



***Mecaster texanus (Echinoidea)*
from Turonian-Coniacian strata
in the Sergipe-Alagoas Basin, Brazil**

Cynthia Lara de Castro MANSO¹
Wagner SOUZA-LIMA²

Abstract: The spatangoid echinoid *Mecaster texanus* (ROEMER) was first described from the Austin Chalk in Texas (USA). In northeast Brazil, this species was recorded from the Upper Cretaceous (Turonian-Coniacian) Jandaíra Formation in the Potiguar Basin. Here we extend the palaeogeographical distribution of *M. texanus* southwards to the Sergipe-Alagoas Basin, where this species occurs in the Turonian-Coniacian Cotinguiba Formation. A key to identification of spatangoids from the Cretaceous-Cenozoic sequence at Sergipe-Alagoas is added and considerations about other spatangoid species from that basin are presented.

Key-words:

- Echinodermata;
- Spatangoïda;
- Crétaceus;
- South America;
- comparison

Citation: MANSO C.L. de C. & SOUZA-LIMA W. (2017).- *Mecaster texanus (Echinoidea)* from Turonian-Coniacian strata in the Sergipe-Alagoas Basin, Brazil.- *Carnets Geol.*, Madrid, vol. 17, no. 11, p. 221-234.

Résumé : Mecaster texanus (Echinoidea) du Turonien-Coniacien du Bassin de Sergipe-Alagoas, Brésil.- *Mecaster texanus* (ROEMER) a été décrit à l'origine dans les calcaires d'Austin au Texas (États-Unis). Au Brésil, cette espèce n'était jusqu'à présent connue que dans la Formation Jandaíra du Crétacé supérieur (Turonien-Coniacien) dans le bassin Potiguar (Nord-Est du Brésil). Cette étude étend paléogéographiquement sa distribution plus au Sud jusqu'au bassin de Sergipe-Alagoas, où l'espèce a été identifiée dans la Formation Cotinguiba du Crétacé supérieur (Turonien-Coniacien). Une clé pour aider à l'identification des spatangoïdes des séries crétacées et tertiaires de ce bassin est proposée. Une dernière partie présente quelques considérations sur d'autres espèces de spatangoïdes rencontrées dans ce bassin.

Mots-clefs :

- Echinodermata ;
- spatangoïdes ;
- Crétacé ;
- Amérique du Sud ;
- comparaisons

Introduction

Echinoids from the Sergipe-Alagoas Basin have been studied for over one hundred years since WHITE (1887) described the first specimens from Sergipe. MAURY (1925) identified numerous

new species for the Albian-Turonian sequence, while BRITO and RAMIREZ (1974) and BRITO (1980, 1981a, 1981b, 1981c) reviewed and reassigned many species from this basin. SMITH (*in* SMITH & BENGTSON, 1991) published a detailed taxonomic review of Albian-Coniacian echinoids from north

¹ Universidade Federal de Sergipe, Departamento de Biociências, Campus Prof. Alberto Carvalho, Av. Olímpio Campos s/nº, Itabaiana, 49500-000, Sergipe (Brazil)
cynthialaramanso@gmail.com

² Fundação Paleontológica Phoenix, Rua Geraldo Menezes de Carvalho, 218, Suissa, 49050-360, Aracaju, Sergipe (Brazil)
wagner@phoenix.org.br

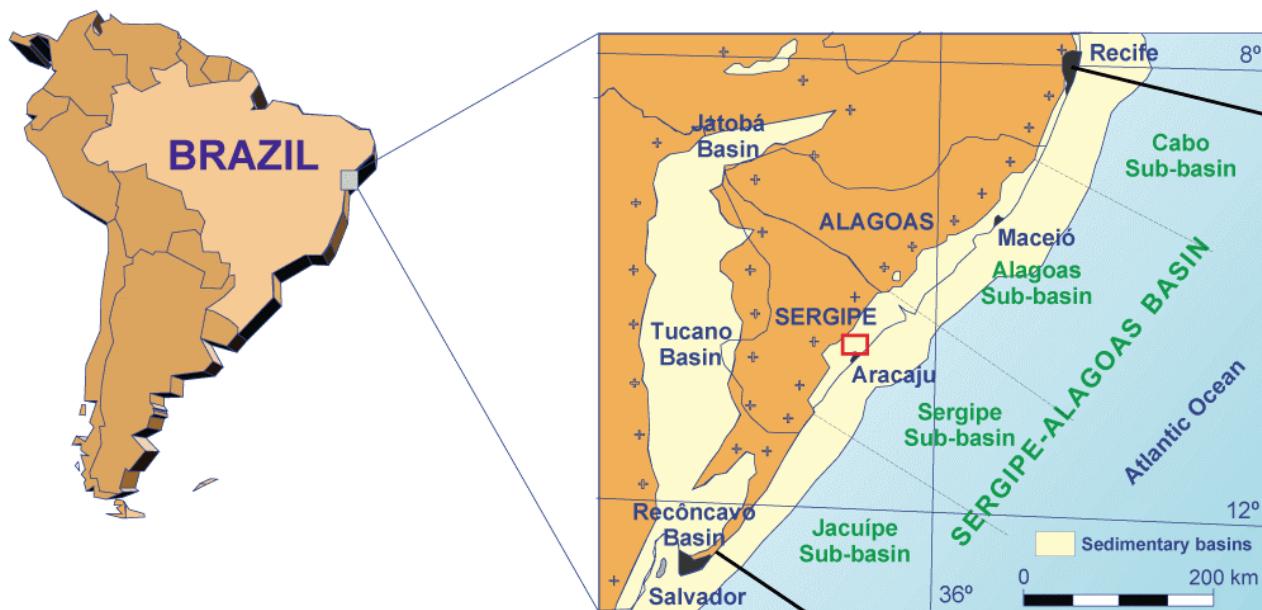


Figure 1: Location map of the Sergipe-Alagoas Basin in northeast Brazil (Souza-LIMA et al., 2002). The red rectangle indicates the map of Figure 4.

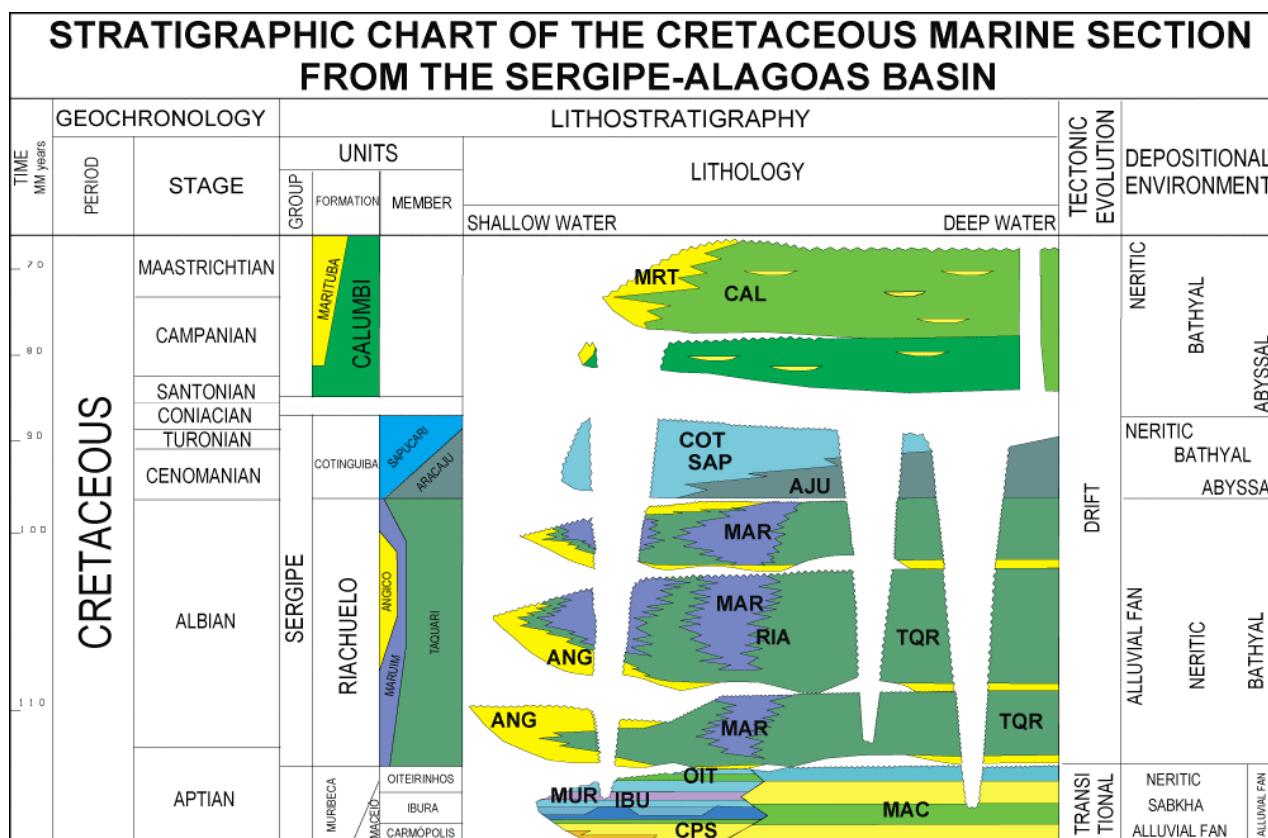


Figure 2: Stratigraphic chart of the marine Cretaceous sequences in the Sergipe-Alagoas Basin (adapted from FEIJÓ, 1995).

east Brazil, including those from Sergipe. MANSO (2003, 2011, 2014), MANSO and Souza-LIMA (2003a, 2003b, 2005, 2011, 2012), MANSO and ANDRADE (2008), and MANSO and LEMOS (2008) studied echinoids mainly from the Aptian-Albian sequence, and established new stratigraphic

distributions, recorded new occurrences and erected new species.

A recent study of echinoids of the genus *Meesteraster* from the Sergipe-Alagoas Basin housed in the Fundação Paleontológica Phoenix collections (Aracaju, Sergipe, Brazil) has resulted in the re-



cognition of some species whose apical system supports their confident assignment to *Mecaster texanus* (ROEMER, 1849), a species previously unknown from this part of Brazil. This new record for the Turonian-Coniacian sequence of the Sergipe-Alagoas Basin is discussed in the present paper, which also focuses on its ontogeny and paleoenvironmental distribution.

Geological setting

The Sergipe-Alagoas Basin, located in the coastal region of the states of Sergipe and Alagoas in northeast Brazil (Fig. 1), features one of the most complete outcrops of Cretaceous sedimentary sequences on either side of the South Atlantic. Its Aptian-Coniacian sequence records a broad carbonate platform that developed in response to a marine ingression that culminated with the establishment of the South Atlantic Ocean during the breakup of Gondwana from the Early Cretaceous onwards. The Aptian-Albian Ria-chuelo Formation represents deposition on a shallow, mixed siliciclastic-carbonate platform. The Cenomanian-Coniacian Cotinguiba Formation documents the drowning of the previous platform, currently recorded by deeper facies, as subsequent tilt of the basin led to erosion of the shallower portions of this sequence (SOUZA-LIMA, 2006).

The material studied comes from the uppermost portion of the Cotinguiba Formation, which is dated as Turonian-Coniacian on the basis of abundant ammonites from throughout the section (BENGTON, 1983) (Fig. 2).

Material and methods

The specimens studied are housed in the fossil echinoderm collections of the Fundação Paleontológica Phoenix (FPH), Aracaju (Sergipe, Brazil). For identification of the taxon studied, a series of biometric analyses of tests were performed: L = test length; W = test width; H = test height; ppalIII = number of differentiated pore-pairs in the ambulacrum III; Lapp = length of anterior paired petals; Lppp = length of posterior paired petals (Fig. 3).

The locality description follows the pattern adopted by BENGTON (1983, pp. 30-31) for the Sergipe-Alagoas Basin, Brazil. The co-ordinates were obtained from the Córrego Alegre datum and rounded off to the nearest 50 metres. UTM co-ordinates are referenced to the central 39° meridian. The code after the location identifies the outcrop on the map (Fig. 4).

Kcsp = Cotinguiba Formation, Sapucari Member

Cajaíba 3 (CJ-03): UTM 8 801 550N/705 700E. Topographical map sheet: SC.24-Z-B-IV

Aracaju. Geological map sheet: SC.24-Z-B-IV-4 Aracaju.

Quarry facing east. Altitude c. 5-20 m.

Kcsp: "Massive, yellowish and brown-grey Laranjeiras limestones with abundant echinoids" (BENGTON, 1983).

References: Probably "Jiquy" of WANDERLEY (1938: 49) and "Pedreira do Jiqui" of BRITO (1980: 572, 575; 1981c: 409).

Cajaíba 7 (CJ-07): UTM 8 801 300N/705 250E. Topographical map sheet: SC.24-Z-B-IV Aracaju. Geological map sheet: SC.24-Z-B-IV-4 Aracaju.

Quarry facing east. Altitude c. 10-20 m.

Kcsp: "Massive, cream and blue-grey Laranjeiras limestones. Large ammonites locally abundant" (BENGTON, 1983).

Mata 11 (MAT-11): UTM 8 799 350N/701 500E. Topographical map sheet: SC.24-Z-B-IV Aracaju. Geological map sheet: SC.24-Z-B-IV-4 Aracaju.

Quarry facing west. Altitude c. 20-30 m.

Kcsp: Hard, cream mudstones, locally with abundant echinoids and inoceramids.

References: "Seção exposta em pedreira ativa com cerca de 110m no Município de Nossa Senhora do Socorro" (ANDRADE, 2005; MANO & ANDRADE, 2008).

Mucuri 6 (MUC-06): UTM 8 796 750N/700 050E. Topographical map sheet: SC.24-Z-B-IV Aracaju. Geological map sheet: SC.24-Z-B-IV-4 Aracaju.

Quarry facing southwest. Altitude c. 50-60 m.

Kcsp: "Cream Laranjeiras limestones, locally with abundant ammonites" (BENGTON, 1983).

Mucuri 15 (MUC-15): UTM 8 796 550N/699 800E. Topographical map sheet: SC.24-Z-B-IV Aracaju. Geological map sheet: SC.24-Z-B-IV-4 Aracaju.

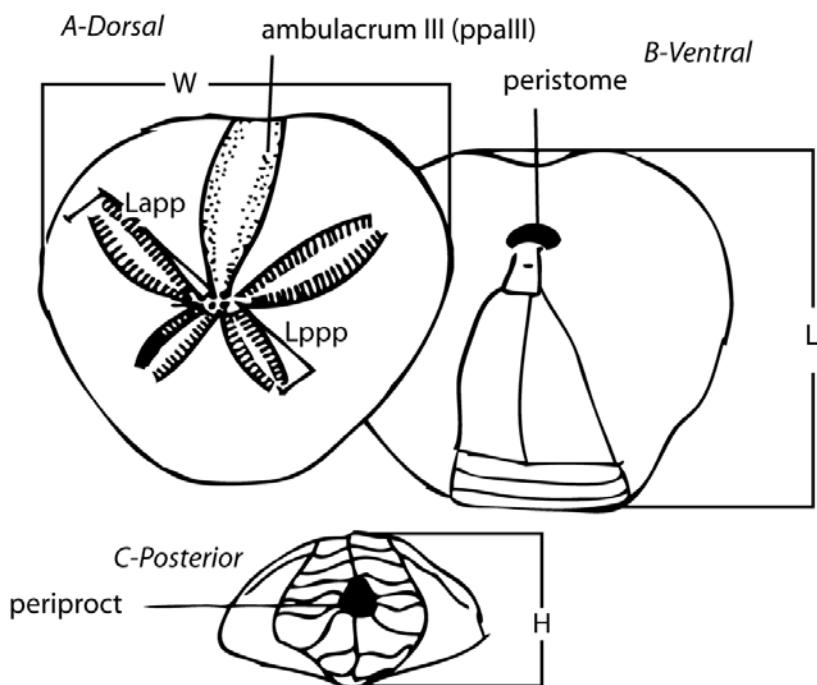
Quarry on hillside facing east. Altitude c. 30-35 m.

Kcsp: "Coquinoid, yellowish Laranjeiras limestones" (BENGTON, 1983).

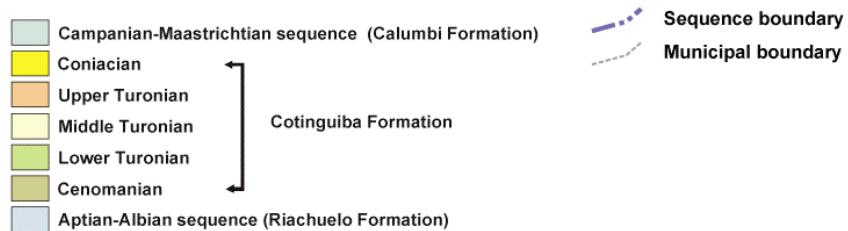
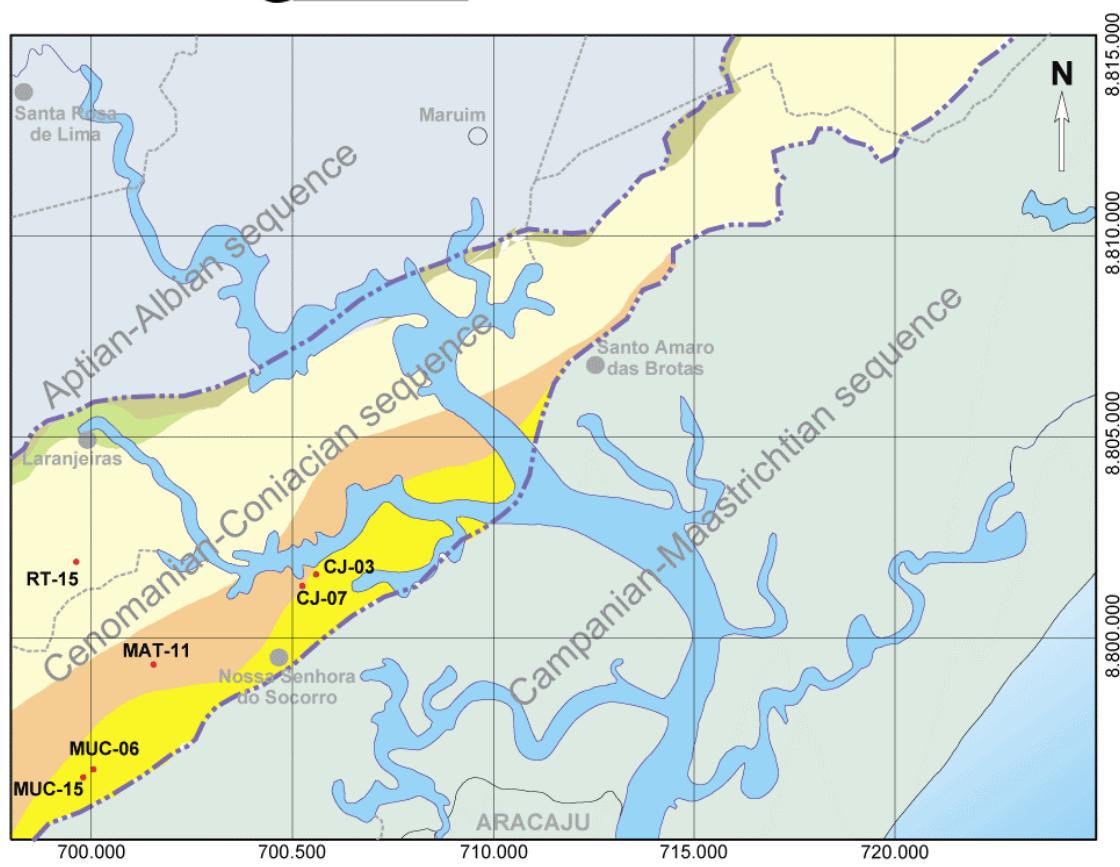
Retiro 15 (RT-15): UTM 8 800 400N/699 450E. Topographical map sheet: SC.24-Z-B-IV Aracaju. Geological map sheet: SC.24-Z-B-IV-4 Aracaju.

Quarry facing northwest. Altitude c. 20-40 m.

Kcsp: "Dominantly massive, cream and blue-grey Laranjeiras limestones with several discontinuity surfaces, some of which are underlain by breccia banks. Also nodular and coquinoid Laranjeiras limestones. Inoceramid bi-valves and small ammonites locally abundant" (BENGTON, 1983).



◀ **Figure 3:** Dimensions of tests of *Mecaster texanus* (ROEMER, 1849).





Mecaster from the Sergipe-Alagoas Basin

Three species of the genus *Mecaster* have been recorded from the Sergipe-Alagoas Basin (SMITH *in* SMITH & BENGTON, 1991), namely *Mecaster batnensis* (Cenomanian-Turonian), *M. founneli* (Turonian-Coniacian) and *M. africanus* (Turonian). According to SMITH, *M. batnensis* usually occurs as a small, widely distributed form in the Cenomanian deposits of the Sergipe-Alagoas Basin. Forms in the mid-Turonian, here called "transitional *Mecaster batnensis*", are characterised by a greater number of pore pairs in ambulacrum III (SMITH *in* SMITH & BENGTON, 1991). The apical system plates' arrangement of these so-called transitional forms is nevertheless similar to that observed in Cenomanian *M. batnensis*, in which the madreporite separates the posterior genitals I and IV, but not the posterior oculars 1 and 5. *Mecaster founneli* differs in having a larger number and narrower plates in ambulacrum III where the two pores of each pair are more closely spaced, and a madreporite separates the two posterior ocular plates. As SMITH noted, they probably form an evolutionary lineage (see also HOOK & COBBAN, 2017). Finally, *Mecaster africanus* stands out for its greater height than in the other species, with more rectilinear distally open petals, and with madreporite not inserted between the posterior ocular plates.

Systematic palaeontology

Phylum Echinodermata BRUGUIÈRE, 1791

Class Echinoidea LESKE, 1778

Cohort Irregularia LATREILLE, 1825

Superorder Atelostomata VON ZITTEL, 1879

Order Spatangoida CLAUS, 1876

Suborder Hemiasterina FISCHER *in* MOORE, 1966

Family Hemiasteridae H.L. CLARK, 1917

Genus *Mecaster* POMEL, 1883

Mecaster texanus (ROEMER, 1849)

Synonymy:

- 1849 *Hemaster texanus* ROEMER, p. 77, 393.
1852 *Hemaster texanus* ROEMER - ROEMER, p. 78, 85, Pl. 10, fig. 4 a-c.
1893 *Hemaster texanus* ROEMER - CLARK, p. 86, Pl. 47, fig. 1a-i.
1915 *Hemaster texanus* ROEMER - CLARK & TWITCHELL, p. 94, Pl. 49, fig. 1a-j.
1925 *Hemaster sancti-sebastiani* MAURY, p. 569, Pl. 24, fig. 13.
1928 *Hemaster texanus* ROEMER - ADKINS, p. 299, Pl. 34, figs. 4-5.

- 1953 *Hemaster texanus* ROEMER - COOKE, p. 33, Pl. 13, figs. 1-4.
1955 *Hemaster texanus* ROEMER - COOKE, p. 109, Pl. 29, figs. 5-10.
1964 *Hemaster catandubensis* MAURY - BEURLEN, p. 157, Pl. 20, figs. 118 a-b, 120 a-b.
1966 *Hemaster sancti-sebastiani* MAURY - BEURLEN, p. 463.
1991 *Mecaster texanum* (ROEMER) - SMITH *in* SMITH & BENGTON, p. 13.
2003 *Hemaster sanctisebastiani* MAURY, 1925 - CASSAB, p. 75.
2003 *Mecaster texanum* (ROEMER, 1852) - CASSAB, p. 76.
2013 *Mecaster texanum* (ROEMER, 1852) - OLIVEIRA *et al.*, p. 11, Figs. 7 A-C, 9 A-I.

Type: *Hemaster texanus* ROEMER, 1849, from the Austin Chalk at the New Braunfels waterfall of the Guadalupe River (ADKINS, 1928, p. 299).

Material: FPH-1457-I; FPH-1500-I; FPH-1887-I; FPH-1888-I; FPH-1889-I; FPH-1890-I; FPH-1891-I; FPH-1892-I; FPH-1955-I.

Localities: Cajaíba 3, Cajaíba 7, Mata 11, Mucuri 6, Mucuri 15 and Retiro 15.

Diagnosis: The peristome is small and surrounded by a well-marked lip. Naked pouches in the interambulacral regions adjacent to the peristome. The apical disc is very elongate, and the madreporite is large and strongly separates the posterior ocular plates (modified from SMITH *in* SMITH & BENGTON, 1991).

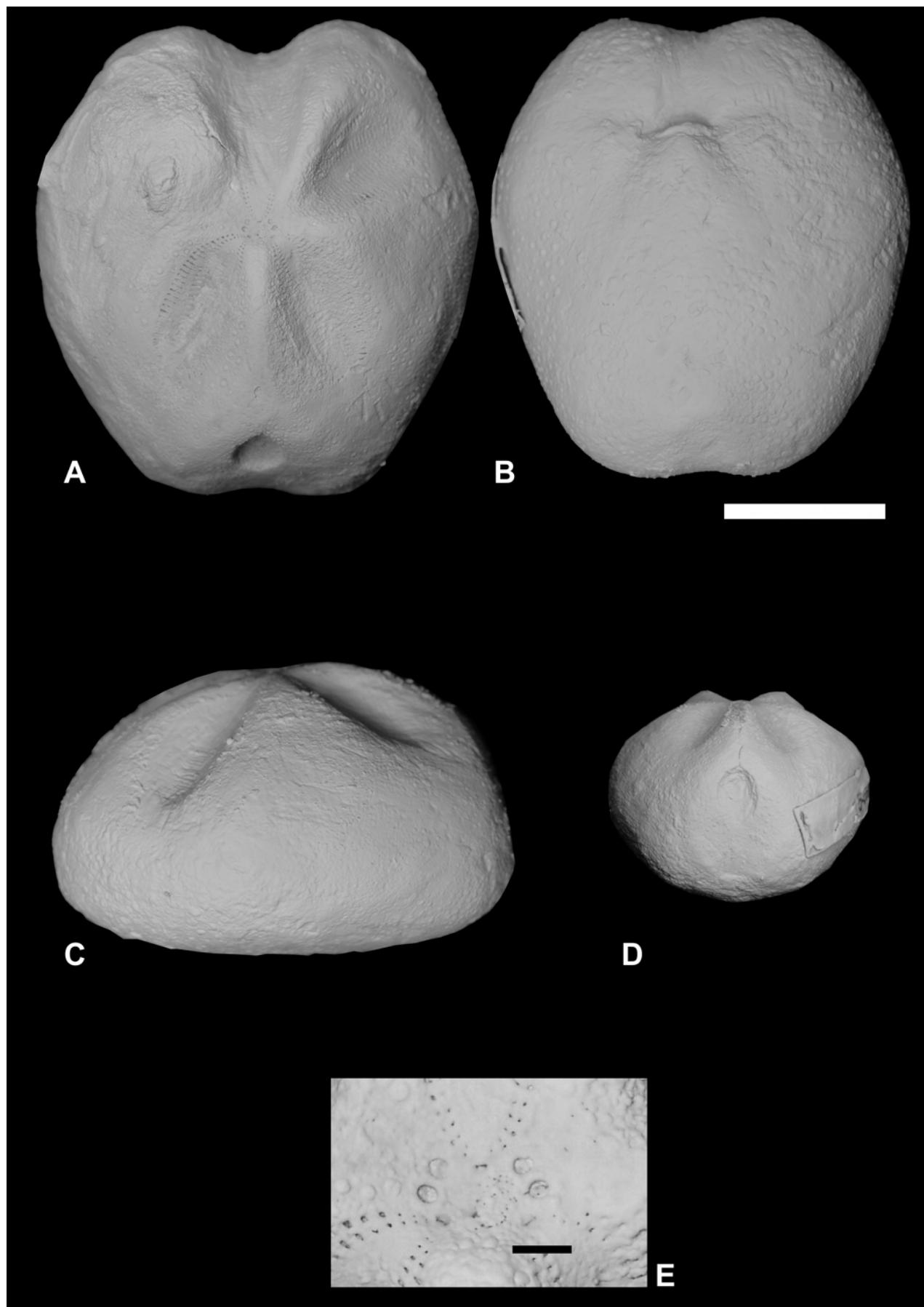
Description (based on FPH-1890-I): test longer than wide, measuring 26.7 mm in length, 25.0 mm in width and 17.5 mm in height, with rounded anterior. The posterior side is inclined so that the periproct is visible from above (Fig. 6.C). The tallest point of the test is just behind the apical plates. A narrow peripetalous orthofasciole can be observed around the petals.

The apical disc, tetrabasal and ethmolytic, is off-centre and transversely wide (Figs. 7.D, 8; Table 1). Genital plate 4 is just in contact with the madreporite and well separated from genital plate 1 (e.g., specimen FPH-1955-I; see Fig. 5.E). The posterior ocular plates are widely separated by the madreporite so that occasionally they go beyond the ocular plates and touch the other plates (Fig. 7.C, E).

The frontal ambulacrum is relatively broad and sunken. There are 35 rounded pore pairs with elevation raised surface between them (Fig. 6.C).

Petals are sunken, and almost closed at the end. There are 39 pore pairs in the anterior pair, 11 mm in length, and 30 pore pairs in the posterior petals, 8 mm in length. The petal pores are elongated and slit-like in both series.

The periproct is small and almost oval in outline and located longitudinally in an elevated position at the posterior end (Fig. 6.C). This feature is well preserved in specimen FPH-1888-I (Fig. 5.D).





◀ **Figure 5:** *Mecaster texanus* (ROEMER) from the Sergipe-Alagoas Basin : A. Dorsal view (FPH-1955-I) ; B. Ventral view (FPH-1457-I); C. Lateral view (FPH-1457-I) ; D. Posterior view (FPH-1888-I) ; E. Detail of apical plating (FPH-1955-I). Scale bar 10 mm (a-d) and 1 mm (e).

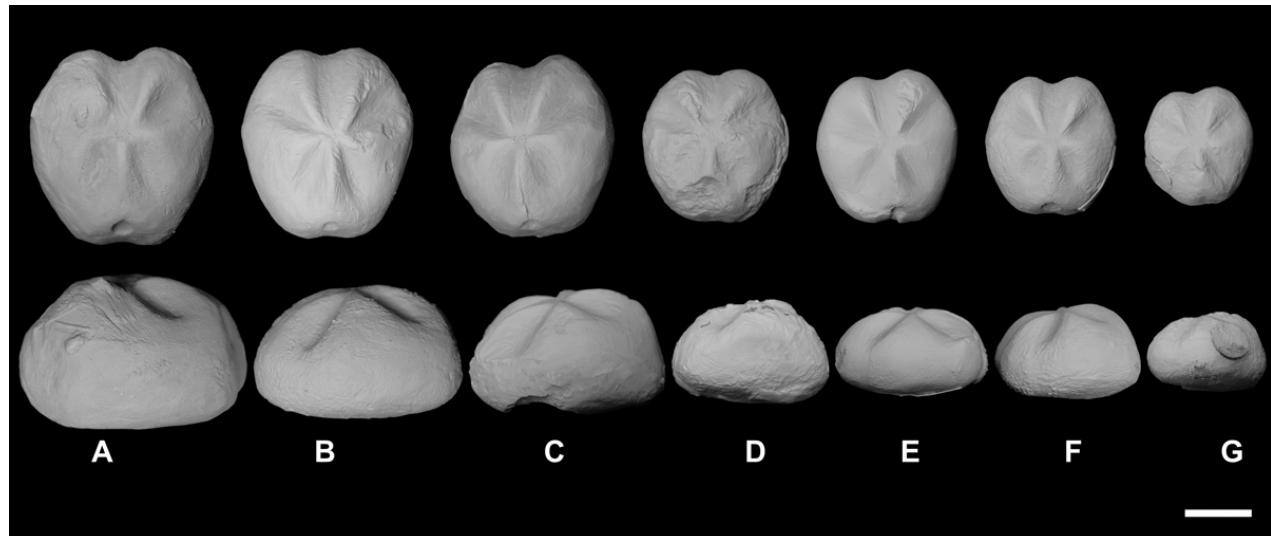


Figure 6: Ontogenetic series of tests of *Mecaster texanus* (ROEMER) from the Sergipe-Alagoas Basin (from larger to smaller, A-G): A (FPH-1955-I), C (FPH-1890-I), D (FPH-1889-I), F (FPH-1888-I), G (FPH-1891-I) (Coniacian); B (FPH-1457-I), E (FPH-1500-I) (upper Turonian). Scale bar 10 mm.

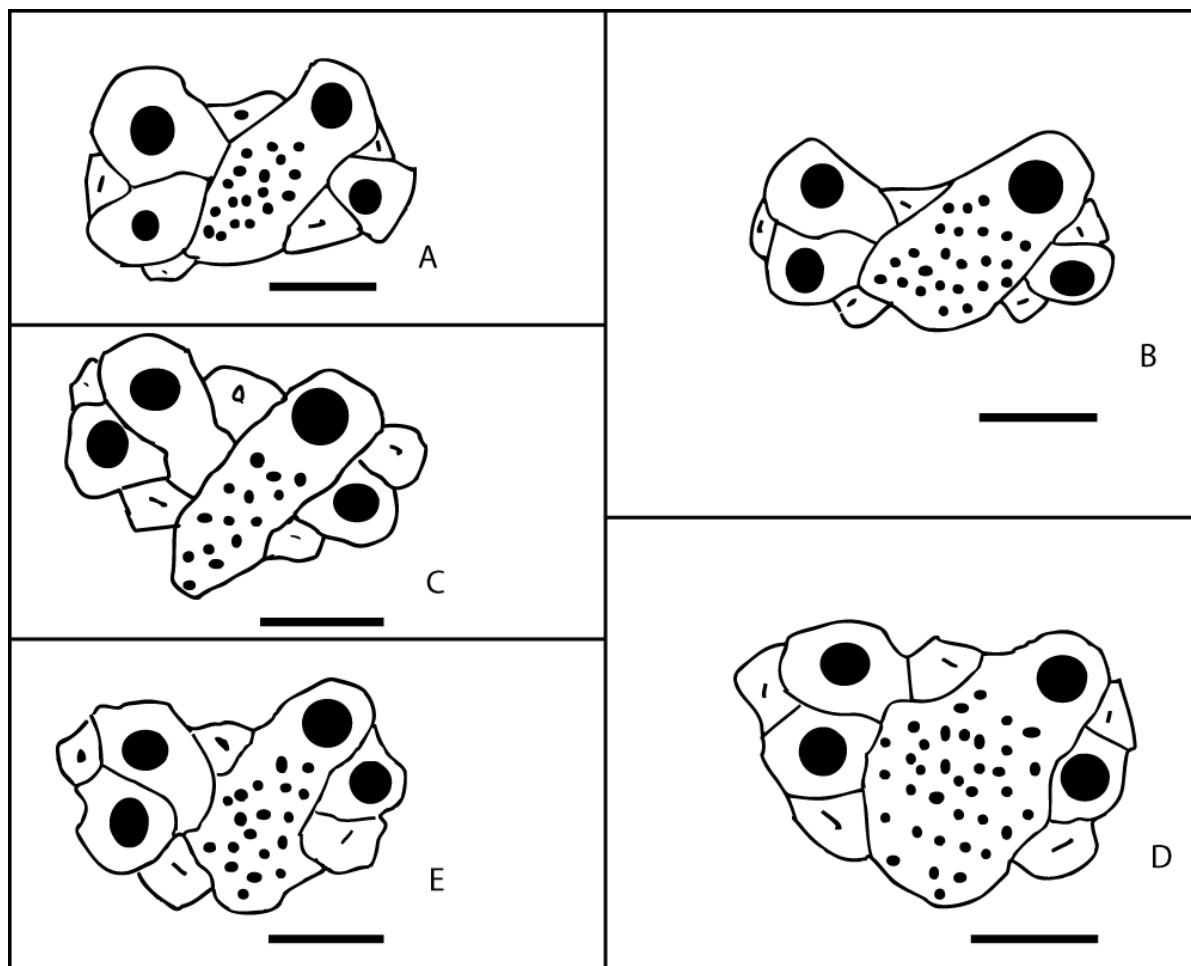


Figure 7: Line drawings of the apical disc of *Mecaster texanus* (ROEMER) from the Sergipe-Alagoas Basin, arranged according to increasing test length: A. FPH-1891-I (test length 16.2 mm), B. FPH-1888-I (21.0 mm); C. FPH-1889-I (23.0 mm), D. FPH-1890-I (26.7 mm); E. FPH-1955-I (30.0 mm). Scale bars 1 mm.

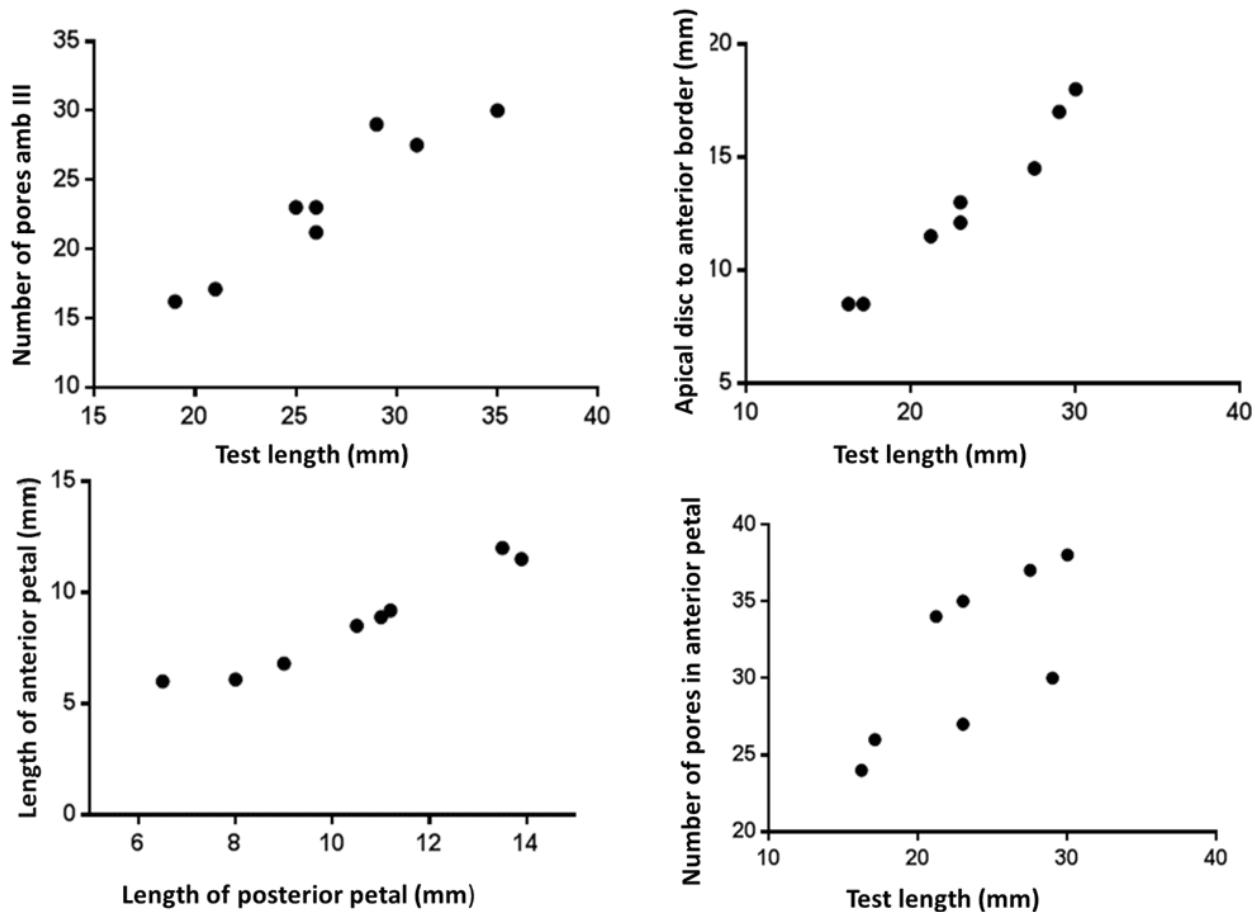


Figure 8: Biometric data of selected specimens ($n = 8$) of *Mecaster texanus* (ROEMER) from Turonian-Coniacian the Sergipe-Alagoas Basin.

The peristome is not preserved in specimen FPH -1890-I, but in FPH-1457-I a well-marked lip is visible around the peristome (Fig. 5.B).

Stratigraphical and geographical distribution: Upper Cretaceous Austin Chalk, Anacacho Limestone and Taylor Marl in Texas (United States;

COOKE, 1953, 1955); upper part of the Napo Series of Late Cretaceous age in Ecuador (COOKE, 1953, 1955); Jandaíra Formation, Potiguar Basin (Turonian-Coniacian) (OLIVEIRA *et al.*, 2013); and Cotinguiba Formation, Sergipe-Alagoas Basin (Turonian-Coniacian) in the present paper.

Table 1 - Biometric data of *Mecaster texanus* (ROEMER). W - Width; H - Height; L - Length; PAIII - Number of differentiated pore-pairs in the ambulacrum III; PAIII/L - Number of differentiated pair pores on ambulacrum III/Length; Adab - Apical disc to anterior border; Npap - Number of pores in anterior petals; Nppp - Number of pores in posterior petals; Lppa - length of anterior pair petals; Lppp - Length of posterior pair petals.

Chrono-stratigraphy	Fossils N=8	Length (mm)	Width (mm)	Height (mm)	W/L	H/L	PAIII	PAIII/L	Adab	Npap	Nppp	Lppa	Lppp
Turonian	FPH-1457-I	29.0	26.5	18.0	0.1	0.62	29	1.0	17.0	30	27	13.5	12.0
Turonian	FPH-1500-I	23.0	22.5	14.0	0.97	0.60	25	1.08	12.1	35	25	10.5	8.5
Turonian	FPH-1955-I	30.0	28.1	20.0	0.93	0.66	35	1.16	18.0	38	31	13.9	11.5
Coniacian	FPH-1889-I	23.0	21.9	15.0	0.95	0.65	26	1.13	13.0	27	23	11.0	8.9
Coniacian	FPH-1890-I	26.7	25.0	17.5	0.93	0.65	31	1.10	14.5	39	30	11.0	8.0
Coniacian	FPH-1891-I	16.2	15.5	11.0	0.95	0.66	19	1.12	8.5	24	22	8.0	6.1
Coniacian	FPH-1887-I	17.1	15.5	11.5	0.94	0.67	21	1.22	8.5	26	20	6.5	6.0
Coniacian	FPH-1888-I	21.0	20.1	14.3	0.87	0.67	26	1.22	11.5	34	26	9.0	6.8



Ontogenetic considerations

In the small specimen FPH-1891-I (16,2 mm), anterior and posterior petals are almost the same in size (Fig. 8). The madreporite is located between genital plates 1 and 4, and is smaller than in other, larger specimens (Fig. 6.G). In this small individual, ocular plates 1 and 5 are widely separated and the madreporite between them has only few pores (Fig. 7.A). We believe that this condition was temporary and, with growth, the madreporite pores could have occupied this place. In madreporites of other specimens larger than 16 mm in test length, the pores occupy almost the entire plate. In specimen (FPH-1888-I; 21 mm) the anterior petals are slightly longer than the posterior ones (Table 1; Fig. 8), the apical system is laterally very wide and the madreporite is located between posterior genitals and ocular plates but does not go beyond these (Fig. 7.B). In individuals larger than 21 mm in test length, the madreporite moves further away from the posterior ocular plates 1 and 5 (Fig. 7.C-E).

Ontogenetic differences observed in the specimens studied suggest a modification of the development of the apical system with growth. It is noted that changes occur in the madreporite, passing from an initial stage with more concentrated pores that became more evenly distributed in adult specimens. Additionally, it is noted that the position of the madreporite shifts progressively more posteriorly with growth, increasing the relative distance between ocular plates 1 and 5.

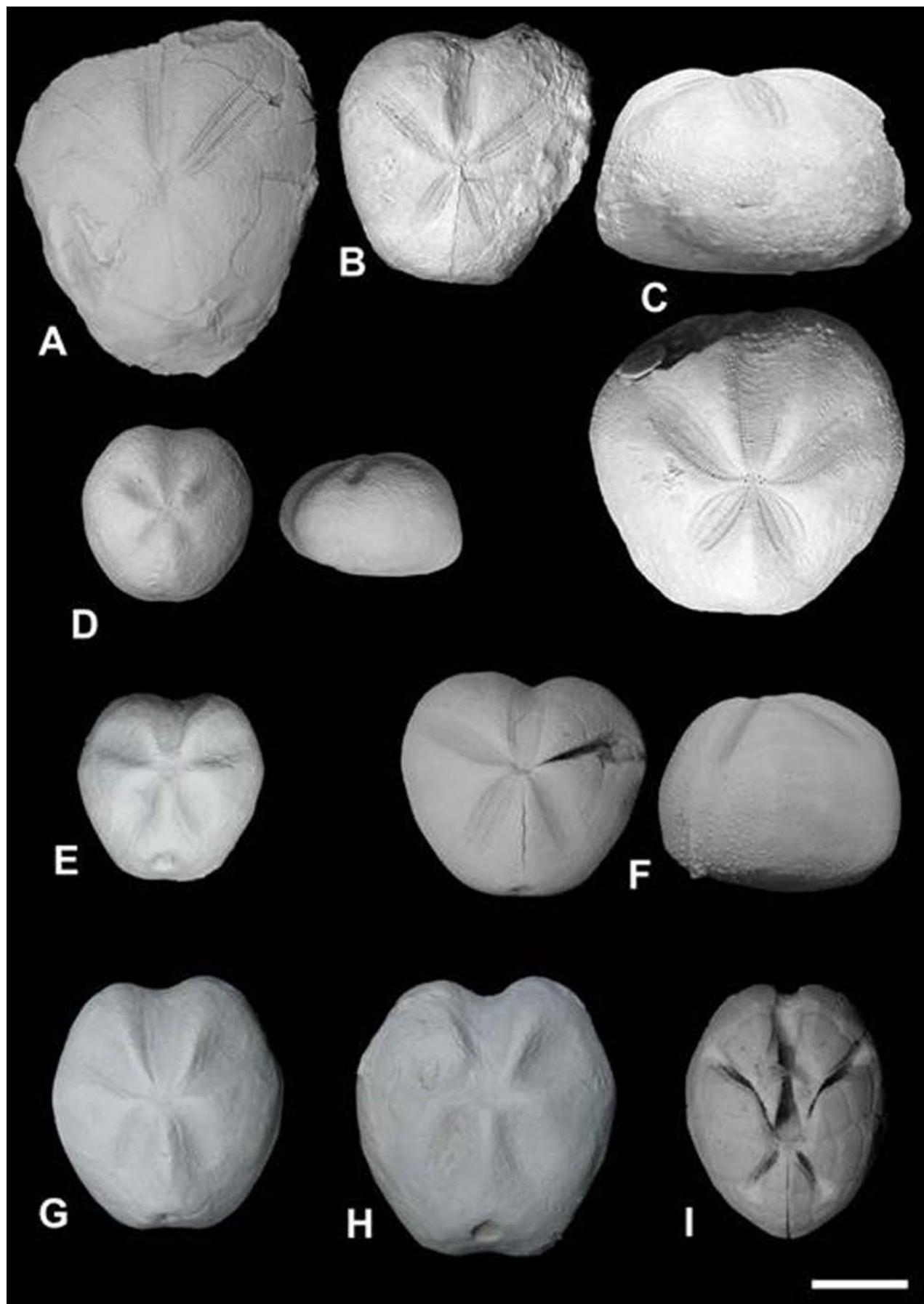
The number of pore pairs in ambulacrum III between the apical system and the fasciole was plotted against the test length (Fig. 8). There is a notable increase of pore pair number with test growth. In comparing these results with the observations of SMITH (in SMITH & BENGTON, 1991, p. 12) for the genus *Mecaster* from the Cenomanian-Coniacian interval in the Sergipe-Alagoas Basin, *M. texanus* is very similar to *M. fournelli*. Different results were observed by SMITH (in SMITH & BENGTON, 1991) for other *Mecaster* species from Cenomanian-lower Turonian which showed fewer pore pairs on ambulacrum III.

Spatangoid occurrences in the Sergipe-Alagoas Basin

The Order Spatangoida accounts for a substantial portion of the Cretaceous echinoid fauna from the Sergipe-Alagoas Basin. Until now, representatives of this order were recorded from the Aptian-Albian (Riachuelo Formation) and Cenomanian-Coniacian interval (Cotinguiba Formation), although unidentifiable isolated fragments are commonly recovered from the Cenozoic section of this basin (Calumbi Formation). One extant species, *Moira atropos*, was recorded from Sergipe by MANSO *et al.* (2002).

Echinoid distribution appears to be strongly linked to substrate type, because the larvae of these organisms can only develop when substrate conditions are favourable (SMITH, 1984). Therefore, irregular echinoids, such as spatangoids, are restricted to certain environments, as they are morphologically adapted to burying themselves and feeding in very specific sediments (SMITH, 1984).

The oldest spatangoid from the Sergipe-Alagoas Basin, *Douvillaster benguelensis* de LORIOL, 1888 (MANSO & SOUZA-LIMA, 2003a), now *Macraster benguelensis* (KROH, 2014), was identified in the upper Aptian. Their tests exhibit evidence to suggest that they lived epifaunally in an anoxic-dysoxic environment (NEUMANN, 1996; MANSO & SOUZA-LIMA, 2003a; VILLIER *et al.*, 2004; MANSO, 2011; KAMYABI SHADAN *et al.*, 2014). *Micraster (Epiaster) dartoni* (COOKE, 1955), now *Epiaster dartoni*, was recorded from the lower Albian. Their tests suggest they were semi-infaunal (MANSO, 2011; MANSO & SOUZA-LIMA, 2012; KROH, 2015). Recorded from the Albian also were *Hemaster proclivus* COTTEAU *et al.*, 1878, with low depressed petals, and *H. zululandensis* BESAIRIE & LAMBERT, 1930, with more deeply sunken petals and rounded tests, suggesting they were capable of burying themselves in arenaceous sediments close to the water/sediment interface (MANSO, 2011). From the Cenomanian to Turonian, a new marine transgression occurred in the Sergipe-Alagoas Basin, with deposition of fine-grained sediments (marls and mudstones of the Cotinguiba Formation), and many species of the genus *Mecaster* appeared. The tests of this genus are adapted for living buried more deeply than the spatangoids from the Riachuelo Formation. Burial capacity involves modification in the disposition of fascioles, the number and disposition of the frontal ambulacrals pores, the depth of petals and even the test layout (SMITH, 1984; KANAZAWA, 1992; SMITH & STOCKLEY, 2005). The establishment of more specialised species for living in sediments can be related to the presence of predators in these palaeocommunities, and burial could have been a defence strategy. According to VERMEIJ (1977), during the Mesozoic modification of the structure of marine benthic communities occurred, caused by the diversification of the gastropods. Previously, gastropods were mainly grazers but, with morphological change, they acquired new feeding habits, becoming predators of other species. These molluscs rapidly diversified towards the end of the Cretaceous. In the sedimentary basins of northeastern Brazil the presence of carnivorous gastropods has previously been recorded, and has been considered in a global Cretaceous evolutionary context (ANDRADE & FÉLIX, 2012).





◀ **Figure 9:** Spatangoid echinoids from the Sergipe-Alagoas Basin: A. *Macraster benguelensis* (FPH-1961-I); B. *Epiaster dartoni* (FPH-423-I); C. *Hemaster zululandensis* (FPH-341-I); D. *Hemaster proclivus* (FPH-645-I); E. *Mecaster batnensis* (FPH-1963-I); F. *Mecaster africanus* (FPH-1964-I); G. *Mecaster fourneli* (FPH-1948-I); H. *Mecaster texanus* (FPH-1955-I); I. *Moira atropos* (FPH-1957-I). Scale bar 10 mm.

On the basis of the diverse record of the Order Spatangoida of the Sergipe-Alagoas Basin, a key is proposed for the identification of such echinoids from this basin; this may prove useful for group identification in other areas as well.

Discussion and conclusions

Mecaster texanus co-occurs with *M. fourneli* (DESHAYES in AGASSIZ & DESOR, 1847) at all localities studied. These species are very close, showing the same number of pore pairs in ambulacrum III. The main difference between them is the larger size of the madreporite plate in *M. texanus* in individuals of the same test size. Another difference concerns the peristome which is wider in *M. fourneli* than in *M. texanus*.

SMITH (*in SMITH & BENGTSON, 1991*), who assessed other species of *Mecaster* of Cretaceous (Cenomanian-Coniacian) age in the Sergipe-Alagoas Basin, concluded that the density of pore pairs between the apical system and the fasciole in ambulacrum III exhibits a general increase through time. Thus, Cenomanian *Mecaster batnensis* has fewer pore pairs than Turonian *M. africanus* and Coniacian *M. fourneli*. This also appears to be true for *M. texanus* which has a similar number of pore pairs to *M. fourneli* from the Turonian-Coniacian of this basin.

Mecaster also exhibits a decrease in test roundness from the Cenomanian to the Turonian. In the Coniacian, the tests again display greater width (SMITH *in SMITH & BENGTSON, 1991*).

Cretaceous spatangoids can be subdivided into two groups on the basis of the length of their even petals (ZOEKE, 1951): those with long petals with many pore pairs and those with short petals (especially the posterior pair) with few pore pairs.

Identification key for species of the Order Spatangoida currently known from the Sergipe-Alagoas Basin and their stratigraphical occurrence.

1 - Apical disc ethmophract with four gonopores;	madreporite not separating genital plates 1 and 4	jump to 2
Apical disc ethmophract with four gonopores;	madreporite separating genital plates 1 and 4	jump to 5
Apical disc ethmolytic with four gonopores;	madreporite separating genital plates 1 and 4 and posterior ocular plates 1 and 5	jump to 6
Apical disc ethmolytic with two gonopores		jump to 7
2 - Petals slightly ridged and distally open;	posterior petals slightly shorter than anterior ones	jump to 3
Petals almost closed;	posterior petals less than approximately half length of anterior pair	jump to 4
3 - Pore pairs in ambulacrum III slit-shaped	<i>Macraster benguelensis</i> (upper Aptian-lower Albian; e.g., MANSO & SOUZA-LIMA, 2003a)	Fig. 9.A
Pore pairs in ambulacrum III rounded	<i>Epiaster dartoni</i> (lower Albian; e.g., MANSO & SOUZA-LIMA, 2012)	Fig. 9.B
4 - Petals shallow; test taller in posterior region	<i>Hemaster proclivus</i> (Albian; e.g., SMITH & BENGTSON, 1991)	Fig. 9.C
Petals more deeply sunken; test profile much more depressed	<i>Hemaster zululandensis</i> (upper Albian; e.g., MANSO & SOUZA-LIMA, 2003b)	Fig. 9.D
5 - Petals deeply sunken and broad; anterior and posterior pairs of almost same size	<i>Mecaster batnensis</i> (Cenomanian-lower Turonian; e.g., SMITH & BENGTSON, 1991)	Fig. 9.E
Petals sunken, straight, distally opened and subequal in length	<i>Mecaster africanus</i> (upper Turonian; e.g., SMITH & BENGTSON, 1991)	Fig. 9.F
6 - Apical disc not very elongate, with madreporite narrowly separating ocular plates	<i>Mecaster fourneli</i> (Turonian-Coniacian; e.g., SMITH & BENGTSON, 1991)	Fig. 9.G
Apical disc very elongate, with madreporite broadly separating ocular plates, occasionally extending beyond these plates	<i>Mecaster texanus</i> (Coniacian; the present paper)	Fig. 9.H
7 - Posterior genital plates widely separated	<i>Moira atropos</i> (Pleistocene to Recent; e.g., MANSO et al., 2002)	Fig. 9.I



As echinoid metabolism is influenced by water temperature and since their distribution may be limited by this variable (SMITH, 1984), some inferences can be made. Those species with longer petals would have higher metabolic rates and would occur in warmer waters. In contrast, those species with shorter petals, with lower metabolism, would be found in colder waters. According to SMITH (1984), hemiasterids that lived around the palaeoequator during the Cretaceous had long petals and species with shorter petals existed in more temperate regions in both hemispheres. In the Sergipe-Alagoas Basin, spatangoids with long petals appeared in the late Aptian and lived on a shallow platform in warm waters in anoxic-dysoxic palaeoenvironments (MANSO & SOUZA-LIMA, 2003a). Organisms with long petals and similar pores and slits in all ambulacra would have more efficient gas exchange (NEUMANN, 1996; MANSO & SOUZA-LIMA, 2003a; KAMYABI SHADAN *et al.*, 2014). During the Albian, species of *Hemaster* with posterior petals shorter than the frontal ones appeared, and were better adapted to colder, oxygenated and probably deeper palaeoenvironments (SMITH & BENGTON, 1991; NÉRAudeau & FLOQUET, 1991; MANSO & SOUZA-LIMA, 2003a). It is assumed that at the start of the Albian the Sergipe-Alagoas Basin was further away from the palaeoequator. From the Cenomanian to Coniacian the position of this basin gradually moved to higher latitudes probably with warmer waters. During this interval there was greater communication between oceanic basins and greater oxygenation of bottom waters globally (SMITH & STOCKLEY, 2005). At higher water temperatures than during Albian, the species of *Mecaster* with longer posterior petals were widely distributed on the Sergipe-Alagoas Basin platform.

Regarding the size of even petals, and the number and arrangement of pores in the anterior ambulacrum in species of *Mecaster* from the Cretaceous of the Sergipe-Alagoas Basin, GUIMARÃES (2016) observed that in the Turonian two distinct morphological groups co-occurred. The first, comprising *M. batnensis* and *M. africanus*, has narrow and open petals and fewer pores in ambulacrum III than their counterparts. The second group, formed by *M. fourneli* and *M. texanus*, exhibits closed petaloids, less rounded tests and a larger number of pores in ambulacrum III. In comparing these two groups with results obtained by NÉRAudeau and FLOQUET (1991) for the Upper Cretaceous of the Castilla and Navarra-Cantabria platforms of Spain, GUIMARÃES (2016) concluded that the species from the Sergipe-Alagoas Basin could have been distributed in a similar way during the Turonian. *Mecaster fourneli* and *M. texanus* would have occupied shallower environments on the inner platform where they would have buried themselves more deeply

into the sediment. *Mecaster batnensis* and *M. africanus* would have preferred deeper areas but buried themselves more closely to the sediment/water interface. NÉRAudeau and FLOQUET (1991) also observed that the spatial distribution of echinoids reflected a palaeoecological control and that differences in depths in distinct geographic outcrops could be related to transgressive and regressive events.

Mecaster texanus and *M. fourneli* were recorded from the Sergipe-Alagoas Basin up to the Coniacian. From the Santonian onwards, a new transgressive event, possibly related to a climatic turnover, laid down siliciclastic strata (Calumbi Formation) over the previous carbonate platform in which these species of *Mecaster* probably could not survive.

Acknowledgements

The authors wish to thank Dr Andreas KROH (Naturhistorisches Museum Wien, Vienna) for suggestions on an earlier typescript, Dr Loïc VILLIER and Dr John JAGT for their valuable suggestions that helped to improve the final manuscript, and Dr Stephen CAREY by the English corrections.

Bibliographic references

- ADKINS W.S. (1928).- Handbook of Texas Cretaceous fossils.- *University of Texas Bulletin*, Austin, vol. 2838, p. 1-381.
- ANDRADE E.J. (2005).- Turonian inoceramids and biostratigraphy of the Sergipe Basin, north-eastern Brazil: An integrated study of the Votorantim and Nassau quarries.- PhD thesis, Universität Heidelberg, 155 p.
- ANDRADE E.J. & FÉLIX I.L.C. (2012).- Gastrópodos marinhos do Turoniano (Cretáceo Superior) da Bacia de Sergipe.- *Cuadernos de Geociências*, Bahia, vol. 9, no. 2, p. 103-111.
- BENGTON P. (1983).- The Cenomanian-Coniacian of the Sergipe Basin, Brazil.- *Fossils and Strata*, Oslo, no. 12, 78 p.
- BEURLEN K. (1964).- A fauna do calcário Jandaíra da região de Mossoró (Rio Grande do Norte).- Coleção Mossoroense, Editora Pongetti, Rio de Janeiro, 215 p.
- BEURLEN K. (1966).- Novos equinóides do Cretáceo do Nordeste do Brasil.- *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, vol. 38, nos. 3-4, p. 455-464.
- BRITO I.M. (1980).- Os equinóides fósseis do Brasil: I. Os endocíclicos.- *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, vol. 52, no. 3, p. 569-590.
- BRITO I.M. (1981a).- Os equinóides fósseis do Brasil: II. Holoctypoides e cassiduloides.- *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, vol. 53, no. 3, p. 513-527.
- BRITO I.M. (1981b).- Os equinóides fósseis do Brasil: III. Espatangóides, exceto Hemiate-



- ridae.- *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, vol. 53, no. 3, p. 569-578.
- BRITO I.M. (1981c).- O gênero *Hemaster* no Cretáceo do Brasil (Echinoidea Spatangoida). In: SANGUINETTI Y.T. (ed.), *Anais do II Congresso Latino-Americano de Paleontologia*.- Editora Pallotti, Porto Alegre, vol. 1, p. 399-414.
- BRITO I.M. & RAMIREZ L.V.O. (1974).- Contribuição ao conhecimento dos equinóides albianos (Cretáceo inferior) do Brasil.- *Anais da Academia Brasileira de Ciências*, Rio de Janeiro, vol. 46, no. 2, p. 275-282.
- CASSAB R. de C.T. (2003).- Paleontologia da Formação Jandaíra, Cretáceo Superior da Bacia Potiguar, com ênfase na paleobiologia dos gastrópodos.- PhD thesis, Universidade Federal do Rio de Janeiro, Instituto de Geociências, Rio de Janeiro, 184 p. URL: <http://www.cprm.gov.br/publique/media/rita.pdf>
- CLARK W.B. (1893).- The Mesozoic Echinodermata of the United States.- *United States Geological Survey, Bulletin*, vol. 97, p. 1-207.
- CLARK W.B. & TWITCHELL M.W. (1915).- The Mesozoic and Cenozoic Echinodermata of the United States.- *United States Geological Survey, Monographs*, vol. 14, 468 p.
- COOKE C.W. (1953).- American Upper Cretaceous Echinoidea.- *United States Geological Survey, Professional Paper*, vol. 254-A, p. 1-44.
- COOKE C.W. (1955).- Some Cretaceous echinoids from the Americas.- *United States Geological Survey, Professional Paper*, vol. 264-E, p. 87-112.
- FEIJÓ F.J. (1995).- Bacias de Sergipe e Alagoas.- *Boletim de Geociências da Petrobras*, Rio de Janeiro, vol. 8, no. 11 (for 1994), p. 149-161.
- FISHER A.G. (1966).- Spatangooids. In: MOORE R.C. (ed.), *Treatise on Invertebrate Paleontology*, Part U, Echinodermata 3.- Geological Society of America, Boulder, and University of Kansas, Lawrence, vol. 2, U543-U628.
- GUIMARÃES C.D.M. (2016).- Identificação e distribuição das espécies de *Mecaster* (Echinodermata: Echinoidea) do Cretáceo da Bacia de Sergipe-Alagoas, nordeste do Brasil.- Dissertação, Departamento de Geologia, Universidade Federal de Sergipe, São Cristóvão, 42 p. URL: <https://ri.ufs.br/handle/riufs/5402>
- HOOKE S.C. & COBBAN W.A. (2017).- *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.- *Acta Geologica Polonica*, vol. 67, no. 1, p. 1-30.
- KAMYABI SHADAN H., VILLIER L., SADEGHI A. & ADABI M.H. (2014).- A revision of the *Macraster* species (Echinodermata, Echinoidea) occurring in the Albian deposits of the Zagros Basin, southwest Iran.- *Annales de Paléontologie*, Paris, vol. 100, no. 1, p. 51-62.
- KANAZAWA K. (1992).- Adaptation of test shape for burrowing and locomotion in spatangoid echinoids.- *Palaeontology*, vol. 35, part 4, p. 733-750.
- KROH A. (2014).- *Macraster benguellensis* (de LORIOL, 1888) †. In: KROH A. & MOOI R. (2017).- World Echinoidea Database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/traits/aphia.php?p=taxdetails&id=746347> on 2017-11-08
- KROH A. (2015).- *Epiaster dartoni* COOKE, 1955 †. In: KROH A. & MOOI R. (2015).- World Echinoida Database. Accessed through: World Register of Marine Species at <http://www.marinespecies.org/echinoidea/aphia.php?p=taxdet&id=755656> on 2016-08-22
- MANSO C.L. de C. (2003).- Paleoecologia, paleobiogeografia e sistemática dos equinóides do Aptiano-Albiano (Cretáceo) do Brasil.- PhD thesis, Universidade Federal da Bahia, Instituto de Geociências, Salvador, 211 p.
- MANSO C.L. de C. (2011).- Adaptação e distribuição dos espatangóides (Echinodermata: Echinoidea) no Cretáceo da Sub-bacia de Sergipe, Brasil. In: CARVALHO I.S., SRIVASTAVA N.K., STROHSCHOEN O. Jr & LANA C.C. (eds.).- *Paleontologia: Cenários da Vida*, Rio de Janeiro, vol. 4, p. 123-132.
- MANSO C.L. de C. (2014).- Os equinodermos como indicadores paleoclimáticos do Cretáceo do Brasil. In: CARVALHO I.S., SRIVASTAVA N.K., STROHSCHOEN O. Jr & LANA C.C. (eds.), *Paleoclimas.- Paleontologia: Cenários da Vida*, Rio de Janeiro, vol. 5, p. 63-70.
- MANSO C.L. de C. & ANDRADE E.J.A. (2008).- Echinóides do Turoniano (Cretáceo Superior) de Sergipe, Brasil.- *Geociências*, Rio Claro, vol. 27, no. 3, p. 319-327.
- MANSO C.L. de C. & LEMOS A.C.C. (2008).- Os Echinoida (Echinodermata) da localidade Cattete Velho I (Cretáceo) em Sergipe, Nordeste do Brasil.- *Revista Brasileira de Paleontologia*, Porto Alegre, vol. 11, no. 2, p. 129-138.
- MANSO C.L. de C. & SOUZA-LIMA W. (2003a).- O equinóide *Douvillaster* LAMBERT, 1917, na Formação Riachuelo, Bacia de Sergipe, Brasil.- *Revista Brasileira de Paleontologia*, Porto Alegre, no. 5, p. 29-37.
- MANSO C.L. de C. & SOUZA-LIMA W. (2003b).- O registro do equinóide *Hemaster zululandensis* BESAIRIE & LAMBERT, 1930, no Cretáceo (Albiano superior) de Sergipe.- *Revista Brasileira de Paleontologia*, Porto Alegre, no. 6, p. 61-67.
- MANSO C.L. de C. & SOUZA-LIMA W. (2005).- Os equinóides *Pygorhynchus colombianus* (COOKE, 1955) e *Pseudholaster altiusculus* (WHITE, 1887) no Neoalbiano da Bacia de Sergipe, Brasil.- *Revista Brasileira de Paleontologia*, Porto Alegre, vol. 8, p. 229-238.



- MANSO C.L. de C. & SOUZA-LIMA W. (2011).- New genus and new species of echinoid (Echinodermata, Orthopsidae) from the Albian (Lower Cretaceous) of Sergipe-Alagoas Basin, Brazil.- *Arquivos do Museu Nacional*, Rio de Janeiro, vol. 68, no. 1-2, p. 41-46.
- MANSO C.L. de C. & SOUZA-LIMA W. (2012).- Novos equinóides para o Aptiano-Albiano (Cretáceo inferior) da sub-bacia de Sergipe, Nordeste do Brasil.- *Geociências*, Rio Claro, vol. 31, no. 4, p. 584-605.
- MANSO C.L. de C., SOUZA-LIMA W. & SOUZA-LIMA R. (2002).- Ocorrência de *Moira atropos* LAMARCK, 1816 (Echinodermata: Echinoidea) no litoral de Sergipe. In: Congresso Brasileiro de Zoologia, 24, Itajaí, Santa Catarina, 2002.- Boletim de Resumos, Sociedade Brasileira de Zoologia, vol. 1, p. 92.
- MAURY C.J. (1925).- Fósseis terciários do Brasil com descrição de novas formas cretáceas.- *Monografia, Serviço Geológico e Mineralógico*, Rio de Janeiro, no. 4, p. 1-305.
- NÉRAudeau D. & FLOQUET M. (1991).- Les échinides Hemiasteridae: marqueurs écologiques de la plate-forme castillane et navarro-cantabre (Espagne) au Crétacé supérieur.- *Palaeogeography, Palaeoclimatology, Palaeoecology*, no. 88, p. 265-281.
- NEUMANN C. (1996).- The mode of life and paleobiogeography of the genus *Douvillaster* LAMBERT (Echinoidea: Spatangoida) as first recorded in the Lower Cretaceous (Albian) of Spain.- *Berliner geowissenschaftliche Abhandlungen*, E18, p. 257-265.
- OLIVEIRA J., MANSO C.L. de C., ANDRADE E.J. & SOUZA-LIMA W. (2013).- O gênero *Mecaster* (Echinodermata: Spatangoida) do Cretáceo superior da Formação Jandaira, Bacia Potiguar, Nordeste do Brasil.- *Scientia Plena*, São Cristóvão, vol. 9, no. 8, p. 1-17.
- POMEI A. (1883).- Classification méthodique et générale des Échinides vivants & fossiles.- 1^{ère} thèse, Docteur ès Sciences Naturelles, Faculté des Sciences de Paris, no. 503, 131 p. URL: [https://www.biodiversitylibrary.org/item/43038#page/5 mode/1up](https://www.biodiversitylibrary.org/item/43038#page/5	mode/1up)
- ROEMER F. (1849).- Texas, mit besonderer Rücksicht auf Deutsche Auswanderung und die physischen Verhältnisse des Landes nach eigener Beobachtung geschildert; mit einem naturwissenschaftlichen Anhange und einer topographisch-geognostischen Karte.- Bonn, Adolph Marcus, 626 p.
- ROEMER F. (1852).- Die Kreidebildungen von Texas und ihre organischen Einschlüsse.- Bonn, Adolph Marcus, 100 p.
- SMITH A.B. (1984).- Echinoid Palaeobiology.- George Allen & Unwin, London, 190 p.
- SMITH A.B. & BENGTON P. (1991).- Cretaceous echinoids from north-eastern Brazil.- *Fossils and Strata*, Oslo, no. 31, 88 p.
- SMITH A.B. & STOCKLEY B. (2005).- Fasciole pathways in spatangoid echinoids: A new source of phylogenetically informative characters.- *Zoological Journal of the Linnean Society*, no. 144, p. 15-35.
- SOUZA-LIMA W. (2006).- Litoestratigrafia e evolução tectono-sedimentar da bacia de Sergipe-Alagoas: Introdução.- *Phoenix*, Aracaju, no. 89, p. 1-10.
- SOUZA-LIMA W., ANDRADE E.J., BENGTON P. & GALM P.C. (2002).- A bacia de Sergipe-Alagoas. Evolução geológica, estratigrafia e conteúdo fóssil [The Sergipe-Alagoas Basin. Geological evolution, stratigraphy and fossil content].- *Phoenix*, Aracaju, Edição Especial, no. 1, p. 1-34.
- VERMEIJ G.J. (1977).- The Mesozoic marine revolution: evidence from snails, predators and grazers.- *Paleobiology*, no. 3, p. 245-258.
- VILLIER L., NÉRAudeau D., CLAVEL B. & NEUMANN C. (2004).- Phylogeny of early Cretaceous spatangoids (Echinodermata: Echinoidea) and taxonomic implications.- *Palaeontology*, no. 47, p. 265-292.
- WANDERLEY A. (1938).- Estado de Sergipe. Estudos geológicos e levantamentos topográficos. In: OLIVEIRA E.P. de (ed.).- Relatório Annual do Director, anno de 1935, p. 46-57.
- WHITE C.A. (1887).- Contribuições à paleontologia do Brazil.- *Archivos do Museu Nacional do Rio de Janeiro*, no. 7, p. 1-273.
- ZOEKE E. (1951).- Étude des plaques des *Hemaster* (Échinides).- *Bulletin du Muséum national d'Histoire naturelle de Paris*, (2), no. 23, p. 696-705.