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Mecaster batnensis (Coquand, 1862), a late Cenomanian echinoid from New Mexico, with a compilation of Late Cretaceous echinoid records in the Western Interior of the United States and Canada

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"April is the cruelest month"
T.S. Elliot, 1922, *The Waste Land*

ABSTRACT:

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Echinoids are rare in the Upper Cretaceous of the Western Interior, where fewer than 60 unique occurrences are known to date, most of these represented by only a few tests or isolated spines. A notable exception is the Carthage coal field (Socorro County, New Mexico), where more than 200 specimens of *Mecaster batnensis*, previously referred to as *Hemiaster jacksoni* Maury, 1925, have been collected from the basal Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale. Prolific occurrences from the same beds are known from elsewhere in west-central and southwest New Mexico. Recorded originally from the Upper Cretaceous of Algeria, *M. batnensis* is a small- to medium-sized, irregular echinoid that is confined to the upper Cenomanian *Euomphaloceras septemseriatum* Zone in New Mexico. Measurements on 169 well-preserved specimens from two localities in New Mexico document a species that is, on average, 21.0 mm long, 19.8 mm wide, and 15.1 mm tall, yielding a width/length ratio of 0.94 and a height/length ratio of 0.72. Graphs plotting width against length and height against length are strongly linear.

The Western Interior echinoid record spans the entire Late Cretaceous, although there are no records from rocks of Santonian age. Localities are spread from New Mexico on the south to Alberta on the north. Preservation ranges from coarse internal molds in high-energy sandstones to original tests in low-energy limestones.

Key words: Cretaceous; Hemiasteridae; North America; Biostratigraphy; Bridge Creek Limestone Beds; Tokay Tongue; Rio Salado Tongue; Mancos Shale; Carthage Coal Field.

INTRODUCTION

Echinoderms are rare faunal elements in the Upper Cretaceous of the Western Interior of the United States (excluding Texas) and Canada, where the assemblages are dominated by mollusks, particularly cephalopods and bivalves (Reeside 1957). Therefore, the occurrence of hundreds of tests of the echinoid *Mecaster batnensis* in thin, upper Cenomanian limestones in the Mancos Shale of central and southern New Mexico is of interest. Although echinoids occur throughout this area at many localities in beds of the same age and lithology, this paper concentrates primarily on an collection of more than 200 individuals (129 of which were well enough preserved for morphometric measurements) from the base of the Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale in the Carthage coal field, Socorro County, New Mexico. The faunas and lithologies of the entire marine section at Carthage are profiled in Hook *et al*. (2012, pp. 130, 131 and fig. 5); those of the Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale at Carthage have been detailed by Hook and Cobban (2015, fig. 4). The major Carthage echinoid occurrence (D14853, see Appendix 1) establishes both the morphological variation of *Mecaster batnensis* in New Mexico and its stratigraphic range, which is confined to the upper Cenomanian *Euomphaloceras septemseriatum* Zone. This morphological information is augmented with data on a collection of 40 specimens from the near the base of the Bridge Creek Limestone Beds of the Rio Salado Tongue of the Mancos Shale at Paradise Canyon, Cibola County, New Mexico (D11739, see Appendix 1).

Although echinoids are rare in the Upper Cretaceous of the Western Interior, they have a published history that dates back more than 150 years and includes six new species and one new genus (Appendix 2). Most occurrences consist of only a few specimens.

Meek and Hayden (1856, p. 147) described the first echinoid known from the Western Interior Upper Cretaceous as a new species, *Hemiaster humphreysanus*. Their specimens came from the Maastrichtian *Baculites baculus* Zone in the Pierre Shale exposed along the Cedar Creek Anticline, Montana (Gill and Cobban 1966, pp. A22, A23). Meek (1876, pp. 5, 6 and pl. 10, fig. 1a–g) redescribed the species and illustrated the holotype, while noting (p. 6) that "It is a little remarkable, that, in all the collections hitherto obtained from the Cretaceous rocks of the Upper Missouri, this is the only species of *Echinoidea* [*sic*] yet found, and it is so rare that but two specimens, and a fragment of another from the same locality, have been met with." Since then, *H. humphreysanus* has been collected from the Campanian *Baculites compressus* Zone in the Pierre Shale of Colorado, the Campanian *B. scotti* Zone of the Sego Sandstone of Utah (Fisher *et al*. 1960, p. 33), and the Campanian *Scaphites hippocrepis* Zone of the Montana Group (J.H. Smith 1961). Almost one hundred years later Reeside (1957, p. 512) drew attention to the molluscan domination of Late Cretaceous faunas of the Western Interior, noting that "The echinoderms [are] so scarce that any occurrence of fossil remains is notable – the echinoids are known at only a few localities and generally as only small forms…."

The only new echinoid genus to come from the Western Interior is *Eurysalenia* Kier (1966, pp. A62–A65, fig. 17) from the Redbird section of the Pierre Shale in Wyoming. *Eurysalenia minima* was collected from a single concretion in the Campanian *Baculites reesidei* Zone. Hundreds of specimens of this diminutive echinoid (< 10 mm diameter) occurred together in the upper six centimeters of a concretion that also contained an even rarer fossil in the Western Interior, a starfish arm. Kier postulated that the echinoids were part of a spawning swarm or were feeding on a dead animal. The species is not known from any other locality.

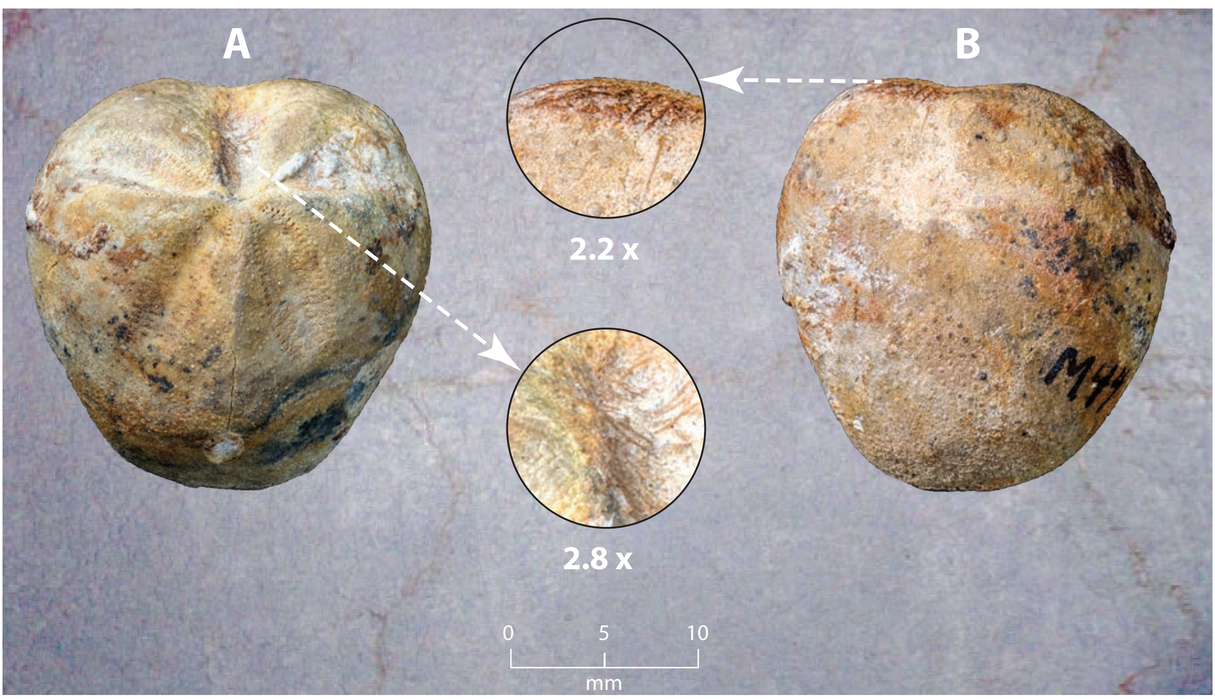
In addition to *Hemiaster humphreysanus* and *Eurysalenia minima*, five other new echinoid species have been described from the Western Interior Upper Cretaceous: *Hardouinia stantoni* (Clark, 1891), *Cardiaster curtus* Clark, 1915, *Hardouinia taylori* (Warren, 1926), *Holaster feralis* Cooke, 1953, and *Porosoma reesidei* Cooke, 1953.

Appendix 2 contains a list of the 54 Upper Cretaceous echinoid localities from the Western Interior known to us from the literature and the USGS Mesozoic invertebrate localities database. These localities are spread between two countries (the United States and Canada) and occur in seven states (New Mexico, Arizona, Colorado, Utah, Wyoming, South Dakota, and Montana), and one province (Alberta). They have been collected from rocks of Cenomanian, Turonian, Coniacian, Campanian, and Maastrichtian age. Some occurrences cannot be placed definitively in an ammonite zone. The occurrences are arranged more-or-less stratigraphically in Appendix 2, with the oldest occurrence at the base of the list. The list may be slightly inflated because some localities may be close enough geographically that they are essentially duplicates of the same information; e.g., the two localities with *Holaster feralis* from the Bridge Creek Limestone Member of Colorado and the two *Hardouinia stantoni* localities from the Codell Sandstone of Colorado. Several localities in the Black Mesa area of northeastern Arizona are represented by a single locality (D9020). The 26 *Mecaster batnensis* localities from the Bridge Creek Limestone Beds of the Mancos Shale in New Mexico are represented by a single Carthage coal field locality (D14853, which yielded more than 200 specimens) in Appendix 2, but are listed in their entirety in Appendix 1.

ECHINOIDS

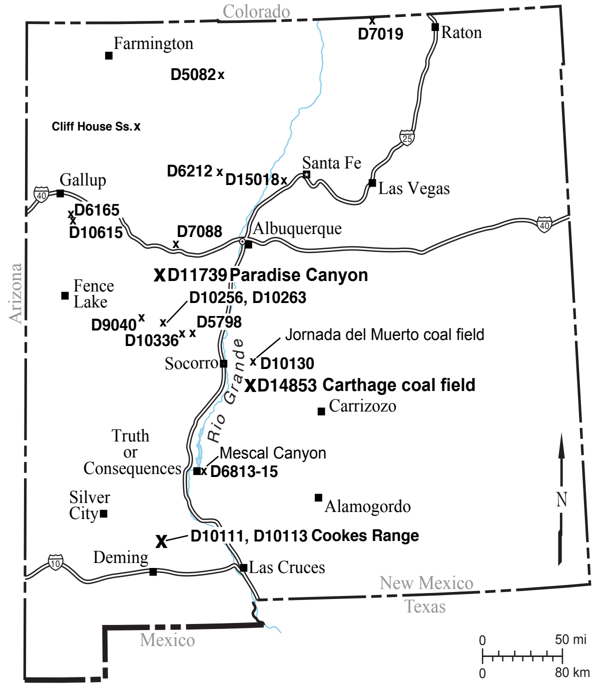
Sea urchins are assigned to the Class Echinoidea within the Phylum Echinodermata and, like their relatives the sand dollars, have exoskeletons that are composed of tightly interlocking calcite plates forming a rigid test. The Class Echinoidea is subdivided informally into two 'subclasses', Regularia and Irregularia. Regular echinoids are epifaunal invertebrates that have radial (pentameral) symmetry and spines of variable size and length, which are used for protection and, in view of sheer numbers, are more likely to be preserved as fossils than the tests. In the list of Western Interior occurrences (Appendix 2), regular echinoids include members of the genera *Eurysalenia* and *Porosoma*, along with occurrences noted as "regular echinoid(s)" or "echinoid spines". Irregular echinoids (e.g., heart urchins, including *Mecaster batnensis*) mostly are infaunal invertebrates that have bilateral symmetry and short spines used for burrowing. In Appendix 2, the irregular echinoids include members of the genera *Holaster*, *Hardouinia*, *Cardiaster*, *Hemiaster,* and *Mecaster.* Twenty-four of the 54 echinoid localities in the Western Interior (Appendix 2) represent infaunal, irregular echinoids whose tests are more likely to be preserved than those of the epifaunal, regular echinoids represented by 11 localities. The additional 19 entries in Appendix 2, often listed in the literature simply as echinoids, cannot be referred to "subclass".

Rock types in which echinoids occur in the Western Interior Upper Cretaceous (Appendix 2) range from lithographic limestones, representing offshore, deep-water environments, to fairly coarse-grained sandstones, representing shallower-water, high-energy settings. An example from quiet water is *Mecaster batnensis* from the Mancos Shale of New Mexico (Text-fig. 1); one of a high-energy setting is *Hardouinia stantoni* from the Codell Sandstone of Colorado (Text-fig. 2). Preservationally, *Mecaster batnensis* occurs as slightly altered original calcite tests that retain detailed morphological features, occasionally including spines (Text-fig. 1). By contrast, *Hardouinia stantoni* is preserved as coarse-grained, internal molds in which only test shape and the positions of the peristome (mouth) and periproct (anus) are preserved. Incidentally, the Codell specimens have been listed in the USGS database simply as "echinoids" ever since their collection in 1965. In part this situation is due to a lack of illustrations and descriptions of *Cassidulus stantoni* Clark, 1891 [now *Hardouinia*] *in* T.W. Stanton's (1893) extremely influential work on the invertebrate fauna of the Colorado Formation of the Western Interior. Meek (1876) and Stanton (1893) provided the standards for identifying invertebrates from the Upper Cretaceous of the Western Interior for more than 140 years, but each work includes merely a single echinoid species. Meek (1876) illustrated and described only *Hemiaster humphreysanus*; Stanton (1893, p. 52) listed, but did not illustrate or describe, *C. stantoni*, which he included "for the sake of completeness."



Text-fig. 1. A single specimen of the irregular echinoid *Mecaster batnensis* Coquand, 1862 weathered matrix-free from the base of the Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale, Carthage coal field, New Mexico. The basal Bridge Creek was deposited in an offshore, relatively deep, generally low energy environment in which original shell preservation of echinoids is the rule and disarticulated echinoid spines are occasionally preserved on tests. Apical (A) and oral (B) views of USNM 642618 with insets showing preserved spines, from USGS Mesozoic locality D14854 in the SE 1/4 NE 1/4 sec. 8, T. 5 S., R. 2 E., Cañon Agua Buena 7.5-min. quadrangle, Socorro County, New Mexico. See Appendix 4A, specimen #100, for measurements. Insets (arrowed) are enlarged 2.2 and 2.8 times relative to the scale of the text-figure

Text-fig. 2. Hundreds of specimens of the irregular echinoid *Hardouinia stantoni* (Clark, 1891) preserved on a slab of Codell Sandstone Member of the Carlile Shale from the Pueblo, Colorado, area. The Codell represents a higher-energy, shallower-water environment than that in which *Mecaster batnensis* (Text-fig. 1) lived. In these Codell Sandstone internal molds, only the shape of the test and the positions of the peristome and periproct of this (semi-) infaunal echinoid are preserved. Top view of a bedding plane from USGS Mesozoic locality D6064 (USNM 642619) in the SE 1/4 SW 1/4 sec. 33, T. 2 S., R. 66 W., Swallows 7.5-minute quadrangle, Pueblo County, Colorado



Text-fig. 3. Map of New Mexico showing localities where Late Cretaceous echinoids have been collected. Collections from the Carthage coal field and Paradise Canyon described in this paper are highlighted in bold. The nine USGS Mesozoic invertebrate localities from Carthage are represented by D14853; the three from Paradise Canyon, by D11739 (see Appendix 1)

MECASTER BATNENSIS IN NEW MEXICO

The first echinoid species known to have been collected from the Upper Cretaceous of New Mexico is *Mecaster batnensis* from the base of the Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale in the Carthage coal field, Socorro County, on April 30, 1967 by W.A. Cobban (Appendix 1). Since then, *M. batnensis* has been reported at 26 localities in New Mexico (Text-fig. 3), all from beds of late Cenomanian age at the base of the Bridge Creek Limestone Member (or Beds) of the Mancos Shale. Fourteen of the New Mexico collections are from Socorro County, with nine of those from the Carthage coal field.

In older field notes and published literature, *Mecaster batnensis* is identified as the Brazilian species *Hemiaster jacksoni*. More recent, detailed taxonomic work on the Late Cretaceous echinoids of Brazil by A.B. Smith (in Smith and Bengtson 1991) has indicated that *H. jacksoni* is a junior synonym of *Mecaster batnensis*. Appendix 3 contains a brief history of the

Stage		Ammonite Zone		Age (Ma)	Range
TURONIAN	lower	*Mammites nodosoides*		92.20	
		Vascoceras birchbyi		92.69	
		Pseudaspidoceras flexuosum		**93.19**	
		Watinoceras devonense		93.32	
CENOMANIAN	upper	*Nigericeras scotti*		93.44	
		Neocardioceras juddii	*Vascoceras hartti*	**93.57**	
		Burroceras clydense		93.63	
		Euomphaloceras septemseriatum		**93.68**	NM & AZ
		Vascoceras diartianum		**93.99**	NM & AZ
		Metoicoceras mosbyense	*Vascoceras gueranger**i*	94.23	Brazil
		? (=*Dunveganoceras* spp.)		94.57	
		Calycoceras canitaurinum		**94.71**	

Text-fig. 4. Upper Cenomanian through lower Turonian ammonite zones for the southern Western Interior showing the documented biostratigraphic range of *Mecaster batnensis*. Areas where *Mecaster batnensis* collections have been dated: NM—New Mexico; AZ – Arizona; and Brazil. An age date in bold text is based on a dated bentonite from the zone; all others are interpolated.

taxonomic problems we faced in finding a valid name for this echinoid species.

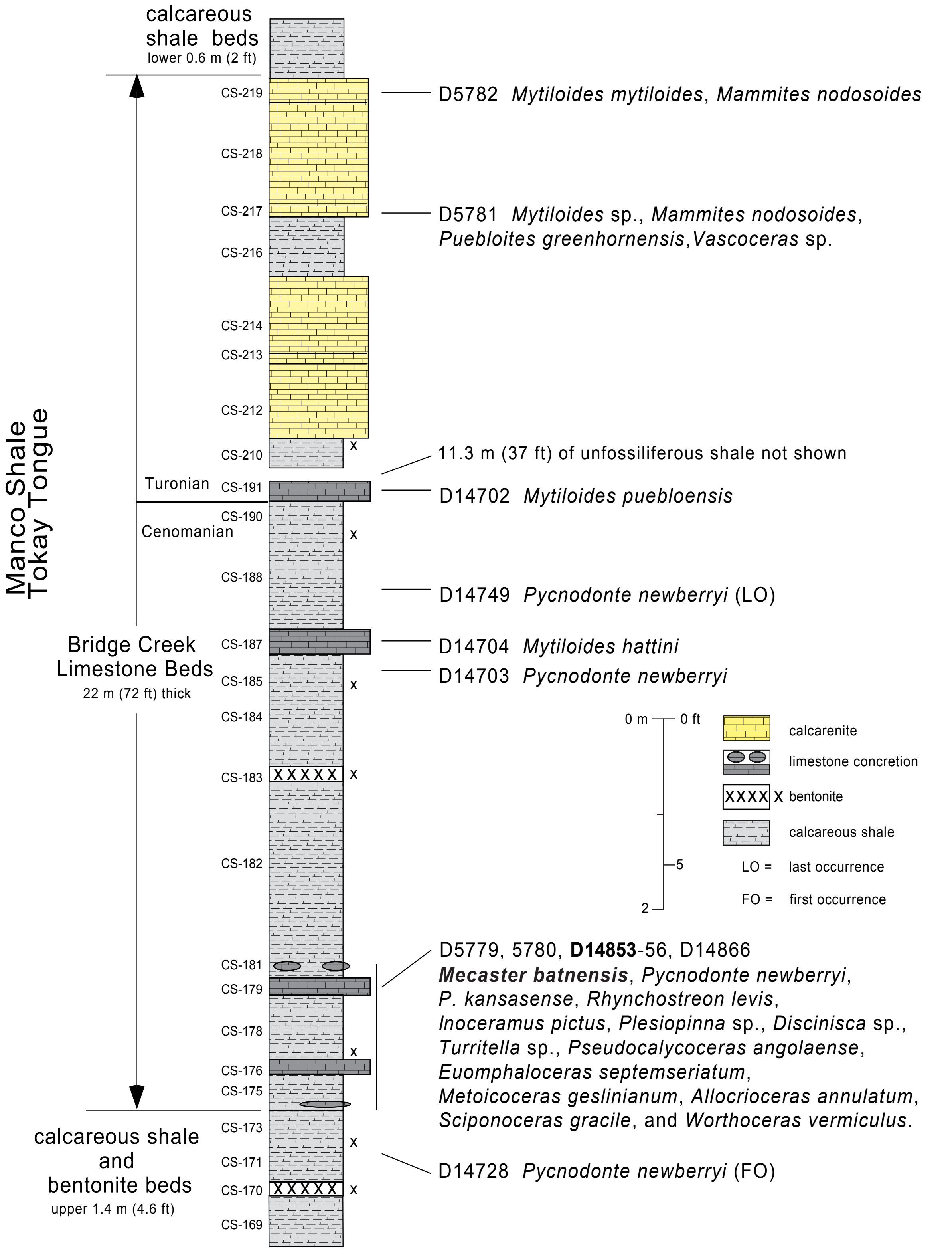
The first published record of *Mecaster batnensis* from New Mexico (as *Hemiaster jacksoni*) is that by Tabet (1979, p. 24), who recorded it to co-occur with the oyster *Pycnodonte newberryi* and the heteromorph ammonite *Sciponoceras gracile* (Appendix 1, D10130) at the base of the Bridge Creek Limestone Beds of the Tokay Tongue in the Jornada del Muerto coal field, Socorro County. Soon after, Hook and Cobban (1981, fig. 3) showed *M. batnensis* (as *H. jacksoni*) to occur at two levels (D10111 and D10113) in the Bridge Creek Limestone Member of the Colorado Formation in Cookes Range, Luna County, in association with *P. newberryi*, *S. gracile*, and *Euomphaloceras septemseriatum*. Hook *et al*. (1983, table 5) showed *M. batnensis* (as *H. jacksoni*) at the base of the Bridge Creek Limestone Beds in the type section of the Rio Salado Tongue of the Mancos Shale. Hook (1983, p. 171) listed *M. batnensis* (as *H. jacksoni*) from the base of the Bridge Creek Limestone Member of the Mancos Shale from the Carthage coal field along with one brachiopod, one bivalve, two oyster, and seven ammonite species, including *E. septemseriatum*. These four occurrences establish that in New Mexico *M. batnensis* occurs unequivocally in the upper Cenomanian *E. septemseriatum* Zone (Text-fig. 4). In Brazil *M. batnensis* has a much greater range, from near the base of the upper Cenomanian throughout the entire lower Turonian (A.B. Smith in Smith and Bengtson, 1991, p. 59; Text-fig. 4).

Cooke (1953, p. 33) reported *Mecaster batnensis* (as *Hemiaster jacksoni*) from the Eagle Ford Formation of central and south Texas and the Indidura Formation of Mexico. These occurrences extended its geographic range in North America from the far southern Western Interior to south Texas and Mexico.

Carthage coal field occurrence

The most prolific occurrence of *Mecaster batnensis* known to date is in the Carthage coal field, Socorro County, New Mexico (Text-fig. 3), where hundreds of specimens have been collected primarily from the third highest (CS-179) of the four, thin, yellowish orange-weathering, limestones at the base of the Bridge Creek Limestone Beds (Text-figs 5 and 6).

Text-fig. 5. Outcrop photograph looking east at the base of the Bridge Creek Limestone Beds in the type section of the Tokay Tongue of the Mancos Shale in the Carthage coal field, Socorro County, New Mexico. All four Scip zone limestone beds yield echinoids, but the major echinoid occurrence is in unit CS-179 (Scip zone limestone #3), where hundreds of echinoids have been collected over the years by students and professors from the New Mexico Institute of Mining and Technology, Socorro, New Mexico. Jacob Staff is 1.5 m (5 ft) long. Modified from Hook and Cobban (2015, fig. 8B). The outcrop is in the SE 1/4 SE 1/4 sec. 8, T. 5 S., R. 2 E., Cañon Agua Buena 7.5-minute quadrangle, Socorro County, New Mexico



Text-fig. 6. Graphic section of the Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale at its type section in the Carthage coal field, Socorro County, New Mexico, showing lithology and positions of USGS Mesozoic fossil collections. Hundreds of specimens of *Mecaster batnensis* have been collected primarily from the third highest (unit CS-179) of the four, thin limestones at the base of the Bridge Creek. Modified from Hook and Cobban (2015, fig. 4). Section measured by S. C. Hook on February 10, 2008 in the SE 1/4 SE 1/4 sec. 8, T. 5 S., R. 2 E., Cañon Agua Buena 7.5-minute quadrangle, Socorro County, New Mexico

The Bridge Creek Limestone Beds of the Tokay Tongue of the Mancos Shale are 22 m- (72 ft-) thick and lie 91 m (302 ft) above the base of the tongue at Carthage. The Bridge Creek Limestone Beds are composed primarily of medium gray, blocky to chippy weathering, highly calcareous shale (77%) with subsidiary amounts of calcarenite (16%), limestone (5%), and bentonite (3%). However, the resistant limestones and calcarenites, which are concentrated at the bottom and top of the unit, respectively, form persistent ridges in the shale valley between the underlying Dakota Sandstone and the overlying Atarque Sandstone Member of the Tres Hermanos Formation. Both the lower and upper contacts of the Bridge Creek, which consist of resistant limestone or calcarenite against non-resistant shale, are conformable.

In southern and west-central New Mexico, the two to six, thin (generally less than 18 cm (7 inches) thick) concretionary to nodular limestones at or near the base of the Bridge Creek Limestone Beds are easily recognized because of their nodular appearance and distinctive golden-brown weathering color. These limestones contain the most diverse fauna in the Tokay Tongue of the Mancos Shale with at least six ammonite, two oyster, one clam, one echinoid, one brachiopod, and several gastropod species. The straight ammonite *Sciponoceras gracile* is so common in the these limestones that they are referred to (informally) as the Scip zone limestones and numbered from #1 at the bottom to #4 at the top at Carthage. Scip zone limestone #1 (CS-174) is concretionary and comes and goes in the section; limestone #2 (CS-176) is bedded and persistent; limestone #3 (CS-179) is a dense, black, almost lithographic limestone that pinches and swells and is as much as 33 cm (13 inches) thick; and limestone #4 (CS-181) is concretionary, but generally present. Each of these four limestones contains the late Cenomanian *Euomphaloceras septemseriatum* fauna. Text-fig. 5 shows an outcrop view of these four limestones exposed in an arroyo at the type section of the Tokay Tongue of the Mancos Shale in the Carthage coal field (see Hook and Cobban 2015). These four Carthage limestones are lithologically and faunally similar to the four limestones at the base of the Bridge Creek Limestone Member of the Greenhorn Formation in the Pueblo, Colorado, area (Cobban and Scott 1973).

A 20-cm- (8 inch-) thick, white-weathering limestone bed (CS-191) that is 6.3 m (20.5 ft) above the base of the Bridge Creek Limestone Beds contains the inoceramid bivalve *Mytiloides puebloensis* (D14702), a taxon that is used to define the base of the Turonian in the Western Interior (Text-fig. 6). *Mytiloides hattini* (D14704), the oldest Cenomanian inoceramid occurs in a 25 cm- (10 inch-) thick limestone, CS-187, 1.5 m (5 ft) below the bed containing *M. puebloensis* (Text-fig. 6).

The brown-weathering, thin-bedded, resistant calcarenites at the top of the Bridge Creek Limestone Beds (CS-217 through CS-219) are composed of comminuted remains of the inoceramid bivalve *Mytiloides mytiloides* (D5782) and contain occasional internal molds of the early Turonian ammonite *Mammites nodosoides* (D5781-5782).

Paradise Canyon occurrence

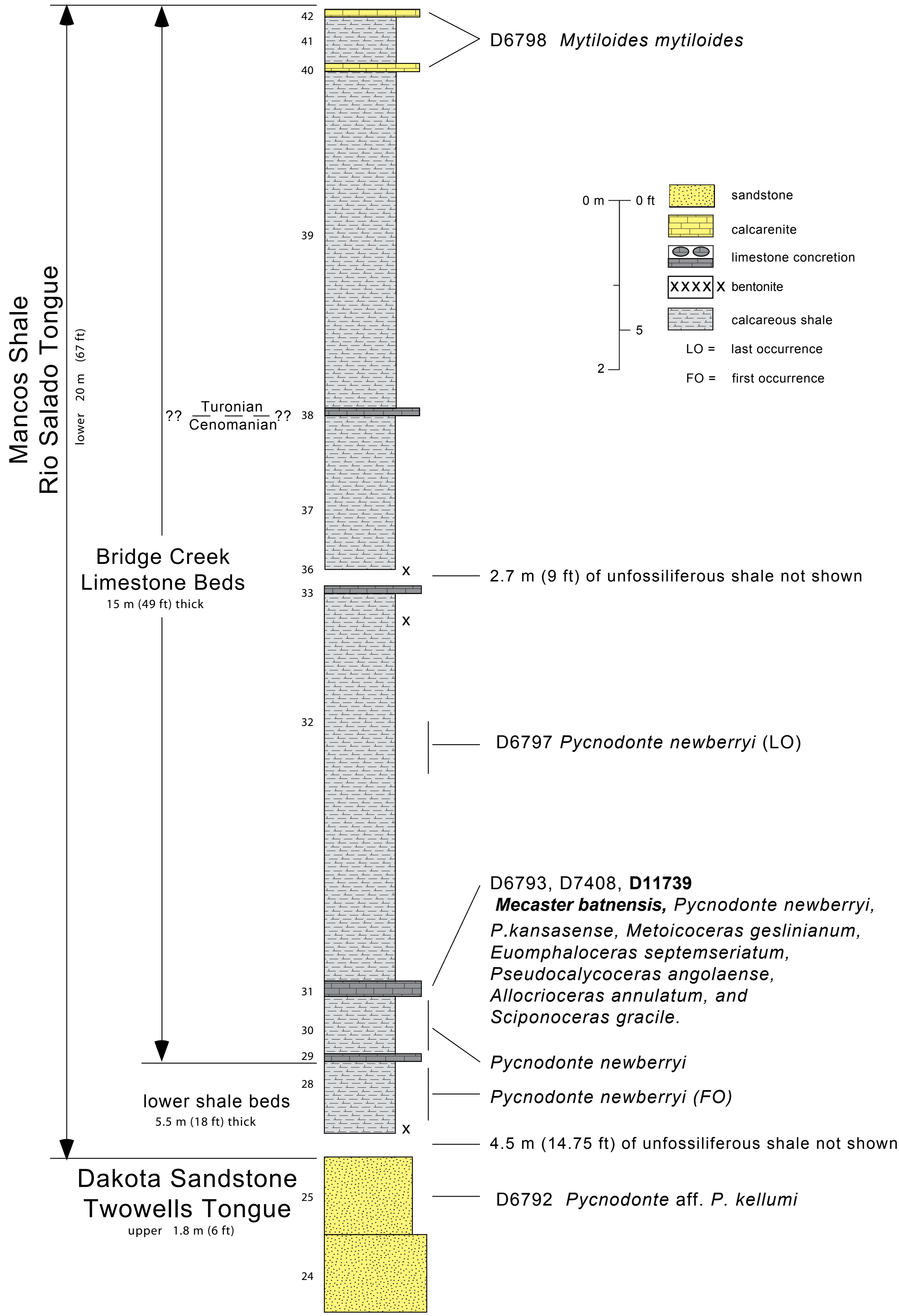
The second most prolific occurrence of *Mecaster batnensis* known to date in New Mexico is from Paradise Canyon, Cibola County, New Mexico (Text-fig. 3). At Paradise Canyon (Text-fig. 7), the echinoids occur in a 18 cm- (7 inch-) thick, gray, nodular limestone (unit 31) that is 73 cm (2.4 ft) above the base of the Bridge Creek Limestone Beds of the Rio Salado Tongue of the Mancos Shale. The Bridge Creek Limestone Beds are 15 m (49 ft) thick; the second Scip zone limestone contains the *Euomphaloceras septemseriatum* fauna (D6793, D7408, and D11739) and the upper calcarenites (units 40 and 42) yield *Mytiloides mytiloides* (D6798), just as they do at Carthage. The basal limestone of the Bridge Creek Beds, 8 cm (3 inches) thick and unfossiliferous, is 6.1 m (17.5 ft) above the top of the 20 m- (66 ft-) thick, massive, cliff-forming Twowells Tongue of the Dakota Sandstone.

The Cenomanian/Turonian boundary has to occur within the Bridge Creek Limestone Beds at Paradise Canyon. The most likely candidates for the boundary are the two thin limestones (units 33 and 38) just above the middle of the Bridge Creek. However, no fossils have been collected from either limestone. The boundary is shown here, albeit questionably, at the higher limestone.

More than 50 matrix-free specimens of *Mecaster batnensis* are available to us from unit 31, of which 40 are suitable for measurement (Appendix 4B). Roney (2013) examined 73 specimens (U.S. National Museum collections) of *M. batnensis* from New Mexico; the vast majority came from the Mancos Shale in Valencia (now Cibola) County, New Mexico, from USGS Mesozoic locality D7408 in Paradise Canyon (Text-fig. 7).

SYSTEMATIC PALEONTOLOGY

Order Spatangoida
Family Hemiasteroidea
Genus *Mecaster* Pomel, 1883



D6798 *Mytiloides mytiloides*
0 m 0 ft
5
2
sandstone
calcarenite
limestone concretion
XXXX X bentonite
calcareous shale
LO = last occurrence
FO = first occurrence
Mancos Shale
Rio Salado Tongue
lower 20 m (67 ft)
?? Turonian / Cenomanian ??
Bridge Creek
Limestone Beds
15 m (49 ft) thick
42
41
40
39
38
37
36
33
32
31
30
29
28
25
24
x
2.7 m (9 ft) of unfossiliferous shale not shown
D6797 *Pycnodonte newberryi* (LO)
D6793, D7408, **D11739**
Mecaster batnensis, *Pycnodonte newberryi, P.kansasense, Metoicoceras geslinianum, Euomphaloceras septemseriatum, Pseudocalycoceras angolaense, Allocrioceras annulatum, and Sciponoceras gracile.*
Pycnodonte newberryi
Pycnodonte newberryi (FO)
lower shale beds
5.5 m (18 ft) thick
4.5 m (14.75 ft) of unfossiliferous shale not shown
Dakota Sandstone
Twowells Tongue
upper 1.8 m (6 ft)
D6792 *Pycnodonte* aff. *P. kellumi*

DESCRIPTION: The small- to medium- sized test is broad and tall relative to length, with an abrupt truncation in the rear and a slight to moderate sinus in the front. The centrally positioned apical system has four gonopores. The frontal ambulacrum is nonpetaloid to semipetaloid and has small round pores. The paired ambulacra have relatively short petals with elongate pores; the frontal pair being longer.

REMARKS: A.B. Smith (in Smith and Bengtson 1991, p. 56) afforded generic status to *Mecaster* (until then considered a subgenus of *Hemiaster*), and differentiated it from the latter on the basis, "… of its subequal peals and laterally elongate apical disc in which the madreporite separates genital plates 1 and 4." The apical disc is centrally located rather than lying posterior of center.

Mecaster batnensis Coquand, 1862
(Text-figs 1 and 8)

1862. *Hemiaster batnensis* H. Coquand, p. 248, pl. 26, figs 6–8.
1887. *Hemiaster cristata* Stoliczka?; White, p. 261 (pars), pl. 27, figs 4–6.
1888. *Hemiaster delgadoi* P. de Loriol, p.104, pl. 20, figs 4–8.
1925. *Hemiaster jacksoni* Maury, pp. 518–521.
non 1930. *Hemiaster jacksoni* Maury; Maury, p. 119, pl. 5, figs 2–7.
1937. *Hemiaster jacksoni* Maury; Maury, p. 279, pl. 3, figs 1, 2, 9.
1937. *Hemiaster cedroensis* Maury; Maury, p. 280, pl. 2, figs 3, 7.
1953. *Hemiaster jacksoni* Maury; Cooke, p. 33, pl. 12, figs 5–11.
1959. *Hemiaster jacksoni* Maury; Santos and Cunha, pp. 11–12, pl. 1, figs 1–4.
1981. *Hemiaster jacksoni* Maury; Brito, p. 404, pl. 1, figs 3, 4, 6, 7.
1981. *Hemiaster cedroensis* Maury; Brito, p. 405, pl. 2, fig. 7.
1991. *Mecaster batnensis* (Coquand, 1862); A.B. Smith in Smith and Bengtson, pp. 56–60, figs 46, 47, 48a, 49; pls 12, 13.
1996. *Hemiaster* sp. cf. H. jacksoni Maury; Kirkland, pp. 109–110, pl. 15, figs L–Q.
1999. *Mecaster batnensis* (Coquand, 1862); Seeling, pl. 7, figs 3–8.
2013. *Mecaster batnensis* (Coquand, 1862); Roney, pp. 11, 12, fig. 5.1–14.

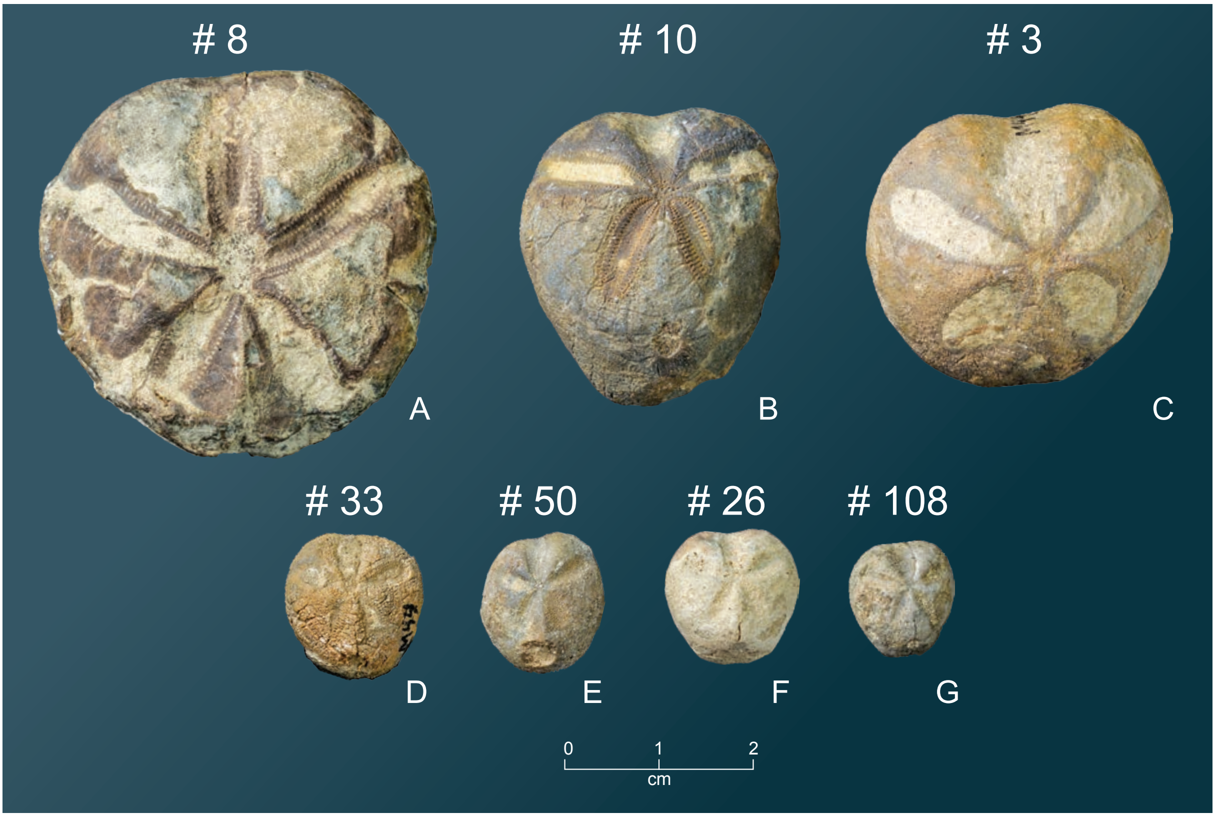
DESCRIPTION: This species group, according to A.B. Smith (in Smith and Bengtson 1991, p. 56), "… is characterized by having a central apical disc in which the madreporite separates the two posterior genital plates but not the two posterior ocular plates. Genital plate 4 maintains broad contact with the madreporite and separates genital plate 3 from ocular V. The interradial suture between sternal plates meets the labral plate close to its right hand margin."

This description is so technical as to be of little use to the field geologist. Fortunately, White's (1887, p. 261) description of *Hemiaster cristata* Stoliczka?, the first Late Cretaceous echinoid species known from Brazil (now placed in synonymy with *Mecaster batnensis*; see above) is much more practical. White's excellent description is paraphrased below. Then, additional morphometric details are added from the literature and the extensive collections from New Mexico.

The test is small, tumid, i.e., subglobose in lateral outline. The length and greatest breadth (width) are nearly equal and crudely hexagonal in outline as seen from above or below. The anal end is a little higher than the anterior end and truncate; its lower portion is a little more prominent than the upper. The fasciole is scarcely perceptible upon any of the specimens in the collection. The oral aperture is situated a little less than one-third the full length of the test from the front. The anal aperture is moderately large and elevated. Tubercles are small but much more distinct upon the under than the upper side of the test. Ambulachral areas are moderately depressed. Interambulachral spaces are prominent; the posterior one is more prominent than the others and somewhat angular or cristate.

Cooke (1953, p. 33) added some additional descriptive information based on an undescribed specimen from White's (1887) original collection from Brazil (USGS 16952). He noted that the apical system is central and has four genital plates. Lateral perforations are closer together than front and back pairs. The anterior petal is sunken into a broad depression, which extends to the peristome where it slightly indents the margin of the test. The peripetalous fasciole is broad and rather ill defined. His figured specimen from Brazil (Cooke 1953, pl. 12, figs 5–8) has a length of 26.7 mm, a width

Text-fig. 7. Graphic section of the Bridge Creek Limestone Beds of the Rio Salado Tongue of the Mancos Shale in Paradise Canyon, Cibola County, New Mexico, showing lithology and positions of USGS Mesozoic fossil collections. More than 100 specimens of *Mecaster batnensis* have been collected from unit 31, the upper of two thin limestones at the base of the Bridge Creek Limestone Beds. The section was measured in the N1/2 sec. 23 and the SW 1/4 NW 1/4 sec. 24, T. 7 N., R. 8 W., Blue Mesa 7.5-minute quadrangle, Cibola County, New Mexico, by E. R. Landis, W. A. Cobban, and C. H. Maxwell on September 26, 1968



Text-fig. 8. Representative selection of well-preserved specimens of *Mecaster batnensis* from USGS Mesozoic locality D14854, Carthage coal field, Socorro County, New Mexico, showing some of the variation in size and aspect ratios that exist in the population (Appendix 4A). Apical views of: **A**. USNM 642620 (Spec. # 8), the largest specimen in the population with both length and width exceeding 40 mm, although it is flattened vertically; **B**. USNM 642621 (Spec. # 10) is one of only eight specimens with a height greater than 20.0 mm; **C**. USNM 642622 (Spec. # 3) is one of only two specimens with a width/ length ratio greater than 1.00; **D**. USNM 642623 (Spec. # 33), although eighteenth smallest, it is just about average in aspect ratios (W/L and H/L); **E**. USNM 642624 (Spec. # 50) and **F**. USNM 642625 (Spec. # 26) are about the same length but **E** is narrower (W/L = 0.93) than **F** (W/L = 0.99); and **G**. USNM 642626 (Spec. # 108), the fourth smallest specimen, is wider than average (W/L = 0.89), but close to average in relative height (H/L = 0.73). USGS Mesozoic locality D14854 is in the SE 1/4 NE 1/4 sec. 8, T. 5 S., R. 2 E., Cañon Agua Buena 7.5-min. quad rangle, Socorro County, New Mexico

of 25.0 mm, and a height of 18 mm; that from Texas (Cooke 1953, pl. 12, figs 9–11) has a length of 26.6 mm, a width of 26.1 mm, and a height of 17 mm.

The 129 measured specimens of *Mecaster batnensis* from the Carthage coal field, New Mexico, (Appendix 4A) illustrate an echinoid population in which individuals are slightly longer (6%) than wide (L/W = 1.06) and about 39% longer than tall (L/H = 1.39). Individuals range from small, probably immature forms to large adults. Fourteen specimens have preserved genital pores, which form when sexual maturity is reached; These 14 specimens range in length from 12.3 mm to 29.8 mm, and suggest that the vast majority of the Carthage echinoids had reached sexual maturity (126 out of 129 specimens have lengths that are 12.3 mm or greater).

The average Carthage specimen has a test length of 20.3 mm, a width of 19.0 mm, and a height of 14.4 mm. The smallest specimen (Appendix 4A, #11) measures 10.4 mm, 9.2 mm, and 7.3 mm, respectively, while the largest (# 8) is a flattened individual that is four times larger areally than the smallest with a length of 41.6 mm and a width of 41.2 mm. Linear regressions of width *vs.* length and height *vs.* length reveal strong linear trends in the Carthage population. The width *vs.* length graph has the stronger linear trend with an r-squared value of 0.96; the width *vs.* length graph shows more scatter about the best fit line, but is still convincingly linear with an r-squared value of 0.87 (Table 1). Several specimens appear to have been crushed slightly, thus reducing both the height and the H/L ratio, which in turn may account for the smaller r-squared value.

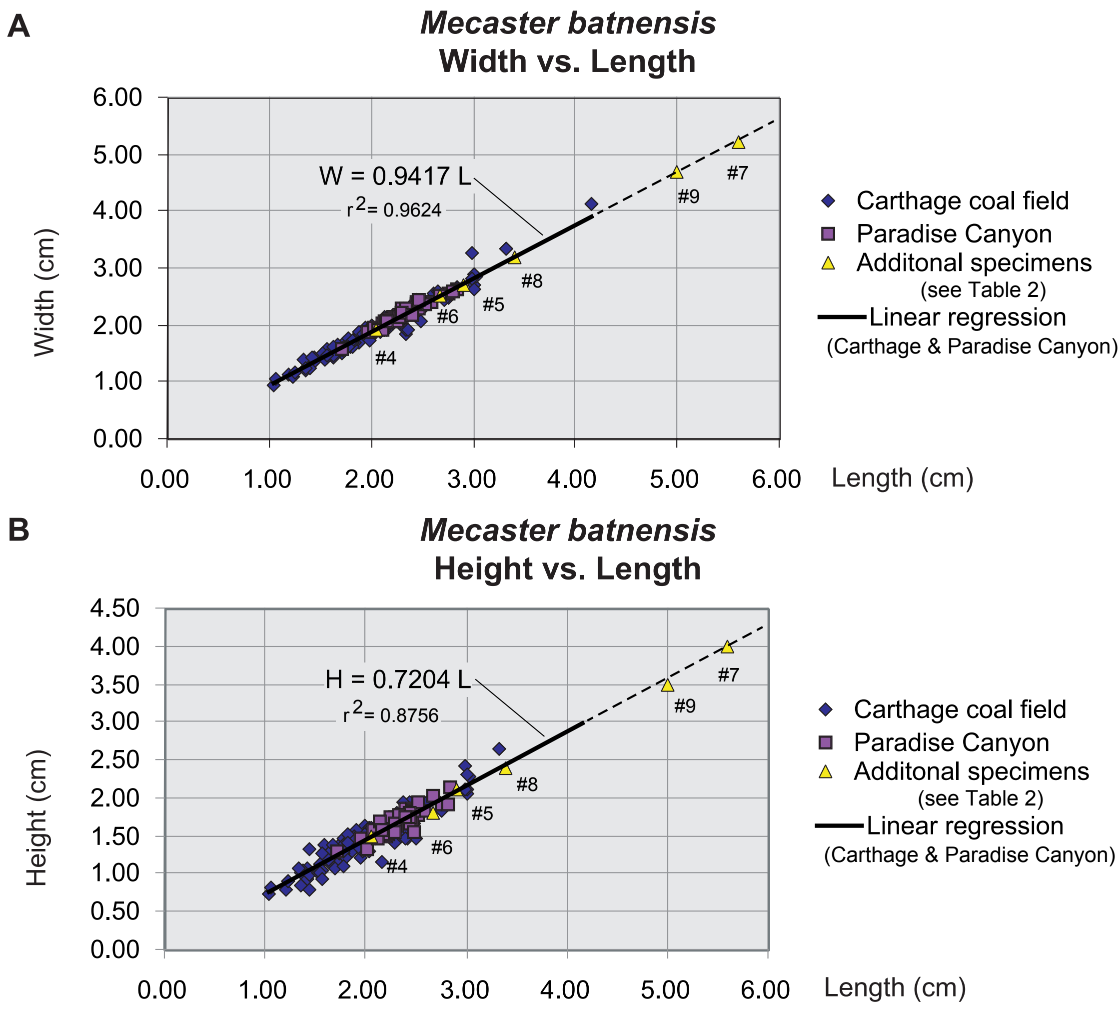
The echinoids from Paradise Canyon (Appendix 4B) show similar patterns. These 40 specimens illustrate an echinoid population almost identical to that from Carthage: tests are slightly (6%) longer than wide (L/W = 1.06) and 39% longer than tall (L/H =1.39). Measured individuals are probably all mature adults

Locality	n =	W/ L	r^2	H/ L	r^2
Carthage	129	0.94	0.96	0.72	0.87
Paradise Canyon	40	0.95	0.94	0.72	0.77
Combined	169	0.94	0.96	0.72	0.88

Table 1. Best-fit linear regression analyses on the aspect ratios of *Mecaster batnensis* for the Carthage and Paradise Canyon collections, along with the combined New Mexico population. Slopes of the best-fit line for width versus length and height versus length are shown along with the r^2 value for each regression

and all are of about the same size. The average specimen has a test length of 23.4 mm, a width of 22.2 mm, and a height of 16.9 mm. The smallest specimen (Appendix 4B, #19) has a length of 17.2 mm, a width of 15.9 mm, and a height of 12.9 mm. The largest specimen (# 18) measures 28.1 mm, 25.8 mm, and 19.0 mm, respectively. Regressions of width *vs.* length and height *vs.* length show strong linear trends with the former having the higher r-squared value and less scatter about the regression line (Table 1).

Appendix 4C combines the 169 specimens of *Mecaster batnensis* from New Mexico and into a single, composite population that has an average length of 21.0 mm, an average width of 19.8 mm, an average height of 15.1 mm, an average width/length ratio of 0.94, and an average height/length ratio of 0.72. Graphs of width *vs.* length (Text-fig. 9A) and height *vs.* length (Text-fig. 9B) for this composite population reveal strong linear trends. The slope of the best-fit regression line for width *vs.* length is 0.94 with an r^2 value of 0.96; that of height *vs.* length is 0.72 with an r^2 value of 0.88. Specimens from each collection are color coded in Text-fig. 9 to



Text-fig. 9. Graphs of aspect ratios of the combined New Mexico population of *Mecaster batnensis* compared with measurements on previously published specimens assigned to *M. batnensis*. In **A,** width is plotted against length; in **B**, height against length for 169 specimens (Appendix 4). In both graphs there is a strong linear correlation between the two variables, but it is much stronger in **A** (r^2 = 0.9624) than in **B** (r^2 = 0.8756). Each of the three collections is color coded to highlight the size distribution in each collection. Table 1 contains the equations for the best fit linear trend for each collection and the combined population. Table 2 contains the summary (average) values for each collection along with a comparison of published measurements of specimens assigned to *Mecaster batnensis*. Note how well each of these published specimens conforms to the trends established by the New Mexico population show their size distribution. The Paradise Canyon collection has a narrower size range than the Carthage lot with most of the specimens clustered near the center of the graph. The Paradise Canyon collection also has a smaller standard deviation for each measured parameter (Appendix 4), suggesting that it represents a single generation of echinoids. Kirkland (1996, p. 110) noted similar trends in size range for echinoids from the *Euomphaloceras septemseriatum* Zone in northeast Arizona. These echinoids, from five locations, are referred to *Hemiaster* cf. *H. jacksoni* by Kirkland (1996). The echinoids occur clustered in large numbers of specimens in the same size range, either all large or all small, suggesting single-generation accumulations.

Table 2 summarizes the average morphometric information on the measured populations of *Mecaster batnensis* from New Mexico, singularly and combined (Items #1 – #3). These average values can be compared directly to five individual specimens (all now referred to *M. batnensis*) whose measurements were either reported in the literature (Items #4 – #6) or can be measured directly on the published plate (items #7 – #9), although not necessarily at natural size.

Published measurements for the three Brazilian specimens (Items #4 – #6) indicate that two are larger than the average specimen from the two localities reported in the present paper, reflecting, perhaps, a bias toward collecting larger specimens. The absolute sizes (L, W, and H) of the Brazilian echinoids fall within the ranges of these size categories in the measured collections from New Mexico (Appendix 4). Thus, the relational values, i.e., the width/length (W/L) and height/length (H/L) ratios, appear to be more important parameters in comparing the specimens from Brazil to the Carthage and Paradise Canyon individuals. The three Brazilian specimens have W/L ratios that range between 0.93 and 0.94 and H/L ratios that range between 0.67 and 0.73. The New Mexico collections have an average W/L ratio of 0.94 and an average H/L ratio of 0.72. Based on these ratios, there is a good fit between New Mexico population and the first two Brazilian specimens. The relational value involving height to length (H/L) of Cooke's (1953) specimen (#6) appears anomalous at 0.67. However, this value is within the range established by the large New Mexico population (Appendix 4) of 0.53 to 0.87. In addition, A.B. Smith (in Smith and Bengtson 1991, p. 56), who did an exhaustive study of the Cretaceous echinoids of northeast Brazil, specifically included Cooke's (1953) specimen into the synonymy of *Mecaster batnensis*.

Biostratigraphically, the fit of these Brazilian specimens seems good as well. The New Mexico and Arizona specimens are confined to the upper Cenomanian *Euomphaloceras septemseriatum* Zone (Text-fig. 4). The Brazilian specimens from Sergipe referred originally to *Hemiaster jacksoni* (# 4, #5, #6) co-occur with the ammonites *Vascoceras hartti* and *Pseudaspidoceras pedroanum,* which were regarded as early Turonian by Cooke (1953, p. 33). Maury (1937, second unnumbered table facing p. 34) correlated the limestone at Bom Jesus, Sergipe, ("calcareo de Bom Jesus com *Vascoceras hartti* e *Pseudaspidoceras pedroanum*") with the lower Turonian of the Eagle Ford in Texas. In southwest New Mexico, Cobban *et al.* (1989, p. 49), working with one of the most diverse late Cenomanian ammonite faunas in the world, reported *V. hartti* from only a single thin bed in association with *Neocardioceras juddii* and *Pseudaspidoceras pseudonodosoides*. This association places *V. hartti* in the *N. juddii* Zone, making it very late Cenomanian in New Mexico (Text-fig. 4).

The measurements for the last three specimens shown in Table 2 (Items #7 – #9) are from published plates of specimens referred by the original authors to *Mecaster batnensis*. The published figures are at

Item	Species/Locality	n	L(mm)	W(mm)	H(mm)	W/L	H/L	References
1	Mb [Carthage]	129	20.3	19.0	14.4	0.94	0.72	Appendix 4A
2	Mb [Paradise Canyon]	40	23.4	22.2	16.9	0.95	0.72	Appendix 4B
3	Mb [NM combined]	169	21.0	19.8	15.1	0.94	0.72	Appendix 4C
4	Hj [lectotype]	1	20.5	19.0	15.0	0.93	0.73	Santos (1960, p. 11)
5	Hj	1	29.0	27.0	21.0	0.93	0.72	Maury (19**37**, p. 279) [Sergipe]
6	Hj (USNM 108395)	1	26.7	25.0	18.0	0.94	0.67	Cooke (1953, p. 33) [Brazil]
7	Mb (PMU SA-362)*	1	**56**	**52**	**40**	0.93	0.71	A.B. Smith (1991, pl. 12E-H) [Sergipe Cen 4]
8	Mb (PMU SA-367)*	1	**34**	**32**	**24**	0.94	0.71	A.B. Smith (1991, pl. 12I-L) [Sergipe Cen 4]
9	Mb (USNM 468535)*	1	**50**	**47**	**35**	0.94	0.70	Roney (2013, fig. 5, 13-14) [NM]

Table 2. Average values of length (L), width (W), height (H), and width/length (W/L) and height/length (H/L) ratios for the two collections and one population (Items #1–#3) of *Mecaster batnensis* documented in the present report (see Appendix 4 for details). These average values are compared against the same parameters for published specimens (Items #4–#9). Mb = *Mecaster batnensis*; Hj = *Hemiaster jacksoni*; * = direct measurement on published plate, shown in bold. See Text-fig. 9 for a graphical comparison

various enlargements. The values given for length (L), width (W), and height (H) of each specimen are the raw, uncorrected measurements taken directly from the plates. The relational values (W/L and H/L) are all within the ranges established by the New Mexico population (Appendix 4). Specimens #7 and #8 are from Sergipe, Brazil; whereas specimen #9 is from USGS Mesozoic locality D7408 in the Mancos Shale at Paradise Canyon, New Mexico (Roney 2013, fig. 5, photos 13 and 14; Text-fig. 7).

The morphometric data in Table 2 are presented in graphical form on Text-figure 9. Data from Carthage are shown as blue diamonds; those from Paradise Canyon as purple squares. Individual specimens, Items #4 through #9 (Table 2), are numbered and shown as yellow triangles. Regression lines with their equations are shown for W/L and H/L; the regression line is forced through the origin (0,0). Note in particular how the data from Paradise Canyon are clustered in the center of the Carthage distribution and how well the individual specimens conform to the linear trends established by the large New Mexico population. This graphical comparison makes a more compelling and easier-to-visualize statement than the written discussion presented above. Sexual dimorphism is not apparent from these graphs.

PALEOECOLOGY

Mecaster batnensis was a detritus-feeding invertebrate that lived buried in the sediment and used its short spines (Text-fig. 1, insets) to burrow and its long tube feet to maintain its burrow (see Kier 1987, fig. 18.77). Recent irregular echinoids live in unconsolidated sediments and use their spines for burrowing and locomotion (A.B. Smith 1984, p. 43). The presence of tens of specimens of *M. batnensis* in thin limestones near or at the base of the Bridge Creek Limestone Beds at Carthage, Paradise Canyon, and elsewhere in New Mexico, attests to the soft nature of the sediments on the seafloor at the time they lived. The infaunal mode of life allowed irregular echinoids to avoid predators, but necessitated building and maintaining burrows that brought in a continuous stream of oxygenated water and allowed waste products to be dissipated behind the individual. As macrophagous sediment eaters ("bulk sediment swallowers", see A.B. Smith 1984, p. 52), they had to move forward, apparently unidirectionally, through the sediment. Although echinoid burrows are relatively rare in the fossil record, A.B. Smith (1984, p. 49) reported that those of heart urchins "…consist of a cylindrical core of sediment with curved, backfill laminae…."

Hook and Cobban (2015, p. 42) postulated (among three considered possibilities) that long, cylindrical, often Y-shaped limestone "tubes" in the shales between the Scip zone limestones in the basal Bridge Creek Limestones Beds at Carthage could be echinoid burrows. At outcrop, these tubes can be more than two meters long and up to 8 cm in diameter, are orientated parallel to bedding, and are Y-shaped (Hook and Cobban 2015, fig. 8E). They are composed of hard, dense micrite that breaks into cylindrical segments that litter the ground. The major problems with the interpretation of these tubes as echinoid burrows are that: (1) they have not been found at other echinoid localities, but only at Carthage where they are common; (2) they consist of dense micrite with no laminae; (3) they have been found only in the shales between the limestones, whereas the echinoids are preserved exclusively in the limestones; and (4) they bifurcate. However, echinoids are the only large, infaunal, invertebrates known from the Bridge Creek at Carthage. Hook and Cobban (2015, p. 42 and fig. 8F) suggested that a depression surrounding an echinoid mold on a bedding surface of limestone slab from Carthage was an echinoid burrow. This interpreted burrow is 2.5 times the length of the echinoid, suggesting that large echinoids with centimeter-length spines could produce burrows the diameter of the tubes. However, the discovery of spines on three echinoids from Carthage (Appendix 4) indicates that the spines were no more than 5 mm long.

Two other interpretations that Hook and Cobban (2015) considered were (1) crustacean burrows and (2) inorganic structures. These two interpretations have similar problems. For the time being, the genesis of these tubes remains unknown.

TAPHONOMY

The presence of hundreds of well-preserved specimens representing several generations of *Mecaster batnensis* at Carthage may testify to their infaunal mode of life, but begs the question of why they died *en masse*. A.B. Smith (1984, p. 11) listed four major ways in which echinoids die: (1) predation, (2) storm action, (3) exposure to high temperatures, and (4) senescence. The last three causes seem improbable to have impacted the Carthage area. Carthage was so far offshore (see Hook and Cobban 2015, fig. 1C) and in such relatively deep water that storms would probably have had little effect on the seafloor. The hard dense limestones and highly calcareous shales at the base of the Bridge Creek Limestone Beds show no evidence of storm bedding. Increases in temperature could have been caused by nearby volcanic activity or a drastic shallowing of water depth, for which there is no evidence either. If senescence had killed the population, then all the specimens would be mature adults of approximately the same size, which is not the case. Sedimentation rates were so slow that it is highly unlikely that the echinoids could have been buried alive to a depth from which they could not escape their burrows. Hook and Cobban (2015, table 2) estimated a compacted sedimentation rate of 1.1 cm (0.4 inches) per thousand years for the entire Bridge Creek Limestone at Carthage. The uncompacted rate could have been 4 to 10 times greater.

The presence of complete internal molds of several species of moderate-sized ammonites (up to 4 cm thick lying on their sides on the seafloor) in the four Scip zone limestones indicates that sedimentation rates for these limy sediments was much greater than the average for the entire Bridge Creek. Assuming that the aragonitic shells of the ammonites would dissolve in seawater within approximately one year, then the sedimentation rate could have been as great as 4 cm/yr, although it was probably less because the filled shell would likely have sunk into the soft mud (see Gill and Cobban 1966, pp. 39–43 for a similar analysis of the Red Bird section of the Pierre Shale in Wyoming). Another line of evidence suggesting that short-lived sedimentation rates were high involves articulated shells of the oyster *Pycnodonte newberryi* in which the valves are preserved in a fully articulated position. This indicates that the oyster was buried so quickly that the pressure of the overlying sediment was greater than the pressure exerted by the ligament to open the valves when the adductor muscle had deteriorated.

In modern oceans, post-larval echinoids are preyed upon by other, regular echinoids, starfish, gastropods, decapod crustaceans, octopuses, and fish. There are no regular echinoids known from the Bridge Creek at Carthage. The tests of the vast majority of irregular echinoids at Carthage are articulated, ruling out starfish, crustaceans, ammonites, and fish as predators, although an occasional *Ptychodus* tooth may be found weathering out of the shale between the limestones. Of course, no starfish, crustaceans, or fish vertebrae have been collected from the Bridge Creek at Carthage, although that does not mean that they did not live there. However, no disarticulated echinoid tests have been found either. Although there is evidence of predatory gastropods at Carthage in the form of small, single, cylindrical holes drilled into numerous oyster shells from the basal Bridge Creek, there is not a single echinoid test from Carthage that has such a hole in it. One possible explanation for the lack of gastropod predation on echinoids is that the irregular echinoids were infaunal, whereas the gastropods and oysters were epifaunal.

Two plausible explanations for the death of the echinoids at Carthage need to be discussed: mass mortality due to sudden erosion and mass mortality due to spawning.

Mass Mortality due to Catastrophic Erosion

Occasional *in-situ* internal molds of the ammonite *Metoicoceras geslinianum* (e.g., at the D14855 level from Scip zone limestone #1) from the Bridge Creek at Carthage are worn on the stratigraphic-up side, but well preserved on the downside. In addition, the corroded upside on these molds is encrusted by oysters, suggesting that the internal mold represents a hiatus concretion, in which encrustation occurred after the hardened mold, eroded out of the sediment, was lying on the seafloor. Hook and Cobban (1981, p. 13) interpreted similar oyster-encrusted molds elsewhere in the Upper Cretaceous of New Mexico as evidence for discontinuity surfaces. Their scenario involved burial of the sediment-filled ammonite shell; dissolution of the aragonitic shell resulting in [pre]fossilization of the sediment filling creating an internal mold; erosion of the softer sediment above and surrounding the hardened internal mold perhaps by currents; colonization by oysters of the discontinuous hardground provided by the internal mold(s), which would form a lag deposit on the seafloor. However, all four Scip zone limestones at Carthage contain the *Euomphaloceras septemseriatum* fauna, which indicates that the hiatus(es), if present, are minor. However, quick erosion of a few to several centimeters of sediment on the seafloor would have resulted in upheaval of echinoids of all sizes (i.e., several generations). In order to be preserved they would have to be reburied rapidly because "…the plates of echinoid tests [disassociate] soon after death because of decomposition of the tissue that bound them together" (Kier 1987, p. 611).

Interestingly, more than one hundred years ago Hyatt (1903, p. 103) came to a similar conclusion about an internal mold of *Vascoceras hartti* from Sergipe, Brazil, collected from a locality close to C.A. White's original echinoid locality. "There is not the slightest fragment of shell upon this cast, but there are the remains of the cemented valves of two or three ostreans. With reference to these I again reiterate the opinions expressed with reference to Hartt's and White's specimens. This cast must, like these, have been a fossil at the time the ostreans were building their shells, since their valves are attached to the surface of the cast and fit into irregularities produced by abrasion before they began to grow on its exposed surface. It [the cast] is not a member of the fauna in which they were found, but came from some earlier strat[um]."

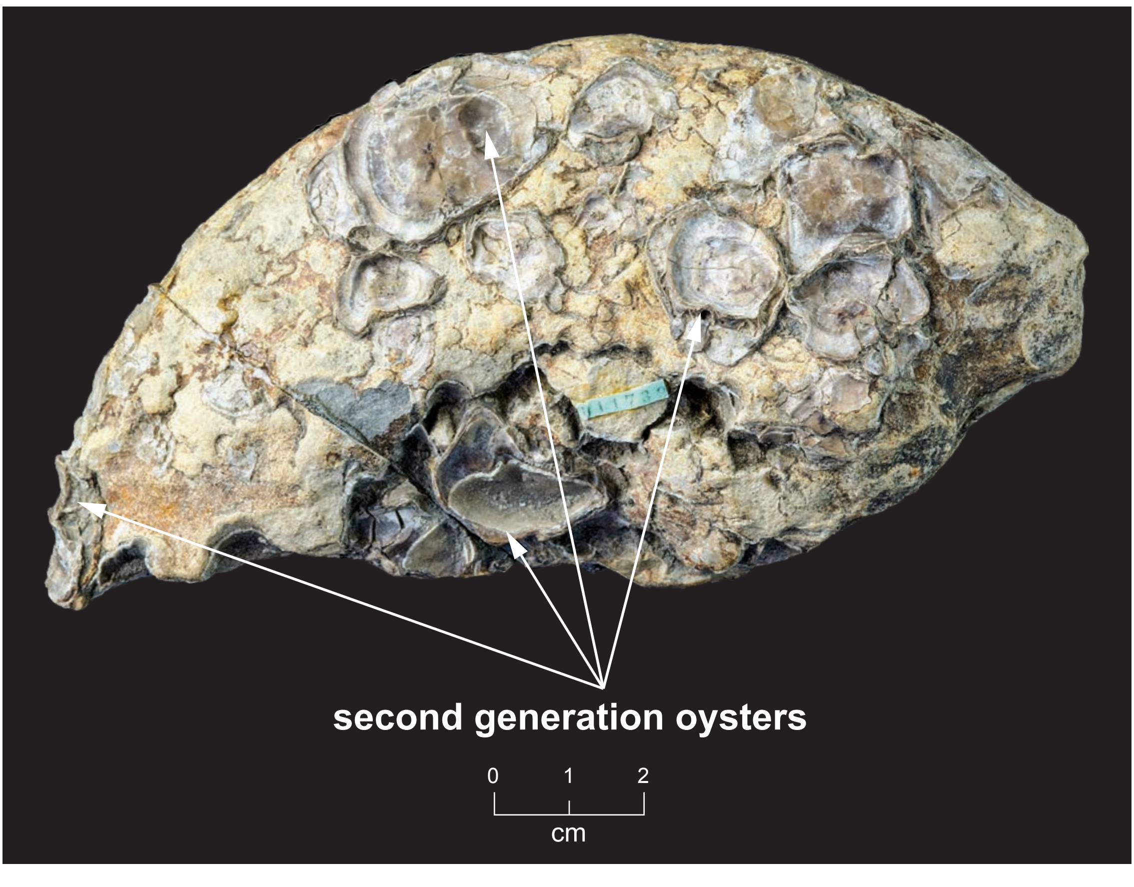
Text-fig. 10 shows a lateral view of a 14-cm- (5.5 inch-) long fragment of an internal mold of the ammonite *Metoicoceras geslinianum* from Paradise Canyon, New Mexico (Text-fig. 7). It was collected from the same bed of Bridge Creek Limestone (D11739) that produced the echinoid collection described in Appendix 4B. This internal mold is encrusted on both sides by the oyster *Pycnodonte kansasense*, indicating that it was encrusted, rolled over at some point on the seafloor, and re-encrusted. Only the cemented left (lower) valves of the oysters are still present on the internal mold. However, there are two generations of oysters preserved on each side of the internal mold, with the left valves of the second (younger) generation attached to the inner portions of the left valves of the first (older) generation.

The photographed side of the ammonite shows more wear and corrosion than the non-illustrated side, on which the ammonite ribs are well preserved and covered by numerous oysters, suggesting that the photographed side was exposed for a longer period of time. Sutures and septal surfaces are well defined in the photograph; on the inner portion of the whorl, the septal surfaces are highly irregular, forming vertical surfaces, which are also encrusted by the oysters (Text-fig. 10). As Hyatt (1903) noted long ago, these irregularities had to have been produced by abrasion on the internal mold (fossil) of the ammonite before the oysters began to grow on them.

The observations discussed above suggest the following geologic history of this encrusted ammonite mold from Paradise Canyon (Text-fig. 10).

Death of the ammonite; filling of the shell with sediment; burial of the filled shell to a shallow depth.

Dissolution of the aragonitic shell and formation of the hardened (prefossilized) internal mold. [Machalski and Olszewska-Nejbert (2016, p. 61) refer to the process of prefossilization as "concretionary lithification" and assume it had to occur prior to dissolution of the ammonite shell.]



Text-fig. 10. Lateral view of an internal mold of *Metoicoceras geslinianum* (d'Orbigny, 1841) from the base of the Bridge Creek Limestone Beds at Paradise Canyon, Cibola County, New Mexico. Although both sides of this specimen are encrusted by two generations of oysters, the outer portion of the whorl on the photographed side is worn smooth, whereas ribs and tubercles are preserved on the other, unillustrated side. Even the vertical portions of the septal surfaces on the photographed side are encrusted by oysters. This specimen (USNM 642627) came from the same bed (unit 31, D11739) as the echinoids described in this paper (see Text-fig. 7). USGS Mesozoic locality D11739 is in the SW1/4 SE1/4 SE1/4 sec. 14 and the NW1/4 NE1/4 NE1/4 sec. 23, T. 7 N., R. 8 W., Blue Mesa 7.5-min. quadrangle, Cibola County, New Mexico

Erosion of the softer sediment surrounding the mold; exposure of the hardened mold on the seafloor.

Encrustation of the mold by oysters as its exposed surfaces are corroded.

Continued erosion of the seafloor such that the mold is overturned (rolled over) and the other side is exposed.

Encrustation of the previously stratigraphic-down side by oysters; death of the oysters that are now facing downward in the sediment. Ligaments open the upper (right) valves of the oysters, which eventually break off the shell.

Two-fold repetition of steps 5 and 6, resulting in two generations of oysters on both sides of the internal mold, with the second generation colonizing the inner portions of the left valves of the first generation.

Encrusted internal molds of ammonites similar to Hyatt's example of *Vascoceras hartti* from Brazil and specimens of *M. geslinianum* from Paradise Canyon (Text-fig. 10) and Carthage occur at several stratigraphic levels in the Upper Cretaceous of New Mexico (Hook and Cobban 1981, p. 13) and are known from the *Euomphaloceras septemseriatum* Zone at Mesa Verde, Colorado (Leckie *et al.* 1996, fig. 31A).

Proponents of the "calcite sea" hypothesis, wherein low magnesium calcite is the primary inorganic precipitate of calcium carbonate, would argue that aragonite is so soluble in a calcite sea that it would dissolve quickly on the seafloor without burial (e.g., Harper *et al.* 1997). This dissolved aragonite could then be a significant source of calcite cement (Palmer and Wilson 2004). Sandberg (1983) discovered that there was an oscillating trend in Phanerozoic oceans in non-skeletal carbonate mineralogy from calcite to aragonite to calcite to aragonite. The Cretaceous was a time of calcite seas. Palmer *et al.* (1988) remarked that "… aragonite fossils [that] have been dissolved out to leave open moulds. The walls of the moulds are encrusted by contemporaneous organisms, confirming the early time of aragonite dissolution." This scenario appears to fit the situation in the Upper Cretaceous of New Mexico described above in which internal molds of ammonites are encrusted by oysters and bryozoans. However, there would still need to be a powerful agent, such as a current, to overturn the pre-fossilized internal molds so they could be encrusted on both sides. Such an agent would also be likely to erode the seafloor to some depth.

Erosion of seafloor sediment as envisioned above would disrupt not only the pre-fossilized molds of ammonites, but also any living infaunal creatures, such as echinoids, and concentrate them as lag deposits at the sediment-water interface. If the erosive force were strong enough, it could also cause the demise of infauna. In the case of echinoids, one to several generations could be eroded during each event. A few hand-size specimens of limestone containing 10 or more tests of at least two generations of echinoids have been collected from the Carthage coal field. All of these hand specimens of "echinoidite" are unoriented because they were collected as float. The D14866 collection from Scip zone limestone #4 in the type area of the Tokay Tongue (Text-fig. 6) contains a cluster of 11 echinoids in a block measuring 50 × 50 × 40 mm. The visible tests range in diameter from 10 to 50 mm. Ten of the tests have the same orientation in the hand specimen; the eleventh is oriented upside down relative the others. A broken-off piece of gray limestone from Paradise Canyon, 40 × 40 × 30 mm (D7408, Appendix 4B, #39), contains a disoriented cluster of at least 10 echinoids; some are upside down relative to others. The largest has a length of 23 mm, the others range down to 7 mm in length.

A spectacular example of an"echinoidite" – called an "accumulate coquina" by A.B. Smith (1984, p. 17) – was collected as float from the Bridge Creek Limestone Member at the Rattlesnake Ridge measured section in the Cookes Range, Luna County, New Mexico, in October 1976 (Text-fig. 3). This unoriented hand specimen (Text-fig. 11) is 110 mm long × 90 mm wide × 40 mm high. It was collected from the uppermost Scip zone limestone (D10113), which is generally a lithographic limestone a few centimeters thick and contains the *Euomphaloceras septemseriatum* fauna. The hand specimen is composed of more than 50 complete, but often abraded, tests of *Mecaster batnensis* along with numerous disarticulated echinoid plates in a fine-grained groundmass of gray limestone, creating a matrix-supported conglomerate in which the clasts are echinoid tests. The visible tests, which are in all orientations, including upside down relative to each other, range in length from 10 to 21 mm. Most of the specimens appear to be about the same size, suggesting they represent a single generation. A few randomly oriented spines are also present on this side. The photographed surface has a thin film of orange-weathering calcarenite. This suggests that the photographed side is the stratigraphic-up side. This accumulation can be interpreted as a death assemblage of living echinoids that were eroded from within the sediment, rolled around on the seafloor, and concentrated as a lag deposit of dead tests and disarticulated plates in a seafloor depression. A recently collected float specimen of a small diameter, internal mold of *Metoicoceras geslinianum* from the D10113 level (USNM 642629) is encrusted by a single oyster and a bryozoan colony (*Membranipora*? sp.). The encrustation is on the side of the mold with a thin film of orange-weathering calcarenite, similar to that on the echinoidite.

Most of the echinoids from the two main New Mexico localities were collected as matrix-free specimens that had weathered out of the limestones. Short, disarticulated spines occur on three echinoids from Carthage and two from Paradise Canyon (Appendix 4). These spines are concentrated primarily, but not entirely, in the natural depressions created by the petals of the echinoid. The presence of more than 100 spines that are up to 5 mm long on specimen #100 (Text-fig. 1), suggests that this individual died *in situ* in its burrow and was not eroded out of the sediment. At Carthage and Paradise Canyon, individual specimens with preserved spines are rare. This may be the case elsewhere in the rock record as well: A.B. Smith (1984, p. 16) reported that the spines of irregular echinoids "… are lost within a matter of hours after death."

Mass Mortality due to Spawning

The infaunal mode of life of irregular echinoids, combined with high productivity and calcitic shells, could have contributed to their preservation at Carthage in large numbers containing several generations. A.B. Smith (1984, p. 15) reported that Recent echinoids have life spans of 1–15 years and that, "…in short-lived and rapidly growing opportunistic species there may be a mass mortality following spawning," which is how Kier (1966, p. A63) interpreted the great concentration of the regular echinoid *Eurysalenia minima* from the Pierre Shale concretion of Wyoming referred to above. The presence of gonopores in the apical system is a simple way of determining between juveniles and sexually mature adults in well-preserved specimens. Unfortunately, only 15 specimens from Carthage are preserved well enough to provide this evidence (Appendix 4). The smallest specimen with preserved gonopores has a length of 14.1 mm, a width of 13.7 mm, and a height of 10.6 mm (Appendix 4, # 9). This specimen is considerably smaller (by two standard deviations) than the average individual, suggesting that *Mecaster batnensis* reached sexual maturity at a small size. Sexes in Recent spatangoids are separate and fertilization is external. Spawning could lead to a large numbers of sexually mature echinoids on the seafloor. After their deaths, the tests could be concentrated by currents or storm events into pockets of conglomerates.

The "echinoidite" from the Cookes Range (Text-fig. 11) with an abundance of tests of approximately comparable size could be the result of mass mortality following spawning, as could the slab of many similar-sized specimens of *Hardouinia stantoni* from the Codell Sandstone of Colorado (Text-fig. 2). Whether mass mortality following spawning occurred at Carthage is not well supported by size distribution, but could have played a part.

Text-fig. 11. Unoriented hand specimen (110 x 90 x 40 mm) of "echinoidite", a matrix- supported conglomerate of echinoid tests, from the uppermost Scip zone limestone (D10113, USNM 642628) from the Rattlesnake Ridge measured section in the Cookes Range, Luna County, New Mexico (Hook and Cobban, 1981, fig. 3). The hand specimen is composed of more than 50 complete, but often abraded tests of *Mecaster batnensis* along with numerous disarticulated echinoid plates. The tests are in all orientations relative to each other, including upside down. D10113 is in the NE 1/4 NE 1/4 sec. 13, T. 21 S., R. 9 W., Massacre Peak 7.5-minute quadrangle, Luna County, New Mexico

GEOLOGIC OCCURRENCE

In Brazil *Mecaster batnensis* has a stratigraphical range – using Western Interior ammonite zones – from the upper Cenomanian *Metoicoceras mosbyense* Zone through the uppermost lower Turonian *Mammites nodosoides* Zone (Smith and Bengtson 1991, fig. 3). The type specimens of *Hemiaster jacksoni* from Brazil have long been regarded as early Turonian in age (Cooke 1953, p. 33). Bengtson (1983, p. 44) assigned the fauna that contained *H. jacksoni* to the lowermost Turonian (his *Turonian 1* level). This fauna includes *Paravascoceras* [*Vascoceras*] *hartti* and *Pseudaspidoceras footeanum* (= *P. pedroanum*). Bengtson (1983, p. 43) noted that this *Paravascoceras hartti* assemblage, "…contains scattered *Euomphaloceras* aff. *septemseriatum*. Some workers might prefer to date this assemblage as latest Cenomanian." A precisely dated ammonite fauna from southwest New Mexico (Cobban *et al*. 1989, p. 49) containing *Vascoceras hartti*, two species of *Euomphaloceras* closely related to *E. septemseriatum*, and *Neocardioceras juddii*, suggests that Bengtson's (1983) *Turonian 1* level, which includes *H. jacksoni*, can be correlated with very late Cenomanian *Neocardioceras juddii* Zone (Text-fig. 4), two zones higher than the Carthage occurrence. More recent ammonite zonations for the Sergipe Basin (Koutsoukos and Bengtson 1993, fig. 4; Ferré *et al*. 2005, fig. 4) have placed the *V. hartti–P. footeanum* fauna in the upper Cenomanian *Neocardioceras juddii* Zone. Smith and Bengtson (1991, fig. 3) showed that the first (= earliest) *M. batnensis* appeared in the *Calycoceras guerangeri* Zone (Cenomanian 3b); i.e., in the *Metoicoceras mosbyense* Zone in the Western Interior (Cobban *et al*. 1989, p. 63; Text-fig. 4 here).

Within the Western Interior, *Mecaster batnensis* is confined to the upper Cenomanian *Euomphaloceras septemseriatum* Zone in New Mexico and Arizona (Text-fig. 4).

GEOGRAPHICAL OCCURRENCE

According to Roney (2013, p. 12), *Mecaster batnensis* is known from the United States (Arizona, New Mexico, and Texas), Mexico, Venezuela, Brazil, Algeria, Tunisia, Egypt, Palestine, and Portugal.

SUMMARY

Mecaster batnensis (Coquand 1862) is a small- to medium- sized, infaunal, Late Cretaceous echinoid that occurs in great numbers in the basal limestones of the Bridge Creek Limestone Beds of the Tokay and Rio Salado Tongues of the Mancos Shale in west-central and southwest New Mexico. The most prolific known occurrence is in the Bridge Creek Limestone Beds of the Tokay Tongue in the Carthage coal field, Socorro County, New Mexico, where more than 200 specimens have been collected. In New Mexico and Arizona, the species is known from only the upper Cenomanian *Euomphaloceras septemseriatum* Zone.

Although echinoids are rare faunal elements in the Upper Cretaceous of the Western Interior, they appear in more than 50 unique localities spread across seven states, one province, and two countries. In these occurrences, there are seven new species and one new genus of echinoid. These echinoids occur in Cenomanian through Maastrichtian rocks, although none are recorded from the Santonian Stage.

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Don Boyd, Socorro, New Mexico, photographed the fossils shown as Text-figures 1, 2, 8, 10, and 11 using a Zeiss 100 mm Makro lens at f22. Little Hawk Studios, Magdalena, New Mexico, drafted Text-figures 3, 4, 5, 6, 7, and 9.

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APPENDIX 1

The 31 known localities where Late Cretaceous echinoids have been collected in New Mexico. All but one of these have been assigned USGS Mesozoic invertebrate (Denver) locality numbers (D#). These localities are plotted in Text-fig. 3.

Locality #	D#_	State	County	Formation	Quadrangle	Fossil
1	5082	NM	Rio Arriba	Lewis Shale	Pounds Mesa	echinoid
2	5780	NM	Socorro	Mancos Shale	Cañon Agua Buena	*Mecaster batnensis*
3	5798	NM	Socorro	Mancos Shale	Carbon Springs	*Mecaster batnensis*
4	6165	NM	McKinley	Mancos Shale	Upper Nutria	*Mecaster batnensis*
5	6212	NM	Sandoval	Mancos Shale	Holy Ghost Spring	*Mecaster batnensis*
6	6793	NM	Cibola	Mancos Shale	Blue Mesa	*Mecaster batnensis*
7	6813	NM	Sierra	Mancos Shale	Elephant Butte	*Mecaster batnensis*
8	6814	NM	Sierra	Mancos Shale	Elephant Butte	*Mecaster batnensis*
9	6815	NM	Sierra	Mancos Shale	Elephant Butte	*Mecaster batnensis*
10	7019	NM	Colfax	Fort Hays Limestone	Vermejo Park	echinoid spines
11	7088	NM	Cibola	Mancos	Laguna	*Mecaster batnensis*
12	7408	NM	Cibola	Mancos Shale	Blue Mesa	*Mecaster batnensis*
13	9040	NM	Socorro	Mancos Shale	D-Cross Mountain	*Mecaster batnensis*
14	10111	NM	Luna	Mancos Shale	Massacre Peak	*Mecaster batnensis*
15	10113	NM	Luna	Mancos Shale	Massacre Peak	*Mecaster batnensis*
16	10130	NM	Socorro	Mancos Shale	Bustos Well	*Mecaster batnensis*
17	10256	NM	Socorro	Mancos Shale	Puertecito	*Mecaster batnensis*
18	10263	NM	Socorro	Mancos Shale	Puertecito	*Mecaster batnensis*
19	10336	NM	Socorro	Gallup Sandstone	Mesa Cencerro	echinoid
20	10615	NM	McKinley	Mancos Shale	Upper Nutria	*Mecaster batnensis*
21	11739	NM	Cibola	Mancos Shale	Blue Mesa	*Mecaster batnensis*
22	14841	NM	Socorro	Mancos Shale	San Antonio	*Mecaster batnensis*
23	14847	NM	Socorro	Mancos Shale	San Antonio	*Mecaster batnensis*
24	14849	NM	Socorro	Mancos Shale	Cañon Agua Buena	*Mecaster batnensis*
25	14853	NM	Socorro	Mancos Shale	Cañon Agua Buena	*Mecaster batnensis*
26	14854	NM	Socorro	Mancos Shale	Cañon Agua Buena	*Mecaster batnensis*
27	14856	NM	Socorro	Mancos Shale	San Antonio	*Mecaster batnensis*
28	14866	NM	Socorro	Mancos Shale	Cañon Agua Buena	*Mecaster batnensis*
29	15010	NM	Socorro	Mancos Shale	Cañon Agua Buena	*Mecaster batnensis*
30	15018	NM	Santa Fe	Mancos Shale	Madrid	small, regular echinoid
31	---	NM	San Juan	Cliff House Sandstone	Pueblo Bonito?	*Hardouinia taylori*

APPENDIX 2

The 54 unique known localities where Late Cretaceous echinoids have been collected within the Western Interior of North America (excluding Texas). Occurrences are arranged more or less chronologically with the oldest at the base of the list. The 26 localities where *Mecaster batnensis* has been collected in New Mexico (Appendix 1) are represented by a single locality, D14853 from the Carthage coal field; the six known localities from Black Mesa, Arizona, are represented by D9020. Symbols: * indicates that the taxon was a new species and ** that the taxon was a new genus and new species. The only taxonomic name updated from the original report(s) is *Mecaster batnensis*, which was referred to originally as *Hemiaster jacksoni*.

No.	Stage	Zone	Formation	Member/Bed	State	Type	Taxon	USGS #	Reference
54	Maastrichtian	*Baculites baculus*	Pierre Shale	upper part	MT	Irregular	*Hemiaster humphreysanus**	6641	Meek and Hayden (1856, p. 147)
53	Maastrichtian	*Baculites baculus*	Pierre Shale		MT	Regular?	*echinoid*	---	Landman *et al.* (2015)
52	Campanian	?? (listed as uppermost)	Pierre Shale		MT	Irregular	*Cardiaster curtus**	---	Clark (1915, p. 84)
51	Campanian	?? (listed as uppermost)	Pierre Shale	Virgin Creek Member	SD	Irregular	*Hemiaster beecheri*	---	Clark (1915, p. 96)
50	Campanian	*Baculites reesidei*	Pierre Shale	Kara Bentonitic Member	WY	Regular	*Eurysalenia minima***	D1954	Gill & Cobban (1966, pp. 23,54,63)
49	Campanian	*Baculites compressus*	Pierre Shale		CO	Regular	echinoid spines	D5864	unpublished
48	Campanian	*Baculities compressus*	Pierre Shale		CO	Irregular	*Hemiaster humphreysanus*	D8089	unpublished (GD-71-5D)
47	Campanian	*Exiteloceras jenneyi*	Pierre Shale	Terry Sandstone Member	CO	??	echinoid	D304	unpublished
46	Campanian	*Exiteloceras jenneyi*	Lewis Shale		NM	??	echinoid	D5082	unpublished (OF-64-6D)
45	Campanian	*Didymoceras stevensoni*	Cozzette Sandstone		CO	??	echinoid	D8278	unpublished (OF-71-11D)
44	Campanian	*Baculites scotti*	Pierre Shale		CO	??	echinoid	D5051	unpublished
43	Campanian	*Baculites scotti*	Pierre Shale		CO	??	echinoid	D5849	unpublished
42	Campanian	*Baculites scotti*	Pierre Shale		CO	??	echinoid	D5854	unpublished
41	Campanian	*Baculites scotti*	Mancos Shale		CO	??	echinoid	D7026	unpublished
40	Campanian	*Baculites scotti*	Mancos Shale		CO	??	echinoid	D6659	unpublished
39	Campanian	*Baculites scotti*	Sego Sandstone		UT	Irregular	*Hemiaster humphreysanus*	13268	Fisher et al. (1960, p. 33)
38	Campanian	*Baculites scotti*	Pierre Shale		CO	Irregular	*Hemiaster humphreysanus*	D4564	unpublished (CD-64-21D)
37	Campanian	*Baculites reduncus*	Pierre Shale		WY	??	echinoid	---	Oral comm., 2009 (S. D. Jorgensen)
36	Campanian	*Baculites gregoryensis*?	Belly River	Birch Lake Sandstone	AB	Irregular	*Hardouinia taylori**	---	Warren (1926, p. 11)
35	Campanian	*Baculites gregoryensis*	Sage Sandstone		CO	Irregular	*Hardouinia taylori*	D7570	unpublished (OF-70-9D)
34	Campanian	*Baculites perplexus*	Mancos Shale	Loyd Sandstone Member	CO	Regular	echinoid spines	D7079	unpublished
33	Campanian	*Baculites perplexus*	Cliff House Sandstone		NM	Irregular	*Hardouinia taylori*	---	Siemers and King (1974, p. 271)
32	Campanian	*Cataceramus balticus*	Montana	probably Eagle	WY	??	echinoids	23115	unpublished (F-50-28))
31	Campanian	*Baculites obtusus*?	Mesaverde Formation	Parkman Sandstone	WY	Irregular	*Hardouinia taylori*	D9352	unpublished
30	Campanian	*Baculites obtusus*?	Mesaverde Formation	Parkman Sandstone	WY	Irregular	*Hardouinia taylori*	D2024	unpublished (F-56-24D)
29	Campanian	*Baculites obtusus*?	Mesaverde Formation	Parkman Sandstone	WY	Irregular	*Hardouinia* sp.	D1169	unpublished (F-56-24D)
28	Campanian	*Baculites* sp. (weak flank ribs)	Cody Shale		WY	Irregular	*Hemiaster* sp.	---	Cavigelli (2005)
27	Campanian	*Scaphites hippocrepis*	Blair Formation		WY	Irregular	*Hardouinia taylori*	D2322, D2262	J.H. Smith (1961, p. 108)
26	Campanian	*Scaphites hippocrepis*	Montana		???	Irregular	*Hemiaster humphreysanus*	---	J.H. Smith (1961)
25	Campanian	??	Pierre Shale		CO	??	echinoid	D24	unpublished
24	Campanian	??	Lewis Shale		WY	Irregular	*Hemiaster humphreysanus*	8424	unpublished
23	Campanian	??	Mancos Shale		CO	Irregular	*Hardouinia taylori*	14699	Cooke (1953, p. 24)
22	Campanian?	*??*	Pierre Shale		CO	??	echinoid	D3954	unpublished
21	Campanian?	??	Mancos Shale	Buck Tongue	CO	Irregular	*Hemiaster humphreysanus*	D2123	unpublished (F-59-11D, 18D)
20	Santonian?	*??*	Mancos Shale		NM	Regular	small, regular echinoid	D15018	unpublished
19	Coniacian	*Cremnoceramus crassus*	Hilliard Shale		WY	??	echinoid	D9310	unpublished (OER-74-36DB)
18	Coniacian	*Cremnoceramus deformis*	Frontier Formation		WY	??	echinoids	---	Love *et al.* (1947, p. 4)
17	Coniacian	??	Frontier Formation	Wall Creek Member	WY	??	echinoid	D9118	unpublished
16	Coniacian	??	Frontier Formation		WY	Regular	*Porosoma reesidei**	19537, 23423	Cooke (1953, pp. 6-7)
15	Coniacian?	??	Hilliard Formation		WY	??	echinoid	D9310	unpublished (OER-74-36D)
14	Turonian	*Prionocyclus germari*?	Gallup Sandstone		NM	??	echinoid	D10336	unpublished
13	Turonian	*Prionocyclus germari*	Frontier Formation	Wall Creek Member	WY	??	echinoids	---'; [D9357]	Reeside (1957, p. 526);[OER-75-35D)
12	Turonian	*Prionocyclus novimexicanus*	Mancos Shale		CO	Regular	echinoid spines	D10449	unpublished (O&G-77-76D)
11	Turonian	*Prionocyclus novimexicanus* ?	Carlile Shale	just below Fort Hays Limestone Member	CO	Regular	echinoid spines	D2967	unpublished
10	Turonian	*Prionocyclus novimexicanus*	Fort Hays Limestone		NM	Regular	echinoid spines	D7019	unpublished
9	Turonian	*Prionocyclus novimexicanus*	Mancos Shale	Fort Hays Limestone	CO	Regular	echinoid spines	D10449	unpublished (O&G-77-76D)
8	Turonian	*Prionocyclus novimexicanus*	Mancos Shale	Juana Lopez Member	CO	Regular	echinoid spines	D10442	unpublished
7	Turonian	*Prionocyclus hyatti*	Carlile Shale	Codell Sandstone Member	CO	Irregular	*Hardouinia stantoni*?	D6064	unpublished
6	Turonian	*Prionocyclus hyatti*	Carlile Shale	Codell Sandstone Member	CO	Irregular	*Hardouinia stantoni**	743	Clark (1891, p. 76)
5	Cenomanian	*Euomphaloceras septemseriatum*	Mancos Shale	Tokay Tongue, Bridge Creek Limestone Beds	NM	Irregular	*Mecaster batnensis*	D14853	The present paper
4	Cenomanian	*Euomphaloceras septemseriatum*	Mancos Shale	lower part	AZ	Irregular	*Mecaster batnensis*	---;[D9020]	Kirkland (1996, p. 109); [Cobban 1975, p. 110]
3	Cenomanian	*Euomphaloceras septemseriatum*	Greenhorn Limestone	Bridge Creek Limestone Member	CO	Irregular	*Holaster feralis*	D3973	Cobban and Scott (1973, p. 24)
2	Cenomanian	Euomphaloceras septemseriatum	Greenhorn Limestone	Bridge Creek Limestone Member	CO	Irregular	*Holaster feralis**	15402, 22899	Cooke (1953, pp. 26-27)
1	Cenomanian	*Plesiacanthoceras wyomingense*	Frontier Formation		WY	??	echinoid	D9329	unpublished (OER-74-36DC)

APPENDIX 3

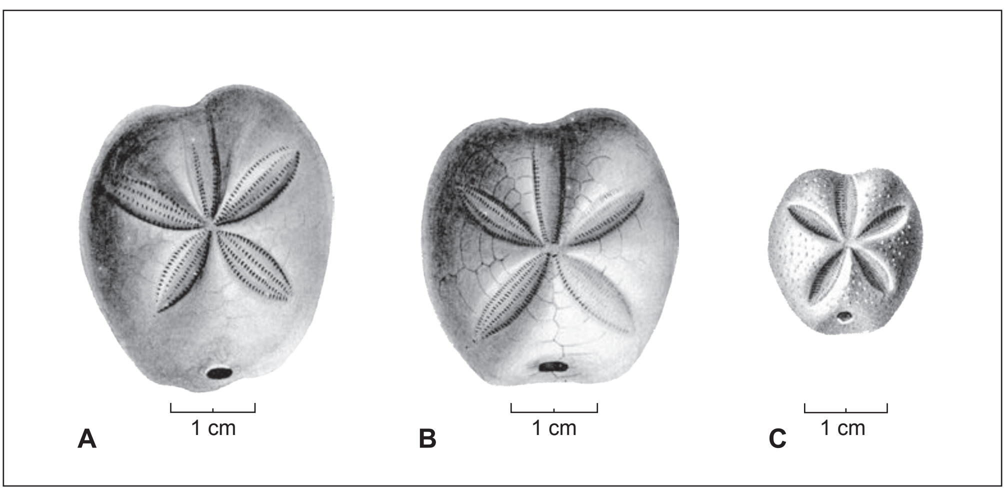
Discussion of the use of *Mecaster batnensis* for the late Cenomanian echinoid from New Mexico

Synonymies tend to be the driest, most boring part of the systematic description of a species. Often, however, there is a fascinating story to be found hidden in that chronological list of names. The following discussion, current through December 31, 2013 when we finished the manuscript, summarizes the problems and hard-won knowledge we had working with a group for which we did not follow the literature or update this regularly, on a species that was named outside the Western Interior.

For more than forty years we have referred irregular echinoids specifically identical to those from the Upper Cretaceous Mancos Shale of the Carthage coal field, New Mexico, to Dr. Carlotta Maury's ** Brazilian species, *Hemiaster jacksoni*. This initial identification was influenced by two factors: (1) the earlier assignment of Turonian echinoids from Texas to *H. jacksoni* by Cooke (1953, p. 33); and (2) the ready availability of Maury's (1936) monograph on the Cretaceous fossils of Sergipe, Brazil, which included a description and illustrations of *H. jacksoni*.

While constructing the synonymy of *Hemiaster jacksoni,* we received two relatively hard-to-obtain Brazilian publications that clarified the use of the specific name *jacksoni*. The first was Santos and Cunha's (1959) paper on *Hemiaster jacksoni* and other echinoids from the Cretaceous of Brazil; and the second was Santos' (1960) note on Cretaceous echinoids from the state of Rio Grande do Norte, Brazil (Text-fig. 1). The first of these restricted the geological range of the

Text-fig. 1. Sketch map of northeastern Brazil. Echinoids from Brazil discussed in this appendix come from the states of Rio Grande do Norte and Sergipe (arrowed)



Text-fig. 2. Original illustrations of Brazilian Late Cretaceous echinoids named by Maury (1925, 1936). **A, B** – Apical views of *Hemiaster sancti-sebastiani* and *Hemiaster rioupanemensis* from Maury (1925, pl. 24, figs. 13 and 10, respectively), placed in synonymy with *H. jacksoni* by Santos (1960, p. 23), but not placed in synonymy with any echinoid species by Smith (1991). Oliveira *et al*. (2013) placed *H. sancti-sebastiani* in synonymy with *M. texanum* and placed *H. rioupanemensis* in synonymy with *M. fourneli*. **C** – Apical view of an echinoid referred to *Hemiaster jacksoni* by Maury (1936, pl. 3, fig. 9), but now assigned to *Mecaster batnensis* by A.B. Smith (in A.B. Smith and Bengtson 1991, p. 56) species; the second bulletin's synonymy of *H. jacksoni* required (actually, demanded) that the specific name be *H. rioupanemensis*. Both bulletins were received in July 2013, when the present work assigning the New Mexico/Texas echinoids to *H. jacksoni* was complete in draft form. Text-fig. 2 reproduces Maury's original illustrations of the three echinoid species that contributed to our taxonomic confusion: *H. sancti-sebastiani*, *H. rioupanemensis*, and *H. jacksoni*.

Santos and Cunha (1959, pp. 16–18) studied the relevant fossil collections reposited in Brazil and restricted *Hemiaster jacksoni* to the lower Turonian (now known to be upper Cenomanian). They (Santos and Cunha 1959, p. 16) emphasized that in the original description of H. *jacksoni*, "… Maury stated that the generic identification was doubtful since the material [from Baixa Verde, state of Rio Grande do Norte] consisted of internal molds which lacked sufficient morphologic details to permit positive identification. Nevertheless, Maury considered the specimens from Sergipe, described by White [1887, p. 261] to be identical with [her] new species, to which they should be referred. Maury did not figure a holotypic specimen." Santos and Cunha (1959) removed Albian and Maastrichtian specimens assigned to *H. jacksoni* that had been mislabeled and mixed in older collections. The Albian specimens were referred by them to *H*emiaster cf. *H. cranium* Cooke, 1946 and the Maastrichtian specimens (e.g., Maury 1930, pl. 5, figs 2, 7) were assigned to the new species *H. oliveirai*. They also designated White's (1887) specimen from the state of Sergipe as the holotype, more correctly, the lectotype for *H. jacksoni* and gave its essential measurements. However, through some error, the photographs of their two holotype specimens were swapped on the published plates. The specimen shown as the holotype of *H. jacksoni* (Santos and Cunha 1959, pl. 1, figs 1–4) is, instead, the holotype of *H. oliveirai* (specimen no. 1069); and the specimen shown as the holotype of *H. oliveirai* (Santos and Cunha 1959, pl. 3, figs 1–4) is, instead, their designated holotype of *H. jacksoni*. In addition, they noted (p. 17) that, "…two specimens were represented by a single composite illustration in White's monograph, a fact not explained in the accompanying text. The two specimens have been found to belong to different species."

After further study of the collections, Santos (1960, p. 23) placed two other new species named by Maury (1925) from the state of Rio Grande do Norte (Text-fig. 1) into synonymy with *Hemiaster jacksoni* (Maury 1925, p. 518). Those two species are *H. rioupanemensis* (Maury, 1925, p. 502) and *H. sancti-sebastiani* (Maury, 1925, p. 508), both from the same age rocks as *H. jacksoni*. All three species were named in the same publication; all three names now referred to the same species. Only one of the three names can be the valid name for the species. Article 23.1 of the International Code of Zoological Nomenclature (ICZN, 1999) states that " [t]he valid name of a taxon is the oldest available name applied to it…"

The solution to this problem becomes apparent when looking at the page number on which each species is described. *Hemiaster rioupanemensis* has to be the namebearer for the species on the basis of appearing first in the publication and thus being the oldest available name. Based on page priority the other two specific names (*H. sancti-sebastiani* and *H. jacksoni*) are junior synonyms. Unfortunately, Santos (1960, p. 23) did not recognize the page priority of *H. rioupanemensis* and continued using *H. jacksoni* as the name for all three species.

Santos (1960, p. 23) assigned *Hemiaster rioupanemensis* and *H. sancti-sebastiani* to *H. jacksoni* after studying all the available collections and considering morphologic variation within populations, along with deformation suffered by the type specimens. An abridged, but literal translation of the Portuguese text of Santos (1960, p. 23) into English follows with our clarifying comments in brackets ([ ]).

"This species [*Hemiaster jacksoni* (Text-fig. 2C)] is very abundant in the Turonian [now upper Cenomanian] faunas of Sergipe, and also occurs in relative abundance in the Cretaceous strata of Rio Grande do Norte [as *H. rioupanemensis* and *H. sancti-sebastiani*].

In 1924 Maury describes *Hemiaster rioupanemensis* [Text-fig. 2A] a new species based on the following differentiating characteristics: form of the narrowing carapace, which is elongate and rounded, and the far anterior position of the apical system. The typical example (type specimen) suffered noticeable deformation that altered its original form. Other characteristics such as petals and apical system allow one to conclude that the species belongs to *H. jacksoni*. In the other material examined by Maury, there is a small specimen, cited in the original description, that has the typical characteristics of *H. jacksoni.*

In the same work, Maury establishes another new species, *Hemiaster sancti-sebastiani* [Text-fig. 2B], considered by her to be very similar to *H. jacksoni*, but separable by its larger height, more angular horizontal contour (outline) and by the more posterior position of the apical system. *H. jacksoni* typically has a hexagonal outline and its height is proportional to that found in *H. sancti-sebastiani*, in which the apical system, partially destroyed, makes it difficult to measure precisely the distances between the apical system and the anterior and posterior borders to within 1 mm, but suggests that is central [as in *H. jacksoni*] and not anterior.

… In the series of specimens examined, we verify that… These diverse individual forms represent local morphological variations [and], therefore are found allied to the typical specimens of [*H. jacksoni*].”

Had no further work been done on the echinoids of Brazil, then *Hemiaster rioupanemensis* would be the name assigned to these New Mexico echinoids from the Bridge Creek Limestone Beds. However, in another paper that we had difficulty obtaining, Smith and Bengtson (1991) published a more up-to-date examination of the Cretaceous echinoids of northeastern Brazil. In this paper, A.B. Smith (in Smith and Bengtson 1991, p. 56) placed *H. jacksoni* Maury, as used by Maury (1925, 1936), Cooke (1953), and others, into the synonymy of *Mecaster batnensis*.

Smith and Bengtson (1991, pp. 7–9) recounted the rather confusing history of research into Brazilian Cretaceous echinoids from 1887 through 1989. Perhaps the most telling comment – and the reason for so much confusion regarding the specific name of the late Cenomanian to early Turonian, Brazilian echinoid – is found in the taxonomic descriptions. Here, under the heading of *Mecaster batnensis*, Smith (1991, pp. 56–58) wrote, “Maury (1925) applied the name *Hemiaster jacksoni* to an indeterminate internal mould of a spatangoid from the limestones of Baixa Verde in the province of Rio Grande do Norte, which she claimed to be identical to the *Hemiaster* species from Sergipe described by White (1887) from “Bom Jesus” …as *H. cristatus*. No type was selected by Maury. … Santos and Cunha (1959, p. 12) designated one of C.A. White’s original specimens, MN 3087-I, holotype; this is the lectotype.” Smith (1991, p. 56) placed White’s (1887) *H. cristatus* and Maury’s (1936) *H. jacksoni* in synonymy with *M. batnensis*. However, Smith’s (1991) work left unresolved the assignments of *Hemiaster rioupanemensis* and *H. sancti-sebastiania,* which Santos (1960) had placed in synonymy with *H. jacksoni*.

Fortunately, while our manuscript was still in draft form, Oliveira *et al*. (2013) published a digital paper on the genus *Mecaster* from the Jandaíra Formation in the Potiguar Basin of northeastern Brazil (Ceará and Rio Grande do Norte). In this paper, they placed *Hemiaster rioupanemensis* Maury in synonymy with *Mecaster fourneli* (Agassiz and Desor, 1847) and placed *H. sancti-sebastiani* in synonymy with *Mecaster texanum* (Roemer, 1849). Both of these later species occur in younger rocks than those in which H. *jacksoni* is found.

These last two papers simplified considerably the task of assigning the New Mexico echinoids to a species. Roney (2013), in his two- and three-dimensional, statistical study of *Mecaster batnensis* and *M. fourneli*, placed several echinoid specimens from the Upper Cretaceous Mancos Shale of New Mexico in *M. batnensis*. This collection (USGS Mesozoic Locality D7408), was identified under contract with the Smithsonian by Andrew B. Smith (The Natural History Museum, Department of Palaeontology, London) as *M. batnensis.* The collection was borrowed from the Smithsonian Institution by Roney (2013) and came from the Bridge Creek Limestone Beds of the Rio Salado Tongue of the Mancos Shale at Paradise Canyon, Cibola County, New Mexico (Daniel Levin, Museum Specialist, Smithsonian Institution, pers. comm., January 2, 2014).

A.B. Smith (1991, p. 54) stated the nature of the taxonomic problem succinctly. “The history of nomenclature for species of *Hemiaster* in Brazil is complex and confused….” We feel comfortable, finally, in using the name *Mecaster batnensis* for the late Cenomanian echinoid from New Mexico previously referred to *Hemiaster jacksoni*.

The interested reader is referred to Santos and Cunha (1959), Santos (1960), and Smith and Bengtson (1991) for greater detail on this rather complicated taxonomic and stratigraphic problem that dates back more than 125 years. Cooke (1953, p. 33) provided details on the original problem of the mixed collections studied by White (1887).

** Brief note about Dr. C.J. Maury – Carlotta Joaquina Maury (1874–1938) is not well known today, but was a well-respected field geologist/paleontologist in the first half of the twentieth century, when it was rare for women to have careers in geology, especially field geology. She worked extensively in Latin America, describing hundreds of new species of fossil invertebrates and plants from Brazil, Venezuela, Trinidad, and the Dominican Republic. She was born on January 6, 1874 in the small of village of Hastings-on-Hudson, New York, and was the younger sister of Harvard astronomer Antonia Caetana de Paiva Pereira Maury (1866–1952). She received a B.S. (1896) and Ph.D. (1902) from Cornell University in geology and later taught at Columbia and Barnard Colleges in the United States and the University of the Cape of Good Hope in South Africa. She was also employed as a paleontologist with the Louisiana Geological Survey (1907–09) and was the official paleontologist of Brazil in 1918. She organized and led a field expedition to the Dominican Republic in 1916 (during the Dominican Revolution) in which she helped lay the geological foundation for the island. She was a fellow of both the Geological Society of America and the American Geographical Society.** Much of the information in this note came from a poster session on Maury’s life and work presented by (Larsen 2011).

APPENDIX 4

Measured specimens of *Mecaster batnensis* from (**A**) the Carthage coal field, New Mexico, and (**B**) Paradise Canyon, New Mexico. Averages, standard deviations, and ranges are provided for each collection and for the combined population (C).
Geographic locations of the USGS Mesozoic invertebrate localities (Denver) are:
D5780 (NE 1/4 SE 1/4 sec. 8, T. 5 S. R. 2 E., Cañon Agua Buena 7.5-min. quadrangle, Socorro County, New Mexico);
D14847 (SE 1/4 NW 1/4 NW 1/4 sec. 8, T. 5 S., R. 2 E., San Antonio 7.5-min. quadrangle, Socorro County, New Mexico);
D14849 (NE 1/4 SE 1/4 SE 1/4 NE 1/4 sec. 8, T. 5 S., R. 2 E., CañonAgua Buena 7.5-min. quadrangle, Socorro County, New Mexico);
D14854 (SE 1/4 NE 1/4 sec. 8, T. 5 S., R. 2 E., Cañon Agua Buena 7.5-min. quadrangle, Socorro County, New Mexico);
D14856 (SW 1/4 SE 1/4 NW 1/4 SE 1/4 sec. 8, T. 5 S., R. 2 E., San Antonio 7.5-min. quadrangle, Socorro County, New Mexico);
D11739 (SW1/4 SE1/4 SE1/4 sec. 14, T. 7 N., R. 8 W., Blue Mesa 7.5-min. quadrangle, Cibola County, New Mexico).

A. Carthage coal field, New Mexico (129 specimens)							
D #	Spec #	L (cm)	W (cm)	H (cm)	W/L	H/L	Notes
14854	1	2.03	1.91	1.29	0.94	0.64	flattened slightly; 4 gonopores
14854	2	1.94	1.94	1.21	1.00	0.62	flattened slightly; 3 gonpores
14854	3	2.98	3.25	2.42	1.09	0.81	distorted lengthwise?; 1 gonopore
14854	4	2.16	1.96	1.51	0.91	0.70	
14854	5	1.88	1.83	1.37	0.97	0.73	2 gonpores
14854	6	1.98	1.93	1.42	0.97	0.72	
14854	7	2.13	1.99	1.53	0.93	0.72	L est.; 4 gonopores
14854	8	4.16	4.12	---	0.99	---	largest; flattened
14854	9	1.41	1.37	1.06	0.97	0.75	2 gonopores
14854	10	3.00	2.70	2.06	0.90	0.69	W-est; 1 gonopore
14854	11	1.04	0.92	0.73	0.88	0.70	distorted; smallest?
14854	12	1.93	1.84	1.38	0.95	0.72	4 gonopores
14854	13	2.00	1.94	1.62	0.97	0.81	
14854	14	2.41	2.33	1.46	0.97	0.61	
14854	15	2.41	2.23	1.78	0.93	0.74	
14854	16	1.74	1.69	1.39	0.97	0.80	
14854	17	3.01	2.64	2.12	0.88	0.70	
14854	18	2.61	2.55	1.93	0.98	0.74	
14854	19	2.31	2.13	1.81	0.92	0.78	
14854	20	2.84	2.68	2.13	0.94	0.75	
14854	21	---	1.85	1.29	---	---	4 gonopores
14854	22	2.31	2.02	1.61	0.87	0.70	
14854	23	2.50	2.35	1.47	0.94	0.59	slighly crushed; 4 gonopores
14854	24	2.09	1.98	1.49	0.95	0.71	
14854	25	2.03	1.89	1.59	0.93	0.78	1 gonopore; 1 spine
14854	26	1.37	1.36	1.04	0.99	0.76	
14854	27	2.17	2.05	1.14	0.94	0.53	
14854	28	2.35	1.85	1.64	0.79	0.70	distorted lengthwise?
14854	29	2.44	2.44	1.94	1.00	0.80	
14854	30	2.27	2.04	1.61	0.90	0.71	
14854	31	2.16	1.93	1.67	0.89	0.77	
14854	32	2.10	1.88	1.45	0.90	0.69	
14854	33	1.54	1.46	1.12	0.95	0.73	
14854	34	2.13	1.91	1.53	0.90	0.72	
14854	35	2.35	2.22	1.78	0.94	0.76	W est.; 2 gonopores
14854	36	1.44	1.44	0.79	1.00	0.55	flattened slightly
14854	37	1.81	1.65	1.36	0.91	0.75	
14854	38	1.77	1.66	1.15	0.94	0.65	
14854	39	1.86	1.74	1.28	0.94	0.69	4 gonopores
14854	40	2.29	---	1.42	---	0.62	L est.
14854	41	1.20	1.11	0.80	0.93	0.67	
14854	42	1.41	1.33	0.99	0.94	0.70	

D #	Spec #	L (cm)	W (cm)	H (cm)	W/L	H/L	Notes
14854	43	1.06	1.04	0.82	0.98	0.77	smallest
14854	44	2.51	2.36	1.73	0.94	0.69	
14854	45	1.57	1.44	1.05	0.92	0.67	
14854	46	1.35	1.20	1.02	0.89	0.76	
14854	47	1.99	1.77	1.41	0.89	0.71	
14854	48	1.81	1.70	1.44	0.94	0.80	
14854	49	1.76	1.62	1.20	0.92	0.68	
14854	50	1.45	1.34	1.31	0.92	0.90	
14854	51	2.00	1.87	1.53	0.94	0.77	
14854	52	1.69	1.59	1.19	0.94	0.70	
14854	53	1.86	1.77	1.50	0.95	0.81	
14854	54	1.33	1.38	1.06	1.04	0.80	
14854	55	1.59	1.55	1.30	0.97	0.82	
14854	56	1.79	1.63	1.26	0.91	0.70	
14854	57	1.61	1.55	---	0.96	---	crushed
14854	58	1.73	1.56	1.26	0.90	0.73	1 gonopore
14854	59	2.34	1.92	1.51	0.82	0.65	
14854	60	1.98	1.93	1.28	0.97	0.65	
14854	61	1.78	1.66	1.46	0.93	0.82	
14854	62	1.94	1.80	1.38	0.93	0.71	
14854	63	1.96	1.85	1.47	0.94	0.75	
14854	64	1.41	1.25	0.94	0.89	0.67	
14854	65	1.60	1.55	1.39	0.97	0.87	
14854	66	1.80	1.72	1.41	0.96	0.78	
14854	67	2.45	2.39	1.77	0.98	0.72	
14854	68	2.75	2.47	1.83	0.90	0.67	1 gonopore
14854	69	2.37	2.26	1.57	0.95	0.66	
14854	70	2.53	2.34	1.75	0.92	0.69	
14854	71	2.43	2.26	1.82	0.93	0.75	
14854	72	2.49	2.08	1.65	0.84	0.66	
14854	73	1.35	1.22	0.83	0.90	0.61	
14854	74	2.22	2.04	1.61	0.92	0.73	
14854	75	1.89	1.70	1.47	0.90	0.78	
14854	76	1.91	1.87	1.57	0.98	0.82	
14854	77	1.23	1.07	0.89	0.87	0.72	1 gonopore; 3 spines
14854	78	2.13	2.12	1.59	1.00	0.75	
14854	79	1.72	1.51	1.28	0.88	0.74	
14854	80	1.44	1.43	0.98	0.99	0.68	
14854	81	1.88	1.88	1.50	1.00	0.80	
14854	82	1.98	1.71	1.39	0.86	0.70	1 gonopore
14854	83	1.64	1.44	1.26	0.88	0.77	
14854	84	1.73	1.63	1.16	0.94	0.67	
14854	85	1.69	1.54	1.07	0.91	0.63	H est.
14854	86	1.57	1.56	1.27	0.99	0.81	1 gonopore
14854	87	1.53	1.50	1.00	0.98	0.65	
14854	88	2.40	2.35	---	0.98	---	crushed; oyster
14854	89	---	2.29	1.84	---	---	
14854	90	1.83	1.67	---	0.91	---	crushed
14854	91	1.55	1.38	1.02	0.89	0.66	
14854	92	1.73	1.52	1.26	0.88	0.73	
14854	93	2.05	1.86	1.59	0.91	0.78	1 gonopore
14854	94	1.78	1.76	1.37	0.99	0.77	

D #	Spec #	L (cm)	W (cm)	H (cm)	W/L	H/L	Notes
14854	95	2.51	2.41	1.71	0.96	0.68	
14854	96	1.64	1.47	1.16	0.90	0.71	
14854	97	2.65	2.58	---	0.97	---	crushed
14854	98	2.01	2.00	---	1.00	---	
14854	99	1.81	1.61	1.20	0.89	0.66	
14854	100	2.38	2.28	1.93	0.96	0.81	100 spines up to 4 mm
14854	101	3.32	3.32	---	1.00	---	top gone
14854	102	1.92	1.82	1.36	0.95	0.71	incomplete
14854	103	1.78	1.65	1.09	0.93	0.61	
14854	104	2.36	1.92	1.50	0.81	0.64	
14854	105	1.82	1.70	1.53	0.93	0.84	
14854	106	2.72	2.43	1.98	0.89	0.73	W est.
14854	107	2.32	2.27	1.63	0.98	0.70	H est.
14854	108	1.23	1.10	0.90	0.89	0.73	
14854	109	2.49	2.28	---	0.92	---	broken. 2 inside?
14854	110	1.68	1.65	1.37	0.98	0.82	
14854	111	2.09	1.95	---	0.93	---	flattened
14854	112	---	1.55	1.27	---	---	broken
14854	113	2.17	2.04	1.54	0.94	0.71	
14854	114	1.64	1.61	1.19	0.98	0.73	
14854	115	1.25	1.16	---	0.93	---	broken
14854	116	1.43	1.43	---	1.00	---	flattened
14847	117	3.33	3.33	2.63	1.00	0.79	
14849	118	2.13	2.00	1.51	0.94	0.71	
14849	119	3.03	2.85	2.28	0.94	0.75	
5780	120	2.27	2.12	1.73	0.93	0.76	
5780	121	1.82	1.72	1.40	0.95	0.77	
5780	122	2.40	2.29	1.46	0.95	0.61	flattened; 1 gonopore
5780	123	1.78	1.60	1.28	0.90	0.72	
5780	124	1.57	1.47	0.92	0.94	0.59	
14849	125	3.01	2.88	2.32	0.96	0.77	
14849	126	2.15	2.00	1.56	0.93	0.73	
14849	127	2.21	2.19	---	0.99	---	flattened
14849	128	---	1.92	1.57	---	---	broken
14856	129	2.99	2.81	2.10	0.94	0.70	
	n =	125	128	117	124	114	
	AVERAGE	2.03	1.90	1.44	0.94	0.72	
	STDEV	0.51	0.50	0.35	0.05	0.07	
Range	from	1.04	0.86	0.73	---	---	
	to	4.16	4.12	2.63	---	---	

B. Paradise Canyon. New Mexico (40 specimens)

D #	Spec #	L (cm)	W (cm)	H (cm)	W/L	H/L	Notes
D11739	1	2.29	2.13	1.75	0.93	0.76	>20 spines up to 5 mm
D11739	2	2.52	2.4	1.77	0.95	0.70	
D11739	3	2.21	2.13	1.5	0.96	0.68	
D11739	4	2.22	2.13	1.53	0.96	0.69	
D11739	5	2.85	2.61	2.13	0.92	0.75	
D11739	6	2.4	2.19	1.85	0.91	0.77	
D11739	7	2.46	2.32	1.79	0.94	0.73	

D #	Spec #	L (cm)	W (cm)	H (cm)	W/L	H/L	Notes
D11739	8	2.21	2.05	1.61	0.93	0.73	
D11739	9	2.59	2.41	1.83	0.93	0.71	
D11739	10	1.96	1.86	1.46	0.95	0.74	
D11739	11	2.46	2.35	1.69	0.96	0.69	
D11739	12	2.12	2.03	1.53	0.96	0.72	
D11739	13	2.38	2.2	1.76	0.92	0.74	
D11739	14	2.17	2.1	1.65	0.97	0.76	
D11739	15	2.43	2.29	1.66	0.94	0.68	
D11739	16	2.75	2.56	1.91	0.93	0.69	L est.
D11739	17	2.68	2.52	2.03	0.94	0.76	
D11739	18	2.81	2.58	1.90	0.92	0.68	largest; H est.
D11739	19	1.72	1.59	1.29	0.92	0.75	smallest; >20 spines
D11739	20	2.46	2.29	1.86	0.93	0.76	
D11739	21	2.47	2.42	1.83	0.98	0.74	
D11739	22	2.29	2.22	1.72	0.97	0.75	
D11739	23	2.53	2.37	1.93	0.94	0.76	
D11739	24	2.25	2.08	1.73	0.92	0.77	
D11739	25	2.44	2.37	1.80	0.97	0.74	
D11739	26	2.31	2.16	1.62	0.94	0.70	
D11739	27	2.02	1.95	1.31	0.97	0.65	
D11739	28	2.27	2.18	1.57	0.96	0.69	
D11739	29	2.44	2.39	1.74	0.98	0.71	4 gonopores
D11739	30	2.07	1.93	1.57	0.93	0.76	
D11739	31	2.29	2.2	1.64	0.96	0.72	best top surface
D11739	32	2.14	2.05	1.69	0.96	0.79	
D11739	33	2.29	2.27	1.65	0.99	0.72	
D11739	34	2.47	2.43	1.56	0.98	0.63	
D11739	35	2.34	2.3	1.78	0.98	0.76	
D11739	36	2.28	2.15	1.67	0.94	0.73	
D11739	37	2.11	1.93	1.46	0.91	0.69	
D11739	38	2.16	2.08	1.58	0.96	0.73	
D7408	39	2.29	2.2	1.54	0.96	0.67	part of a cluster; H est.
D11739	40	2.4	2.18	1.74	0.91	0.73	
	n =	40	40	40	40	40	
	AVERAGE	2.34	2.22	1.69	0.95	0.72	
	STDEV	0.23	0.21	0.18	0.02	0.04	
Range	from	1.72	1.59	1.29	---	---	
	to	2.81	2.56	2.13	---	---	
C. Combined New Mexico Populations (169 specimens)							
	n =	165	168	157	164	154	
	AVERAGE	2.10	1.98	1.51	0.94	0.72	
	STDEV	0.48	0.47	0.34	0.04	0.06	
Range	from	1.04	0.86	0.73	---	---	
	to	4.16	4.12	2.63	---	---	