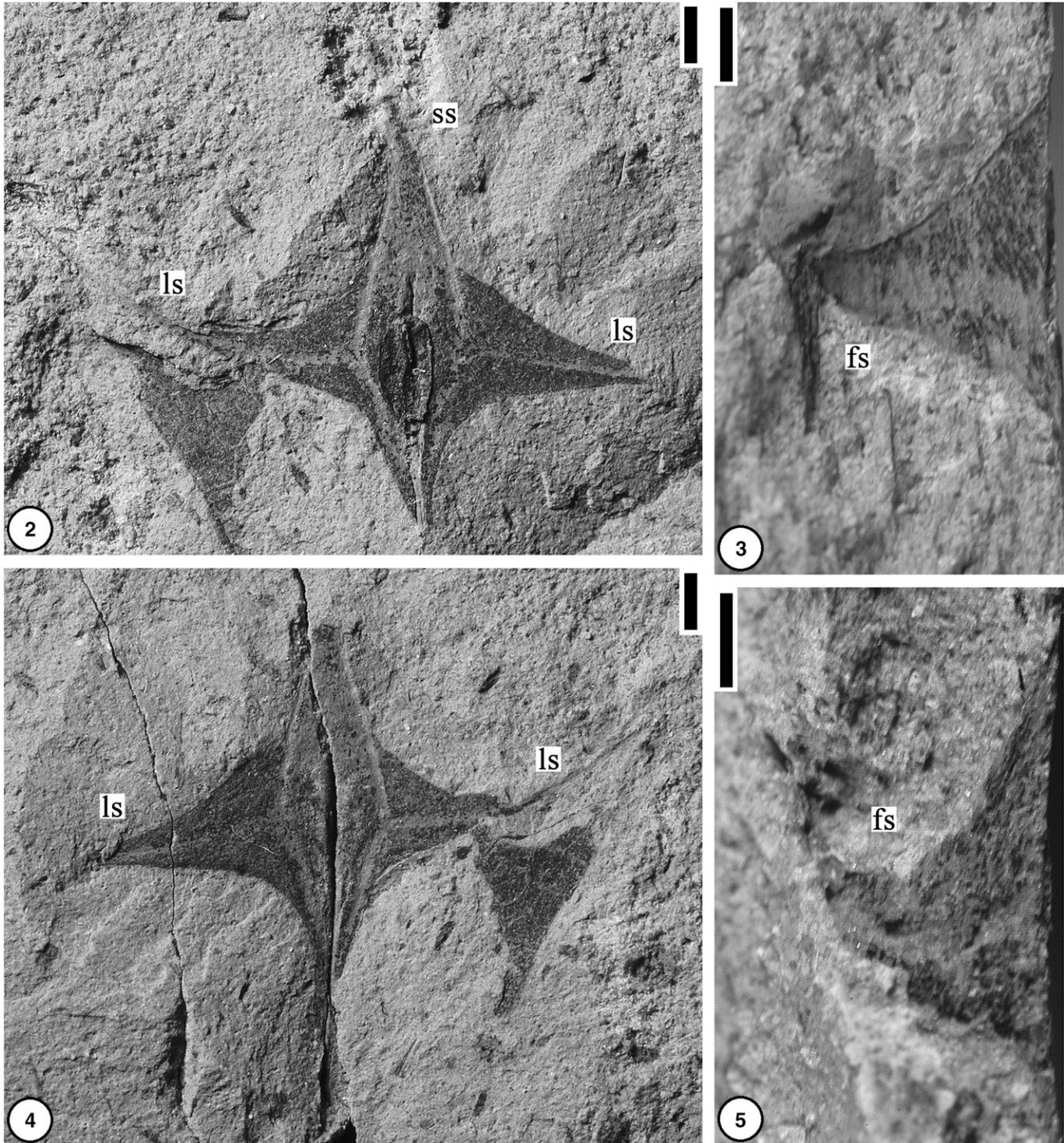
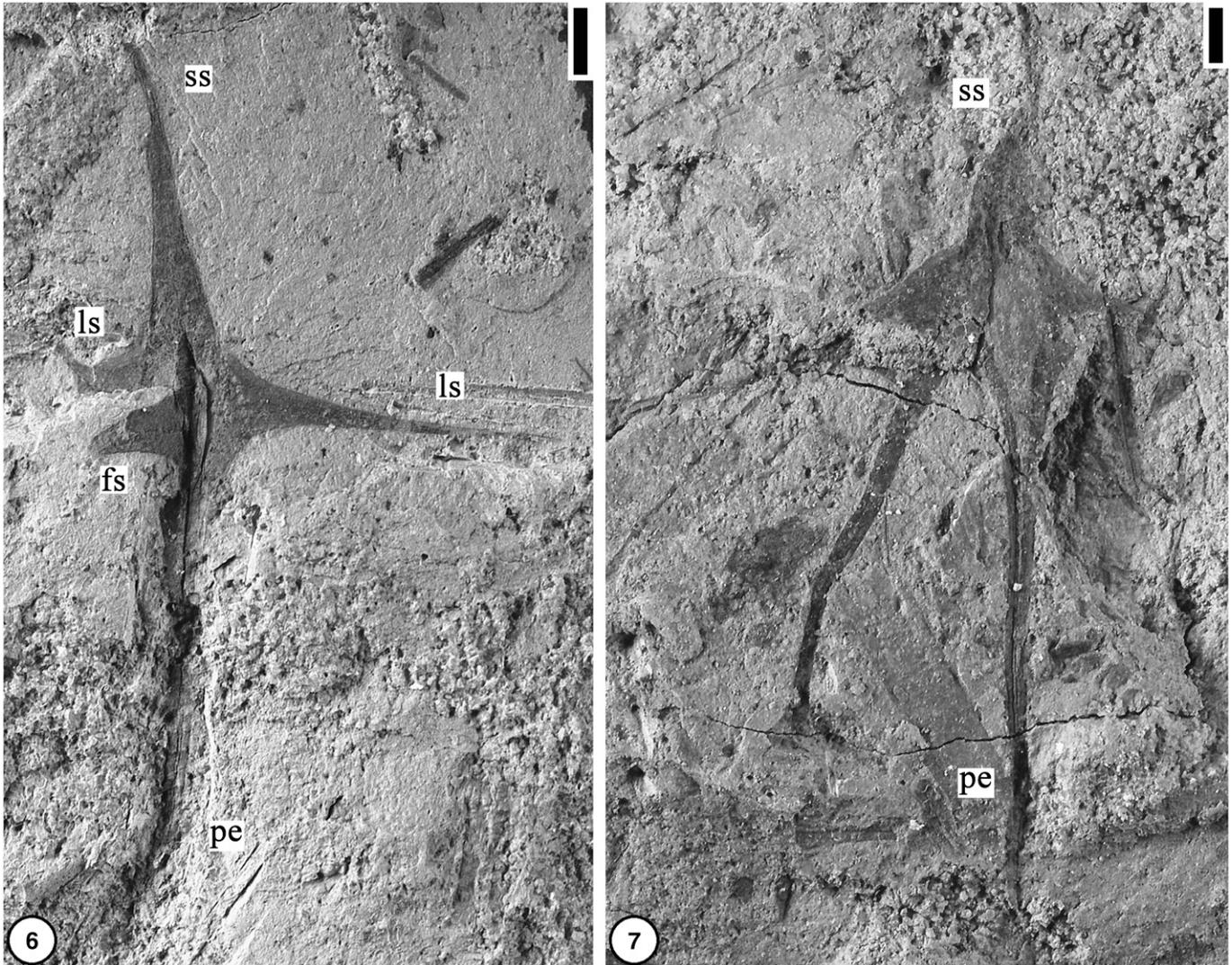


Fig. 1. (A) Regional outcrop of the Dakota Formation and location of the plant fossil localities discussed in the text. * The Acme Brick Co. I (UF15708) and II (UF18730), Kansas. The lower right inset map shows the location of the study area in USA. Outcrop map is based on Witzke and Ludvigson (1996). (B) Diagram showing the division of the Cretaceous strata from central Kansas to eastern Nebraska, USA. The plant fossils described in this paper were collected from the Terra Cotta Clay Member of the Dakota Formation (late Albian, Early Cretaceous).



Figs. 2–5. *Donlesia dakotensis* gen. et sp. nov. UF15708–5332, 5332', part and counterpart of the holotype specimen, revealing two winged lateral spines, and two winged facial spines after the specimen split. **2.** UF15708–5332', specimen showing two winged lateral spines (ls), a stylar spine (ss), and the seed tegma in the middle. Scale bar = 1 mm. **3.** Right part of Fig. 2 photographed after being split and rotated 90° clockwise along the longitudinal axis of the fruit, showing the compressed winged facial spine (fs). Note that the distal portion of the facial spine is broken but still attached. Scale bar = 0.5 mm. **4.** UF15708–5332, counterpart of Fig. 2 showing two lateral spines (ls). Scale bar = 1 mm. **5.** Right part of Fig. 4 photographed after being split and rotated 90° clockwise along the longitudinal axis of the fruit, revealing the second facial spine (fs). Scale bar = 0.5 mm.



Figs. 6–7. *Donlesia dakotensis* gen. et sp. nov. All scale bars equal 1 mm. 6. UF15708–49579, specimen showing one stylar spine (ss), two winged lateral spines (ls), and one facial spine (fs). 7. UF15708–33642, specimen showing three undifferentiated lateral and facial spines, a long peduncle (pe), and a stylar spine (ss).

the winged facial spines is slightly narrower than that of the winged lateral spines. This is a character that can be used to distinguish lateral and facial spines when fruits are compressed. Only one complete facial spine with a length of 9.8 mm has been observed (Fig. 8; Table 1).

The average length of the lateral spines is 8.0 mm (range 5–12 mm, $N = 23$; Table 1). The basal width of the lateral spine wing can be the same as the length of the fruit body, while the base of the facial spine wing is slightly shorter than the length of the fruit body. The average basal width of lateral spine wings is 2.5 mm (range 1.5–4 mm, $N = 38$) and that of the facial spine wings is 2.1 mm (range 1.5–3 mm, $N = 5$). The width of the wing reduces abruptly toward the apex of the lateral spine, resulting in a triangular-shaped wing and a long and sharp spine (Figs. 2, 4, 6, 8).

The average length of the stylar spines is 6.8 mm (range 5–12 mm, $N = 8$; Table 1). The stylar spine tapers gradually toward the attenuate apex (Figs. 2, 6, 8). The demarcation between the stylar spine and the fruit body is indistinct, making the mea-

surement of fruit length somewhat arbitrary (Table 1). At the base, the stylar spines typically have the same width as the fruit body when compressed (Figs. 2, 4). No stylar groove or pore is observed. The peduncle of the fruit is very long relative to the fruit length, with an average of 9.9 mm (range 6–14 mm, $N = 14$). Each peduncle has a distinctive groove, which extends from the seed body to a truncated peduncle end (Figs. 8, 9, 12). This groove in the peduncle probably is the impression of a compressed vascular bundle. A portion of the groove within the fruit body is probably the impression of the compressed winged facial spine. No vascular bundles are observed in the fruit body or the stylar, facial, and lateral spines.

The tegmina (tegma = inner coat of the seed) of the fruits are occasionally exposed as cuticularized compressions clinging to one half of the specimen when it is longitudinally split into two halves (Figs. 2, 6, 8, 9, 12). The shape of the seed varies from ovoid (Figs. 13, 14) to obovate (Figs. 2, 10, 11). The average seed size is 3.9 mm long (range 3–5.5 mm, $N = 22$) and 1.8 mm wide (range 0.6–2.5, $N = 22$; Table 1). When the tegma is

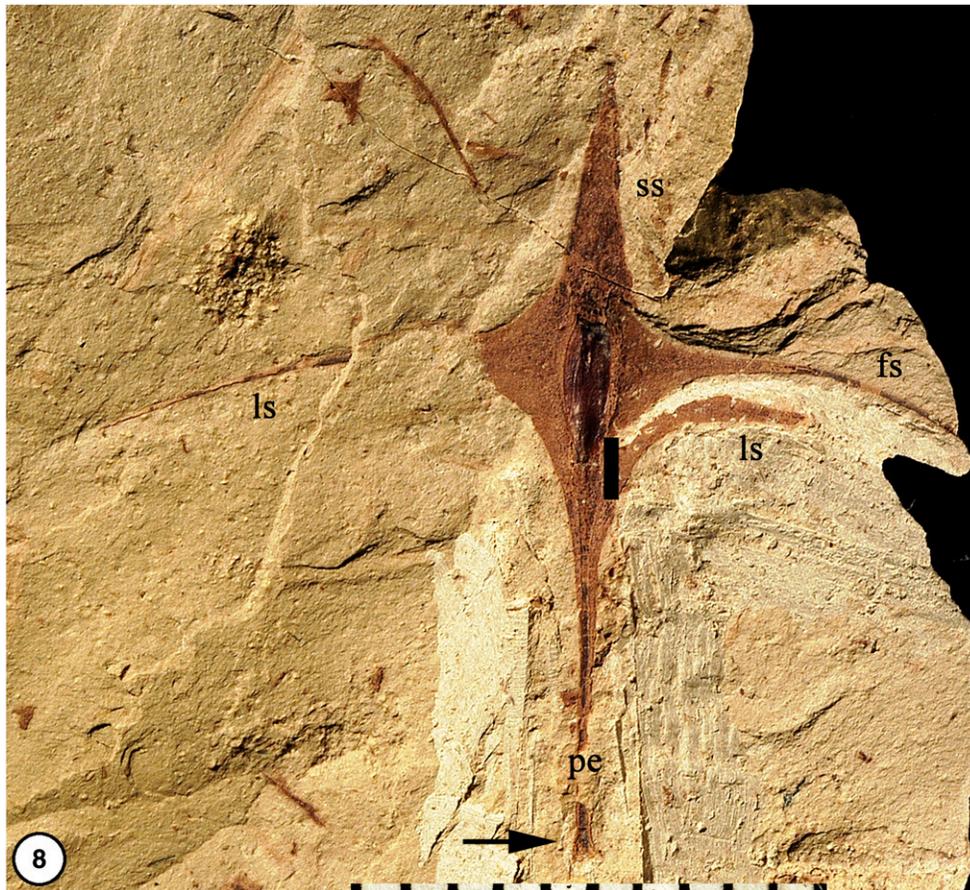


Fig. 8. *Donlesia dakotensis* gen. et sp. nov. UF15708–8418, specimen showing two lateral spines (ls), one facial spine (fs), the stylar spine (ss), and the peduncle (pe). Note the truncated base of the peduncle (arrow). Scale bar = 1 cm.

removed from the matrix without washing, it clearly shows the impressions of two cotyledons and the position of the plumule (Figs. 10–11, 13–14). There are two cotyledons in each seed (Figs. 10–11, 13–14). The plumule is about 0.25 mm wide and is slightly shorter than the seed length.

Species epithet—Referring to the occurrence of this species in the Dakota Formation.

Locality, horizon, and age—Acme Brick Co. I locality, Kansas (UF15708), Dakota Formation, Late Albian, Early Cretaceous.

Number of specimens examined—58.

Holotype—UF15708–5332, 5332' (Figs. 2–5).

Paratypes—UF15708–49579 (Fig. 6); 33642 (Fig. 7); 8418 (Fig. 8); 33636 (Figs. 9–11); 33637b (Figs. 12–14).

DISCUSSION

Donlesia dakotensis differs from extant and other fossil *Ceratophyllum* species by the following characters: (1) tetra-radially symmetric fruits, (2) presence of two winged facial spines

and a long peduncle, and (3) lack of other appendages on the fruit surface. This suite of characters warrants the establishment of a new genus. The long peduncle of *D. dakotensis* is unique because all extant and other fossil fruits possess very short or inconspicuous peduncles (Wilmot-Dear, 1985; Les, 1993; Fu and Les, 2001).

Another unique feature of *Donlesia dakotensis* fruits is the presence of winged facial spines. Facial spines are only present in members of the “facially-spined” group of extant *Ceratophyllum*, i.e., *C. platyacanthum* subsp. *oryzetorum* and *C. platyacanthum* subsp. *platyacanthum* (Les, 1988b, 1989), but the spines of these species lack wings or the wings of their facial spines are not as developed as in the lateral spines. Fruit morphology of *D. dakotensis* is similar to and therefore appears to be related to the “facially-spined” group, i.e., *C. platyacanthum* subsp. *platyacanthum* and *C. platyacanthum* subsp. *oryzetorum* (Les, 1988b; also see *C. demersum* var. *platyacanthum* in Wilmot-Dear, 1985) because of the facial appendages on the fossil fruits. Flattened, spiny wings only occur on fruits of *C. platyacanthum* (Les, 1988b). While the wings of *C. platyacanthum* fruits are more complicated and there are several spines on each wing, there is only one spine on each lateral wing on the fruits of *D. dakotensis*. The arrangement of facial and lateral spines of *D. dakotensis* differs from that of *C. platyacanthum* subsp. *oryzetorum* (Les, 1989, Fig. 4E), because fruits of *D. dakotensis* have two lateral spines and two facial spines, while



Figs. 9–11. *Donlesia dakotensis* gen. et sp. nov. **9.** UF15708–33636, specimen showing the longitudinal groove and its extension toward the peduncle (pe). Scale bar = 1 mm. **10.** Enlargement of the seed tegma detached from Fig. 9 with the same orientation to show two compressed cotyledons (co) and position of the plumule (pl, indicated by arrow), and position of chalaza (ch). Scale bar = 0.5 mm. **11.** Opposite side of Fig. 10 to show two compressed cotyledons (co) and position of the plumule (pl, indicated by arrow), and position of chalaza (ch). Scale bar = 0.5 mm.

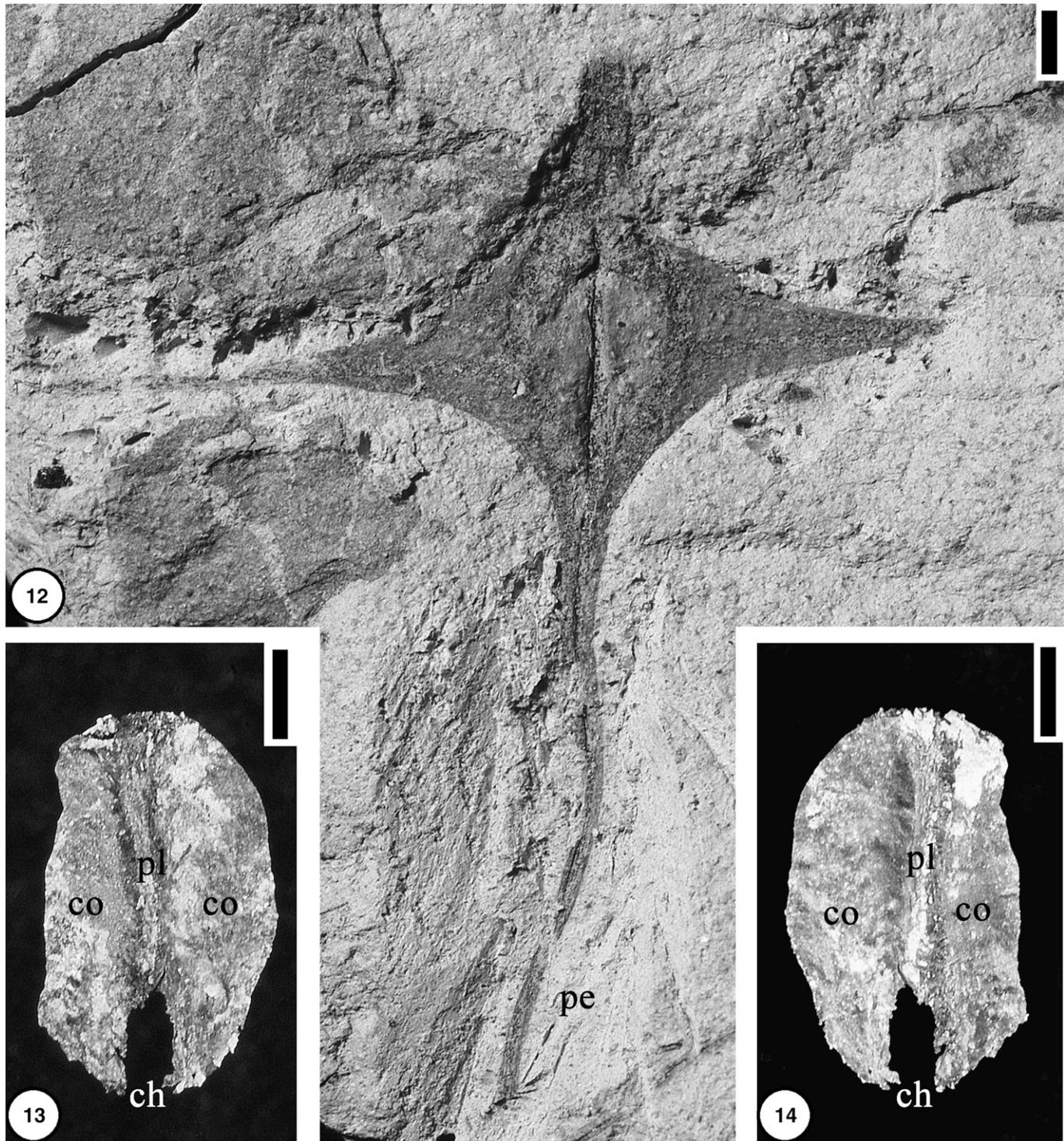
fruits of *C. platyacanthum* subsp. *oryztorum* have two basal spines and two lateral spines (Fig. 15).

Donlesia dakotensis fruits, like those of extant *Ceratophyllum* (Figs. 15–17), possess one seed with two cotyledons and a plumule between them (Les, 1985). In extant *Ceratophyllum* mature fruits, after the chalaza is removed, there is a notch on the apical side of the seed (Fig. 17) denoting the position of the placenta. By contrast, two fruits of *D. dakotensis* (Figs. 10–11, 13–14) clearly show these distinct notches on the basal end of the seeds. This suggests that the position of placenta for the fossil fruits is basal.

Fruits of *Donlesia dakotensis* co-occur, but are not found in attachment with whorled, petiolate dichotomously branching leaves at the Acme Brick Co. localities (Figs. 18–20). We follow Les (1997) using “leaf-order” to describe forking pattern of the lamina. The leaf-order is the maximum number of consecutive dichotomous forkings (starting at the petiole) necessary to

yield a pair of adjacent, ultimate segments. For example, leaves that do not fork are 0-order, and they consist only of a primary segment. Leaves are 1st-order if they fork once and their ultimate segments are secondary. Leaves are 2nd-order if at least one secondary segment forks and their ultimate segments are tertiary, and so on.

One specimen (Fig. 18) shows two whorls of leaves attached to the nodes. Each node has four leaves with petioles about 1.5–2.2 cm long and 0.3–0.6 mm wide; a single vein is present within each petiole (Fig. 18) and each lamina segment (Fig. 19). The leaf is at least 5th-order and the leaf lamina is 1 cm long (from the first dichotomy to lamina apex) with a single vein in each of the terminal segments (Fig. 20). Denticles are absent on the leaf segments. The other specimen (Fig. 20) shows a dispersed leaf lamina that has an incomplete petiole about 4 mm long and 0.6 mm wide before first branching. The lamina is 2 cm long (from first dichotomy to lamina apex) and is 5th-order



Figs. 12–14. *Donlesia dakotensis* gen. et sp. nov. 12. UF15708–33637b, fruit with an ovate seed and a long peduncle (pe). Scale bar = 1 mm. 13. Seed tegma removed from Fig. 12 with the same orientation to show two cotyledons (co), position of the plumule (pl) and chalaza (ch) notch. Scale bar = 0.5 mm. 14. Opposite side of Fig. 13 to show two cotyledons (co), position of the plumule (pl) and chalaza (ch) notch. Scale bar = 0.5 mm.

with a single vein entering each final segment. Leaf segment is about 0.6 mm wide, and no denticles are observed.

On the basis of (1) the co-occurrence of leaves and fruits from the same horizon and a small geographic area and (2) lack of other aquatic leaves or fruits from the same locality and ho-

rizon, we tentatively propose that these dispersed leaves and fruits are from the same plant species. Other aquatic plants reported from the Dakota Formation include *Aquatifolia*, *Azolla*, *Brasenites*, *Isoëtes*, *Marsilea*, and *Salvinia* (Kovach and Dilcher, 1985; Skog and Dilcher, 1992, 1994; Skog et al., 1992;

TABLE 1. Measurement of fruit size for *Donlesia dakotensis* gen. et sp. nov. Seed length and width are measured based upon the seed tegma or the impression of the seed tegma. Fruit length is measured as the distance between the two points where lateral spine wing meets with stylar spine and peduncle. Stylar spine length is measured from the point where the distal portion of the seed ends to the tip of the style. Peduncle length is measured from the point where the proximal portion of the seed ends to the base of the peduncle. Basal width of the lateral and facial spines is the direct distance between the two points where distinctive decurrent tissue of wing ends on the fruit. The length of lateral and facial spines is measured from the midpoint of the convex spine wing base to the tip of the spine. Only one complete facial spine length is measured. All measurements are in millimeters. * Mean length or width (length or width of each spine measured).

Specimen number	Fruit		Seed		Peduncle length	Style length	Facial spine		Lateral spine	
	Length	Width	Length	Width			Length	Basal width	Length	Basal width
15708-5332	4.5	3	4	1.5		5		2.75 (3, 2.5)*	7.5	3.25(4, 3.5)
15708-5333	4	3.5	4	1.5		6			7 (7, 7)	2.5 (2, 3)
15708-8384	5	3	5	2	10	12			11.5 (12, 11)	2.5 (2, 3)
15708-8385	4	2.5	4	1.8					11	2.5 (2, 3)
15708-8416	5.5	2	5.5	1.8	7				9	3 (3, 3)
15708-8418	4	3.5	4	1.5	9	6	9.8	3	10	4
15708-8419	5	2.5	5	2.3		6				4
15708-8420	5	3.5	4	2.5						4 (4, 4)
15708-33636	4	2.5	4	1.7	8				6 (7, 5)	3(3, 3)
15708-33637a	5	3.5	5	2	11				8	3 (3, 3)
15708-33638a	3	2.8	3	2.5	6	5			7	1.5 (1.5, 1.5)
15708-33639	4	2	3	1	8			2	10	3
15708-33641	3	2.5	3	2					9	2.5 (2.5, 2.5)
15708-33642a	5	2.5	5	2	12				10 (10, 10)	3
15708-49571a	3.5	2	3.5	1.5		7			5.5 (5, 6)	2.5 (2, 3)
15708-49571b	3.5	2	3	2	9				6.5	2.25 (2, 2.5)
15708-49571c	4	2.5	4	2	10				5	2.25 (2, 2.5)
15708-49572	3	2.5	3	1.5	9				7.5	2.5 (2.5, 2.5)
15708-49577	4	3	4	2	14				10	2.5 (2, 3)
15708-49578	5	4	5	2.5						4 (4, 4)
15708-49579	3	1.6	3	0.6	10	6		1.5	6.5	2
15708-51207	4	3	4	2.5	10					2
Mean (range)	4.0 (3-5.5)	2.7 (1.6-4)	3.9 (3-5.5)	1.8 (0.6-2.5)	9.9 (6-14)	6.8 (5-12)	9.8	2.1 (1.5-3)	8.0 (5-12)	2.5 (1.5-4)

Wang and Dilcher, 2006), but none of these plants have leaf or fruit morphology similar to that of *Ceratophyllum*.

GENERAL DISCUSSION

Fossils of various ages from the Cretaceous to the Holocene assigned to the genus *Ceratophyllum* have been reported around the world (see Les, 1988c, Table 8; Hu and Chaney, 1940; Backman, 1943; Hessland, 1946; Terasmae and Craig, 1958; Avakov, 1962; Dorofeev, 1963, 1974; Ritchie and DeVries, 1964; Watts and Bright, 1968; Gruger, 1973; Knobloch, 1977; Gregor, 1978; Mai and Walther, 1978, 1988; Van Zant 1979; Griffin, 1980; Pals et al., 1980; Ohlhorst et al., 1982; Palamarev, 1982; van der Burgh, 1983, 1987; Axelrod, 1985; Pierce and Tiffney, 1986; Geissert et al., 1990; Herendeen et al., 1990; Ozaki, 1991; Huang and Dilcher, 1994; Dyjor et al., 1998; Mai and Wähnert, 2000; Manchester, 2000; Wilf, 2000; Mai, 2001; Johnson, 2002; Gümbel and Mai, 2004, 2006; Wang et al., 2005; Serbet et al., 2008; Estrada-Ruiz et al., 2009). *Donlesia dakotensis* differs from extant and other fossil *Ceratophyllum* species by the following characters: (1) tetra-radially symmetric fruits, (2) presence of two winged facial spines and a long peduncle, and (3) lack of other appendages on the fruit surface.

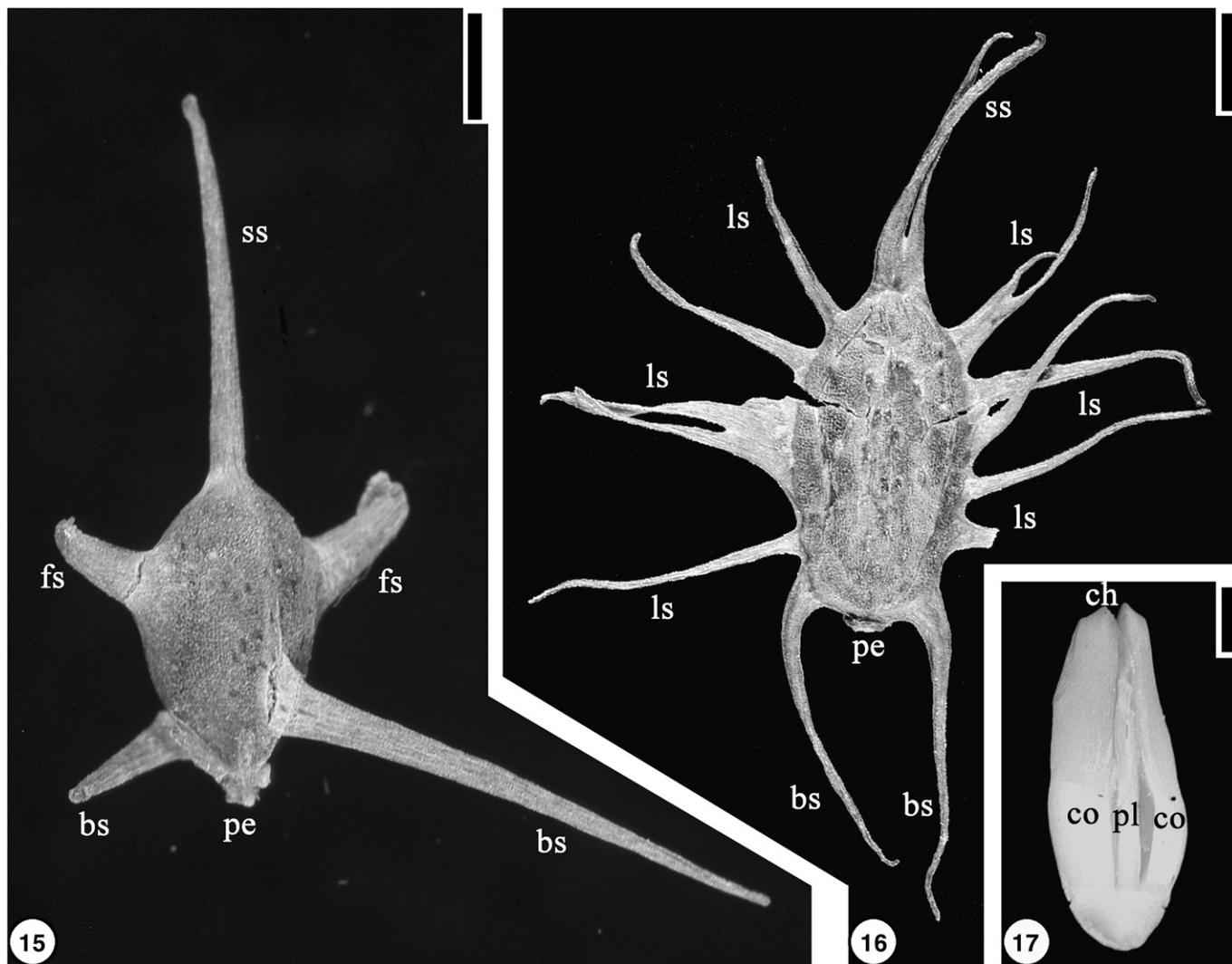
Ceratostratiotes is a form genus established by Bůžek (1982) for fossil fruits from the Miocene of Europe that are regarded as belonging to a different genus in the Ceratophyllaceae (Bůžek, 1982; Les, 1988c, table 9). However, others (Meller and van Bergen, 2003) consider that its systematic affinity is unresolved based upon its morphological-anatomical features. Comparison

of the achene features of *Donlesia dakotensis* with extant *Ceratophyllum* and *Ceratostratiotes* is presented in Table 2. The table shows that *D. dakotensis* differs from *Ceratostratiotes* in having a long peduncle, two planes of symmetry of the fruit, a smooth surface, and the presence of winged facial and lateral spines.

Donlesia dakotensis can be distinguished from *Hemitrapa* Miki reported from the late Cenozoic of Eurasia (Kovar-Eder et al., 2002; Wójcicki and Kvaček, 2002a) and the "Awned Seeds" from Cretaceous of Australia (Douglas, 1969; Drinnan and Chambers, 1986) by its winged spines, a long peduncle, a stylar spine and a smooth surface. In gross morphology, it is similar to *Schenkiella* Wójcicki and Kvaček, a fossil genus of unknown affinities from the Lower Miocene of central Europe (Wójcicki and Kvaček, 2002b), but they differ in that *Schenkiella* does not possess a long peduncle and long facial, lateral, or stylar spines.

Donlesia dakotensis is similar to *Ceratophyllum platyacanthum* in that both have facial spines (Les, 1988b, 1989). However, it is unlikely that these two species are particularly closely related, given the number of other differences that justify their recognition as distinct genera. It is conceivable that species known from the other two sections of *Ceratophyllum*, i.e., sect. *Submersum* and sect. *Muricosa* could be derived from an ancestor similar to these Cretaceous fossils through modification of fruit features. However, such modification would be extensive from a *Donlesia*-like ancestor, which most likely represents a close sister group to *Ceratophyllum*, with no known direct extant descendants. Its affinity to *Ceratophyllum* seems closer than that of *Ceratostratiotes* in any case.

If one regards *Donlesia dakotensis* as the outgroup of *Ceratophyllum*, then an interpretation of certain morphological characters is possible. Notably, the presence of winged spines



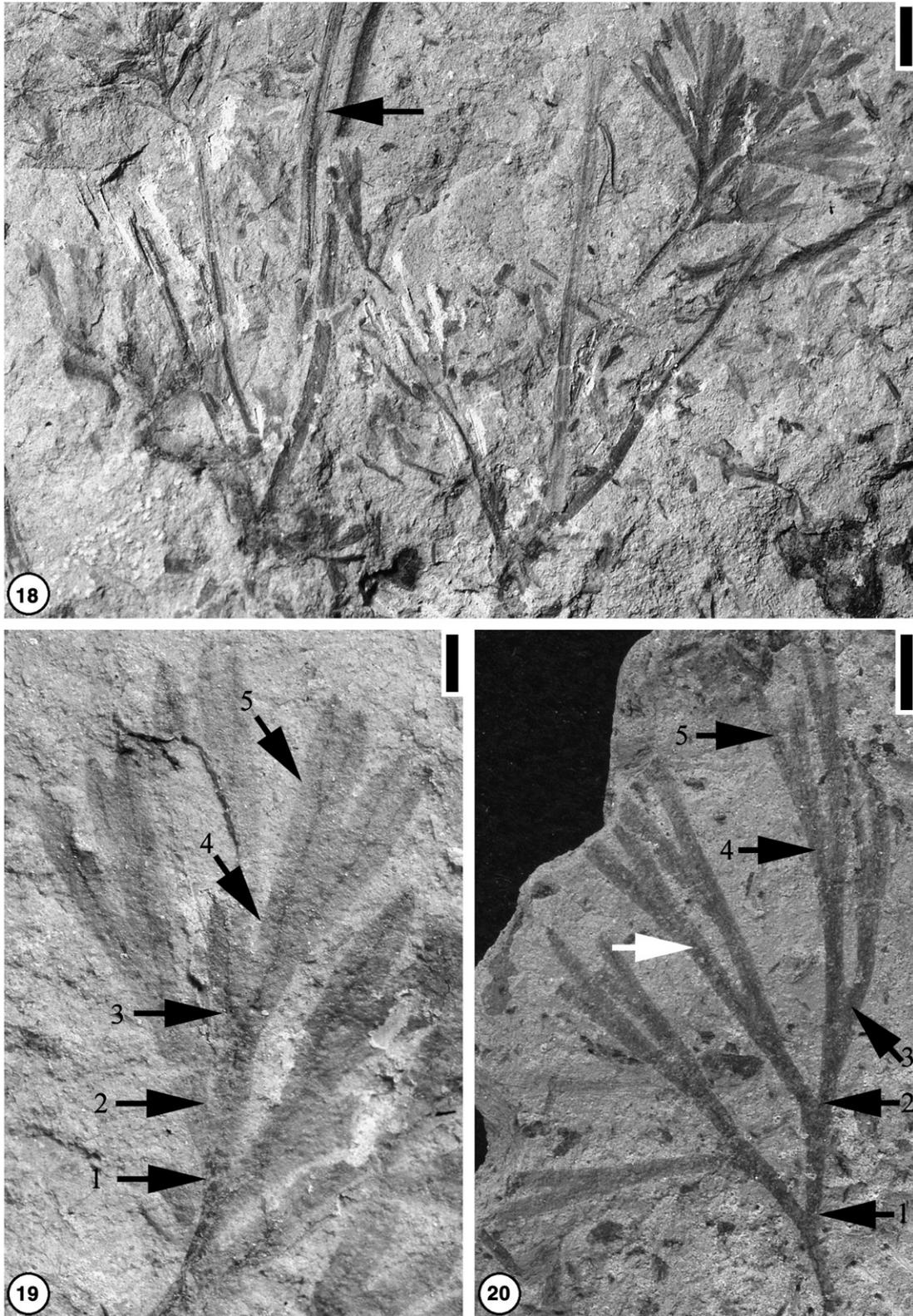
Figs. 15–17. Fruits of extant *Ceratophyllum*. **15.** *C. platyacanthum*, UF1388, fruit showing two broken facial spines (fs), two basal spines (bs, one is broken and incomplete), a stylar spine (ss) and a short peduncle (pe). Scale bar = 1 mm. **16.** *C. muricatum*, UF0114, fruit showing two stylar spines (ss) fused at the base, lateral spines (ls), two basal spines (bs), and the short peduncle (pe). Scale bar = 1 mm. **17.** Seed removed from Fig 16 with the same orientation as in the fruit showing two cotyledons (co), the plumule (pl), and the position of the chalaza (ch). Scale bar = 0.5 mm.

in *Donlesia* would indicate that winged spines in *Ceratophyllum* (e.g., *C. platyacanthum* subsp. *platyacanthum*, *C. echinatum*, *C. muricatum*) conceivably represent an ancestral condition in the genus. Thus, wingless spines such as those of *C. demersum* and *C. platyacanthum* subsp. *oryzetorum*) would indicate a derived condition. By this interpretation, the wing in taxa such as *C. platyacanthum* subsp. *platyacanthum*, would not have originated *de novo* as Les (1988a, 1989) previously hypothesized. A similar argument could be applied to suggest the ancestral condition of facial spines in *Ceratophyllum*.

Of the two facially spined subspecies of *Ceratophyllum platyacanthum*, *C. platyacanthum* subsp. *platyacanthum* occurs exclusively in Western Europe and *C. platyacanthum* subsp. *oryzetorum* only occurs in eastern Asia (Les, 1986c, 1988b). Hypotheses to interpret the current distribution and disjunction for these two subspecies are proposed next.

After its origin, *Donlesia dakotensis* may have undergone rapid evolutionary changes like other early angiosperms (Doyle and Hickey, 1976; Hickey and Doyle, 1977; Upchurch

and Wolfe, 1993; Wing and Boucher, 1998). By the late Early Cretaceous, environments such as quiet freshwater lakes and streams with abundant light and nutrients were widespread. By this time, the paleoenvironments, the warm, equitable, and perhaps ice-free paleoclimate (Fassell and Bralower, 1999), and the propagation mechanism all favored the rapid production and widespread distribution of *Ceratophyllum*. As in extant *Ceratophyllum*, the ability to reproduce vegetatively and the dispersal of fruits by birds enabled *D. dakotensis* to migrate along coastal water bodies and occupy many of these stable aquatic environments throughout the northern hemisphere (Retallack and Dilcher, 1981b; 1986). In North America, *D. dakotensis* became extinct, whereas in Europe, it underwent morphological changes, reducing its peduncle length and complicating its lateral wings, and in East Asia it underwent the reduction of wings on facial and lateral spines, and the reduction of peduncle length. If correct, this hypothesis predicts the occurrence of *Donlesia* in the fossil record of the Old World.



Figs. 18–20. Leaves associated with *Donlesia* fruits from the Acme Brick Co I (UF15708) and II (UF18730), Kansas. **18.** UF18730–49574, specimen showing long petioles of the leaves; note the single vein in the petiole (arrow). Scale bar = 2 mm. **19.** Enlargement of the leaf in Fig. 18 to show that the leaf is 5th-order (indicated by numbers 1–5 and arrows); note the single vein in each lamina segment. Scale bar = 0.5 mm. **20.** UF15708–8383, specimen showing a dispersed leaf of 5th-order (indicated by numbers 1–5 and arrows); note the single vein in each lamina segment (white arrow). Scale bar = 2 mm.

TABLE 2. Comparisons of achene features for *Donlesia dakotensis* gen. et sp. nov., modern *Ceratophyllum*, and *Ceratostratiotes*. Data for extant *Ceratophyllum* and *Ceratostratiotes* are from Les (1988c, Table 8). “?” indicates that a feature is not observed.

Character	<i>Donlesia dakotensis</i>	<i>Ceratophyllum</i>	<i>Ceratostratiotes</i>
Fruit stalk	Long stalked (peduncle)	Stalked (short or inconspicuous)	Sessile
Planes of symmetry	Two	Two	One
Surface	Smooth	Punctate or papillate	Polygonally pitted
Spines	In two planes	In two planes	Radiate in circular plane
Vasculature of apical style	Nonvascularized	Vascularized	Nonvascularized
No. of locules	Unilocular	Unilocular	Unilocular
No. of seeds	One	One	One
Placentation	Basal	Apical/ventral	Basal/ventral
No. of endocarp layers	?	Two	Two
“Micropylar” canal	?	Present	Present

Whether the close morphological similarities of these fossil and extant *Ceratophyllum* fruits can be used to suggest a close genetic relationship should be open to question. These similarities may be explained by morphological stasis, a concept that was proposed by Parks and Wendel (1990) and has been applied to explain the morphological similarities between eastern Asian–eastern North American disjunct taxa (Hoey and Parks, 1991; Qiu et al., 1995a, b; Shi et al., 1998; Wen, 1999, 2000; Wen et al., 2002; Nie et al., 2006). The stable and similar habitats (i.e., freshwater lakes) and the generic level stability of aquatic plants (Hutchinson, 1975) may have played a major role in maintaining the morphological similarities between *Donlesia* and extant *Ceratophyllum* (Williamson, 1987; Williams, 1992). However, these fossil fruits are from the Early Cretaceous (Albian), about 100 million years before present. Their age raises questions about how long do species or genera live, can morphological characters be used to define general/species through 100 million years of time, and do close morphological characters also mean close genetic relationships?

Williamson (1987) proposed two mechanisms, i.e., evolutionary constraints and stabilizing selection, for morphological stasis. Morphological stasis caused by evolutionary constraints is the lack of significant change through intrinsic features of the genetic and/or developmental architecture, whereas stasis through stabilizing selection results from the elimination of all phenotypes that deviate significantly from the populational mean. The relative contributions of the two mechanisms to generating and maintaining morphological stasis are not well understood, and they both may act together (Williamson, 1987; Wen, 2001).

Here, accepting that the morphological similarities between *Donlesia* and extant *Ceratophyllum* as indicating a close genetic relationship suggests that evolutionary constraints played a main role in maintaining the morphological stasis. Water is a sheltered and stable environment (Hutchinson, 1975) and ancient aquatic plants, such as *Aquatifolia*, *Azolla*, *Brasenites*, *Donlesia*, *Isoetes*, *Marsilea*, and *Salvinia*, hold some similarities to extant taxa. Other aquatic taxa such as *Archaeofructus* have become extinct and leave no extant relatives (Sun et al., 1998, 2002).

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