Phylogenetic and Biogeographic Analysis of Cretaceous Spatangoid Echinoids from the Western Interior Seaway

By

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Abstract

Members of the echinoid order Spatangoida, a highly diverse and abundant marine invertebrate clade, were important denizens of the Cretaceous Western Interior Seaway (WIS), an epicontinental seaway that divided North America in two during an interval of greenhouse conditions between roughly 100 and 65 million years ago. Despite being well represented in the Cretaceous rocks of Texas and surrounding areas, the phylogenetic patterns of spatangoid echinoids of the WIS, especially at the species level, have yet to be fully resolved. Further, because of their complex morphologies, they represent one of the few marine invertebrate groups from this time period that are amenable to phylogenetic study. Another interesting question pertaining to taxa found in the WIS is their biogeographic origins and whether they represent an endemic radiation or are instead derived from one or more invasions from other regions. In order to reconstruct a hypothesis of spatangoid phylogenetic relationships, a parsimony analysis was conducted using a character matrix of 32 characters collected from 20 species. Species that occur in the WIS were considered comprehensively; species from other regions such as South America, Europe, and North Africa were additionally incorporated into the analysis. Phylogenetic biogeographic analysis was then conducted on the spatangoid phylogeny using a modified version of Fitch Parsimony Analysis, and several episodes of vicariance and range expansion were identified across the phylogeny. These were possibly further related to some of the various major episodes of sea-level rise and fall during the Cretaceous.

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Chapter 1: Phylogenetic Analysis of WIS Spatangoids

Introduction

The Western Interior Seaway (WIS) was an epicontinental sea that existed during the Cretaceous Period, effectively dividing North America into two terrestrial regions and originated due to tectonic forces associated with the Sevier orogeny that formed the Rocky Mountains (Kauffman & Caldwell 1993; Frakes 1999) and extremely warm climatic conditions which may serve as a proxy for those likely to be experienced in Earth's near-term future (Myers et al. 2013; Frakes 1999). Today the WIS is preserved as a spectacular set of fossil deposits running from Texas, through Kansas, and up into Alberta, Canada. The WIS supported a highly diverse marine ecosystem comprising a richly abundant fossil record of microorganisms, invertebrates, and vertebrates. These deposits have been collected from extensively by paleontologists for over 140 years, and the fossils from the WIS played a pivotal role in the history of North American paleontology (Shore 1971; Lanham 1973; Mayor 2005). Fossils from this region have also provided a wealth of macroevolutionary and biogeographic data (e.g. Kauffman 1984; Glancy et al. 1993; Cochran et al. 2003; Myers & Lieberman 2011; Myers et al. 2013).

Echinoids are a highly successful group of marine invertebrates present in a plethora of habitats today, including interdidal zones, continental shelves, and deep water (Kroh & Smith 2010). They are characterized by a rich and diverse fossil record dating back to the Ordovician period (Smith 1984). The group experienced a sharp diversity decline at the end of the Paleozoic in which the majority of stem group echinoids went extinct after the end-Permian mass extinction (Thompson et al. 2016). However, their diversity rebounded in the Mesozoic era with the appearance of irregular echinoids, which express bilateral symmetry superimposed over the typical radial symmetry of other echinoderms. Echinoids were also abundant denizens of the

shallow benthic communities of the southern parts of the WIS, in what is today part of the southwestern United States (e.g. Texas, New Mexico) and northern Mexico (Sonora, Coahuila). This is where the WIS opened into the much larger North Atlantic/West Tethys for much of its duration (Blakey 2014). Many of the first echinoids found in this region were described in various 19th century studies (e.g. Roemer 1849, 1852; Clark 1893). Subsequent works include descriptions by Clark & Twitchell (1915), Cooke (1946, 1953, 1955), and publications focused on taxa from Texas (Adkins 1928; Whitney & Kellum 1966; Smith & Rader 2009; Thompson 2016).

Among the irregular echinoids, the most diverse and abundant are the heart urchins of the order Spatangoida. In the present day, spatangoids, like other echinoids, inhabit all oceans and a wide array of habitats (Stockley et al. 2005). Spatangoids are deposit-feeding burrowers that became diverse in the Cretaceous and survive into the present day (Smith 1984). Spantangoida are currently subdivided into the suborders Micrasterina, Brissidina, Hemiasterina, Paleopnuestina, and the extinct stem families Toxasteridae and Somaliasteridae (Smith & Kroh 2011). Spatangoid taxonomy has been studies throughout the 20th century, with a special emphasis on the family and subordinal levels (Mortensen 1950; Fischer 1966). More recently, echinoids have been the subject of phylogenetic study (Kroh & Smith 2010), including analyses that incorporated both living and fossil spatangoids (Villier et al. 2004; Stockley et al. 2005). However, there have been no previous studies that focused on species-level phylogenetic relationships of the Cretaceous spatangoids of North America. The goal of the present study is to rectify this gap in knowledge and develop a more detailed picture of spatangoid phylogeny, with special emphasis on taxa in the WIS. Additionally, this study aims to use that phylogenetic

perspective to increase our understanding of the biogeographic relationship between the WIS and other parts of the Cretaceous world.

Methods

Taxonomic Sampling – In order to analyze the phylogenetic relationships within WIS Spatangoida, 20 taxa were selected for phylogenetic analysis, comprising representatives of the families Toxasteridae, Hemiasteridae, and Micrasteridae (Table 1). Specimens were examined from the collections of: the University of Kansas Museum of Invertebrate Paleontology (KUMIP); the Non-Vertebrate Paleontology Laboratory at the University of Texas in Austin (UT); and the New Mexico Museum of Natural History (NMMNH). In addition, loans of type specimens from the National Museum of Natural History (NMNH) were obtained. High quality stacked images were sourced from specimens housed at the aforementioned institutions, as well as Universität Bonn, The Natural History Museum London (NHM), and online from *The NHM Echinoid Directory* (Smith & Kroh 2011). Due to the large number of species, not all spatangoids could be considered in the analysis, including Cenozoic and modern forms. Additional Cretaceous spatangoid species from outside the WIS were selected using the criteria that: 1) type specimens or quality photographs of these needed to be accessible; 2) species needed to be defined such that at least 50% of characters could be coded; 3) and all major Cretaceous biogeographic regions should be represented. This meant that species that were the subject of more recent systematic treatments were better represented in the analysis. Although analyzing additional species would be beneficial, expanding the number beyond those considered would entail approaching the n-1 character-to-taxon limit, utilizing species defined on the basis of poorly preserved specimens, and incorporating species that had not been revised in a very long time to the point that status of types would be difficult to verify. *Toxaster retusus* (Lamarck,

1816) was selected to represent the outgroup, as previous phylogenetic analysis by Stockley et al.

(2005) suggests that it comprises a basal representative of the clade.

Table 1. List of species considered in phylogenetic analysis, including the temporal stage(s) they occur in, geographic distribution, all material examined or a relevant reference. Select specimen images can be found in Appendix.

Species	Age	Location	Material examined
Toxaster retusus (Lamarck, 1816)	Valanginian-Hauterivian	France, Switzerland	NHM Echinoid Directory; UT 11704
Heteraster oblongus (Brongniart, 1821)	Valanginian-Barremian	France	NHM Echinoid Directory; UT 14575
Heteraster texanus (Roemer, 1849)	Albian	Mexico; Texas, USA	KUMIP 370536, 370548–370556; UT BEG 34165; Universitat Bonn Texas No org 157

Washitaster riovistae (Adkins, 1920)	Albian	Texas, USA	UT BEG 21491–21493; NHM Echinoid Directory
*Washitaster wenoensis (*Adkins, 1920)	Albian	Texas, USA	UT BEG 21496
Macraster elegans (Shumard, 1853)	Albian	Texas, USA	KUMIP 420253, 490608, 490611; UT BEG 21497, 34161
Mecaster fourneli (Agassiz & Desor 1847)	Turonian-Maastrichtian	Algeria, Brazil	UT 14285; NHM Echinoid Directory

Mecaster batnensis (Coquand, 1862)	Cenomanian-Turonian	Brazil; Mexico; New Mexico(?) & Texas, USA	UT 14252, 83026
Mecaster texanus (Roemer, 1849)	Santonian-Campanian	Texas, USA	UT BEG 34771; Universität Bonn Texas No org 156; NHM Echinoid Directory
Micraster schroederi Stolley, 1892	Campanian	Germany	UT 53845
Pliotoxaster comanchei (Clark, 1915)	Albian	Texas, USA	USNM 103893; UT BEG 21264, 21270

Proraster dalli (Clark, 1891)	Albian	Texas, USA	USNM 19114; UT 83036
Palhemiaster calvini (Clark, 1915)	Albian	Texas, USA	UT BEG 21268, 21487; NHM Echinoid Directory
Hemiaster bufo (Brongniart, 1822)	Cenomanian	United Kingdom	NHM Echinoid Directory
Hemiaster bexari Clark, 1915	Albian	Texas, USA	USNM 8330

Hemiaster cranium Cooke, 1946	Albian	Texas, USA	USNM 103890
Hemiaster estepi Lucas, 2000	Albian	New Mexico, USA	NMMNH P-26501, 26508, 26515
Hemiaster humphreysanus Meek & Hayden, 1857	Maastrichtian	Montana, USA	USNM 331
Diplodetus americanus Stephenson, 1941	Maastrichtian	Texas, USA	UT 83001; USNM 76285

Diplodetus parvistella Schluter, 1900	Maastrichtian	Netherlands	NHM Echinoid Directory

Phylogenetic Methods - Phylogenetic relationships were determined using a parsimony analysis implemented via PAUP 4.0 (Swofford 2003). Data were subjected to a branch and bound search in order to find the most parsimonious tree (Hendy & Penny 1982). Consistency index and retention index were recorded. In the event of multiple trees, a strict consensus was calculated. A bootstrap analysis was conducted using PAUP 4.0 to determine support for each node appearing in the most parsimonious tree(s), using 100 bootstrap replicates in a stepwise search that employed 5 random replications per bootstrap replication. Jackknife analysis was also used, with the percentage of characters removed value chosen at 10%, which equates to 3 characters. For both support tests, groups were retained that were compatible with the 50% majority rule consensus tree. In addition, a Bremer branch support analysis (Bremer 1994) was conducted to calculate node support using the difference between the length of the most parsimonious tree and the largest tree in which a node is maintained.

Characters and Character States - Character and character state descriptions were developed via detailed comparative examination of the exterior tests of specimens. The pre-existing literature was additionally considered to identify characters that had been used previously to diagnose groups and to infer relationships between groups. Villier et al. (2004) and Stockley &

Smith (2005) were especially helpful regarding character data sets used in phylogenetic analyses of echinoids, including spatangoids. In total, 32 characters were identified (listed below), including a combination of qualitative and quantitative characters. Quantitative characters were measured from photographs of spatangoid specimens using the program *ImageJ* (Schneider et al. 2012), scale was set with with known measurements for determining ratios of measured features as well as for angle measurements. Character states are non-continuous relative to each other and multi-state characters were treated as unordered.

Apical disc

1.	Plating: genital plate 2 does not extend between the posterior genital plates – referred to as Ethmophract (0)/ genital plate 2 extends between posterior genital and ocular plates – referred to as Ethmolytic (1).

2.	Position: Below midpoint of test (0) / at midpoint (1) / above midpoint (2).

Frontal ambulacra (III)

3.	Width is much narrower than central width of paired petals (0) / width is much broader than central width of paired petals (1) / width is approximately equal to width of central width of paired petals (2).

4.	Frontal ambulacra depth shallow (0) / frontal ambulacra depth substantial (1).

5.	Distal end of frontal ambulacra tapers to form a "notch" present at ambitus (0) / distal end of frontal ambulacra does not form "notch" at ambitus (1) / deep "notch" formed by frontal ambulacra (2).

6.	Pore pairs of the frontal ambulacra are uniform and uniserial (0) / pore pairs are heterogenous and not uniform (1).

7.   Tubercles located between ambulacra pore pairs: absent (0) / present (1).

Anterior paired ambulacra

8.   Angle axis of petals forms relative to apical disc: 6–14 degrees (0) / 18–22 degrees

(1). This character describes the degree at which the ambulacra inflects from a straight

line to the apical disc.

9.   Relative size of pairs of pores on both axes: equally developed (0) / not equally

developed (1).

10.   Termination of paired petals: subpetaloid (0)/ divergent (1) / in linear branches (2) /

closed (3).

 Posterior paired ambulacra

11.   Angle axis of petals forms relative to apical disc: 2–7 degrees (0) / 10–11 degrees (1) /

more than 14 degrees (2). This character describes the degree at which the ambulacra

inflects from a straight line to the apical disc.

12.   Relative size of pairs of pores on both axes: equally developed (0) / not equally

developed (1).

13.   Termination of paired petals: subpetaloid (0)/ divergent (1) / in linear branches (2) /

closed (3).

Fasciole

14.   Subanal fasciole: absent (0) / present (1).

15. Partially developed fasciole that does not fully encircle the test (sometimes called peripetalous parafasciole): absent (0) / present (1).

16. Fully developed peripetalous fasciole: absent (0) / present (1).

17. Multiple fasciole bands on the test: absent (0) / present (1).

18. Ambulacral plates: decrease in size at fasciole (0) / do not decrease in size such that ambulacra are not "pinched" (1).

Interambulacra

19. Interambulacra: flush or level with paired ambulacra (0) / raised above ambulacra (1).

Periproct

20. In posterior view of the test, the periproct: positioned at the midline (0) / positioned above the midline (1).

Plastron

21. Plates 2a and 2b: asymmetrical (protamphisternous) (0) / symmetrical (mesamphisternous) (1).

Peristome

22. Labrum: does not project over the peristome (0) / projects over the peristome (1).

23. Peristome shape: rounded (0) / pentagonal (1).

24. Peristome: not surrounded by apparent rim (0) / surrounded by apparent rim (1).

25. Peristome orientation: flat (0) / oblique (1) / strongly oblique (2).

Test Shape

26.   From an adapical view, posterior end shape: rounded (0) / truncate (1).

27.   Anterior end in lateral view: has flat angular slope (0) / has inflated curvature (1).

Labrum

28.   Posterior termination of labral plate extends to: 2nd ambulacral plate (0) / 3rd ambulacral

        plate (1) / 4th ambulacral plate (2).

29.   Sternal suture: straight or lightly curved (0) / concave (1).

Measurements

30.   Anterior ambulacra length/ length to ambitus ratio: 0.5–0.55 (0) / .65–.68 (1) / 0.72–1.0

        (2).

31.   Posterior ambulacra length/ length to ambitus ratio: 0.3–0.47 (0) / 0.51–0.60 (1) / 0.65–

        1.0 (2).

32.   Anterior ambulacra length/posterior ambulacra length ratio: 0.9–1.3 (0) / 1.54 –1.9 (1) /

        2.5–2.8 (2).

Character codings for the taxa analyzed are shown below in Table 2.

Table 2. Character state distributions for taxa used in phylogenetic analysis. Missing data is indicated by "?". Character numbers are listed at the top of the table.

										1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	3	3	3
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2
Toxaster retusus	1	0	1	0	0	0	1	1	1	1	0	0	0	0	0	0	0	?	0	1	0	0	0	0	0	1	1	2	1	2	2	0
Heteraster oblongus	1	0	1	0	1	1	0	1	1	1	2	1	1	0	0	0	0	1	0	1	1	0	0	0	0	0	2	0	2	2	2	1
Heteraster texanus	1	0	1	0	0	1	0	1	1	1	2	1	2	0	0	0	0	1	0	1	1	0	0	0	0	1	1	1	0	2	1	1
Washitaster riovistae	1	0	1	0	0	0	1	1	1	1	2	1	2	0	0	0	1	0	0	1	1	1	0	1	1	1	0	1	0	2	1	2
Washitaster wenoensis	1	0	1	0	0	1	0	1	1	1	2	1	2	0	0	0	1	?	0	1	1	0	0	0	0	1	0	?	?	1	0	2
Macraster elegans	1	2	0	0	0	0	0	0	0	2	0	0	2	0	1	0	0	1	1	0	0	0	0	0	1	0	1	2	1	2	2	0
Mecaster fourneli	0	0	2	0	0	0	1	0	0	3	1	0	3	0	0	1	0	0	1	1	1	1	1	0	1	1	1	1	0	2	2	0
Mecaster batnensis	1	2	0	0	0	0	1	0	0	3	1	0	3	0	0	2	0	0	1	1	0	1	0	0	1	1	1	1	1	2	2	0
Mecaster texanus	0	1	1	0	0	0	1	0	1	3	1	0	3	0	0	2	0	0	1	0	1	1	0	0	1	1	1	2	1	2	1	0
Micraster schroederi	1	1	0	0	0	0	1	0	1	2	0	0	2	1	0	0	0	1	1	0	1	1	0	0	2	2	0	0	0	0	0	0
Pliotoxaster comanchei	1	1	0	0	0	0	1	0	0	2	0	0	2	0	1	0	0	1	1	1	0	0	1	0	1	1	1	1	1	2	2	0
Proraster dalli	0	0	1	1	2	0	1	1	0	2	2	0	3	?	0	2	0	0	1	?	?	1	1	1	2	0	0	?	?	2	2	1
Palhemiaster calvini	1	1	1	0	0	0	1	0	0	3	0	0	3	0	0	1	0	?	1	1	0	1	1	1	1	1	1	1	1	2	1	0
Hemiaster bufo	1	1	0	0	1	0	1	0	0	3	1	0	3	0	?	2	0	1	1	1	0	1	0	1	1	0	1	1	1	2	1	0
Hemiaster bexari	1	0	1	0	0	0	1	0	0	3	1	0	3	0	0	2	0	?	1	1	?	1	1	0	1	0	0	?	?	2	1	1
Hemiaster cranium	1	1	0	0	1	0	1	0	0	3	1	0	3	0	0	1	0	0	1	1	0	1	0	1	1	1	1	1	1	1	0	1
Hemiaster estepi	1	2	0	0	0	0	1	0	0	2	1	0	2	0	0	2	0	0	1	1	0	0	0	0	1	0	1	1	1	2	0	1
Hemiaster humphreysanus	1	0	1	0	0	0	1	0	0	3	2	0	3	0	0	2	0	0	1	1	0	1	1	?	0	0	1	1	1	2	1	2
Diplodetus americanus	1	2	0	0	0	0	1	0	0	2	0	0	2	1	0	1	0	1	1	1	0	1	0	1	1	0	1	1	1	2	1	0
Diplodetus parvistella	1	1	0	0	1	0	1	0	0	1	0	?	1	1	0	0	0	0	1	1	?	1	1	0	1	1	0	?	?	0	0	0

Results

  The phylogenetic analysis resulted in a strict consensus of four most parsimonious trees of length 111 steps, consistency index (CI) of 0.41, and retention index (RI) of 0.60 (Figure 1). To assess whether this result might be influenced by the inclusion of relatively incompletely preserved taxa, an additional analysis was run. Two taxa, *Proraster dalli* and *Hemiaster bexari*, which could only be coded for ~ 80–90% of the characters and creating a polytomy, were removed, and a branch and bound analysis was performed again. This resulted in a strict consensus of two trees of length 100 steps, a CI of 0.44, and an RI of 0.61 (Figure 2) that had a topology identical to that of Figure 1, indicating that the result was not influenced by including these incomplete taxa. In terms of tree support statistics, four nodes of the cladogram in Figure 1 were supported by bootstrap values greater than 60%, with 15 nodes supported by jackknife values greater than 60% (with 5 jackknife values above 80%). Bremer support was found for four nodes in the tree.
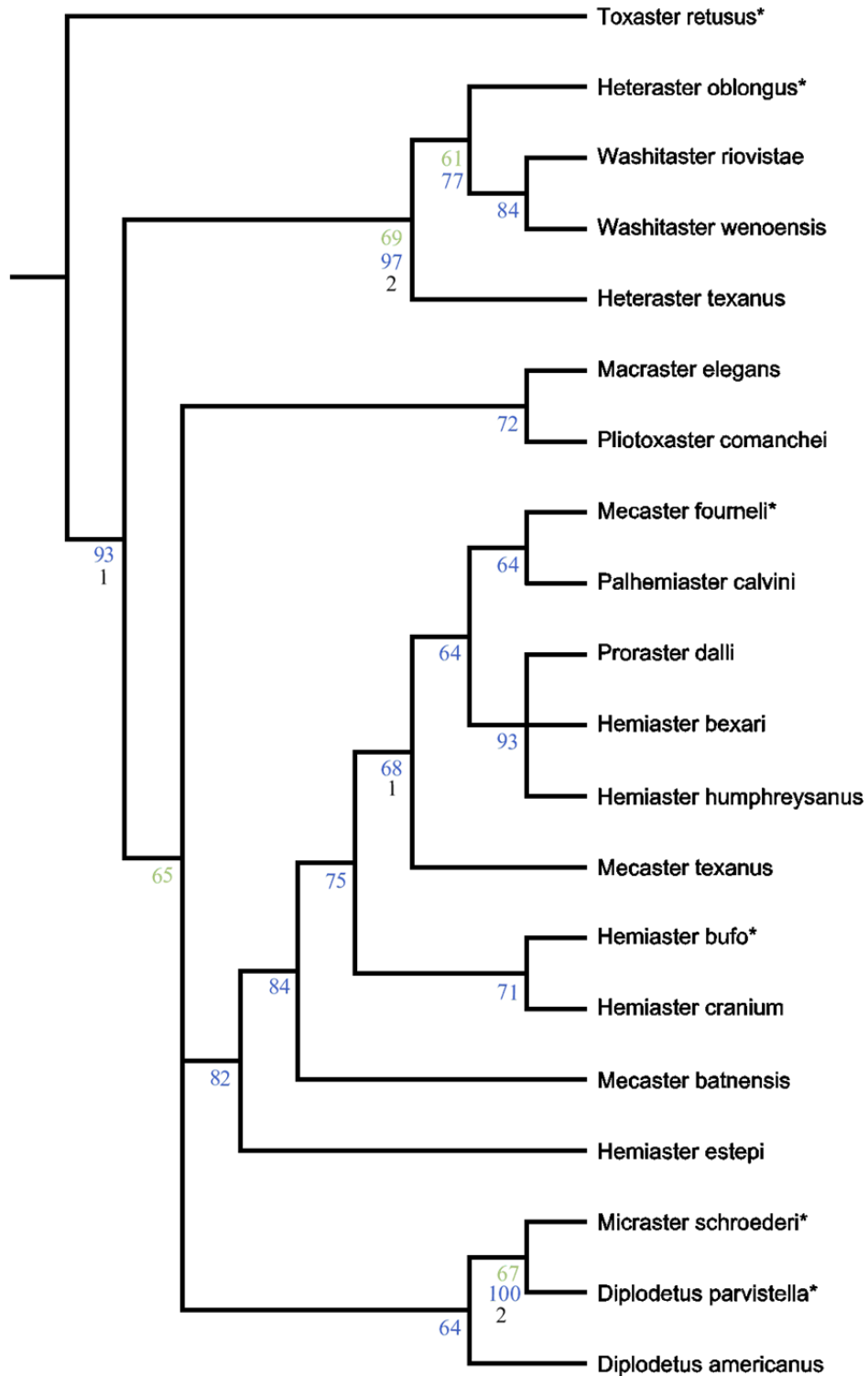
Figure 1. Strict consensus of four most parsimonious trees of length 111 with 20 taxa. Numbers in blue refer to Jackknife support values, numbers in green represent Bootstrap support values, remaining numbers are Bremer support values. Asterisk represents non-North American species.
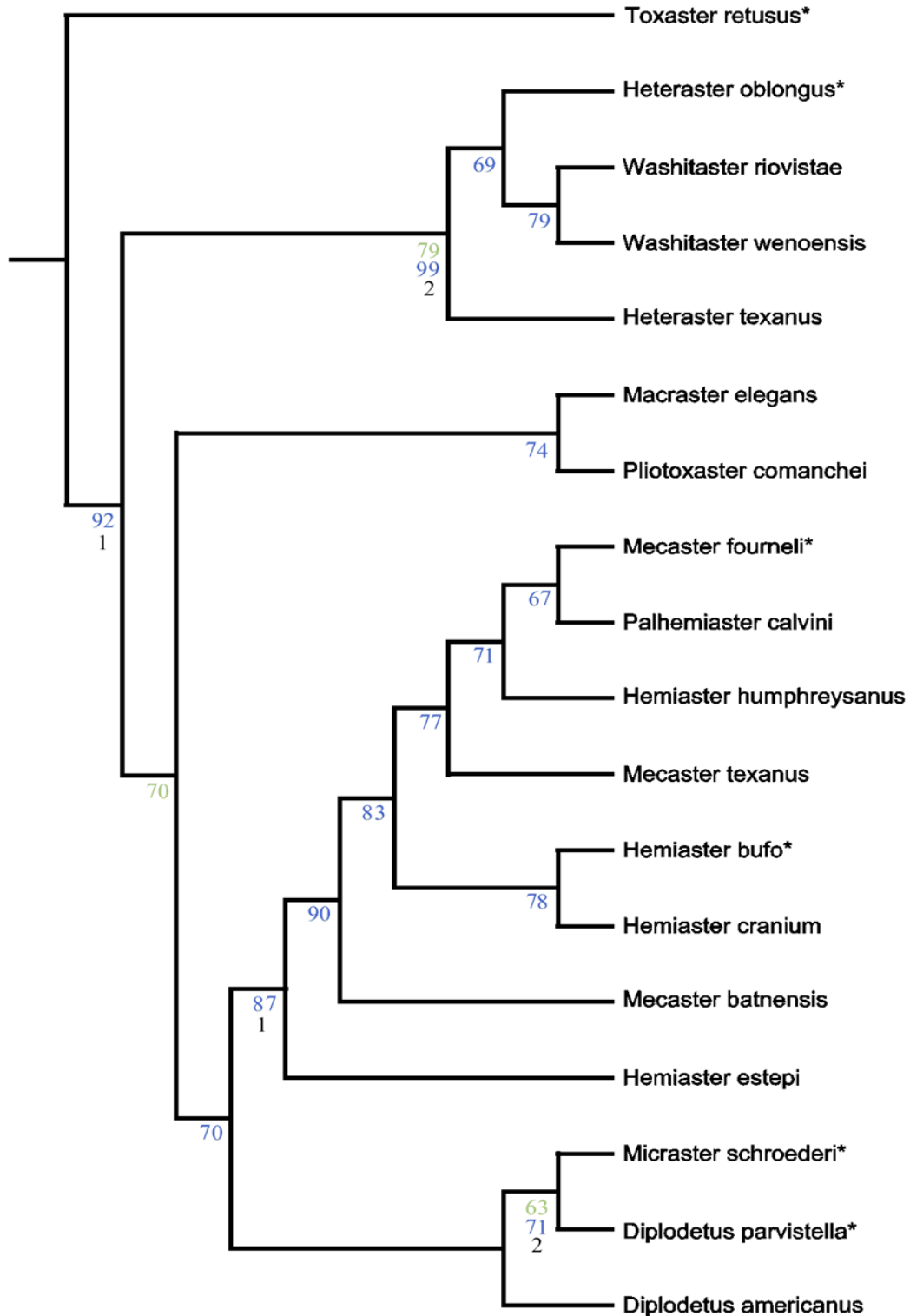
Figure 2. Strict consensus of the two most parsimonious trees of length 100 excluding two taxa (*Proraster dalli, Hemiaster bexari*). Numbers in blue refer to Jackknife support values, numbers in green represent Bootstrap support values, remaining numbers are Bremer support values. Asterisk represents non-North American species.

The analysis suggests several notable relationships relative to traditional groupings and previous analyses. Regarding traditional groupings, the genera *Hemiaster*, *Mecaster*, *Heteraster*, and *Proraster* are paraphyletic or even polyphyletic (see also Smith & Bengston 1991 and Neredeau 1994). To make the classification more compatible with the phylogeny, several taxonomic changes were made, including lumping some species within other genera to produce monophyletic groupings (Figure 3). For instance, *Proraster* is defined herein to contain *P. dalli*, *P. humphreysanus*, and *P. bexari* (Figure 3). In addition, some genera were designated as paraphyletic using the within quotes convention of Wiley (1979). These are: "*Heteraster*" t*exanus*; "*Hemiaster*" *batnensis*; "*Hemiaster*" *texanus*; "*Hemiaster*" *estepi*; and "*Diplodetus*" *americanus* (Figure 3). At this time this seemed preferable to establishing several new monotypic genera, as not all relevant species could be considered in the present analysis. In broad terms, the phylogeny indicates that *Mecaster fournelli* and *Palhemiaster* are closely related, with *Proraster* comprising the sister group of these; a paraphyletic set of species referable to *Hemiaster* and "Hemiaster" comprise several successive lineages sister to these. *Diplodetus* and *Micraster* are also all closely related, as are *Washitaster* and *Heteraster*, and *Pliotoxaster* and *Macraster*. Further, *Washitaster* plus *Heteraster* comprise the sister group to all spatangoids (excluding *Toxaster*).
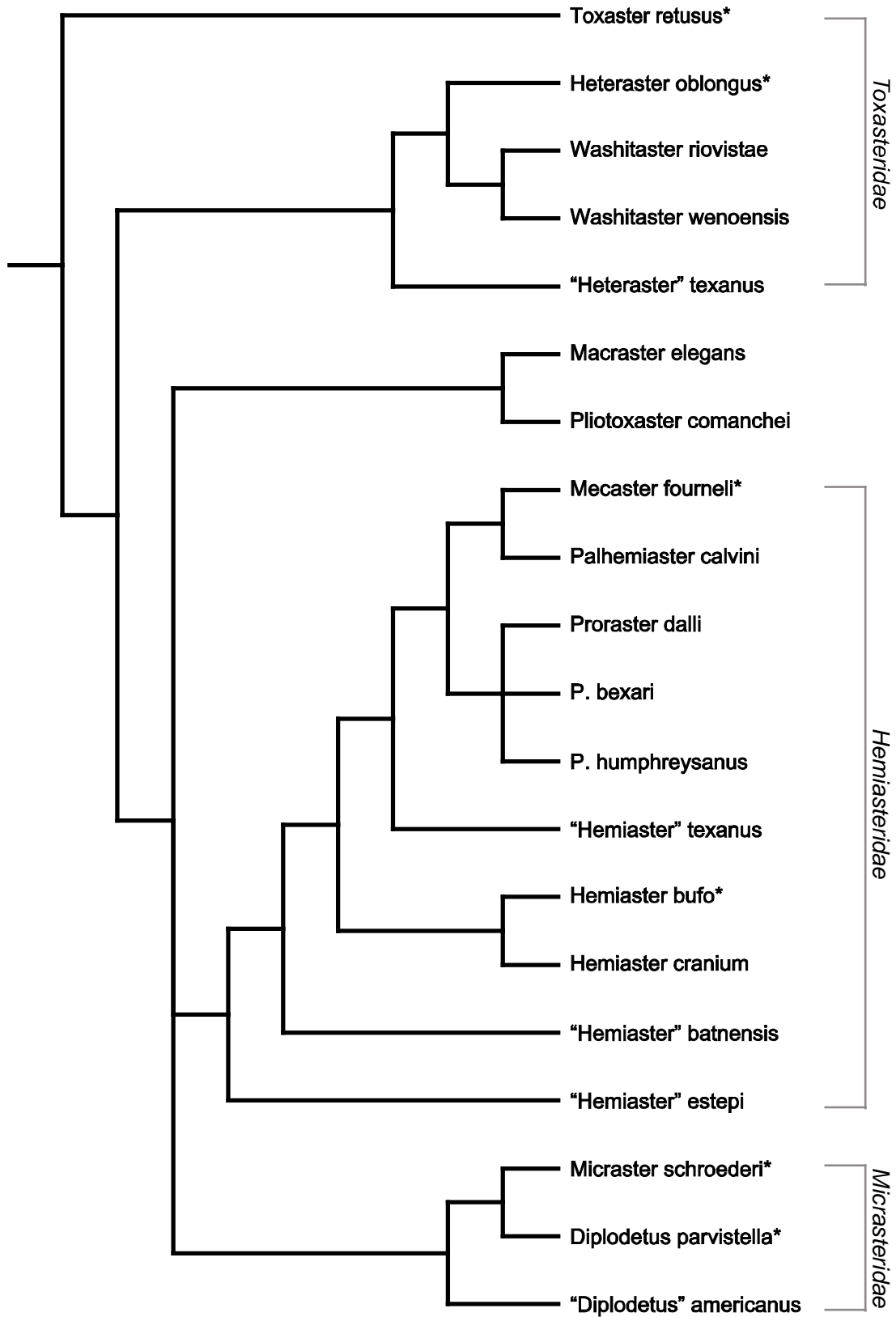
Figure 3. Strict consensus of four most parsimonious trees of length 111 with 20 taxa, with taxonomic changes applied.

Discussion

In general, the phylogenetic results match various aspects of previous interpretations. For instance, *Micraster* and *Diplodetus* had previously been grouped into a Micrasteridae clade due to the shared presence of an ethmophract apical disc and similarly-patterned subanal fasciole (Smith & Stockley 2005), although part of *Diplodetus* was found to be paraphyletic. Several species of *Mecaster* were originally described as *Hemiaster* (Agassiz & Desor 1847; Roemer 1849; Coquand 1862), matching the placement herein of the species within Hemiasteridae.
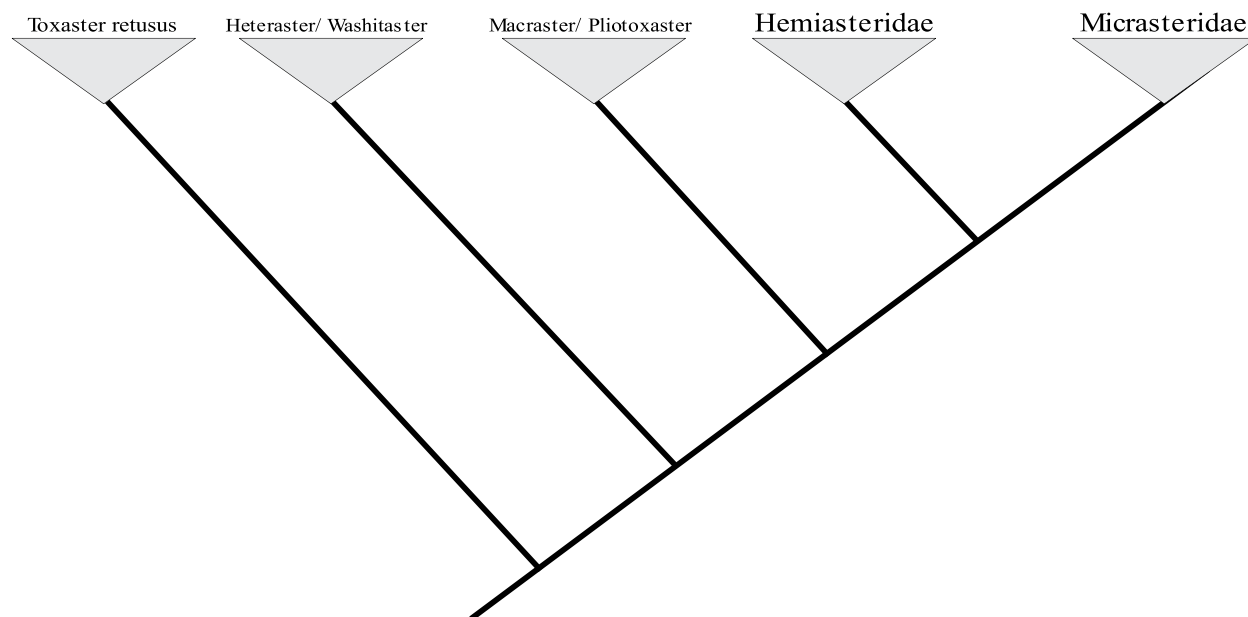

Figure 4. Simplified branching patterns of clades represented in the phylogenetic analysis.

The phylogenetic analysis of Villier et al. (2004) is not directly comparable to the analysis performed herein as they focused on Early Cretaceous taxa and had fewer WIS representatives. However, some similarities emerge between the results retrieved in the present study and the fifty percent majority rule consensus tree they presented. For instance, they also retrieved a monophyletic clade of *Heteraster oblongus*, *"H." texanus*, and *Washitaster riovistae*. In addition, Villier et al. (2004) found that a clade containing *Macraster elegans* was sister to

two clades, one that includes Micrasteridae and the other that includes Hemiasteridae. They did not, however, retrieve *Macraster* as closely related to *Pliotoxaster comanchei* (referred to as *Palhemiaster comanchei* in their study).

Some aspects of the phylogeny (Figure 1) were also in agreement with the phylogeny presented in Stockley et al. (2005), although they included a much broader range of taxa. For instance, they too found *Mecaster* and *Hemiaster* to be closely related, although they did not retrieve a monophyletic Hemiasteridae. They also held *Toxaster* to be the basal member of the spatangoids.

Moving forward, it will be valuable to increase the number of taxa considered in phylogenetic analyses of fossil spatangoids, perhaps through the employment of supertree methods (see Lieberman 2002). In addition, several of the spatangoid taxa found in the WIS have not been revised since their original descriptions in the 1900's so it would be useful to provide detailed taxonomic descriptions and revisions for these.

Chapter 2: Phylogenetic Biogeographic Analysis of WIS Spatangoids

Introduction

In addition to phylogenetic relationships, another focus of this thesis was unraveling the biogeographic patterns within spatangoids. Of special interest is the origins of taxa found in the WIS and determining whether these taxa represent an endemic radiation or instead were derived via invasions from one or more other regions. Several studies of Cretaceous echinoid biogeography have been conducted over the years. For instance, Smith (1984) summarized general patterns of echinoid biogeography (in the absence of a detailed phylogeny) and argued that: during the Cretaceous the present-day Mediterranean region (then Tethys) was a biodiversity hotspot for echinoids; and the group subsequently dispersed to colonize other regions throughout the world. In addition, Neraudeau & Mathey (2000) focused on the biogeography of echinoids found in the Cretaceous of the present day South Atlantic region. Like Smith (1984), they also were unable to incorporate phylogenetic information in their study but posited a migration between the Mediterranean region (Tethys) and parts of Africa and South America. Further, they suggested that both pre-Aptian and Aptian South American spatangoids were closely related to similar-aged species found in the WIS.

Rosen and Smith (1988) and Smith (1992) later rejected the earlier more "narrative" approaches to echinoid biogeography and endorsed phylogenetically-focused biogeographic studies. Rosen and Smith (1988) used parsimony analysis of endemicity (PAE) on Campanian-Maastrichtian echinoids, and found the WIS, in particular a joint region comprising Texas and Mexico, to be the sister region to North Africa plus Europe. Smith (1992) analyzed patterns in Cenomanian echinoids using distance-based methods, cladistic biogeography, and PAE (see Lieberman 2000 for discussion of these various methods). The PAE indicated Brazil and Angola

were closely related biogeographically and sister to the Texas region. Smith's (1992) cladistic

biogeographic analysis indicated that Texas could be sister to western European and northern

African faunas, or in fact part of a cosmopolitan fauna present across the multiple habitats.

Aside from these studies, there has been little research on the biogeography of Cretaceous

spatangoid echinoids, and no previous studies have focused on elaborating biogeographic

patterns at the species level for WIS spatangoids. The purpose of this chapter is to conduct a

biogeographic analysis of Cretaceous Spatangoids of the WIS and infer the timing and overall

nature (i.e. involving vicariance or dispersal or within region differentiation) of biogeographic

events.

Methods

The biogeographic approach utilized follows the method described in Lieberman (2000).

In particular, the species names on the phylogeny presented in Figure 1 were replaced by their

areas of geographic distribution. The following regions were considered: Western Europe

(comprising Portugal, France, Spain, England, Germany, and The Netherlands) [0]; North Africa

(comprising Algeria, Egypt, Libya, Morocco, and parts of the present-day Middle East) [1];

South America (comprising Brazil and Peru) [2]; and North America (comprising Mexico, the

United States, and Canada) [3] (Figure 5). These all represented regions of significant faunal

endemism (including echinoid endemism) during the Cretaceous Period. Further, each of these

regions represent either separate tectonic blocs or broad parts of cratons that were separated from

other such regions by geographic barriers, and they, or similarly defined regions, had also been

identified by Smith (1984). Geographic distributions were determined by a comprehensive

consideration of the literature and museum specimen records. Biogeographic distributions in the

literature were only treated as valid if actual specimens or photographs of specimens could be examined to ground truth taxonomic assignments.

Figure 5. Paleomap of the Late Albian from Scotese (2013). Numbers indicate locations of taxa selected for analyses.[0] represents Western Europe, [1] represents North Africa, [2] represents South America and [3] represents the WIS.

Biogeographic areas were optimized to the nodes of the strict consensus tree of the previous chapter (Figure 3) using the modified version of Fitch (1971) parsimony described in Lieberman (2000). This was done in order to consider how geographic range changed at cladogenetic events. For instance, if range expansion occurred during the transition between adjacent nodes on the tree or adjacent nodes and terminals it was treated as compatible with

some type of dispersal (either traditional or geodispersal *sensu* Lieberman 2000). If range

contraction occurred, it was treated as compatible with vicariance. If range remained unchanged

it was treated as within region diversification which could involve either sympatry or within-

region allopatry. To infer the timing of various biogeographic transitions, information on the

temporal duration of fossil species was also considered. Species were assigned to the resolution

of stage using information from the literature and then the ghost lineage method described in

Norell et al. (1992) was applied.

Results

Biogeographic patterns provide evidence for vicariance within the spatangoids (Figure 6).

For instance, following an initial range expansion by the group from being jointly distributed in

western Europe and north Africa to being jointly distributed in these areas and the WIS during

the Valanginian, there was subsequent vicariance between northern Africa and the WIS &

Western Europe during the Albian along the backbone of the tree and in the clade comprising

Heteraster and *Washitaster*. There is further vicariance between Western Europe and the WIS

within *Heteraster* and *Washitaster*. Another vicariance event occurs in the Campanian associated

with the divergence of the WIS *"Diplodetus" americanus* and the western European *Micraster*
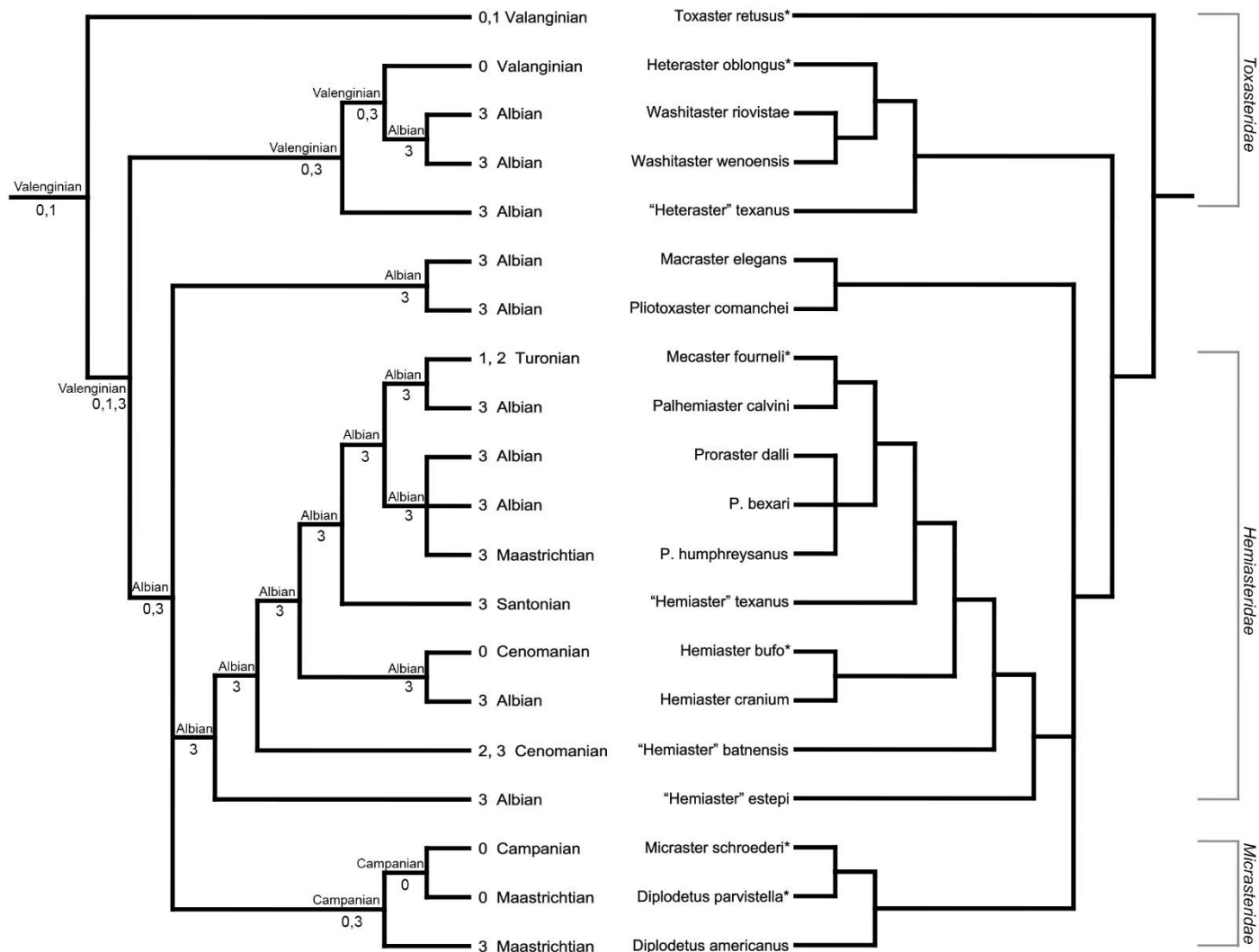
and *Diplodetus parvistella*.

Figure 6. The biogeographic distribution and ages of terminals, along with the biogeographic distribution of ancestral nodes, calculated using the modified version of Fitch parsimony described in Lieberman (2000), and minimum divergence age of nodes, determined using the ghost lineage method described in Norell & Novacek (1992). [0] represents Western Europe, [1] represents North Africa, [2] represents South America and [3] represents the WIS (left). The consensus phylogeny from the previous section is provided for comparison (right)

There also appears to have been range expansion by spatangoids from the WIS into Europe, North Africa and South America, but it is not possible at this time to determine if these comprise geodispersal or traditional dispersal *sensu* Lieberman (2000) because phylogenetic biogeographic information from other groups is not available. For instance, at some time

between the Albian and the Cenomanian there was a range expansion by the lineage leading to *Hemiaster bufo*. There was also a range expansion from the WIS into South America during the Cenomanian associated with the origin of *"Hemiaster" batnensis*. Finally, sometime between the Albian and the Turonian there was a range expansion from the WIS into North Africa and South America associated with the origin of *Mecaster fourneli*.

The rest of the diversification within the clade comprises speciation occurring within the WIS, though at this time it could not be determined whether this involved smaller scale vicariant events within the WIS or actual sympatric differentiation. The pattern of substantial within-region speciation in the WIS suggests that the WIS itself might also have served as another biodiversity hotspot for echinoids, beyond just the Mediterranean (Tethyan) region, at least in the spatangoids.

Discussion

It is clear that sea-level changes would have had a major impact on the biogeography and evolution of marine taxa like echinoids (Smith & Rader 2009), and thus it is highly useful that multiple studies have been conducted that investigated changes in sea level during the Cretaceous (e.g Hallam 1992; Haq 2014). For instance, prominent sea-level changes are associated with the following transgressive-regressive cycles seen in the North American Cretaceous carbonate platform series: the Coahuilan (Valanginian – mid Aptian); the Comanchean (late Aptian – early Cenomanian); and the Gulfian (mid-Cenomanian – Maastrichtian) (Scott 1993; Smith & Rader 2009). The results from the biogeographic analysis presented herein suggest a possible connection between specific transgressive-regressive cycles and patterns of echinoid vicariance and range expansion. For instance, a regression during the Coahuilan series may coincide with the vicariance event that led to the diversification both of,

and within, the WIS "toxasterids", including *Heteraster* and *Washitaster* (Figure 6); the

regression during the Comanchean series may have also led to the vicariance involving the

divergence at the base of all spatangoids excluding the "toxasterids" (Figure 6); another sea-level

drop during the Gulfian series may coincide with Campanian vicariance in the Micrasteridae

(Figure 6). In addition, sea-level rise associated with the Comanchean could account for the

range expansions associated with *Mecaster fourneli*, *Hemiaster bufo*, and *"Hemiaster" batnensis*

(Figure 6). However, ultimately a broader range of marine taxa will need to be considered to see

if these are patterns that consistently emerge in other groups, thereby indicating biogeographic

congruence and an overarching earth history control (e.g. Lieberman 2000), or instead do not,

and then may be related to specific aspects of spatangoid ecology.

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Appendix

All scale bars represent 1cm unless otherwise noted.

Toxaster retusus (Lamarck, 1816) (From Smith & Kroh, 2011)
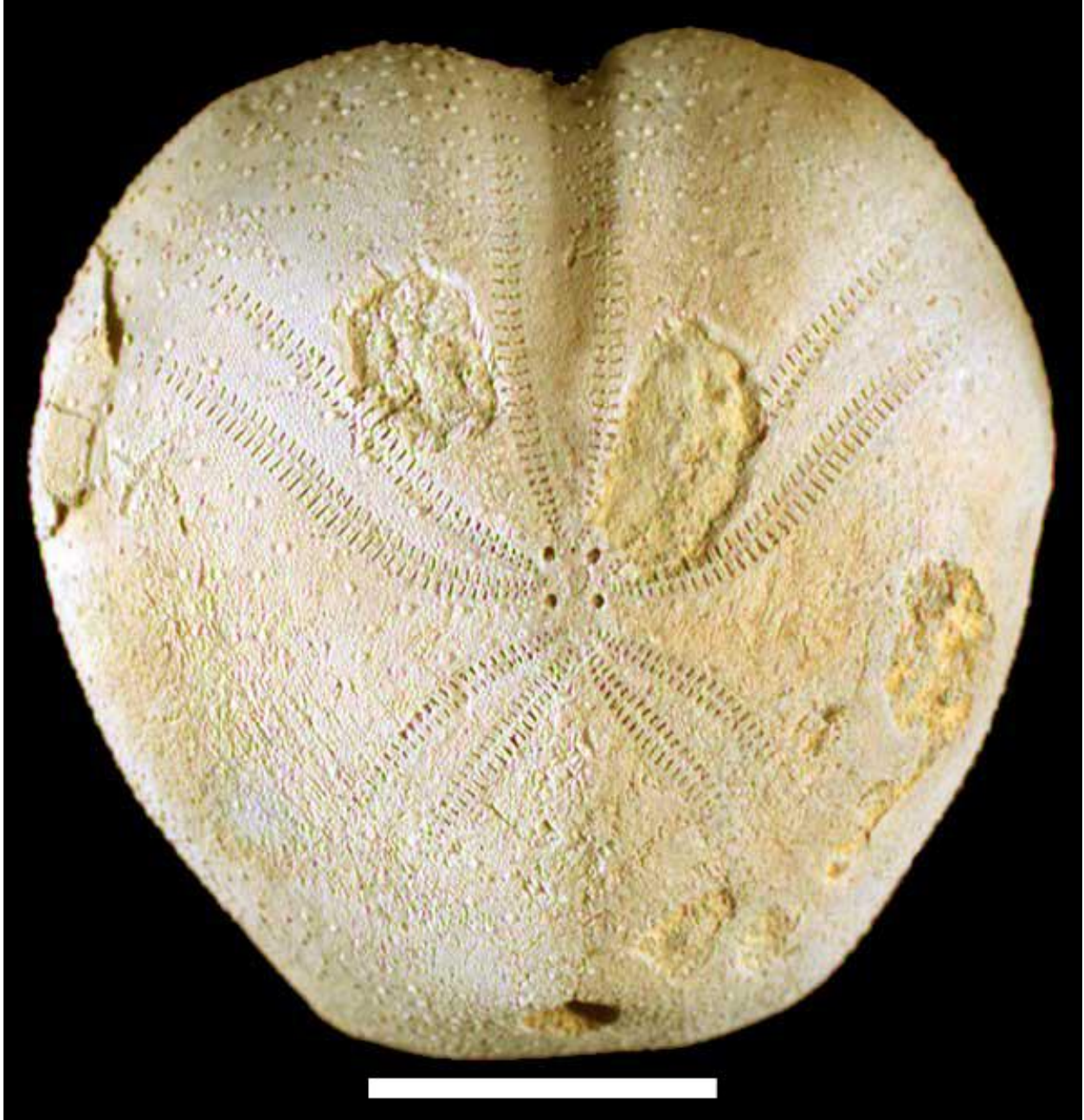
Heteraster oblongus (Brongniart, 1821) (From Smith & Kroh, 2011)

"Heteraster" texanus (Roemer 1849)

UT BEG34165

Washitaster riovistae (Adkins 1920)

UT BEG 21491

Washitaster wenoensis (Adkins, 1920)
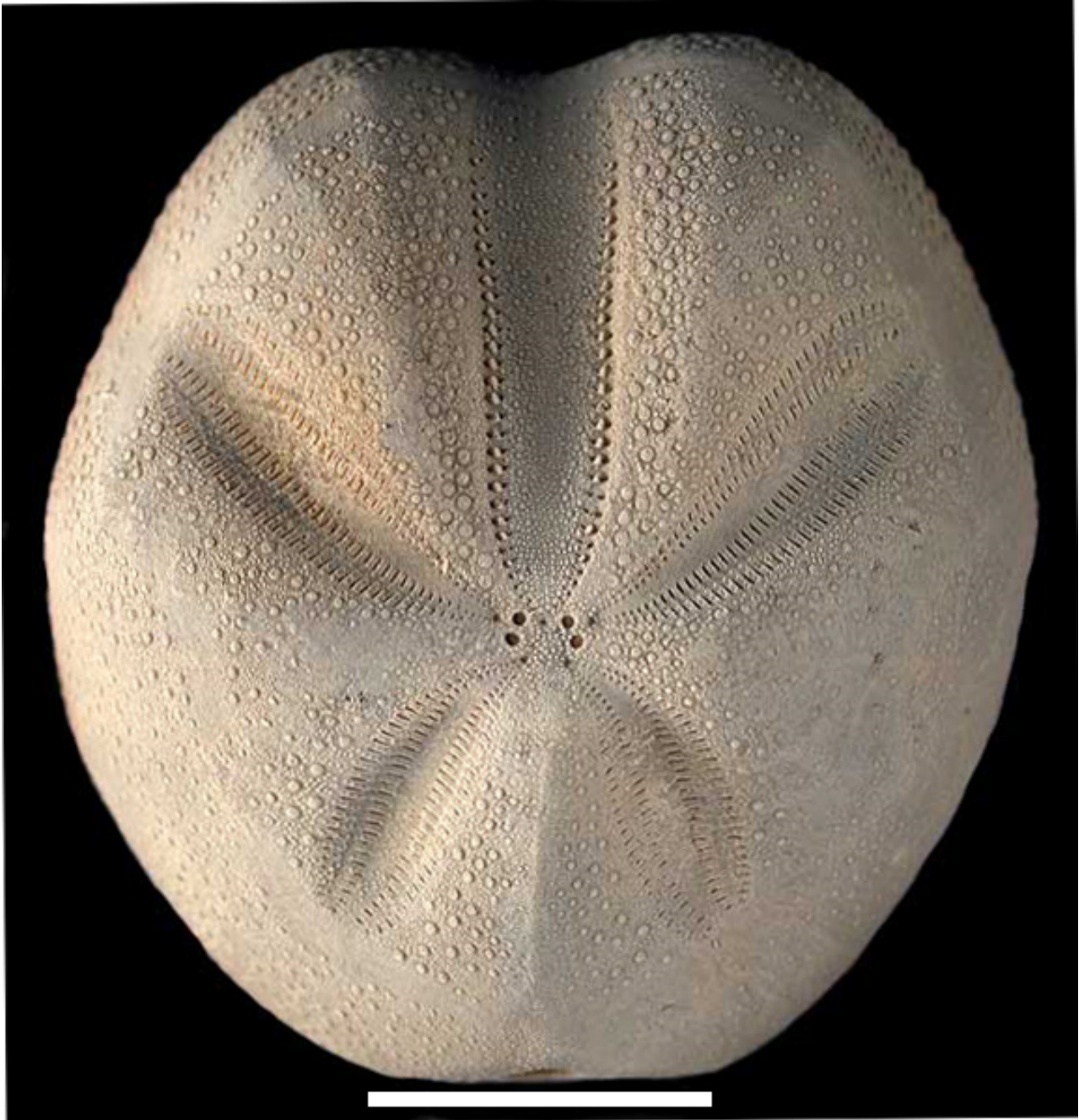
UT BEG 21496

Macraster elegans (Shumard, 1853)

UT BEG34161

Mecaster fourneli (Agassiz & Desor 1847) (From Smith & Kroh, 2011)

"Hemiaster" batnensis (Coquand, 1862)

UT83026

"Mecaster" texanus (Roemer, 1849)

Universität Bonn Texas No org 156

3 mm

Micraster schroederi Stolley, 1892

UT 53845

Pliotoxaster comanchei (Clark, 1915)

USNM PAL 103893

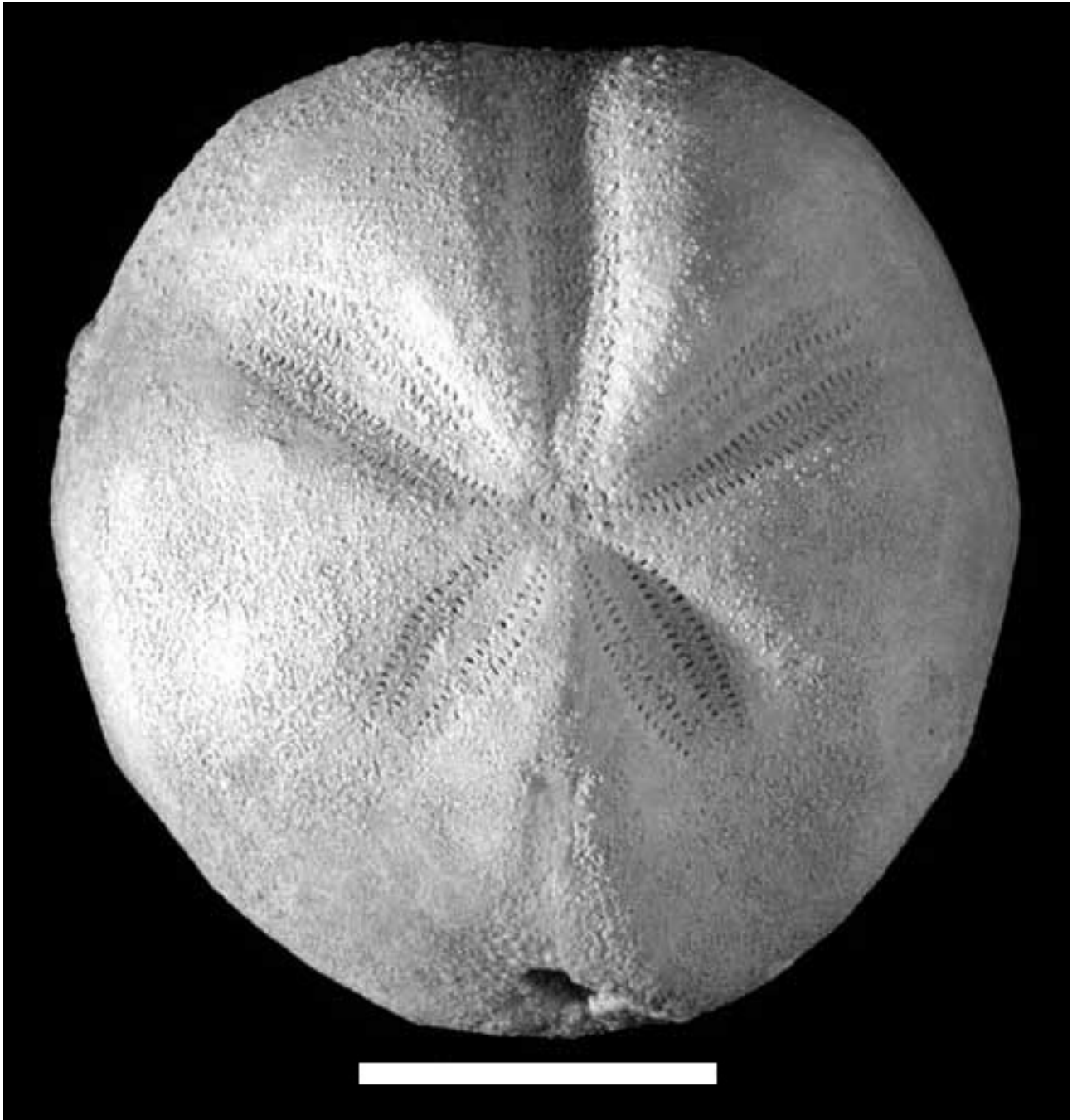*Proraster dalli* (Clark, 1891)

USNM PAL 191114

Palhemiaster calvini (Clark, 1915)

UT BEG21487

Hemiaster bufo (Brongniart, 1822) (From Smith & Kroh, 2011)

Proraster bexari Clark, 1915

USNM PAL 8330

Hemiaster cranium Cooke, 1946

USNM PAL 103890

"Hemiaster" estepi Lucas, 2000

NMMNH P-26515

Proraster humphreysanus Meek & Hayden, 1857
USNM PAL 331

"Diplodetus" americanus Stephenson, 1941

USNM PAL 76285

Diplodetus parvistella Schluter, 1900 (From Smith & Kroh, 2011)