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Lakotacrinus brezinai n. gen. n. sp., a new stalked crinoid from cold methane seeps in the Upper Cretaceous (Campanian) Pierre Shale, South Dakota, United States

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Abstract.—Despite a rich and varied record, Mesozoic stalked crinoids are relatively rare in the Western Interior Seaway of North America compared to those found in Northern Europe. A unique example of Mesozoic stalked crinoid is described from cold methane seeps (hydrocarbon seep mounds also called "tepee buttes") from the Upper Cretaceous (upper Campanian) of the Northern Great Plains of the United States; the first crinoids to be described from such an environment. The Late Cretaceous Western Interior Seaway has never before yielded any identifiable stalked crinoid remains. Nevertheless, there have been significant studies on both free living and stalked crinoids from other locations in the Upper Cretaceous of North America that provide a good basis for comparison. *Lakotacrinus brezinai* n. gen. n. sp. is characterized by a tapering homeomorphic column with through-going tubuli, lacking any attachment disc. The arms are unbranched and pinnulate, with muscular and syzygial articulations. The unique morphology of the column justifies the establishment of Lakotacrinidae new family. A new suborder Lakotacrinina n. subord., is also proposed as there exists no corresponding taxon within the Articulata that can accommodate all the characteristics of this new genus. This new crinoid shares many features with other members of the articulates, including bathycrinids, bourgueticrinids and guillecrinids within the Order Comatulida, as currently defined in the revised Treatise of Invertebrate Paleontology. Reconstructing the entire crinoid using hundreds of semi-articulated and disarticulated (well preserved) fossils, reveals a unique paleoecology and functional morphology specifically adapted to living within this hydrocarbon seep environment.

Introduction

Despite a rich and varied global record, Mesozoic stalked crinoids are relatively rare in the Western Interior Seaway of North America. We describe a unique example of a stalked crinoid from cold methane seeps (hydrocarbon seep mounds or "tepee buttes") from the Upper Cretaceous (upper Campanian) of the Northern Great Plains of the United States. Herein we describe a new suborder, family, genus and species of crinoid, *Lakotacrinus brezinai*, as part of the existing order Comatulida within the Articulata. The Late Cretaceous Western Interior Seaway has never before yielded any identifiable stalked crinoid remains.

The existing knowledge of Upper Cretaceous crinoids from North America is extensive and comparable to that of Europe (Rasmussen, 1961; Jagt, 1999; Salamon et al., 2007; Salamon et al., 2009; Salamon and Gorzelak, 2010; etc), the Former USSR (Klikushin, 1982, 1987) and Japan (Oji, 1985; Oji et al., 1996; Hunter et al., 2011a). Previous studies on Upper Cretaceous North American crinoids, specifically from the USA, include specimens from Utah (Marsh, 1871), New Jersey (Gabb, 1876; Clark, 1893), Kansas (Grinnell, 1876; Meek, 1876; Clark, 1893; Logan, 1896; Springer, 1900, 1901, 1911; Clark and Twitchell, 1915; Miller et al., 1957; Miller, 1968; Milsom et al., 1994; etc.), Alabama (de Loriol, 1882; Clark, 1893; Clark and Twitchell, 1915), Mississippi (Springer, 1911; Clark and Twitchell, 1915; Moore, 1967), Texas (Peck, 1943; Peck and Watkins, 1972), Wyoming (Koch, 1962; Keefer and Troyer, 1964; Cobban, 1995), Colorado (Cobban, 1995), Montana (Cobban, 1995) and Washington (Moore and Vokes, 1953). They have also been described from Mexico (Rasmussen, 1961) and Jamaica (Donovan et al., 1996). Moore (1967) described a diverse range of deep-water stalked forms within the fauna from the Maastrichtian Stage of the Prairie Bluff Chalk in northeastern Mississippi. While neither stalked nor free living crinoids have previously been recorded from the Pierre Shale itself, the Santonian Stage of the underlying Niobrara Formation from Kansas has one of the major crinoid Lagerstätten, containing *Marsupites* and *Uintacrinus* (Cobban, 1995; Hess, 1999).

Geological setting

The crinoid specimens (both articulated and fragmentary) occur in cold methane seep deposits within the Pierre Shale in western South Dakota (see Fig. 1). These structures appear as conical mounds (often referred to as “tepee buttes”) composed of carbonate limestones, up to 60 m in diameter and 10 m in height (Fenneman, 1931). These unusual conical features were formed by the erosion of the surrounding softer sediments and have been recognized since the late 19th century (Gilbert and Gulliver, 1895). Hendricks et al. (2011) reported that in Colorado, seeps are expressed by four different kind of facies including dense lucinid limestone, vuggy limestone with only a few lucinids, brecciated limestone and ‘ropy-textured limestone; however all four of these facies may not be present at all seeps. Seeps range in age from the late-middle Campanian to the early Maastrichtian (Howe, 1987; Kauffman et al., 1996; Metz, 2008) (see Fig. 2) and have been documented from Montana to Texas and from the Front Range of the Rocky Mountains to western Kansas (Metz, 2008).

“Tepee Buttes” are widely thought to be the sites of cold methane seeps (Kauffman et al., 1996; Metz, 2008). The source of the methane is still disputed but may have originated from nutrient rich brines or connate waters trapped within the Pierre Shale and possibly the underlying Niobrara Formation. Chemosynthetic bacteria oxidized the methane thereby increasing the concentration of CO_2 in the water; this promoted the authigenic precipitation of carbonate minerals. Isotopic analyses of the carbonate cements at these sites reveal very light values of δ^{13} C. Kauffman et al. (1996) reported that the carbonate cements in vent deposits from Colorado are extremely depleted in δ^{13} C (−40‰ to −45‰). Similarly negative values have been reported from Cretaceous vents in the Canadian Arctic (Beauchamp and Savard, 1992). Such negative values indicate that the carbon was derived from methane oxidation.

The seeps support an abundant and diverse community in addition to the crinoids that includes bivalves (notably inoceramids and aggregations of chemosymbiotic-harboring lucinids), gastropods, nautilids *(Eutrephoceras)*, ammonites (*Solenoceras, Menuites*, *Baculites*, *Hoploscaphites*, *Placenticeras*, *Didymoceras*, *Spiroxybeloceras*), irregular (spatangoid) and regular echinoids, ophiuroids, crabs (Bishop and Williams, 2000), shrimp, sponges, corals (*Microbacia*), (serpulid) worm tubes, algae, chemosynthetic bacteria (forming stromatolite like masses or microbialites), foraminifera, radiolarians, bryozoans and fish. A total of ~30 individual molluscan species were reported from single seeps in the upper Campanian of Colorado (Howe, 1987). In their studies of these sites, Kauffman et al. (1996) documented a zonation of macrofaunal and microfaunal assemblages distributed from the center of the vents to the adjacent sea floor, reflecting, according to

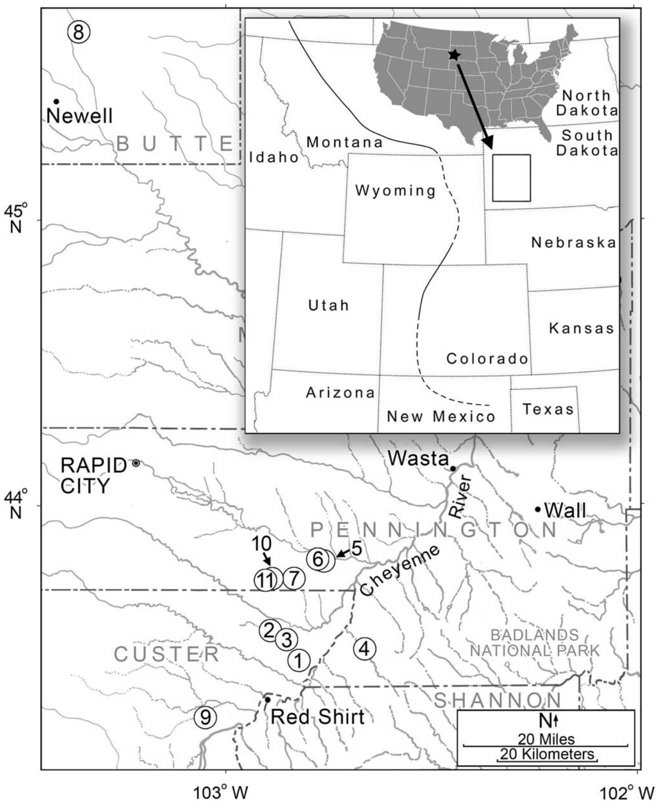
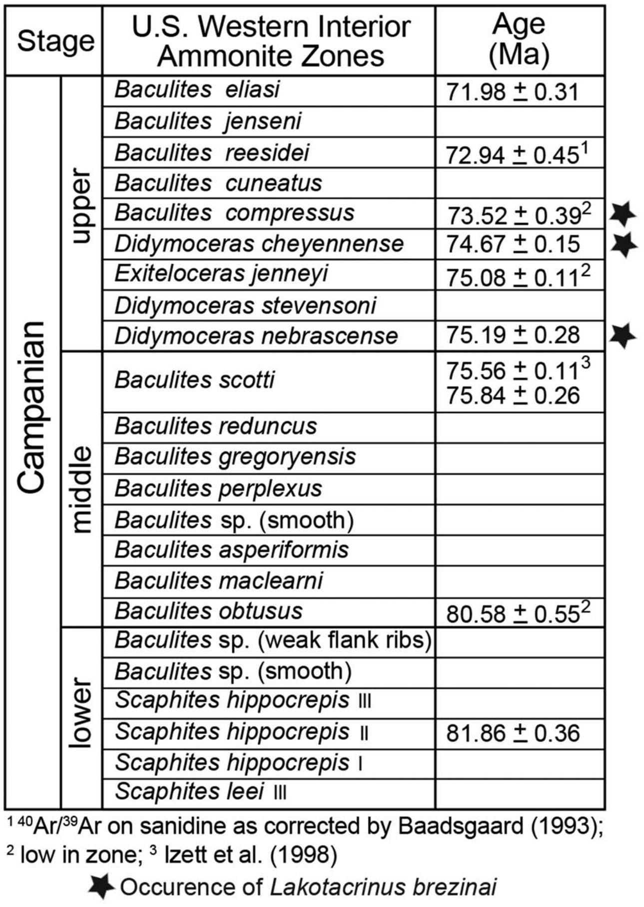


Figure 1. Map of southwestern South Dakota showing the crinoidal bearing methane seep mounds. (**1**) AMNH loc. 3456; (**2**) AMNH loc. 3418; (**3**) AMNH locs. 3419, 3420, 3457a,b,c; (4) AMNH loc. 3489; (**5**) AMNH loc. 3505; (**6**) AMNH locs. 3467, 3468, 3469; (**7**) AMNH loc. 3488; (**8**) AMNH loc. 3440, (**9**) AMNH loc. 3506; (**10**) AMNH loc. 3507; and (**11**) AMNH loc. 3509. Solid and dashed line in upper map indicates the western margin of the Western Interior Seaway during the deposition of the *Baculites compressus* Zone.



Stage		U.S. Western Interior Ammonite Zones	Age (Ma)	
Campanian	upper	*Baculites eliasi*	71.98 ± 0.31	
		Baculites jenseni		
		Baculites reesidei	72.94 ± 0.45[1]	
		Baculites cuneatus		
		Baculites compressus	73.52 ± 0.39[2]	★
		Didymoceras cheyennense	74.67 ± 0.15	★
		Exiteloceras jenneyi	75.08 ± 0.11[2]	
		Didymoceras stevensoni		
		Didymoceras nebrascense	75.19 ± 0.28	★
	middle	*Baculites scotti*	75.56 ± 0.11[3] 75.84 ± 0.26	
		Baculites reduncus		
		Baculites gregoryensis		
		Baculites perplexus		
		Baculites sp. (smooth)		
		Baculites asperiformis		
		Baculites maclearni		
		Baculites obtusus	80.58 ± 0.55[2]	
	lower	*Baculites* sp. (weak flank ribs)		
		Baculites sp. (smooth)		
		Scaphites hippocrepis III		
		Scaphites hippocrepis II	81.86 ± 0.36	
		Scaphites hippocrepis I		
		Scaphites leei III		

[1] $^{40}Ar/^{39}Ar$ on sanidine as corrected by Baadsgaard (1993);
[2] low in zone; [3] Izett et al. (1998)
★ Occurence of *Lakotacrinus brezinai*

Figure 2. Upper Cretaceous (Campanian and Maastrichtian) ammonite zonal table of the U.S. Western Interior, designating the zones of the crinoid occurrence (after Cobban et al., 2006).

them, an environmental stress gradient with decreasing H_2S. The most diverse assemblage consists mostly of molluscs and occurs on the upper part of the flanks, down-current from the immediate vicinity of the methane emissions. In contrast, the surrounding grey shale contains few fossils.

The topographical relief of the seeps on the sea floor is unknown. Some may have represented topographical highs, while others formed below or at the sediment-water interface (Shapiro and Fricke, 2002; Hendricks et al., 2011). However, the presence of fallen slump blocks on the sides of some seeps, dipping away from the central conduits, suggests that some must have exhibited higher relief (Kauffman et al., 1996), although we are not inferring that the seeps described in this study did and further research into modern seeps will be the key to understanding their ancient analogues.

The geographic distribution of cold seep deposits in the Western Interior of North America may be related to underlying structural features. For example, in certain biostratigraphic zones in South Dakota, they form a ring around the Black Hills (see Fig. 1), suggesting that they originated from a series of tectonic faults that must have developed in this area during the upper Campanian as a precursor to the Black Hills uplift. Howe (1987, p. 13–18, 46) suggested that "tepee buttes" reflect faults since the buttes can be traced for several miles paralleling uplifts, indicating that tectonic activity was the underlying source in the creation and deposition of the seeps near Pueblo and elsewhere in Colorado.

In an analysis of the geographic and temporal distribution of cold seeps in the Western Interior Basin, Metz (2008) suggested that they are associated with the development of the forebulge depozone. Metz argued that transgressive episodes, which involved an increase in sediment loading near the orogenic belt and an increase in the degree of flexure of the forebulge, promoted the formation of cold seeps. In contrast, regressive episodes, which involved a decrease in sediment loading near the orogenic belt and a decrease in the degree of flexure of the forebulge, acted against the formation of cold seeps. Landman et al. (2012) suggested that seep activity was related to faults that were active at the time of deposition.

The longevity of a single seep is difficult to estimate but it may have persisted over a time span of up to 1.25 Myr, during which time, it may have episodically stopped, started, collapsed, and restarted again nearby, depending on the source of the methane and the intricacies of the plumbing network (Kauffman et al., 1996). We infer a long lifespan for a seep in Fall River County, South Dakota (AMNH loc. 3342), where the lower part of the deposit contains fossils from the *Baculites scotti* Zone and the upper part of the deposit (more than 30 m higher) contains abundant fossils from the *Didymoceras nebrascense* Zone (Fig. 2).

We collected and examined fossil material from several methane seeps from the *Didymoceras cheyennense* and *Baculites compressus* Zones, in both Custer and Pennington counties in western South Dakota (Figs. 1, 2), as well as from older seeps in Butte County, South Dakota (not shown on Fig. 1 but labeled on Fig. 2). These zones are radiometrically dated as 74.67 Ma, 73.52 Ma and 75.19 Ma respectively (Cobban et al., 2006). The discovery of a single columnal from a seep in the D. *nebrascense* Zone in Butte County indicates that these crinoids first appeared in the lowermost, upper Campanian.

A seep from the *Didymoceras cheyennense* Zone is exposed in cross-section at AMNH loc. 3418. The outcrop is nearly vertical and is ~13 m high and 20 m wide. The central area consists of multiple, anastomosing pipe like conduits, surrounded by grey shale with orange-weathering partings. Fossils are abundant over a distance of ~6 m on either side of the central area; however, perhaps due to sampling bias caused by the predominance of spot sampling rather than bulk sampling (Hunter and Donovan, 2005), relatively few crinoid remains were discovered here. Fossils are preserved in both the sediment and carbonate (limestone) concretions; in both instances, they retain their original morphologies and in some specimens the shell material itself (Landman et al., 2012). The sediments on the outer margins of the seep, up to 20 m away, are much darker, with fewer fossils. The fossils on either side of the central area include the cephalopods: *Hoploscaphites nodosus*, *H. brevis*, *Baculites corrugatus, B. undatus*, *Didymoceras cheyennense*, *Spiroxybeloceras meekanum*, *Placenticeras intercalare*, *P. meeki, Eutrephoceras nebrascensis*; the bivalves: *Nympholucina occidentalis*, "*Inoceramus*" *altus*, "*I.*" *nebrascensis*, *Cataceramus*? *gandjaensis*; the gastropods: *Drepanochilus nebrascensis*, *Ellipsoscapha occidentalis*, *Euspira obliquata*, *Oligoptycha concinna*; (serpulid) worm tubes, dinoflagellates, and some indeterminate sponges.

All but one of the crinoid specimens are from seep deposits in the *Didymoceras cheyennense* and *Baculites compressus* Zones in Custer County, South Dakota (AMNH locs. 3418, 3419, 3420 and 3456) and Pennington County (3505, 3507, 3509), South Dakota (see Fig. 1). In Custer County we recorded six mounds within 200 m of each other representing a vent field (3419, 3420, 3457, 3457a, 3457b and 3507). AMNH loc. 3420 is a large, extremely fossiliferous mound ~25 m across and 4 m high; three smaller mounds (locs. 3457, 3457a, 3457b) are within 10 m of loc. 3420. AMNH loc. 3419 (5–10 m across by 3 m high) is ~125 m away and is also very fossiliferous. AMNH loc. 3507 (5–6 m across by 2 m high), 150 m away from locs. 3419 and 3420 contains crinoids, inoceramids and ammonites.

Figure 3 shows a reconstruction of the likely environment that these crinoids inhabited. The seeps containing crinoids are riddled with inoceramid hash, cemented by thin layers of carbonates as well as abundant microbialite nodules and conduits filled with limestone and vuggy calcite. The center of the core at the majority of these seeps consists of a heavily cemented carbonate (limestone) structure surrounded by abundant microbialite nodules and thin layers of cemented shell hash and carbonates separated by shale with abundant invertebrate fossils surrounding the entire structure. This high degree of cementation suggests a late stage in vent development, as described by Beauchamp and Savard (1992) for Late Cretaceous vents from the Canadian Arctic.

Taphonomy and paleoecology

The large number of columnals found at seeps but nowhere else in the Western Interior Seaway suggests that *Lakotacrinus* n. gen. preferred the carbonate substrate of the seeps and the nutrients the seeps provided over an otherwise expansive, soft and muddy sea floor. They were gregarious, living in small local communities (of tens to perhaps a hundred individuals) occupying only a small portion of the carbonate mounds and not the

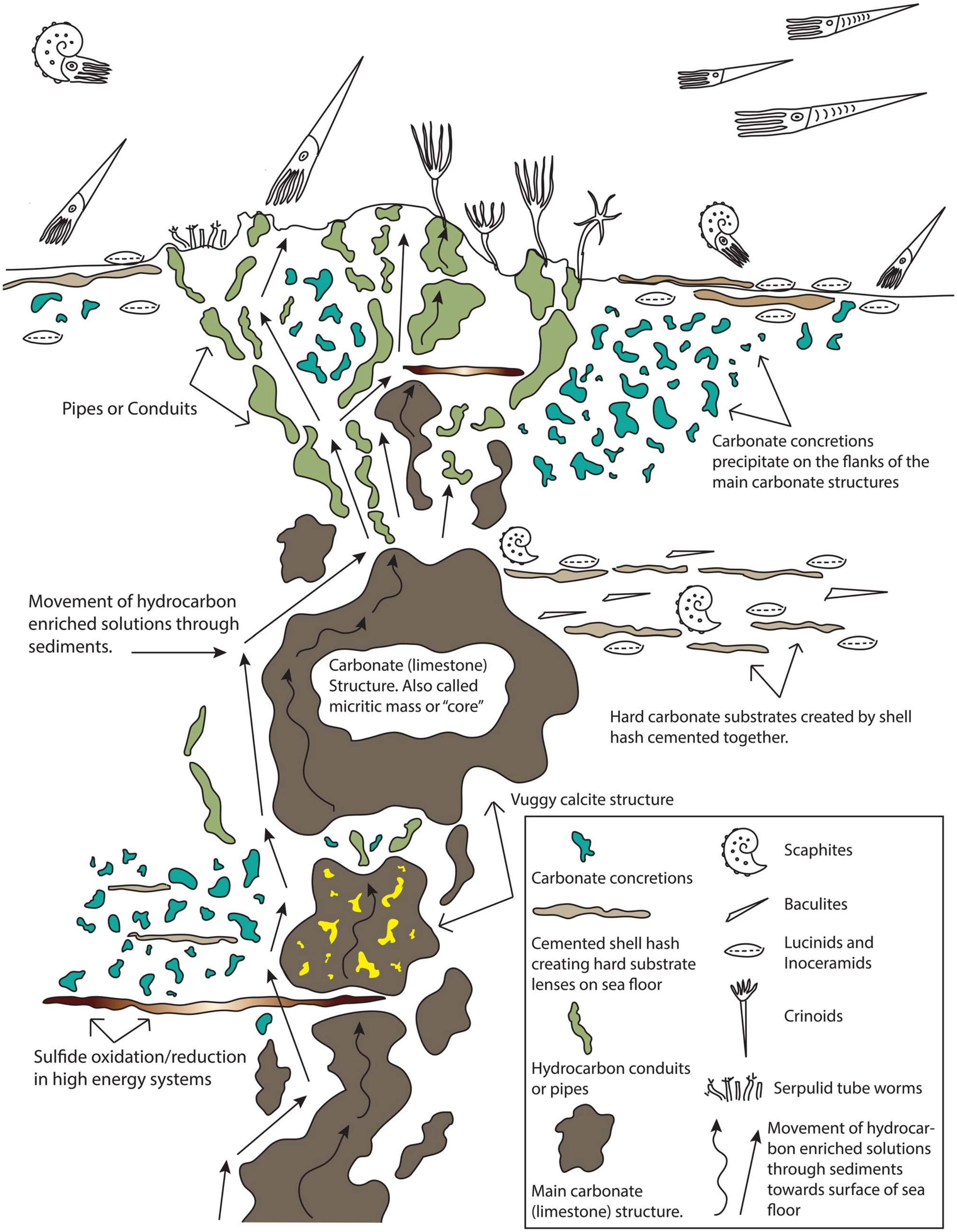


Figure 3. Reconstruction of the hydrocarbon (methane) seep environment (courtesy of Jamie Brezina).

entire surface. Most crinoids need to attach to some sort of hard surface to serve as an anchor when feeding. Since no attachment disc and instead only terminal columnals (AMNH-FI 85668 (AMNH loc. 3522)) have been discovered for *Lakotacrinus*, it is possible that it was not cemented to the surface but may have instead anchored itself within the substrate for stability (refer to functional morphology for further discussion).

The seeps undoubtedly attracted vast amounts of organic matter derived from seep associated communities, as well as phytoplankton and zooplankton; these would have provided abundant sources of food for the crinoids. Based upon measurements of reconstructed crinoid skeletons, *Lakotacrinus* is estimated to have been between 150 to 500 mm tall and would have been able to rise above the surrounding surface of the seeps, allowing them to feed freely in the rich sea currents and from the seep itself.

Sedimentation was probably relatively constant over the life of the seep (Hendricks et al., 2011); however, the unique environmental setting implies that sedimentation rates are unlikely to have been a primary factor influencing the taphonomic gradients described below. Seeps are primarily composed of carbonates from chemosynthetic bacteria (e.g Beauchamp et al., 1989). In oceans today, microorganisms produce carbonate structures in and around hydrothermal vents and methane seeps using chemosynthesis (Aharon, 1994). These chemosynthetic microorganisms are in turn consumed by other organisms in the ocean, possibly providing food for not only the crinoids but for sponges, (serpulid) worm tubes, lucinids and many other animals on the seep. Thus, large populations of many different animals could have been supported by chemosynthetic production at these different structures.

Amongst the echinoderms, some species of holothurians and ophiuroids are reported from hydrothermal vents and cold methane seeps in the modern deep sea (Segonzac, 1992; Stöhr and Segonzac, 2005), but reportedly echinoderms are underrepresented in such environments compared with other marine phyla. The present species described herein represents the first record of crinoids associated with cold methane seeps.

Lakotacrinus seems to have avoided the dense, lucinid limestone deposits so typically recognized in Colorado (Kauffman et al., 1996; Metz, 2008) and in the *Didymoceras nebrascense* Zone seeps around the Black Hills. Rather, these crinoids seem to have preferred seeps with lower populations of lucinids and a more diverse fauna rich in sponges, (serpulid) worm tubes, algae, chemosynthetic bacteria, ammonites, inoceramids and gastropods. This is indicated by the crinoids being far more prolific in seep deposits with abundant microbialite nodules around a central core (e.g., AMNH locs. 3419, 3420, 3456, 3505) than from the pipe like conduit vents where lucinids are more common (e.g., AMNH loc. 3418).

The lack of any specimens in the surrounding sedimentary facies strongly suggests that *Lakotacrinus* spent their entire life on or near the seep. These crinoids appear to be autochthonous (see Fig. 4) or para-autochthonous (see Figs. 5, 6) in that very few specimens appear outside the seep mounds. Specimens are preserved either articulated or show little disarticulation or abrasion in the ossicles, probably due to a lack of transportation. This lack of transportation may have resulted from their having been trapped in algal mats or pipe conduits (see below). A few ossicles are more distinctly abraded but are still found in the seep environment. In contrast with other Mesozoic crinoids, these specimens are exceptionally well preserved, allowing the majority of their skeleton to be reconstructed (Fig. 7). On close inspection however, these crinoids reveal a complex taphonomic history. For instance, to date, there are no preserved fully mature articulated specimens (Figs. 4.2, 5.7, 5.8). In contrast, immature growth forms are better preserved (Fig. 8), with all stages of ontogenetic development of the cup represented (Fig. 9). Specimens that are preserved with both the cup and proximal column lack articulated arms (with the exception of Figure 4.8), with only the most proximal section of the arms still present (Figs. 4.3, 5.7, 5.8). Typically crinoids are preserved as a single columnal (Fig. 5.1, 5.2), a group of columnals (pluricolumnals) (Figs. 5.9, 6.6, 6.8), or fully articulated (Figs. 8.1, 8.9). Those not preserved at an early secondary stage of decay (see Hunter and Zonnerveld, 2008), are almost always preserved as single columnals with the majority of these subject to abrasion or bioerosion (Fig. 5.1), revealing the unique internal tubuli structure in *Lakotacrinus* (Fig. 6.1, 6.6, 6.8). In addition, there are no obvious signs of predation or epizoan activity on the column (Fig. 5.7–5.9). This is quite unlike ammonites that show evidence of predation, such as bite marks, in almost every specimen (Landman et al., 2010). The numerous syzygies in the arms (Figs. 4.5, 5.4), (which in Recent forms are observed to operate as an articulation of autotomy in response to physical stimuli (personal observation, Oji)), would have permitted easy breakage, and are perhaps an indication of a defense mechanism against predation (personal communication, H. Hess, 2012), which is further supported by the lack of preserved articulated arms (Fig. 5.1, 5.2) and evidence of pathological regrowths in the proximal part of the cup (Figs. 8.7).

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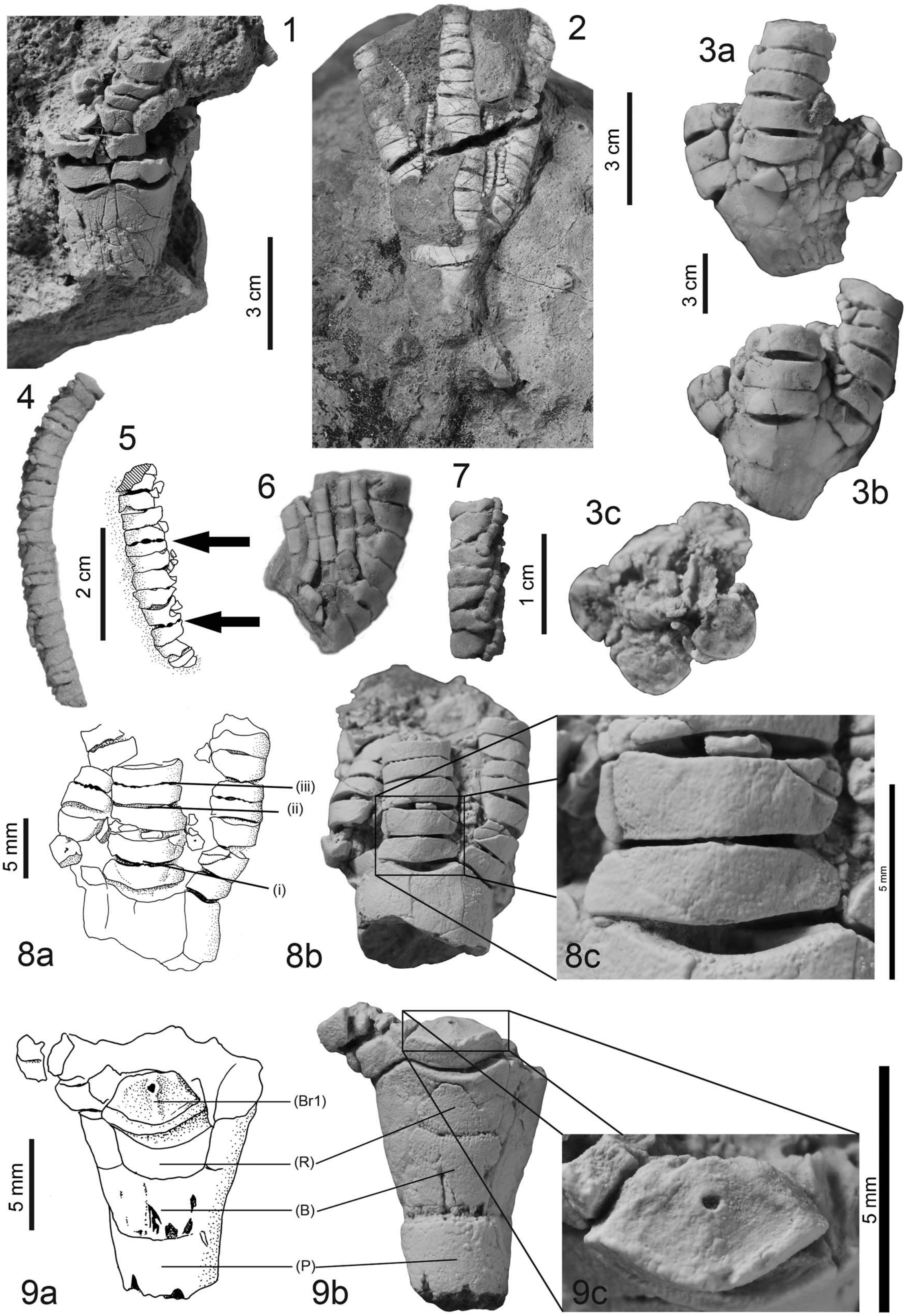
Figure 4. Holotype and paratypes of *Lakotacrinus brezinai* n. gen., n. sp. in the type collections of the American Museum of Natural History and Black Hills Museum of Natural History: (**1**) cup and slightly disarticulated proximal brachials, paratype AMNH-FI 83026 (AMNH loc. 3420); (**2**) cup (basal, radial circlet), proximal stalk and proximal brachials, Holotype AMNH-FI 69618 (AMNH loc. 3420); (**3a–3c**) articulated cup and proximal brachials, paratype AMNH-FI 63498 (AMNH loc. 3509); (**3a**) cup showing articulated section of proximal arms up to fifth brachial; (**3b**) clear view of interradial plates (interradials) sandwiched between proximal arms and located below first pinnule; (**3c**) top view of small cup showing muscular articulations and attachment of single pinnule; (**4**) distal arm segment showing arm pinnule sockets, AMNH-FI 84503 (AMNH loc. 3507); (**5**) Camera Lucida drawing of distal arm showing syzygy articulations (arrows), other articulations are all muscular, paratype AMNH-FI 83027 (AMNH loc. 3420); (**6**) intermediate arm with articulated pinnules, AMNH-FI 84502 (AMNH loc. 3419); (**7**) intermediate arm with well-preserved pinnules, AMNH-FI 85669 (AMNH loc. 3522); (**8a–8c**) partial cup (radials only) and articulated proximal arms, paratype AMNH-FI 83027 (AMNH loc. 3420); (**8a**) Camera Lucida drawing of cup and arm articulations, showing radial circlet and proximal brachials with synarthrial, syzygial and muscular articulations, note (i) synarthrial ligamentary articulation between the first and the second brachials (ii) muscular articulation between the third and fourth brachials (iii) ligamentary syzygy articulation between the fourth and the fifth brachials, exhibiting a typical "dotted line" like appearance from the exterior; (**8b**) distal edge of a basal, radial circlet and proximal brachials; (**8c**) enlarged view of first and second brachials showing synarthrial articulation with central transverse ridges on each side of brachials forming a slightly raised fulcral ridge; (**9a–9c**) cup with proximal columnal and proximal brachials, paratype BHMNH-7123 (AMNH loc. 3419); (**9a, 9b**) Camera Lucida drawing and original image showing structure of cup, (P) proximal columnal (B) fused basals (R) radials (Br1) first brachial; (**9c**) enlarged view of distal facet of first brachial showing synarthrial articulation with a transverse ridge.


1
3 cm
2
3 cm
3a
3 cm
3b
3c
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5
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6
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(iii)
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8c
5 mm
9a
5 mm
(Br1)
(R)
(B)
(P)
9b
9c
5 mm

The majority of articulated Mesozoic crinoids were preserved entombed in either sand or mud (see Hess, 1999). However no such 'obrution' deposit exists within these carbonate mounds. One of the features of the heavily cemented carbonate seeps is the presence of filamentous algal mats that would have trapped crinoid skeletal debris (as well as other faunal debris and sediment (Riding, 2000)), thus preventing transport of the material and contributing to a high preservation potential. The carbonate also presented an irregular surface providing crevices for the debris to fall into and accumulate. This leads us to suggest that the crinoids persisted 'entombed' for a significant amount of time within the substrate, and only then preserved by syn-depositional lithification of the sediment surface or within the pipe walls (carbonate structures) of the hydrocarbon seep (for example the holotype Figure 4.2). Some specimens were also shielded from decay by being preserved inside large bivalve shells (Fig. 5.1, 5.2). Finally, the unique fused structure of the proximal cup of *Lakotacrinus* implies that this component may have had a much higher preservation potential than other body parts (Fig. 6.1–6.5, 6.7).

Crinoids have an endoskeleton usually composed of high magnesium calcite, typical of all echinoderms. However it should also be mentioned that calcitic organisms are generally not well preserved or readily observed in the Pierre Shale. Most calcitic organisms seem to be dissolved or are completely fused during the formation of the abundant concretions (see Landman et al., 2010, p. 61).

Functional morphology

As this is the first crinoid to be documented living within a cold methane (hydrocarbon) seep environment, coupled with its unique form, it is reasonable to suggest that this crinoid had a unique adaptive morphology. Evidence of this comes firstly from the arms. There is no evidence for arm branching (Fig. 5.5) and the lack of axillaries (Fig. 5.6) in the bulk samples suggests that this crinoid would not have been able to form an efficient parabolic fan with which to feed. Pinnulation on the arms is evident from pinnule sockets (Figs. 4.4, 4.5, 5.3) and preserved pinnules (Fig. 4.6, 4.7) along the length of the arms. Fig. 5.5 shows preserved pinnules and pinnule sockets in the intermediate to distal sections but poor pinnulation in the proximal section, however this may be taphonomic. It is therefore possible that with the high nutrient conditions within the seep environment, and therefore wide availability of food, this crinoid may not have had to form an efficient fan system in which to thrive, instead relying on the large surface area of its long pinnulate arms. Barnes (1980) postulated that crinoids living in rich environments have fewer arms and a shorter life span than those which live in environments with relatively little plankton. Baumiller (1993) also concluded that the fine-meshed filter feeder is generally a specialist adapted for feeding in a strong current, and these fossil species had shorter lineage duration on average.

The column morphology of *Lakotacrinus* n. gen. also might result from its unique environment. The through-going tubuli (Figs. 6.1, 6.6, 9.8b, 9.9) could provide canals for through flowing ligaments running from the distal ossicle to the radials that could provide extra support, making the crinoid column a far more rigid structure capable of withstanding high current conditions (see Remarks).

Finally the manner by which *Lakotacrinus* attached itself to the substrate and remained stable remains a mystery, as we are yet to find any attachment structure. The discovery of two examples of terminal columnals AMNH-FI 80013 (Fig. 8.4) and AMNH-FI 85668 (AMNH loc. 3522) with rounded smooth bases, sealed and lacking lumen, which would have completed the tapering column as it diminished to a diameter of ~2 mm (Figs. 8.9, 8.10), show no evidence of an attachment disc as is seen in other articulate groups. We postulate that the immature column with low columnals and a symplectial articulation (Figs. 8.9, 8.10) could provide ample curvature and rigidity to hold its crown in strong currents, whereas the large columnals and longer column of the adults, combined with an almost smooth synostosial articulation (Fig. 6.8, 6.9, 6.10, 6.11) would have reduced the flexibility of the column, resulting in a far more rigid, strong stalk structure with some flexibility. Hess et al. (1999, p. 12) discussed that some shallow water Paleozoic crinoids, without any appendages (radicular cirri or holdfast), and with only a distally tapering column (as observed in *Lakotacrinus*) (Fig. 8.8, 8.10), were able to exist in a high-energy environment. Thus, *Lakotacrinus* might have either used its column to anchor itself or its long arms to cling to the substrate (much like that observed in Recent comatulids, such as *Oxycomanthus parvicirrus*, which has only a small number of cirri, but attaches to the substrate using its arms by curling the proximal sections outwards (personal observation, Oji)), or the inside of the pipe conduits in the seep complex (as indicated by some of the crinoids, including the holotype (Fig. 4.2), being preserved within the pipes themselves). Alternatively, cementation of sediment around the column may have in fact occurred due to the high CO_2 levels forming an environment of rapid cementation and syn-depositional lithification of sediment. The low number of terminal columnals discovered is possible evidence of this, with those columnals found representing individuals which failed to attach fully and the terminations of cemented specimens being lost or preserved as part of the substrate.

Materials and methods

Crinoids were found at approximately 35 individual seeps; 11 of which are cited in this study (AMNH locs. 3418, 3419, 3420, 3440, 3456, 3457, 3457a, 3457b, 3457c, 3467, 3468, 3469, 3488, 3489, 3505, 3507, 3509, [see Fig. 1]), although most of the cited specimens came from just six seeps (AMNH locs. 3419, 3420, 3456, 3488, 3505, 3507 and 3509). The material was collected between 2005 and 2014. Specimens were collected from weathered outcrops both in carbonate rocks and loose in the shale. Crinoids are not found over the entire surface of the seeps. At AMNH loc. 3420 crinoids are found sparingly on the top, and abundantly only from about one-quarter of the seep (on one side, about 1 m below the top).

At AMNH locs. 3505 and 3509 the crinoid material was so abundant in one portion of the seep that sediments were washed, screened and sorted. At locs. 3419 and 3420 the outcrops were first raked in 2009 and allowed to weather out naturally. This allowed for many more new specimens to be found in both the

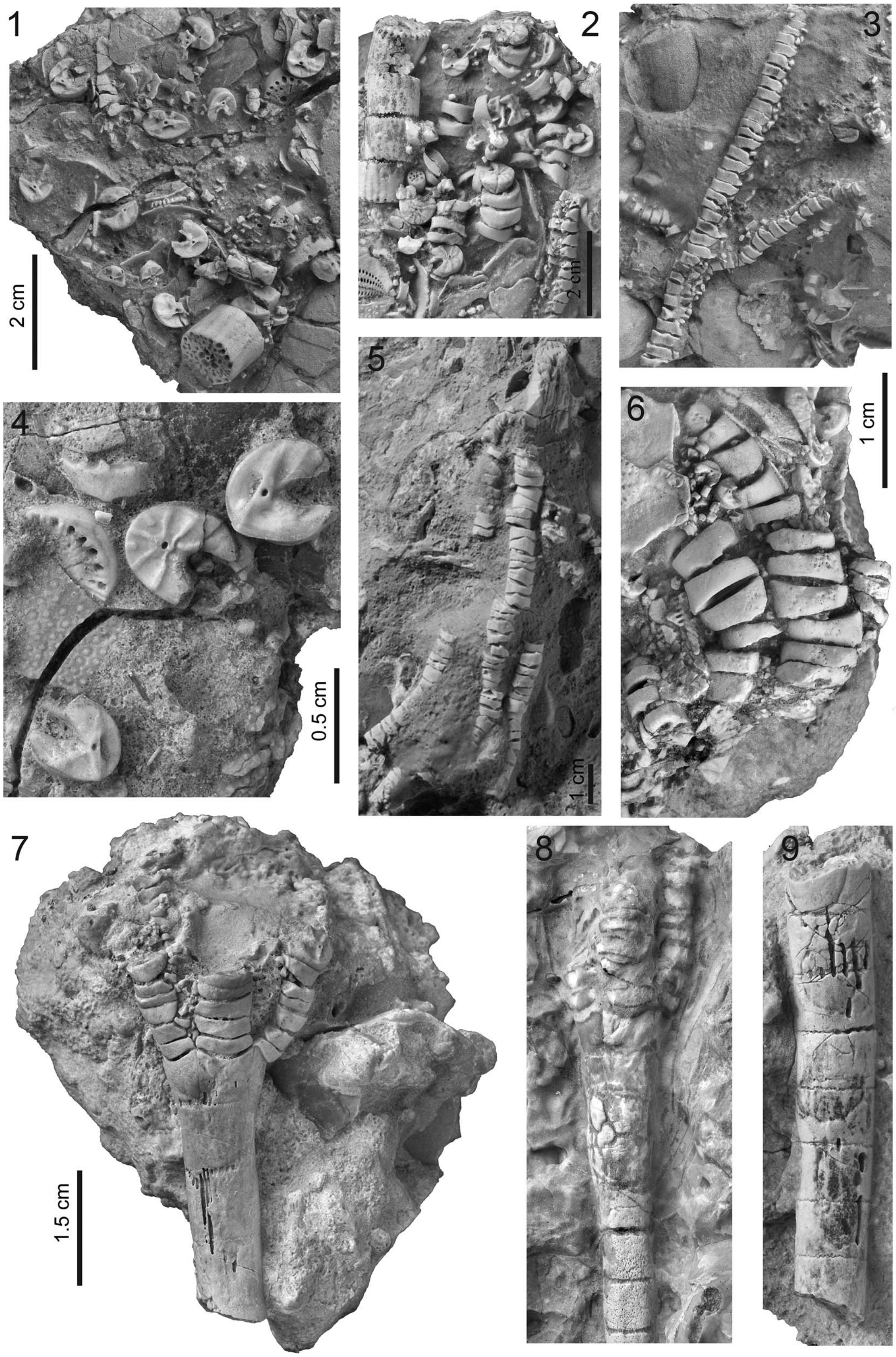


Figure 5. Crown morphologies of mature individuals of *Lakotacrinus brezinai* n. gen., n. sp. including AMNH and BHMNH paratypes: (**1**) disarticulated brachials and columnals, BHMNH-7023 (AMNH loc. 3419); (**2**) disarticulated proximal brachials, articulated distal brachials and semi-articulated columnals, note preservation adjacent to irregular echinoid test, BHMNH-7024 (AMNH loc. 3419); (**3**) articulated distal arms, BHMNH-7023 (AMNH loc. 3419); (**4**) enlarged view of disarticulated syzygial and muscular brachial ossicles, note preserved echinoid fragment, BHMNH-7026 (AMNH loc. 3419); (**5**) semi-articulated calyx including cup and unbranched arms with preserved distal pinnules, paratype AMNH-FI 63502 (AMNH loc. 3509); (**6**) semi-articulated section of proximal brachials, BHMNH-7024 (AMNH loc. 3419); (**7**) mature growth stage articulated cup (basal and radial circlet) with proximal column and brachials, paratype BHMNH-7028 (AMNH loc. 3419); (**8**) articulated cup with long proximal ?(sub)adult column (4-5 columnals) and proximal brachials, note preserved pinnules, BHMNH-7025 (AMNH loc. 3419); (**9**) section of proximal ?(sub)adult column (7-8 columnals), BHMNH-7027 (AMNH loc. 3419).

underlying sediments and in the freshly weathered microbialite nodules. Specimens in the lab were washed and cleaned by blasting crushed sodium bicarbonate through an air-abrasive system. Both the matrix and the crinoids are composed of calcium carbonate and neither acetic acid preparation nor base etching seemed to produce any favorable results.

Repositories and institutional abbreviations.—AMNH, American Museum of Natural History; BHMNH, Black Hills Museum of Natural History; BMNH, Natural History Museum, London; NUM, Nagoya University Museum.

Systematic paleontology

Class Crinoidea Miller, 1821
Subclass Articulata von Zittel, 1879
Order Comatulida Clark, 1908
Suborder Lakotacrinina new suborder
Fig. 4–9

Diagnosis.—Medium-small sized stalked crinoid. Cup funnel shaped, smooth and low with weakly rounded fused basals; five radials with outward sloping facets; radial cavity narrow. Basals and proximale commonly fused into a single plate. Infrabasals absent. Radials deeper than, but as wide as brachials. Arms unbranched; proximal brachials wide, the first two brachials united by synarthry, following brachials muscular and syzygial, first pinnule on IBr2 but pinnules more prevalent in intermediate and distal sections. Column moderately long, with smooth latera tapering towards a tiny distal end with rounded smooth terminal columnal lacking lumen; cirri and attachment disk absent. All columnals high, cylindrical and barrel shaped; articular facets cryptosymplectial to synostosial. Axial canal narrow, surrounded by extensive ringed network of five central large irregular through-going tubuli and abundant smaller regular marginal tubuli. Columnals never with synarthries.

Comparison.—We believe that the erection of a new suborder is required as no existing suborder or family within the Articulata can accommodate the characteristics of *Lakotacrinus* n. gen. from the upper Campanian of South Dakota. Diagnostic characters are summarized in Appendix 1.

This new suborder shares many features with other members of the Articulata including well-developed muscular articulations and a slender cup with five (fused) basals (but no infrabasals) and five radials (Fig. 4.1, 4.2, 4.3a, 4.3b, 4.8a, 4.8b, 4.9a, 4.9b). The arms are uniserial, long, unbranched and five in number with synarthrial, muscular and syzygial articulations (Fig. 4.8, 5.3, 5.4, 5.5).

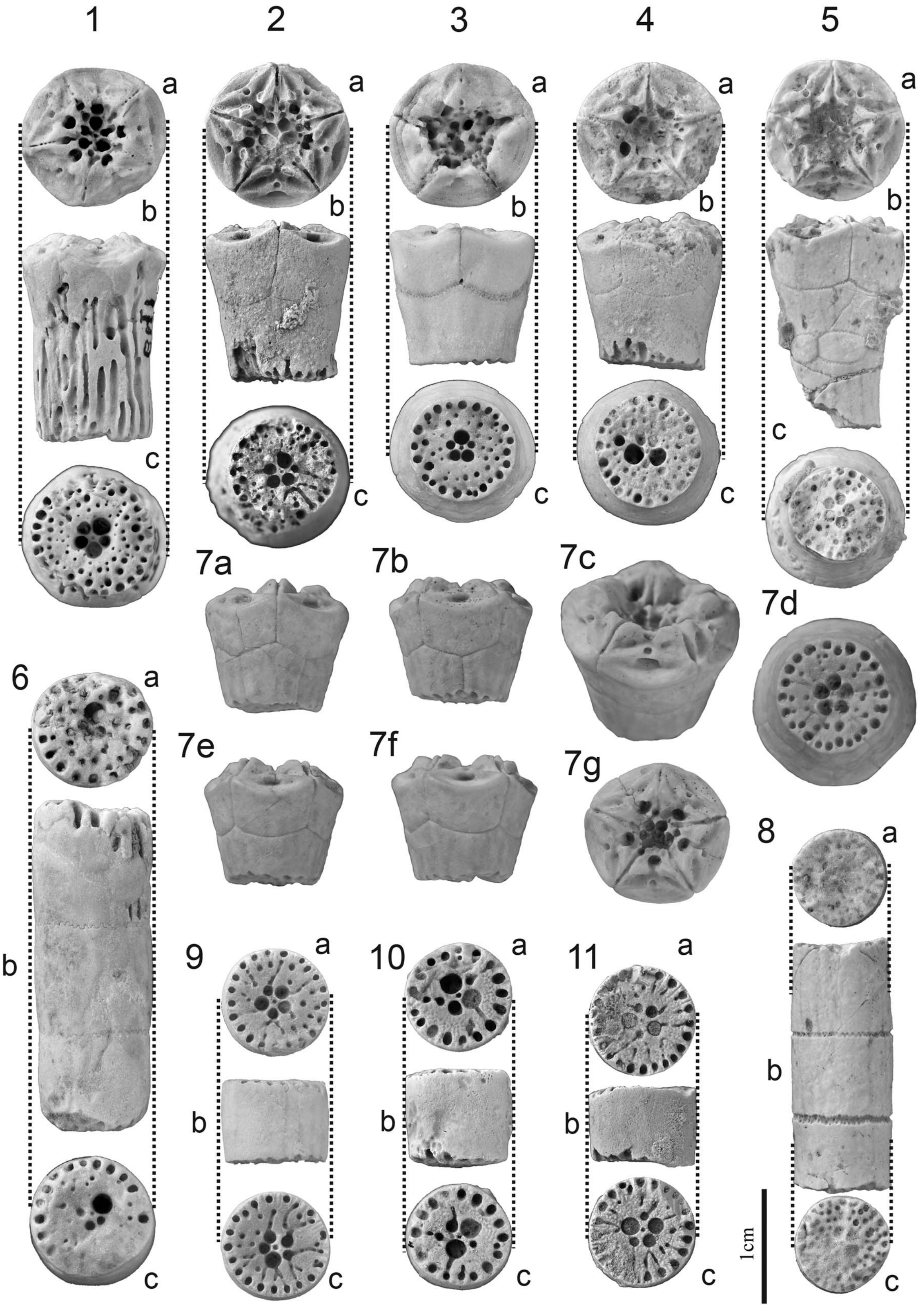
We think that Lakotacrinina n. subord. can confidently be assigned as a clade within the Order Comatulida (personal communication, H. Hess, 2012). The new family shares the defining characters of the order including "proximal most pinnule on second brachial" (Hess et al., 2011, p. 72), the development of five radials, and syzygial and muscular articulations along the length of the arms (Fig. 4.5) (Hess et al., 2011). Lakotacrinidae n. fam. also shows many similarities with other stalked members of the Comatulida including bathycrinids, bourgueticrinids and guillecrinids.

It is confirmed that Lakotacrinidae cannot be assigned to either the orders Hyocrinida (Rasmussen, 1978) or Isocrinida (Sieverts-Doreck, 1952) due to the significant differences in diagnostic characteristics. The Isocrinida have a bowl shaped cup, basals commonly much lower than radials, well developed cirri, columnals with distinct cryptosymplectial and symplectial articular (sometimes pentagonal) facets (Hess et al., 2011). The Hyocrinida have a large hollow cup, formed by basals and radials, which is very much larger in proportion to its narrow arms; non muscular articulations are smooth (synostosial) and united on IBr1-2. However the hyocrinids have a homeomorphic cylindrical column and an absence of infrabasals, and their relationship to other groups, including the millericrinids and cyrtocrinids, remains controversial (Hess et al., 2011).

Despite superficial similarities to *Ailsacrinus* Taylor (1983), within the Millericrinida (Sieverts-Doreck, 1952), Lakotacrinina is distinct from the Millericrinida. Similarities include a cylindrical, homeomorphic, tapering column devoid of cirri with symplexies and smooth latera (Figs. 5.7, 5.8, 5.9, 8.1, 8.9), radials are as wide as brachials (Fig. 4.9), brachial articulations have cryptosynarthry, including at IBr1-2 (Fig. 4.9), more distal brachials with muscular and syzygial articulations (Fig. 5.4), and partly fused basals with accessory plates developed between (Fig. 6.5). However, Lakotacrinina differs from the Millericrinida, as Lakotacrinina has a funnel shaped cup (conical in the Millericrinida), fused basals (more distinct than for *Ailsacrinus*) (Fig. 6.2–6.4), five unbranched arms with well-developed syzygies (Fig. 4.2, 4.5) (only seen with certainty in *Ailsacrinus* within the Millericrinida [Hunter et al., 2011b]) and the column having synostoses but lacking synarthries (Fig. 8.1, 8.9) (Hess et al., 2011). The Millericrinida also have a large modified attachment disc (except for *Ailsacrinus*), not found in Lakotacrinina. These differences strengthen the assignment to Comatulida.

Within the Comatulida, Lakotacrinina is allied to the Bourgueticrinina, including Bathycrinidae (Bather, 1899) and

Figure 6. Columnal and cup morphologies of mature individuals of *Lakotacrinus brezinai* n. gen., n. sp., including BMNH paratype: (**1a–1c**) articulated cup and proximal columnal, note exposed tubuli running length of cup from the radials through the proximale, BHMNH-7029 (AMNH loc. 3419); (**2a–2c**) articulated cup with well-preserved radial articulations, note completely fused basals and partly fused radials, BMNH EE14845; (**3a–3c**) articulated cup, note separated radials and completely fused basals, AMNH-FI 66551 (AMNH loc. 3420); (**4a–4c**) articulated cup, note asymmetric central tubuli, AMNH-FI 66552 (AMNH loc. 3420); (**5a–5c**) articulated cup with proximal column, note small unfused accessory plates (infrabasal candidates) developed beneath and between the radials and basals, paratype BHMNH-7029; (**6a–6c**) slightly abraded section of column (3 columnals), AMNH-FI 66512 (AMNH loc. 3419); (**7a–7g**) articulated cup with clear longitudinal sutures between basals, specimen shows a partly fused basal section, with two small unfused basals (one fifth of the basal circlet) and one large fused basal section (presumably the three other basals), AMNH-FI 63496a (AMNH loc. 3509); (**8a–8c**) slightly abraded section of column (three columnals), note flat synostosial articulation between columnals, AMNH-FI 66563 (AMNH loc. 3420); (**9a–9c**) individual columnal showing weakly symmetric central tubuli arrangement with smaller marginal tubuli, AMNH-FI 66569 (AMNH loc. 3420); (**10a–10c**) individual columnal showing strongly asymmetric central tubuli arrangement with larger marginal tubuli, AMNH-FI 66570 (AMNH loc. 3420); (**11a–11c**) individual columnal showing weakly asymmetric central tubuli arrangement with medium sized marginal tubuli, AMNH-FI 66571 (AMNH loc. 3420).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Bourgueticrinidae (de Loriol, 1882). Similarities with the Bathycrinidae such as *Bathycrinus* Thomson (1872) include a funnel shaped cup with five radial plates (Fig. 6.7) (which are free with clear sutures), basals commonly fused (when present) and a lack of infrabasals. Brachials have cryptosynarthrial articulations, including on IBr1-2 and syzygial articulations. Adult column articulations have synostoses and cirri are absent. However, there are significant differences which prevent the assignment of Lakotacrinidae to this family. These include often absent basals, no interradials, ten arms instead of five with cryptosynarthrial articulation on IBr2-3 and a lack of syzygy between primibrachials IBr4-5. The column is not homeomorphic in adults, with discoidal proximal columnals and synarthrial distal columnals (Hess et al., 2011).

A comparison with the Bourgueticrinidae, such as *Dunnicrinus* Moore (1967), also shows similarities. This includes in the arms, which are undivided, with articulations that are cryptosynarthrial, including between IBr1-2 (although note that cryptosynarthry on IBr1-2 are thought to have been replaced with possibly muscular articulations in *Dunnicrinus mississippiensis*), syzygial and muscular; the first pinnule is always on second primibrachial (Fig. 4.8) (Hess et al., 2011). Cirri are absent in the column and the upper part of column has synostosial articulation (but only in part of proximal column in *Dunnicrinus*). However there are some key differences that confirm Lakotacrinidae cannot be united within the same family. For example *Dunnicrinus* has a conical to cylindrical cup which is almost as high as wide, basals and radials are high with clear sutures separating each plate and circlet (seen in some pathological specimens of *Lakotacrinus* [Fig. 8.3]). Additionally, *Dunnicrinus* does not have a homeomorphic column, the most proximal columnals are thin, the remaining proximal columnals are low, and distal columnals have narrow lumen, are elliptical in section and joined by synarthries (Hess et al., 2011). Finally, all Bourgueticrinidae share "the formation of new columnals below the proximale is restricted to juveniles; form and size of columnals changing during growth and varying through a single column" (Hess et al, 2011, p. 149); this is not shared by *Lakotacrinus* which exhibits more uniform growth patterns.

It is confirmed that we cannot assign Lakotacrinina to the Bourgueticrinina (personal communication, H. Hess, 2011), both from the evidence above (summarized in Appendix 1) and because "synarthrial columnal articulations, the characteristic feature of bourgueticrinids" (Hess et al., 2011, p. 148) are lacking in Lakotacrinina. Additionally, the Bourgueticrinina have a clearly developed holdfast or branched radices (Hess et al., 2011). Lakotacrinina is also unique in having a tapering column and a central canal with a well-developed network of marginal and central through-going tubuli (Figs. 6.1, 8.9, 8.10, 9.8a, 9.9).

It is possible to see from the comparative Appendix 1, that *Lakotacrinus* n. gen., Lakotacrinidae, n. fam., Lakotacrinina, n. subord., has the greatest affinity to the Genus *Guillecrinus* Roux, 1985, Bourseau et al., 1991, Family Guillecrinidae, Suborder Guillecrinina (Mironov and Sorokina, 1998), (personal communication, H. Hess, 2012). Similarities include comparable characters in the proximal column and cup, along with the occurrence of five undivided arms and similar structure of the brachials, with both muscular and syzygial articulations along the length of the arms (with *Lakotacrinus* having more syzygial articulations). For example, members of the Suborder Guillecrinina have a small and low cup (not including the proximale as seen in *Lakotacrinus*), rounded basals (weakly in *Lakotacrinus*) and an absence of infrabasals; "first primibrachial as wide as radial" (Hess et al., 2011, p. 158). The first pinnule is from the second primibrachial. The unique characters that *Lakotacrinus* shares with the Suborder Guillecrinina are syzygial articulations between primibrachials IBr4-5 (Fig. 4.8), the articular face of syzygial articulations have widely spaced ridges (although in *Lakotacrinus*, they are further widely spaced and far more comatulid like [Fig. 5.4]) and a homeomorphic column in adults (with cirri absent) and "columnals never with synarthries" (Hess et al., 2011, p. 158) (unlike members of the Bourgueticrinina).

The main difference between *Lakotacrinus* and *Guillecrinus* is the presence of deep ligamentary depressions in the columnals of *Guillecrinus*, whereas depressions are more numerous and seem to have developed into through-going tubuli in *Lakotacrinus* n. gen. The arms of *Guillecrinus* lack cryptosynarthrial articulations, having syzygies between IBr1-2, IBr2-3, and IBr4-5 (Hess et al., 2011), whereas in *Lakotacrinus* IBr1-2 is cryptosynarthrial (Fig. 4.8–4.9), IBr2-3 and IBr3-4 muscular (Fig. 4.8), and only after IBr4-5 are the brachials syzygial (Fig. 4.4, 4.5) (Appendix 2); *Guillecrinus* may also have divided arms at more distal brachials. Basals are not fused in *Guillecrinus*, unlike *Lakotacrinus*, that not only has fused basals but uniquely, these are in turn fused to the most proximal columnal (proximale). Unlike *Lakotacrinus* the columns of juvenile *Guillecrinus* do not taper and articulations with weak marginal symplexy are unconfirmed, and the adult column articulations do not have synostoses (Hess et al., 2011). In addition, *Guillecrinus* is attached by a terminal disk the width of its homeomorphic column, while the column of *Lakotacrinus* tapers distally towards to a very small terminal columnal with no apparent attachment disc (Fig. 8.4, 8.8, 8.10).

Although it is evident that Lakotacrinina shares many similarities with the Guillecrinina, the authors have decided that at this stage, the differences are too significant to place Lakotacrinidae in the suborder Guillecrinina and therefore assign Lakotacrinidae to new Suborder Lakotacrinina.

Occurrence.—*Didymoceras nebrascense*, *Didymoceras cheyennense* and the *Baculites compressus* Range Zones (upper Campanian, Upper Cretaceous), Pierre Shale, Custer, Pennington, Butte Counties, South Dakota, USA (see Fig. 2).

Family Lakotacrinidae new family
Figs. 4–9

Diagnosis.—As for suborder.

Comparison.—The authors think that the erection of a new family is required as no existing family within the Articulata can accommodate the characteristics of the new genus *Lakotacrinus* from the upper Campanian of South Dakota. Refer to comparison above.

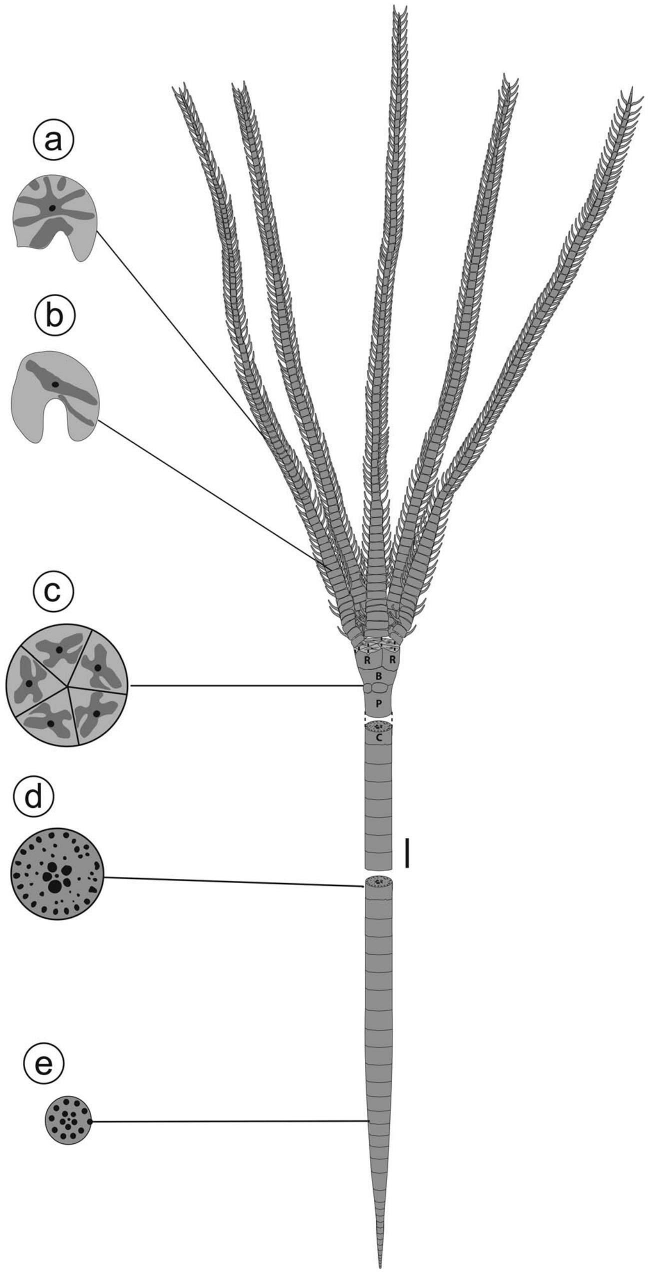


Figure 7. Reconstruction of an individual of *Lakotacrinus brezinai* n. gen., n. sp., scale bar = 1cm: reconstruction of mature growth stage; a, syzygial brachial articulation; b, muscular brachial articulation; c, radials (R = radials; B = basal; P = proximal columnal; C = columnal); d, proximal columnal; e, distal columnal.

Occurrence.—As for suborder.

Genus *Lakotacrinus*, new genus
Figs. 4–9

Type species.—The holotype AMNH-FI 69618 (Fig. 4.2) is reposited in the type collection of the American Museum of Natural History. AMNH-FI 69618 is the most complete specimen known preserving a partial articulated column, cup and five proximal arms. The following paratypes AMNH-FI 83026 (Fig. 4.1), AMNH-FI 63498 (Fig. 4.3), AMNH-FI 83027 (Fig. 4.8), BHMNH-7123 (Fig. 4.9), AMNH-FI 63502 (Fig. 5.3), BHMNH-2208 (Fig. 5.7), BHMNH-7205 (Fig. 5.8), BMNH EE14845 (Fig. 6.2), BHMNH-7029 (Fig. 6.5), from the American Museum of Natural History, The Black Hills Museum of Natural History, and The Natural History Museum in London preserve further diagnostic characters.

Diagnosis.—Articulata having funnel shaped cup with five radials and interradials, fused basals, and proximale fused into single, cylindrical plate. Infrabasals not confirmed; accessory plates sometimes present. Arms long and wide, with both synarthrial and syzygial articulations. IBr1-2 cryptosynarthrial; IBr2-3 and IBr3-4 muscular; IBr4-5 syzygial, wide ridges on the articular face, giving broken line-like suture from exterior, slightly raised central ridge separating two fossae on both sides. Cylindrical barrel-shaped columnals, predominately synostosial articulation in mature forms; symplectial marginal crenulae on articular face of immature and distal columnals, narrow through-going tubuli. Column homeomorphic in mature growth stage, tapering at distal end towards smooth terminal columnal.

Description.—Medium sized crinoid, height 150–500 mm in life (see reconstruction Fig. 7). Cup: funnel shaped or cylindrical, blends into separated and unfused trapezoidal radials, forming clearly round circlet of plates with slightly rugose appearance, with many canals in the central theca (Fig. 4.1–4.2, 4.9a, 4.9b, 6.2–6.5). Radials have clear small axial canal, prominent fulcral ridge, wide ligamentary field and muscular fossae (Fig. 4.9c). Basal plates commonly fused (Figs. 4.2, 6.2, 6.3, 5.7, 8.7), but separated in some immature individuals (Figs. 4.3, 6.1, 6.7, 8.9). Basals and proximal columnals fused into single plate in some specimens (Figs. 4.1, 4.2, 4.8, 4.9a, 4.9b, 5.7–5.9, 8.7, 8.9). Infrabasals absent (Fig. 6.1–6.4), candidates for unfused infrabasals preserved in some specimens (see Remarks) (Figs. 6.5b, 8.3, 8.7); accessory plates sometimes present (Figs. 6.5, 8.3). Radials deeper than, but as wide as brachials (Fig. 4.9b). Interradials present, inserted between proximal arms below first pinnules (Fig. 4.3b, 4.6); some immature growth stage specimens show several irregular shaped interradials (Fig. 4.3b). Arms: from cup genus has five radiating, unbranched arms, uncertain length, taper distally (Figs. 4.1, 4.2, 4.3a, 4.8a, 4.8b, 4.9a, 4.9b, 5.5, 8.1). AMNH-FI 63502 (Fig. 5.5) has allowed reconstruction of arms (Fig. 7). Brachial ossicles semicircular and low, variable widths (Fig. 5.6), one-third to one-half height of radials, reducing in size distally (Fig. 5.3, 5.5). Brachials 5–6 mm wide in proximal part of the crown, 3–4 mm in the distal parts (Fig. 5.3, 5.5, 5.6). Brachials resemble those of isocrinids, however there are noticeable differences, *Lakotacrinus* n. gen. have both muscular (Fig. 5.4) and syzygial (Fig. 5.4) articulations rather than cryptosyzygies seen in isocrinids; arms of *Lakotacrinus* are more similar to those of many comatulids. Proximal brachials, IBr1-2 cryptosynarthrial (Fig. 4.8a(i), 4.8b, 4.8c, 4.9b, 4.9c), IBr2-3 and IBr3-4 muscular (Fig. 4.8a(ii), 4.8b, 4.8c). IBr4-5 syzygial (Fig. 4.5, 4.8a(iii), 4.8b), with several prominent, widely spaced ridges on articular facet (Fig. 4.5, 5.4), giving broken line-like suture from exterior (Fig. 4.8a(iii), 4.8b, 4.8c). Further brachial articulations are muscular and syzygial only (Fig. 4.5), with syzygies usually in every four or five brachials but sometimes in irregular intervals

(Figs. 4.5, 5.5). First pinnule on IBr2 (Figs. 4.3, 4.9, 5.7). Pinnule socket small, basal pinnulars low and shape nearly trapezoidal (Fig 4.3b). Proximal arms have fewer pinnules (Figs. 4.2, 5.5, 5.7); distal and intermediate pinnulation far more prevalent (Figs. 4.4–4.7, 5.3); further pinnules appear, alternating on either side of each brachial (see Appendix 2); proximal brachial of syzygial pair does not bear pinnules (Fig. 4.5). Majority of arms disarticulated in specimens (Fig. 5.1, 5.2), AMNH-FI 63502 clearly shows unbranched arms (Fig. 5.5). Column: columnals barrel shaped (Fig. 6.9), long, cylindrical and high, with smooth latera surface (Figs. 5.7–5.9). All columnals undifferentiated and homeomorphic proximally, except for most proximal (proximale) fused with basals (Figs. 5.7, 5.8, 6.5). Columnals have flat predominantly synostosial articulations, weakly developed external symplexy around margin in mature individuals (Figs. 6.6, 6.8–6.11, 8.2), symplexy better developed near margin of articular face of small-sized immature or most distal columnals (Figs. 8.2, 8.10). Columnals never with synarthries (Figs. 8.1, 8.8), or cirri throughout ontogeny (Fig. 8.9). Columnals have very tiny axial canal or lumen surrounded by five large straight through-going tubuli, usually differing diameters (Figs. 6.1, 6.6, 6.9–6.11, 9.8), either symmetric (Fig. 6.9) or asymmetric (Figs. 6.10, 6.11); small-sized columnals, only three or four tubuli surround axial canal (Fig. 8.2). Each columnal has series of smaller, more regular through-going tubuli around margin (Figs. 6.1, 6.6, 9.8c). Proximal columnals have non through-going accessory tubuli (absent in distal columnals) (Fig. 6.6), columnals appear porous. Mature growth stage columnals homeomorphic proximally, tapering towards tiny distal end (1 cm to ~2 mm), rounded smooth terminal columnal (Figs. 4.2, 5.7–5.9, 8.4, 8.8); immature columns taper throughout (Figs. 8.9, 8.10). Column columnals vary in height, 3 mm in immature specimens, 8–9 mm in more mature growth stages; immature adult column (Fig. 8.9) represents only nearly complete column found; 105 mm long, composed of 27 columnals, decreasing in height distally from 5 mm to 3 mm. Other column examples represent only distal or proximal parts of immature or intermediate growth columns, range 50–90 mm (at least 14 columnals). Estimated from analysis of many disarticulated columnals and full immature column of 27 columnals (Fig. 8.9), columns of mature individuals may have reached 250 mm (500 mm including crown); however, this cannot be extrapolated accurately at this stage, as uncertain whether distal columnals in mature stages remain smaller or whether columnals become uniform in height (Figs. 5.7–5.9, 6.8–6.11, 7, 8.8, 8.9). Attachment structure: based on several specimens (Figs. 8.1, 8.8), columnals taper in width to few millimeters toward distal end (Figs. 8.8–8.10), terminating with smooth rounded terminal columnal (Fig. 8.4). No attachment structure (Figs. 8.1, 8.8–8.10) or radicular cirri (Figs. 8.8, 8.9) confirmed.

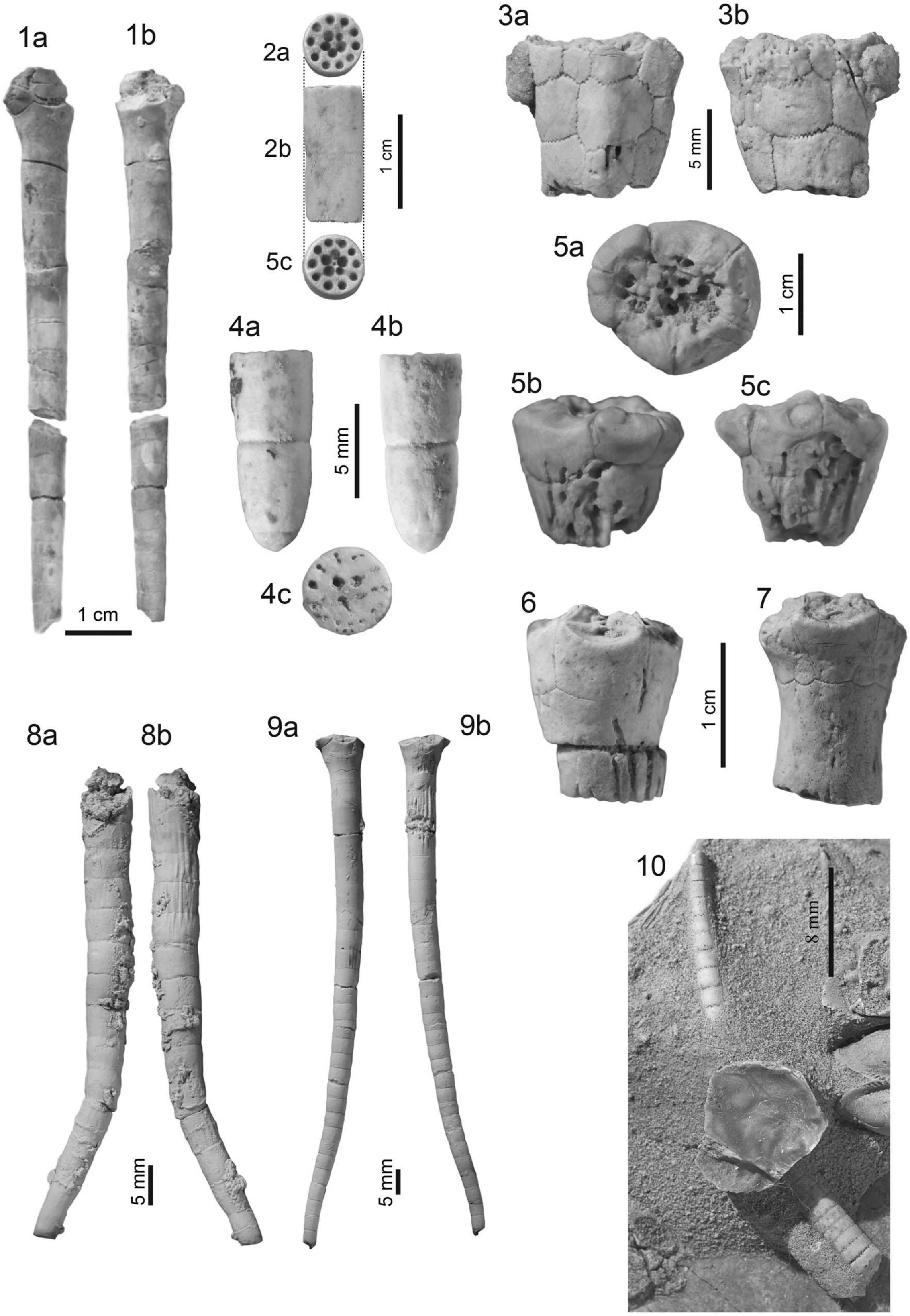
Etymology.—After the Lakota people. The Lakota are a Native American confederation of seven related Sioux tribes that once owned and controlled all of the lands in western South Dakota.

Remarks.—*Lakotacrinus* has no preserved anal plates as is true of other members of the adult Articulata. The aboral cup is made up of a circlet of plates (including the fused basals), with five radiating unbranched arms with cryptosynarthrial, muscular and syzygial articulations throughout the arms (Figs. 4.5, 4.8, 4.9, 5.4); some pinnulate structures are well preserved, particularly on the distal and intermediate arms (Fig. 4.4, 4.7); pinnules less on proximal section of arms (Figs. 4.2, 5.5, 5.7).

In most preserved specimens, *Lakotacrinus*, like members of the Millericrinida, have no infrabasal plates (Figs. 4.1–4.3, 5.7) between the basals as is seen in Isocrinida. Although candidates for infrabasals are observed in three specimens, these are in fact more likely to be pathological accessory plates (Figs. 6.5, 6.7, 8.3); however, it is unclear whether these formed through predation or ontogeny (see Remarks).

The column structure of *Lakotacrinus* with through-going tubuli is unique for post-Triassic articulates. Through-going tubuli also occur in the Triassic *Traumatocrinus* (Order Encrinida, Family Traumatocrinidae; Hess et al., 2011), where they are called tubuli, these longitudinal tubuli run parallel to the narrow axial canal. Like these Triassic forms, *Lakotacrinus* also has a narrow axial canal (Figs. 6.9, 6.11, 9.8c, 9.10). Each columnal has a cavernous structure with straight >1 mm sized through-going longitudinal tubuli. This microstructure is confirmed by eroded ossicles and thin sections (Figs. 6.1, 6.6, 6.8, 9.8b), which show these are actually through-going pores through the stereom (Fig. 9.9). The ligamentary articulations are concentrated around the outside of the ossicle, with a single central lumen surrounded by five tubuli (Figs. 6.9–6.11, 9.8a–9.8c). Further stereom structures are difficult to recognize due to infilling by sparry calcite (Figs. 9.8b, 9.8c). Hagdorn et al. (2007, p. 190–191), postulate that in *Traumatocrinus* “the enigmatic pore systems of the intercolumnar fossulae and the tubuli that ran longitudinally through the entire system were likely to have contained strings of mutable collagen that enabled the animal to stiffen and smooth its stem, possibly depending on, or reacting to, changing current velocities. The animal may even have improved its filtration effectively by active motion of the stem.” Although the structure of the column and facets differ and it is not a long-stemmed pseudoplanktonic crinoid, like *Traumatocrinus*, it is still possible that *Lakotacrinus* developed this same ability.

Figure 8. Adult growth morphologies of *Lakotacrinus brezinai* n. gen., n. sp.: (**1**) column morphology of intermediate growth stage individual of *Lakotacrinus brezinai* n. gen., n. sp.; (**1a, 1b**) restored articulated proximal column section with fused proximale, AMNH-FI 66347 (AMNH loc. 3505); (**2a–2c**) distal immature columnals, note symmetric central tubuli arrangement and reduced number of marginal tubuli, AMNH-FI 66517 (AMNH loc. 3456); (**3a, 3b**) articulated cup “pathological specimen”, with three unfused circlets and lower set of accessory plates (either infrabasal candidate plates or “aberrant” columnal plates) BHMNH-7121 (AMNH loc. 3420); (**4**) terminal columnal with smooth rounded base and no attachment disc, AMNH-FI 80013, (AMNH loc. 3419); (**5**) articulated cup with extra pathological radial plate, AMNH-FI 84501 (AMNH loc. 3419); (**6**) cup with fused basals, but not fused to proximal columnal, AMNH-FI 83030 (AMNH loc. 3420); (**7**) articulated cup with radials, and completely fused basals and proximale, BHMNH-7162 (AMNH loc. 3420); (**8a, 8b**) restored distal column section of intermediate growth stage individual, note almost cylindrical columnals with gradually diameter decreasing distally, AMNH-FI 83032 (AMNH loc. 3488); (**9a, 9b**) restored articulated slender full column of immature growth form, note gradual distal tapering and partly fused proximale, no attachment disc preserved, AMNH-FI 83031 (AMNH loc. 3419); (**10**) distal tapering column section from intermediate or adult form? AMNH-FI 56712 (AMNH loc. 3419).


1a
1b
1 cm
2a
2b
5c
1 cm
3a
3b
5 mm
4a
4b
5 mm
4c
5a
1 cm
5b
5c
6
7
1 cm
8a
8b
5 mm
9a
9b
5 mm
10
8 mm

Finally it is clear from several of the more articulated specimens (Fig. 8.1, 8.8–8.10) that these crinoids have a tapering column, which goes down to <2.07 mm and ends with a rounded terminal columnal (Fig. 8.4). We have yet to find any form of attachment disc for the column of *Lakotacrinus*, leading to the conclusion that such a structure might be absent. The lack of lumen in both terminal columnal specimens (AMNH-FI 80013 [Fig. 8.4] and AMNH-FI 85668 [AMNH loc. 3522]) indicates that the terminus is sealed and thus the through-going tubuli are sealed, supporting the suggestions that there was no attachment disc and that ligaments could have been contained within the tubuli.

The unique column structures, including through-going tubuli and tapering column, with smooth termination lacking an attachment disc, along with the fused basals and absent infrabasals justify the establishment of a unique genus (suborder and family) within the Articulata.

Occurrence.—As for suborder.

Lakotacrinus brezinai new species
Figs. 4–9

Diagnosis.—Same as genus, monotypic.

Etymology.—In honor of Jamie Brezina who discovered the localities and these unusual crinoid specimens. While collecting Fairburn agates he stumbled across the methane seeps and, after finding echinoderms, recognized the significance of these deposits.

Types.—By monotypy.

Occurrence.—Only found in the hard substrates of methane seeps and associated with microbialite nodules and thin layers of cemented shell hash and carbonates (Fig. 3). The crinoids are concentrated in the *Baculites compressus* Zone (Fig. 2), and underlying *Didymoceras cheyennense* Zone (AMNH-FI 76275, AMNH loc. 3418), (upper Campanian, Upper Cretaceous) of the Pierre Shale in Custer and Pennington Counties, South Dakota (Figs. 1, 2). A total of 35 of 100 mapped seep sites have yielded crinoid fragments, indicating that 35% of the discovered seeps contain crinoidal remains. Based on disarticulated fragmentary remains, it appears that *Lakotacrinus* n. gen. may also have occurred in the underlying *Didymoceras nebrascense* (lower upper Campanian, 75.19 Ma) and *Didymoceras stevensoni* zones of the Pierre Shale (Fig. 2).

AMNH localities 3418, 3419, 3420, 3456, 3467, 3468, 3469, 3505, 3506, 3509, *Baculites compressus* (73.52 Ma-type material) and *Didymoceras cheyennense* Zones (74.67Ma) of the Pierre Shale, Custer and Pennington Counties, South Dakota, USA.

Remarks.—Currently *Lakotacrinus* is monospecific. However, there are three adult morphotypes: one larger mature form whose column tapers only at the distal end (Figs. 4.2, 5.7, 5.8, 6.8, 7), those representing intermediate growth stages (Figs. 5.5, 8.1, 8.8) and an immature morphotype whose column tapers gradually from a diameter of >10 mm (at the base of the crown) to <2 mm (at the most distal columnal) (Fig. 8.9).

Additionally, there are several morphological variations in the growth of the cup. Variations from the more common characteristic of basal plates entirely fused and in turn fused to the most proximal columnal (proximale) (Figs. 4.2, 5.7, 8.7), include those that have unfused basals and accessory plates (Figs. 6.5, 6.7, 8.3, 8.6). Although interpreted as pathological differences, regrowth of plates resulting from predation is uncommonly observed in extant forms (unpublished data, Hunter, 2008); therefore the definitive cause of these anomalies remains unclear. Other examples of where the cup has been radically altered by pathological regrowths, more certainly due to predation, include Figure 8.5 which shows a duplicated radial plate, and swollen basal plates observed in an uncited and unfigured specimen from a private collection.

Other variations seen are interpreted as being ontogenetic. Several small cups have been recovered from at least six seeps, including localities AMNH 3419, AMNH 3420, AMNH 3488 and AMNH 3509b showing what is thought to be at least six stages of ontogeny within the cup (Fig. 9.1–9.6), with a mature adult cup (Fig. 9.7) for comparison. This shows that the juvenile and immature growth stages would have developed within the seep environment from an early larval stage. However, at site AMNH 3509b, only juvenile crowns were found compared to AMNH 3509a 30 m away, where only mature forms were discovered, indicating the possible existence of trophic levels within the seep inhabited by different growth stage populations. The ontogenetic trend (Fig. 9.1–9.6) shows that the smallest specimen (Fig. 9.1) already possesses essentially similar morphological features to those of the more common mature specimens, with many through-going tubuli in the stalk and proximal cup (although number of tubuli appears to increase during ontogeny). The arrangement of fused plates within the cup is also essentially unchanged, supporting the suggestion that examples of unfused plates may be pathologic rather than ontogenetic and reaffirm that we are not currently in a position to erect more than one species within the new genus.

Conclusions

Lakotacrinus n. gen. (n. fam., n. subord.) is unique among other Mesozoic and indeed all other crinoids. So far the authors have been unable to conclusively assign this taxon to any existing suborder within the Order Comatulida. The column structure with through-going tubuli that run parallel to a narrow axial canal is distinctive from other Mesozoic articulates, with the exception of the Triassic *Traumatocrinus* (Hess et al., 2011). The column of *Lakotacrinus* is also unique in that it tapers gradually from a diameter of up to 10 mm at the base of the crown to less than a few mm at the distal columnals, terminating in a smooth rounded columnal, with no attachment structure observed. *Lakotacrinus brezinai* n. gen. n. sp. is the first recorded occurrence of crinoids in the Pierre Shale, and for stemmed crinoids within the Late Cretaceous of the Western Interior Seaway. The absence of *Lakotacrinus* elsewhere within the Western Interior Seaway indicates that this crinoid was specifically adapted to living within the environment of a cold methane (hydrocarbon) seep; the first recorded example of such an occurrence.

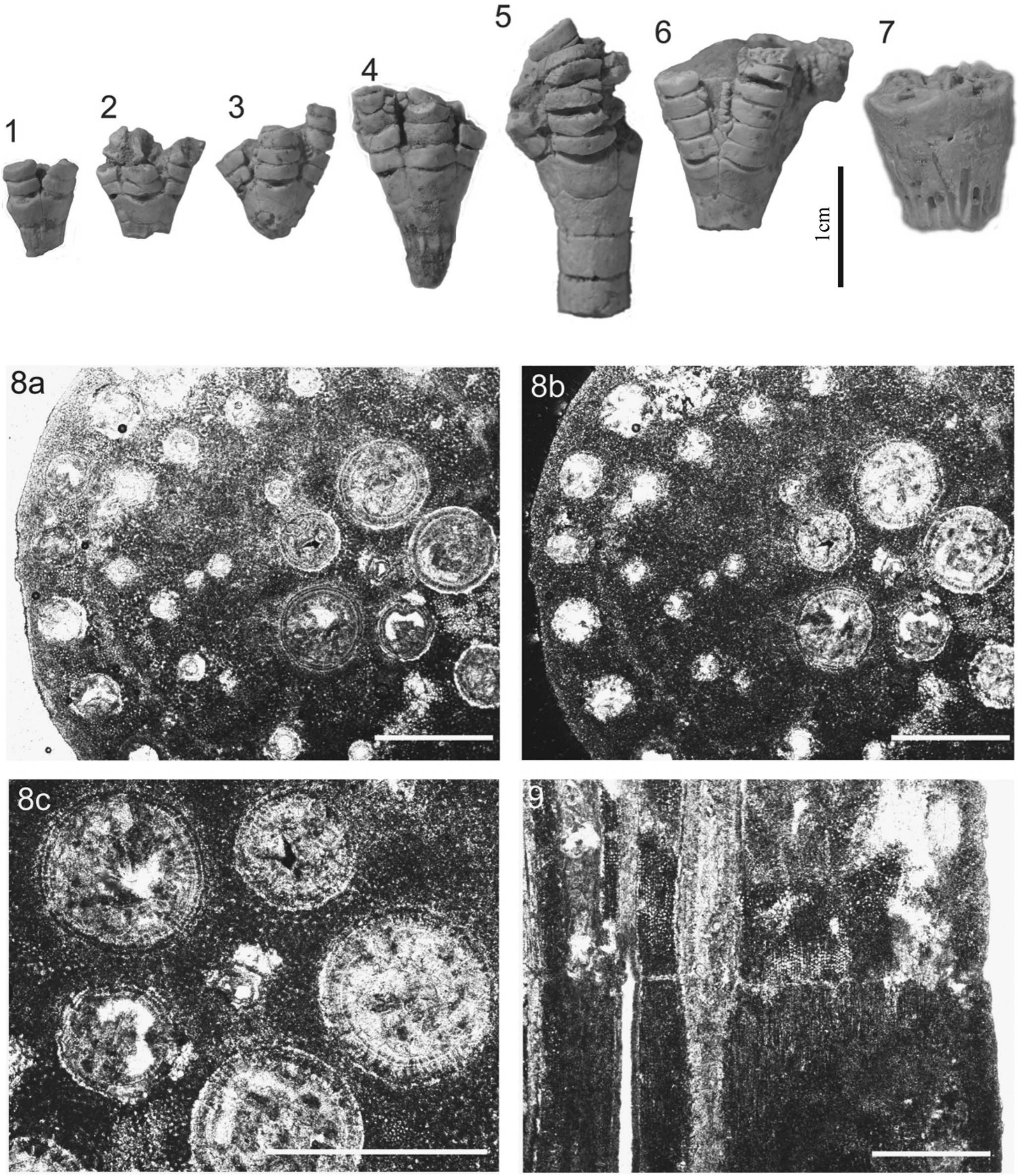


Figure 9. The ontogenetic trend in cup morphology and columnal thin sections of *Lakotacrinus brezinai* n. gen., n. sp.: (**1–6**) gradational cup growth stages of immature *Lakotacrinus brezinai* n. gen., n. sp., (**1**) AMNH-FI 84495 (AMNH loc. 3509); (**2**) AMNH-FI 84499 (AMNH loc. 3509); (**3**) AMNH-FI 84498 (AMNH loc. 3509); (**4**) AMNH-FI 84496 (AMNH loc. 3488); (**5**) AMNH-FI 84497 (AMNH loc. 3488); (**6**) AMNH-FI 84500 (AMNH loc. 3509); (**7**) adult cup for comparison, AMNH-FI 84504 (AMNH loc. 3419); (**8**) columnal thin-sections showing arrangement of through-going tubuli, NUM-FA182 (AMNH loc. 3509); (**8a**) PPL thin-section clearly showing arrangement of marginal and central tubuli in cross-section; (**8b**) XPL thin-section showing tubuli in-filled with sparry calcite; (**8c**) magnified XPL thin-section of (8b), showing central in-filled tubuli with small lumen; (**9**) PPL thin-section of planar view through two columnals showing in-filled tubuli passing through the columnals, NUM-FA183 (AMNH loc. 3509). Scale bars represent 1 mm unless specified.

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Appendix 1. Family level comparative table of diagnostic characters for Lakotacrinidae n. fam. against its nearest morphological relatives (nearest comparable *genera* from each family given in brackets). ✓ present; ? unconfirmed character. Order Comatulida represented by Pentametrocrinidae.

		LAKOTACRINIDAE (*Lakotacrinus*)	GUILLECRINIDAE (*Guillecrinus*)	BOURGUETICRINIDAE (*Dunnicrinus*)	PENTAMETROCRINIDAE (*Pentametrocrinus*)	BATHYCRINIDAE (*Bathycrinus*)	MILLERICRINIDAE (*Ailsacrinus*)
Arms	IBr1-2 is (crypto)synarthrial	✓		✓	✓	✓	✓
	Brachials have (crypto)synarthrial articulations	✓		✓	✓	✓	✓
	Brachials have syzygial articulations	✓	✓	✓	✓	✓	✓
	Syzygy between primibrachials 1Br 4-5	✓	✓				
	Pinnulars are semicircular (cresent shaped)	?	✓	?	?		
	First pinnule always on primibrachials 2 or 3	✓	✓	✓		?	✓
	Always have undivided arms	✓	✓	✓	✓		
	Always have five arms	✓	✓		✓		
	Details of "syzygies" ridges widely spaced	✓	✓	?	✓		✓
	Interradials present	✓					
Cup	Radials are as wide as brachials	✓	✓				✓
	Small funnel-shaped - low cup	✓	✓			✓	
	Infrabasals always absent	✓	✓	?	✓		?
	Basals are fused in adults	✓				✓	✓
Column	Stem in adult stage	✓	✓	✓		✓	
	Cirri absent	✓	✓	✓		✓	✓
	Columnals never with synarthies	✓	✓				
	Through going tubuli	✓					
	Stem in adults homeomorphic	✓	✓				✓
	Stem in tapers in immature forms	✓					
	Adult stem articulations have synostosis	✓				✓	
	Juvenile stem articulations have symplexy	✓					
	Terminal attachment disc	?	✓				?

Appendix 2. Diagrams showing position and type of brachial articulation and pinnulations (position and orientation of pinnules). R, radial; –, synarthry; +, syzygy; . (dot), muscular articulation; / \ (oblique short lines above or below numbers), pinnules.

ANMH-FI 83027 (ANMH loc. 3420), (see Fig. 4.8).

$$R \bullet 1 - \underset{\backslash}{2} \bullet \overset{/}{3} \bullet 4 + \underset{\backslash}{5} \bullet \overbrace{6 \bullet 7 \bullet 8 \bullet 9}^{\text{pinnulation unknown}}$$

$$R \bullet 1 - \overset{/}{2} \bullet \underset{\backslash}{3} \bullet 4 + \overset{/}{5} \bullet$$

$$R \bullet 1 - \overset{/}{2} \bullet \underset{\backslash}{3} \bullet 4 + \overset{/}{5} \bullet \underset{\backslash}{6} \bullet \overset{/}{7}$$

ANMH-F1 83026 (ANMH loc. 3420) (see Fig. 4.1).

$$R \bullet 1 - \overset{/}{2} \bullet$$

$$R \bullet 1 - \overset{/}{2} \bullet \underset{\backslash}{3} \bullet 4 + \overset{/}{5} \bullet \overset{/}{6} \bullet$$

$$R \bullet 1 - \overset{/}{2} \bullet \underset{\backslash}{3} \bullet 4 + \underbrace{5 \bullet 6 \bullet 7}_{\text{pinnulation unknown}} \bullet$$