

PALAEODIVERSITY OF CARIBBEAN ECHINOIDS INCLUDING NEW MATERIAL FROM THE VENEZUELAN NEOGENE

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ABSTRACT

The extensive Venezuelan coastline is very important for understanding the evolution of the Caribbean marine fauna. We report new fossil material collected from three Neogene fossil sites in the Falcón Basin and present the first diversity analysis of the known fossil echinoids from Venezuela and other Caribbean regions. Five species are reported for the first time from Venezuela. Each of the three fossil sites shows a different taxonomic composition, which may be a consequence of differing palaeoecological conditions during the Neogene. Furthermore, the environmental changes caused by the closure of the Central American Isthmus may also have played a role. The analysis of the Venezuelan echinoid fossil record, including the new herein described material, reveals three major diversity decreases and a maximal diversity peak in the Middle Miocene instead of the Eocene as it is the case in other Caribbean echinoid faunas. The first diversity decrease at the end of the Early Cretaceous, recognised by a gap in the fossil record, unfolds new research potential. The second one, around the Eocene-Oligocene boundary, is interpreted as an extinction event, as has been recognized for other echinoid and invertebrate faunas throughout the Caribbean. In contrast to other Caribbean invertebrate faunas, the cause of the third diversity decrease of echinoids throughout the Caribbean appears to be the beginning, instead of the end, of the closure of the Central American Isthmus. Although Venezuela plays a special ecological role in the Caribbean due to its seasonal upwellings, this study provides (1) a basis to better understand the fossil Venezuelan echinoid fauna, (2) a contrast to other Caribbean regions, and (3) insights into the Caribbean echinoid evolutionary patterns.

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INTRODUCTION

Studies of fossil echinoids in Venezuela have been sporadically conducted in past decades, resulting in records from the Permian to the Neogene (Jeannot 1928; Cooke 1941; Von der Osten 1957; Cooke 1961; Anisgard 1954; Weisbord 1969; Hoover 1981; Mooi and Peterson 2000). In spite of the limitations resulting from the low sample sizes, some patterns in echinoid ecology and evolution in this country are recognizable. There are about 2,800 km of coast line in Venezuela, and this vast area is particularly relevant for understanding changes in the Caribbean echinoid assemblages in the last portion of the Cenozoic period. However, one has to be aware that Venezuela plays a special ecological role in the Caribbean because of seasonal upwelling, a phenomenon otherwise absent or less important in the rest of the Caribbean. Our material comes from the Late Miocene to the Early Pleistocene which was the time around the closure of the Central American Isthmus, when major changes in marine environments occurred (Lessios 2008).

The new fossil material was collected by M. R. Sánchez-Villagra, O. Aguilera and associates mostly in June of 2008 from three localities in Falcón State in north-western Venezuela (Figure 1). This savannah-like region contains outcrops of mostly Neogene deposits (Johnson et al. 2009). At two of our fossil sites (Cocuiza West: N 11°18'38.4" N 70°14'26.2" and Cocuiza East: N 11°18'37.8" W 70°14'21.2"), sediments of the Cocuiza Member of the San Gregorio Formation are exposed, and at the third fossil site (La Vela: N 11°30'0.2" W 69°31'50"), the La Vela Formation crops out.

The Cocuiza Member constitutes the middle portion of the San Gregorio Formation and is 80 m thick at its type section. This section is characterized by the presence of numerous conspicuous fossil beds separated by siltstones. The fossiliferous beds are usually sandy and unconsolidated to slightly lithified. Palaeoenvironmental reconstructions are based mostly on ostreid-colonies and crustacean burrows and suggest a low to moderate wave energy coastline environment with local

occurrence of terrigenous sediments and local sea-level fluctuations (Aguilera et al. 2010). The age of this member is estimated to be of Late Pliocene to Early Pleistocene age (Ministerio de Energía y Minas 1997).

The La Vela Formation is exposed in the Coro-La Vela region in the north-northeastern area of the Falcón Basin. Stratigraphically, it lies above the Taratara Member of the Caujarao Formation. The La Vela Formation is characterized by sandy siltstones and blue-grey shales that are interrupted by sandstone beds. Foraminiferan assemblages suggest a middle neritic habitat (30-60 m deep). The age of this formation is estimated to be Late Miocene to Pliocene (Smith 2008).

Here, we document the taxonomy of new echinoid material, discuss palaeoecological differences among fossil localities and compare the diversity pattern of the echinoid fossil record of Venezuela with that of the entire Caribbean. All specimens are stored in the collection of Universidad Nacional Experimental Francisco de Miranda in Venezuela.

SYSTEMATIC PALAEOONTOLOGY

ECHINOIDEA Leske, 1778

CIDARIDAE Gray, 1825

CIDARINAE Mortensen, 1928

PRIONOCIDARIS Agassiz, 1863

Type species. - *Prionocidaris pistillaris* (Lamarck, 1816), by original designation.

Range and distribution. - Lower Cretaceous (Albian) to Recent, worldwide.

Prionocidaris sp.

Figure 2.1

Description. - The fragment is 12 mm long (UNEFM-IF-001). By applying the circle perimeter equation, the test diameter was reconstructed to be 12.7 mm. The somewhat sinuous ambulacral plating is simple (unigeminate). Each plate comprises conjugate pore-pairs and distinct primary and secondary tubercles (Figure 2.2). Primary tubercles on interambulacral plates are perforated and non-crenulate (Figure 2.3). Ovate areoles are surrounded by almost uniform scrobicular tuber-



FIGURE 1. Map of the Falcón Basin with the three fossil localities (Venezuela, South America).

cles. The narrow extrascrobicular zones are covered with secondary tubercles and granules. The small spine fragments embedded in the surrounding sediment are cylindrical with traces of a coarse granular ornamentation.

Remarks. - Fossils of the genus *Prionocidaris* are known from the Late Cretaceous to Miocene. Therefore, our Late Miocene to Pliocene specimen appears to be the youngest known fossil of this genus. Furthermore, the genus *Prionocidaris* shows a different geographical distribution of fossil and extant species (Mortensen 1928). *Prionocidaris* fossils are known from Europe and the Mediterranean as well as from the entire Caribbean. Extant species, however, are known from the Indian and the Pacific Ocean.

Stratigraphic range. - The La Vela Formation (Late Miocene to Pliocene).

Locality. - La Vela region, Falcón State, Venezuela.

Material. - Fragment showing one interambulacrum and adjacent ambulacra broken along the perradial suture on both sides, UNEFM-IF-001.

ARBACIOIDA Gregory, 1900

ARBACIIDAE Gray, 1855

ARBACIA Gray, 1835.

Type species. - *Arbacia lixula* (Linnaeus, 1758), by subsequent designation of Agassiz & Clark, (1908: 67).

Range and distribution. - Miocene to Recent, Mediterranean, both coasts of Central and South America.

Arbacia punctulata (Lamarck, 1816)

Figure 3

Description. - The test measures 25 mm in diameter and 12 mm in height (UNEFM-IF-002). It is hemispherical with a flattened oral side. Throughout the whole ambulacra, trigeminate plating is visible. The pore zones become wider towards the oral surface. Tuberculation is small and irregular on the aboral surface increasing in size towards the ambitus. Mostly naked interambulacral plates

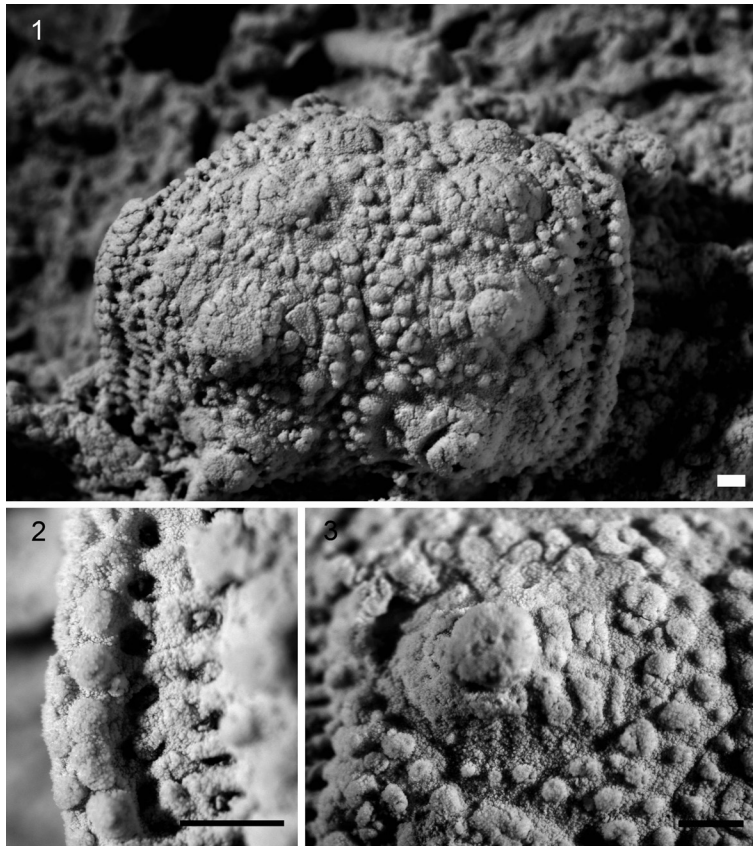


FIGURE 2. 1, *Prionocidaris* sp., La Vela Formation, Falcón state, Venezuela, UNEFM-IF-001. 2, *Prionocidaris* sp., ambulacral plates with conspicuous pore pairs. 3, interambulacral plate with perforate and non-crenulate primary tubercle. Scale bar equals 1 mm.

stand out on the aboral surface. Imperforate and non-crenulate primary tubercles show relatively large mamelons with poorly defined areoles. The inner interambulacral tubercles on the aboral side are of the same size as those in the adradial series. On the badly preserved oral side, a rather large peristome is recognizable.

Remarks. - *Arbacia punctulata* is a well known species of Pliocene age. It is distributed throughout the western Atlantic seaboard and the whole Caribbean. It is very similar to the two Pacific coast species *A. spatuligera* (Valenciennes, 1846) and *A. stellata* (Blainville, 1825). Aside from coloration and spine morphology, which are not preserved, *A. punctulata* appears not to have any morphological differences to *A. stellata*. The difference to *A. spatuligera* is more obvious since *A. punctulata* has tubercles of equal size both on the interambulacra and the adradial series in contrast to its Pacific coast relative with smaller tubercles on the inner interambulacra (Mortensen 1935).

Stratigraphic range. - Cocuiza Member of the San Gregorio Formation (Late Pliocene to Early Pleistocene); Pliocene to Recent.

Locality. - Cocuiza West locality, Codore Adentro region, Falcón State, Venezuela.

Spatial distribution. - The western Atlantic seaboard, the whole Caribbean.

Material. - One rather poorly preserved specimen (UNEFM-IF-002).

ECHINOIDA Troschel, 1872
TOXOPNEUSTIDAE Troschel, 1872
LYTECHINUS Agassiz, 1863

Type species. - *Lytechinus variegatus* Lamarck, 1816, by monotypy.

Range and distribution. - Eocene (*Scoliechinus*), Oligocene to Recent, both coasts of the Americas, but mainly in the Gulf of California and the Caribbean.

Lytechinus cf. *euerces* Clark, 1912

Figure 4.1

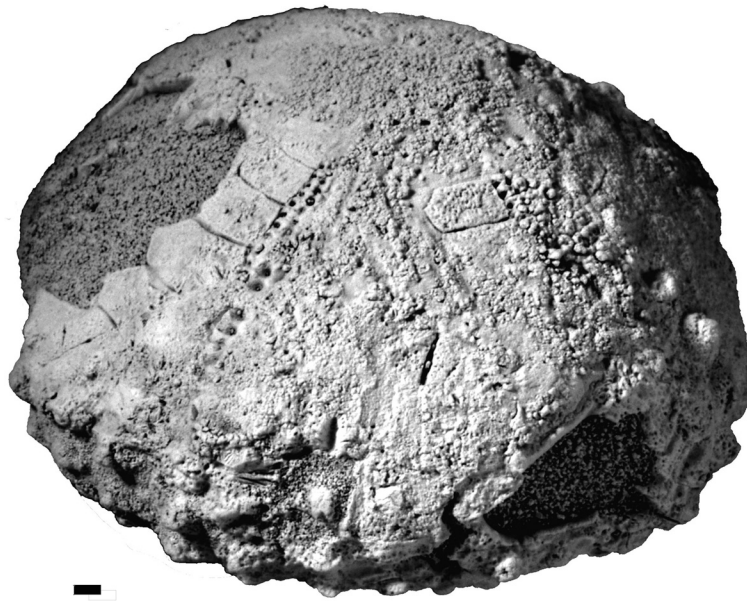


FIGURE 3. *Arbacia punctulata* (Lamarck, 1816), San Gregorio Formation, Falcón state, Venezuela, UNEFM-IF-002. Scale bar equals 1 mm.

Description. - The diameter of the best preserved test measures 16 mm (UNEFM-IF-004). Each ambulacral trigeminate compound plate has both primary and secondary tubercles (Figure 4.2). The latter are small and irregularly dispersed. The conjugate pore pairs form oblique lines of three. Interambulacral plates carry a rather small, non-crenulate primary tubercle and several, well-spaced, slightly smaller secondary tubercles (Figure 4.3). The rest of the tuberculation is small and irregularly distributed. The peristome margin is defined by sharp and distinct buccal notches.

Remarks. - Although the material's preservation is not outstanding, the prominent buccal notches are sufficiently well preserved to assign the material to the family Toxopneustidae. Since the here described specimens do not preserve the peristome plating, which is usually applied for the identification of the genus *Lytechinus*, pattern and tuberculation of both ambulacral and interambulacral plates were used for the determination. Recent *L. euerces* are known from the Caribbean from the Gulf of Mexico to Barbados (Smith 2005).

Stratigraphic range. - The La Vela Formation (the Late Miocene to the Pliocene).

Locality. - La Vela region, Falcón State, Venezuela.

Spatial distribution. - Gulf of Mexico to north-west of Tortuga and to Barbados.

Material. - Three specimens: one is compressed UNEFM-IF-003, one has a rather well preserved oral side UNEFM-IF-004 and one shows a rather damaged surface UNEFM-IF-005.

CLYPEASTEROIDA Agassiz, 1835

CLYPEASTERIDAE Agassiz, 1835

CLYPEASTER Lamarck, 1801.

Type species. - *Clypeaster rosaceus* Linnaeus, 1758, by original designation.

Range and distribution. - Late Eocene to Recent, worldwide in tropical to temperate regions.

Clypeaster rosaceus Linnaeus, 1758

Figure 5.1

Description. - The test is sturdy due to a double-walled margin created by inner peripheral partitioning (UNEFM-IF-006). The oral surface is concave. The petals become wider distally. On the ridges between the pore pairs 8 to 9, primary tubercles are aligned in a regular series (Figure 5.1). The furrows between primary tubercle series are narrow but fairly deep and sharp. The interambulacral tuberculation is conspicuous (primary tubercle diameter 0.5 mm) and irregularly arranged.

Remarks. - The genus *Clypeaster* is distributed throughout tropical to temperate regions from the Late Eocene to today. *Clypeaster* represents a paraphyletic or even a polyphyletic genus with more than thirty species (Mortensen 1948). A detailed revision and subdivision of this genus is



FIGURE 4. 1, *Lytechinus* cf. *euerces* Clark, 1912, La Vela Formation, Falcón state, Venezuela, UNEFM-IF-004. 2, trigeminate ambulacral plates. 3, interambulacral plate with one rather small, non-crenulate primary and several secondary tubercles. Scale bar equals 1 mm.

needed. *Clypeaster rosaceus*'s test is characteristic for its highly rounded but not limited edge and gradual transition towards the moderately high, rounded apex. It is a common species in shallow waters, down to depth of 50 m, of the West Atlantic and Caribbean coasts from South Carolina to Venezuela.

Stratigraphic range. - The La Vela Formation (the Late Miocene to the Pliocene); Plio-Pleistocene to Recent.

Locality. - La Vela region, Falcón State, Venezuela.

Spatial distribution. - The Caribbean and the south-eastern USA.

Material. - Three fragments with a rather well preserved surface: UNEFM-IF-006, UNEFM-IF-007, UNEFM-IF-008.

Clypeaster subdepressus (Gray, 1825)

Figure 5.3

Description. - The test measures more than 100 mm in length and displays a subpentagonal outline with a rounded margin (UNEFM-IF-009). The test shows no indication of convergence on the oral side. The apical disc is somewhat distorted but the presence of five gonopores is clearly visible. Both the anterior and posterior pairs of petals are well-developed and almost closed distally. The anterior petal is damaged anteriorly; therefore, it is not clear if it is completely closed. All petals are slightly inflated and show a leaf-shaped form. The ridge between the pore pairs carries 13 to 15 regularly arranged primary tubercles (Figure 5.2). Interambulacral tuberculation is rather small (primary tubercle-diameter 0.25 mm) and irregularly arranged.

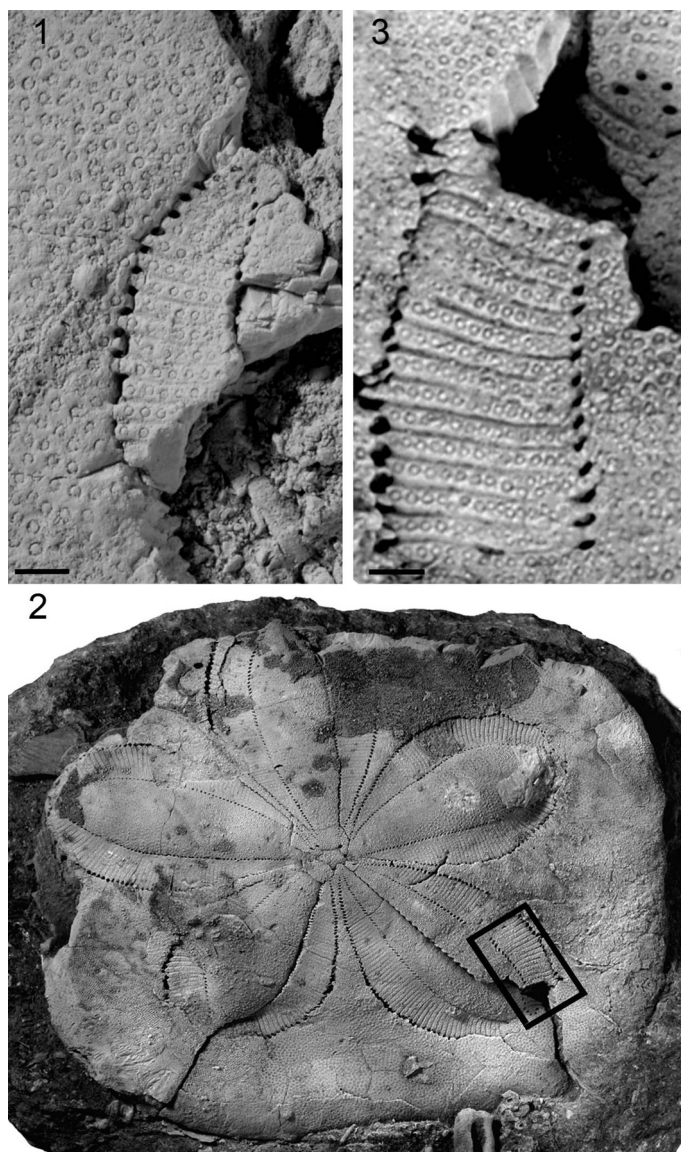


FIGURE 5. *Clypeaster* sp., La Vela Formation, Falcón state, Venezuela. 1, *Clypeaster rosaceus* Linnaeus, 1758, detail of petal, UNEFM-IF-007. 2, *Clypeaster subdepressus*, UNEFM-IF-009, aboral view; rectangle borders the petal detail shown in 3. 3, *Clypeaster subdepressus* (Gray, 1825), detail of posterior petal, UNEFM-IF-009. Scale bar equals 1 mm.

Remarks. - Due to the exceedingly high number of synonyms and misidentifications, the description of *C. subdepressus* remained dubious until Mortensen (1948) published a comprehensive revision. Due to the above mentioned reasons, the spatial distribution of *C. subdepressus* is uncertain, but this species appears to be distributed throughout the entire Caribbean from Florida to the Atlantic coast of Brazil.

The key trait that distinguishes *C. subdepressus* from other similar *Clypeaster* species is the high number of primary tubercles (13-15) on ridges

between the pore-pairs. This feature is unfortunately not referred to in Kier's (1963a) description of Florida's *C. sunnilandensis* Kier, 1963, for which he states that its only difference to *C. subdepressus* is an opened anterior (III.) petal. Since the anterior petal in our specimen is damaged, it is hard to verify this. However, due to the spatial distribution of both species, we are confident to assign our material to *C. subdepressus*.

Stratigraphic range. - The La Vela Formation (the Late Miocene to the Pliocene); Pliocene to Recent.

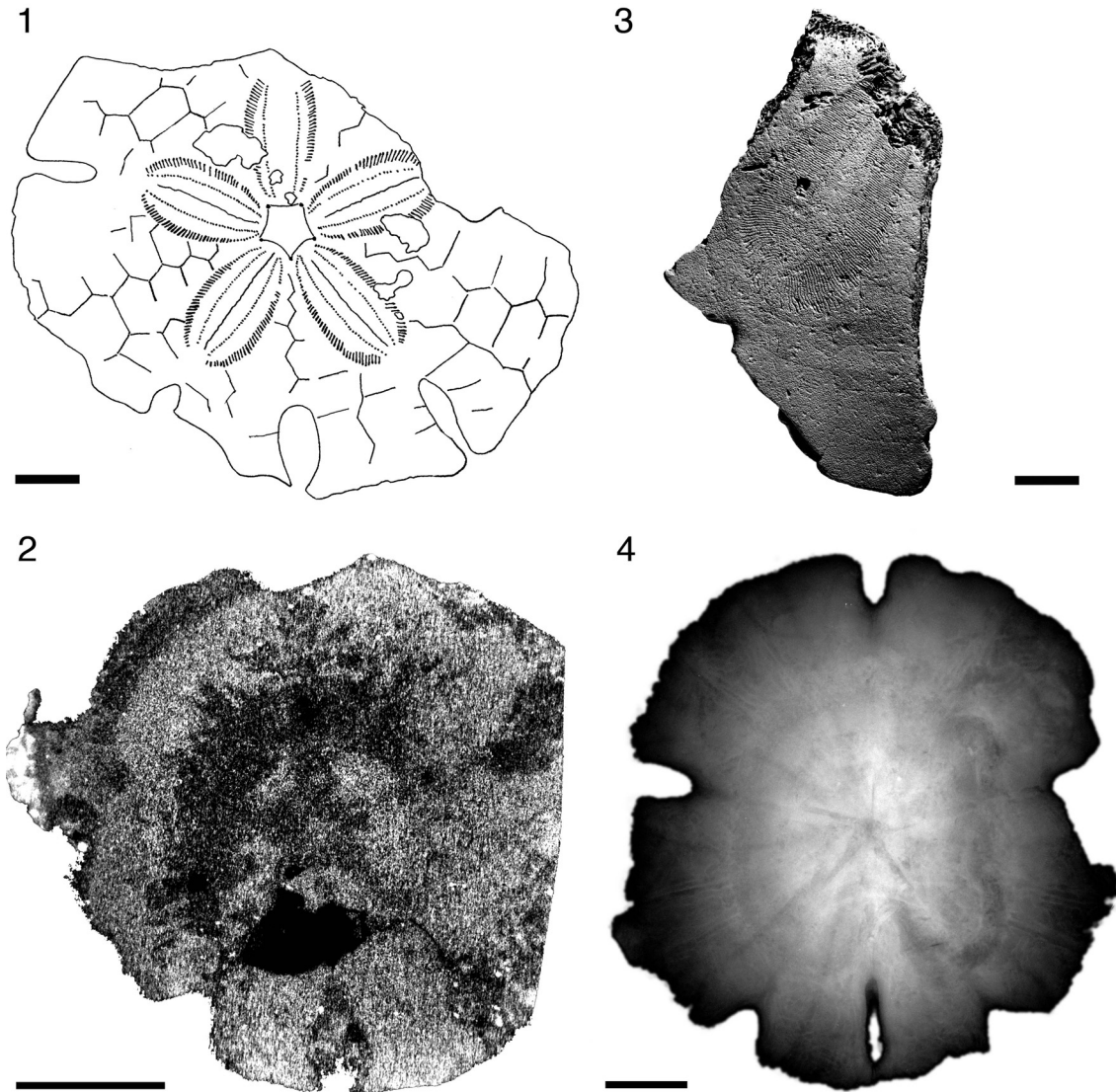


FIGURE 6. Mellitidae, San Gregorio Formation, Falcón state, Venezuela. 1, *Melitella falconensis* Cooke, 1961, aboral plate diagram, UNEFM-IF-016. 2, *Melitella falconensis* Cooke, 1961, CT- exposure, showing Aristotle's lantern and a series of buttresses UNEFM-IF-021. 3, *Encope* cf. *emarginata* (Leske, 1778), UNEFM-IF-029. 4, *Encope secoensis* Cooke, 1961, x-ray, showing internal buttressing and intestine tract cavity UNEFM-IF-025. Scale bar equals 10 mm.

Locality. - La Vela region, Falcón State, Venezuela.

Spatial distribution. - The Caribbean from Florida to northern Brazil.

Material. - The best preserved specimen has a well preserved aboral side UNEFM-IF-009. The additional specimens represent fragments mostly showing parts of the petals (UNEFM-IF-010, UNEFM-IF-011, UNEFM-IF-012, UNEFM-IF-013).

MELLITIDAE Stephanini, 1912
MELLITELLA Duncan, 1889.

Type species. - *Encope stokesii* Agassiz, 1841, by subsequent designation.

Range and distribution. - Miocene to Recent, East Pacific and Caribbean.

Melitella falconensis Cooke, 1961
Figure 6.1

Description. - The test sizes range between 30 and 50 mm in diameter. The horizontal outline of the test is subcircular with a posterior truncation. Five ambulacral notches on different specimens show different degrees of closure. The anal lunule is small and situated near the posterior margin, i.e.,

it always lies completely behind the posterior petals UNEFM-IF-016, (Figure 6.1). On the apical surface, five gonopores are clearly visible, as well as weakly bowed petals that are converging distally but remain opened. All petals are rather short and approximately half as wide as long UNEFM-IF-016. The periproct is situated midway between the peristome and the margin and does not reach the fifth basicoronal interambulacral plate UNEFM-IF-018. The peristome is small, central and pentagonal. Conspicuous food grooves are bifurcating immediately distal to the basicoronal plates and are converging around the ambulacral notches UNEFM-IF-018.

Remarks. - The literature is ambiguous in defining the taxon *Mellitella*; by some authors, it is defined as an independent genus (Smith 2005; Mooi 1989) and by others as a subgenus (Mortensen 1948; Cooke 1961; Schultz 2006) within the genus *Encope*. These two taxa share significant taxonomic traits, such as five gonopores, five well-marked ambulacral notches or lunules and a periproct that does not indent the basicoronal plates in the fifth interambulacrum. *Mellitella*'s simpler inner structure and more fragile separation of the intestine tract from the central cavity are the most distinctive features (Mortensen 1948). To study these and other features we made a tomography of UNEFM-IF-021 (Figure 6.2). However, the small anal lunule is situated near the posterior margin that always lies completely behind the posterior petals; this is, for the analysis of our material, the most important feature that distinguishes *Mellitella* from *Encope*.

Mellitella includes, besides *M. falconensis*, the two species *M. stokesii* (Recent) and *M. angelensis* Durham, 1950 (Pliocene). These are, however, known from the Pacific coast only (Smith 2005). The Chiguaje formation (Miocene) and the San Gregorio Formation (Pliocene) in Venezuela appear to be the only known localities where *M. falconensis* is found.

Cooke (1961) mentioned that ambulacral notches are not yet closed in smaller specimens. During the examination of this new material, however, no such correlation between size and notch closure could be found. During the examination of this new material, however, no such correlation between size and notch closure could be found, consistent with the material of *M. falconensis* in the collection of the Natural History Museum Basel that also does not show this ontogenetic closure of the ambulacral notches. It appears likely that more factors (environment, injuries) other than just the onto-

genetic stage have an influence on the degree of notch closure.

Stratigraphic range. - Cocuiza Member of the San Gregorio Formation (the Late Pliocene to the Early Pleistocene).

Locality. - Cocuiza West und Cocuiza East locality, Codore Adentro region, Falcón State, Venezuela.

Spatial distribution. - Falcón State, Venezuela.

Material. - The fossil material includes eleven fragments of varying preservation quality (UNEFM-IF-014 to -024).

ENCOPE Agassiz, 1841.

Type species. - *Encope grandis* Agassiz, 1841, by original designation.

Range and distribution. - Early Miocene to Recent, both coasts of Central and South America but mainly in the Gulf of California and Florida.

Encope cf. *emarginata* (Leske, 1778)

Figure 6.3

Description. - This species is characterized by its long and somewhat irregular anal lunule. The anal lunule incises deeply between the posterior petals (UNEFM-IF-029). The petal is slightly curved and converges distally but remains open. The food grooves are bifurcating and become highly branched distally. Internal structures are sponge-like, i.e., the internal buttressing is extremely dense.

Remarks. - *Encope emarginata* is widely distributed from the Pliocene until today in the entire Caribbean, from the intertidal zone to a depth of about 50 m. The length of the anal lunule and the lunule/test length-ratio were used to estimate the size of the actual specimen. The lunule/test length-ratio was calculated using figure 658 from Schultz (2006). The estimated length is 115 mm which is within the range of intraspecific variability known from *E. emarginata* (Schultz 2006).

Stratigraphic range. - Cocuiza Member of the San Gregorio Formation (Late Pliocene to Early Pleistocene); Pliocene to Recent.

Locality. - Concuiza West locality, Codore Adentro region, Falcón State, Venezuela.

Spatial distribution. - The Caribbean, south-eastern USA and north-eastern South America.

Material. - One poorly preserved fragment showing the fifth ambulacra and the left part of the anal lunule, probably Recent (UNEFM-IF-029).

Encope secoensis Cooke, 1961

Figure 6.4

Description. - The diameter of the completely preserved test amounts to 62 mm (UNEFM-IF-025). The test shows a discoidal shape with a flat oral side and the highest point being located anteriorly. Test margin is interrupted by five well-marked ambulacral notches that show the tendency to close by bending their edges toward each other. The anal lunule is elongated, narrow and extends between the distal tips of the posterior petals. The apical disc is star-shaped showing five gonopores. All petals are open distally, although the poriferous zones are approaching each other. Posterior petals are somewhat longer than the anterior petals. The periproct is elongated and situated closer to the anal lunule than to the peristome, although it does not approach the basicoronal plates of the fifth interambulacrum. The peristome is situated orally, directly beneath the apical disc on the aboral surface. The food grooves are branching immediately behind the basicoronal plates and converging distally around the ambulacral notches.

Remarks. - Like *Melitella falconensis*, *E. secoensis* is also known only from the Chiguaje formation (Miocene) and the San Gregorio Formation (Pliocene) in Venezuela. Because of the thin test margin, incompletely closed ambulacral notches, the food groove shape and the elongated narrow anal lunule, *E. secoensis* somewhat resembles *E. michelini* L. Agassiz, 1841. Nevertheless, the test of *E. secoensis* has its highest point anterior to the centre which distinguishes it from *E. michelini*. An elongated periproct, situated closer to the anal lunule than to the peristome, is an additional diagnostic feature of *E. secoensis*. To document the inner structure of *E. secoensis*, we took an x-ray image (Figure 6.4) for the first time.

Stratigraphic range. - Cocuiza Member of the San Gregorio Formation (Late Pliocene to Early Pleistocene).

Locality. - Cocuiza East locality, Codore Adentro region, Falcón State, Venezuela.

Spatial distribution. - Falcón State, Venezuela.

Material. - One well-preserved specimen (UNEFM-IF-025) and three rather well-preserved fragments, all darker coloured (UNEFM-IF-026, UNEFM-IF-027, UNEFM-IF-028).

SPATANGOIDA Agassiz, 1840

PRENASTERIDAE Lambert, 1905

AGASSIZIA Valenciennes, in Agassiz and Desor, 1847.

Type species. - *Agassizia scrobiculata* Valenciennes in Agassiz and Desor, 1847, by original designation.

Range and distribution. - Middle Eocene to Recent, mainly Caribbean.

Agassizia excentrica Agassiz, 1869

Figure 7.1

Description. - The longest diameter of the ovate test without anterior sulcus is 23 mm long and the shortest 21 mm (UNEFM-IF-030). The long, weakly sunken anterior petal is broadening anteriorly and carries only one row of pore pairs (Figure 7.2). The posterior column of the anterior petal pair is developed whereas the anterior series is inconspicuous. All petals are slightly depressed. The posterior petals are short, just about 1/3 of the length of the anterior ones, and show a less developed upper part of the anterior series of pore pairs (Figure 7.2). The well-developed peripetalous fasciole is situated very low anteriorly, passing three plates below the end of the anterior petals, and rises steeply towards the end of the posterior petals forming a parabolic trace. Behind the anterior pair petals, the peripetalous fasciole is touching the lateroanal fasciole that is running towards the periproct and passes beneath it. Due to poor preservation of the oral surface, one can only suspect the position of a D-shaped peristome.

Remarks. - *Agassizia excentrica* is distributed throughout the entire Caribbean. The reduced pores of anterior series of pore pairs on the posterior petals are the main difference to the pacific species *A. scrobiculata* Valenciennes, 1846. The posterior petal in our specimen has fewer plates with reduced pores in the outer column than shown in Mortensen (1951, figure 157).

Stratigraphic range. - Cocuiza Member of the San Gregorio Formation (Late Pliocene to Early Pleistocene); Recent.

Locality. - Cocuiza West locality, Codore Adentro region, Falcón State, Venezuela.

Spatial distribution. - The Caribbean.

Material. - One specimen which is missing the first and second petals UNEFM-IF-030, and a second specimen showing just one half of the test with the lateroanal fasciole UNEFM-IF-031.

SCHIZASTERIDAE Lambert, 1905

MOIRA Agassiz, 1872.

Type species. - *Moira atropos* (Lamarck, 1816), by ICZN designation, 1948.

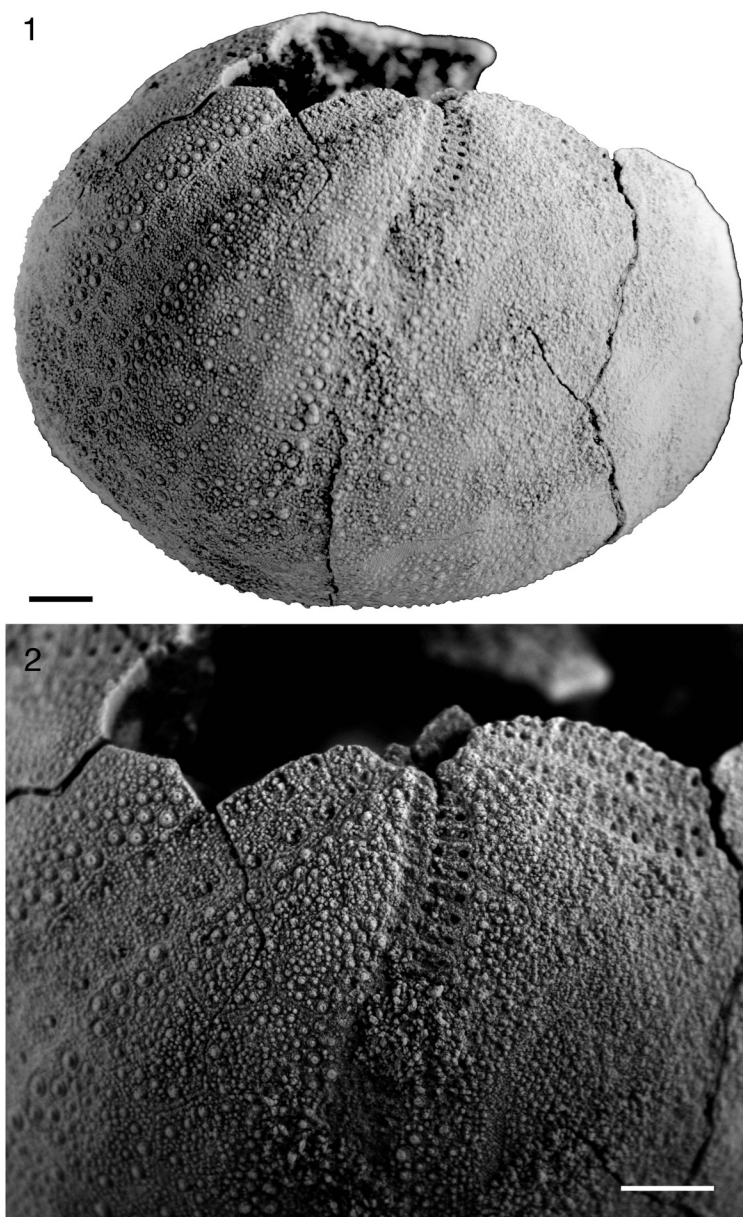


FIGURE 7. *Agassizia excentrica* Valenciennes, in Agassiz & Desor, 1847, San Gregorio Formation, Falcón state, Venezuela, UNEFM-IF-030. 1, detail of petals, showing anterior petal with only one row of pore pairs, and short posterior petal with less developed upper part of the anterior series of the pore pairs. 2, test, lateral view. Scale bar equals 1 mm.

Range and distribution. -Miocene to Recent, Indo-Pacific, Caribbean, western Atlantic.

Moira atropos (Lamarck, 1816)
Figure 8

Description. - The test lengths range from about 20 to 40 mm and the maximum test height varies between 10 and 15 mm. The test is ovate in outline with an anterior sulcus and vertically truncated at its posterior end (UNEFM-IF-032). The aboral test

side is highly vaulted in contrast to the oral side that is flattened. The aboral surface of the test is characterized by deeply sunken ambulacra (Figure 8.1). The anterior ambulacrum is the deepest, but it is shallowing near the ambitus. The posterior petal pair is half as long as the anterior petal pair. The periproct is situated high up on the vertical posterior end (Figure 8.2). The peripetalous and lateral fascioles are well developed. The kidney-shaped peristome is wider than long and is situated close

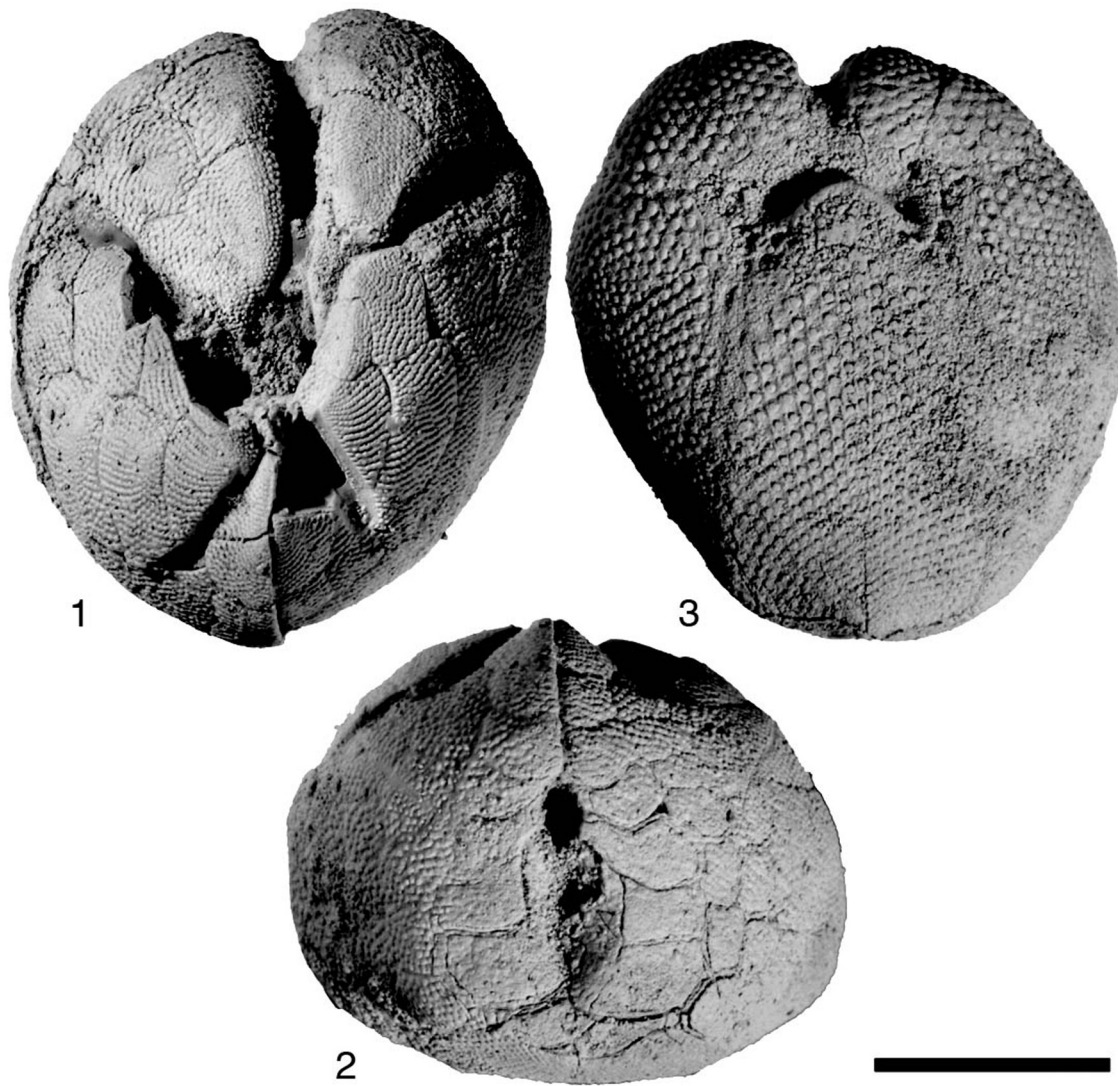


FIGURE 8. *Moira atropos* Agassiz, 1872, San Gregorio Formation, Falcón state, Venezuela, UNEFM-IF-032. 1, aboral view. 2, oral view. 3, posterior view. Scale bar equals 10 mm.

to the anterior end. The wide and short labial plate is prominent but not extending posteriorly beyond the first ambulacral plates (Figure 8.3). The sternal plates are long and slightly widened posteriorly (2/3 as broad as long). Tuberculation on both aboral and oral sides is uniform and dense, but somewhat more prominent on the oral side.

Remarks. - *Moira* is easily recognizable by its deep ambulacra. These ambulacra appear to be an adaptation to an infaunal mode of life, allowing water to flow through the ambulacra which are kept free of sediment by spines and tube feet. Mortensen (1951) emphasized that most spatangoids, although lacking deep ambulacra, may well have lived infaunally, independent to some extent of the sediment composition.

Due to the vertically truncated shape of the posterior end of the test, *M. clotho* Michelin, 1855 resembles *M. atropos*. However, in contrast to *M. atropos*, *M. clotho*'s sternum is strongly widened posteriorly: it is 3/4 as broad as long. *Moira atropos* is known from the east coast of the Americas, from Massachusetts, USA to Sao Paulo, Brazil.

Stratigraphic range. - Cocuiza Member of the San Gregorio Formation (Late Pliocene to Early Pleistocene); Recent.

Locality. - Cocuiza West locality, Codore Adentro region, Falcón State, Venezuela.

Spatial distribution. - The east American coast from North Carolina to Brazil, the Caribbean.

TABLE 1. Species lists of the three localities.

| Cocuiza West | Cocuiza East | La Vela |
|-------------------------------------|-------------------------------|--------------------------------------|
| <i>Arbacia punctulata</i> | <i>Mellitella falconensis</i> | <i>Prionocidaris</i> sp. |
| <i>Mellitella falconensis</i> | <i>Encope secoensis</i> | <i>Lytechinus</i> cf. <i>euerces</i> |
| <i>Encope</i> cf. <i>emarginata</i> | | <i>Clypeaster subdepressus</i> |
| <i>Agassizia excentrica</i> | | <i>Clypeaster rosaceus</i> |
| <i>Moiria atropos</i> | | |

Material. - Four well-preserved specimens: UNEFM-IF-032 to -035.

RESULTS AND DISCUSSION

Palaeoecology

The Neogene sediments of Falcón State in northwestern Venezuela yielded 10 echinoid species. Although we cannot make any statistically well-founded statement about echinoid diversity and palaeoecology in this region, our study demonstrates the potential of the region to provide both taxonomic and palaeoecological information.

Each of these localities shows a different species assemblage (Table 1). Only one of 10 species, *Mellitella falconensis*, occurs in two of the three sites (in both San Gregorio sites). *Encope secoensis* is the only other fossil species found in the Cocuiza East site. The Cocuiza West site comprises five species, *Mellitella falconensis*, *Encope* cf. *emarginata*, *Agassizia excentrica*, *Moiria atropos* and *Arbacia punctulata*. The two San Gregorio sites are situated only 1 km apart and belong to the same stratigraphic unit; therefore, we hypothesize that these sediments and fossils come from the same habitat. The difference in the species composition may be the result of lateral variation within the habitat and the low sample size.

The site in the La Vela Formation displays a different species composition to the San Gregorio sites. At this locality, four species were found, two of the genus *Clypeaster* and two regular echinoids *Prionocidaris* sp. and *Lytechinus* cf. *euerces*.

The three localities studied here are rich in other invertebrate fossils such as bivalves and gastropods. In contrast to the San Gregorio formation sites, the La Vela site preserves coral fragments indicating different habitat-properties. This is confirmed with known palaeoenvironmental records (Ministerio de Energía y Minas 1997; Smith 2008). As previously stated, the deposits of the Cocuiza Member display characters of a moderate wave energy coastline habitat and the La Vela sediments

were deposited in a middle neritic habitat, indicating a depth gradient within the Falcón Basin (Smith 2008; Sánchez-Villagra et al. 2010). After analyzing the habitat preferences (Mortensen 1928-1951; Schultz 2006) of extant relatives of the sampled fossil taxa, we compared these modes of life to the species found in the Cocuiza sites, which accordingly inhabited still and shallower waters than the living representatives of the species found in the La Vela site. These habitat differences may be one possible explanation for the heterogeneous occurrence of echinoid genera in the San Gregorio and the La Vela formations. Difference in age of deposits and geological events occurring at the time may have caused the local environmental differences described above.

Palaeogeographic Implications and the Closure of the Central American Isthmus

The most significant geological event in the Caribbean Neogene was the gradual closure of the Central American Isthmus completed in the late Pliocene, about 2.8 m.y.a. (Lessios 2008). The closure was accompanied by significant global environmental changes (Cronin and Dowsett 1996). One of them, the change in the Global Ocean Conveyor, had an impact on the global climate. On a more local scale, the formation of this land bridge resulted in contrasting environmental conditions on the Pacific and the Caribbean coasts (Lessios 2008). Hence, the Caribbean waters, in contrast to the Pacific ones, are characterized by the absence of upwelling (except in Venezuela), low seasonality, increase of carbonate deposition and decrease of the plankton productivity (Aguilera et al. 2010). The relation between the age of the deposits studied here and the degree of closure of the Central American Isthmus (Coates and Obando 1996) may have affected the differing species compositions of the collections from the three localities.

The physical changes, such as fluctuations in sea level, salinity, ocean currents and temperature, caused by the closure of the Central American Isthmus, had a great impact on benthic communities

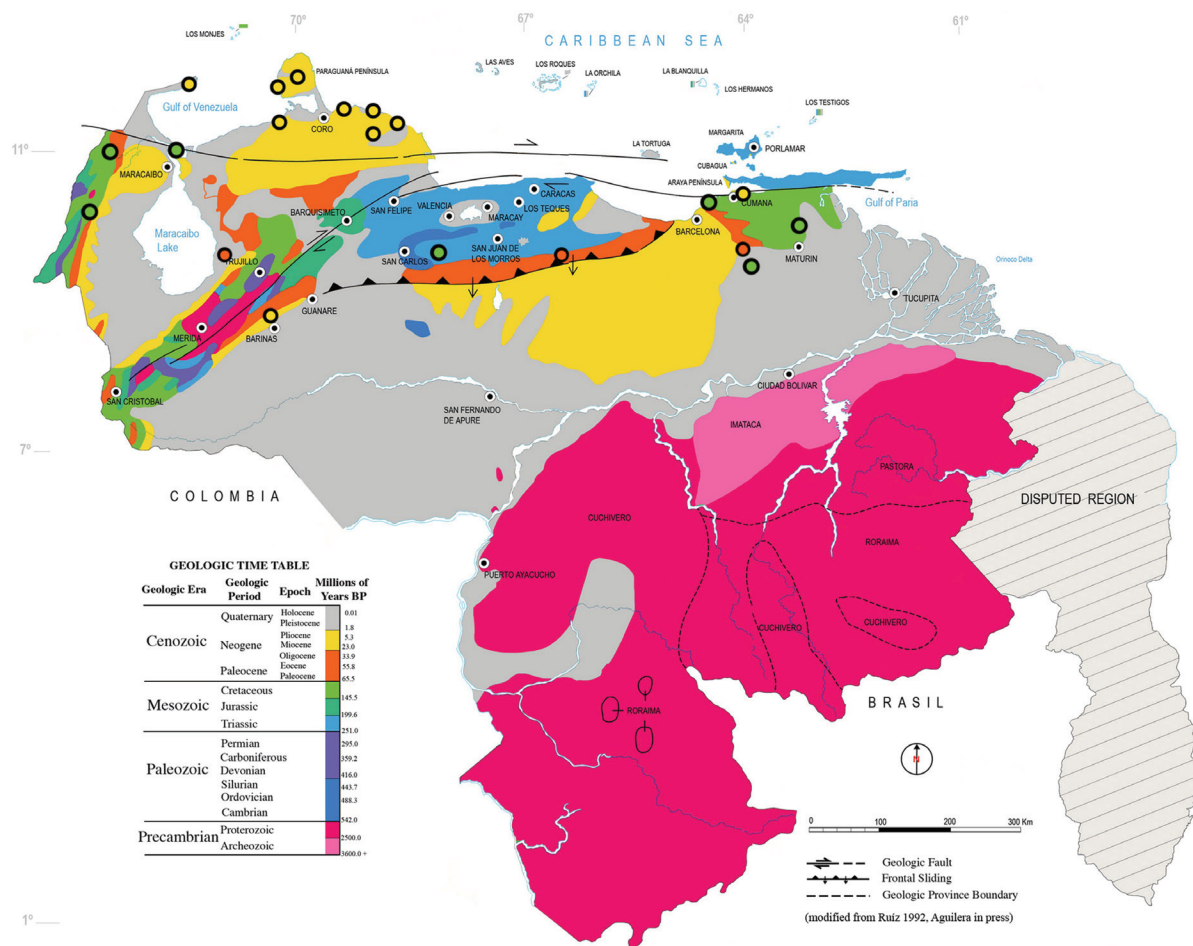


FIGURE 9. Simplified geological map of Venezuela with marked fossil sites. Based on Table 2.

(Aguilera et al. 2010). The described material contains three taxa, *Mellitella falconensis*, *Encopeseconoensis* and *Prionocidaris*, that appear to have been affected by the accompanying effects of the closure. *Mellitella falconensis* and *Encopeseconoensis* are known only from the Venezuelan San Gregorio Formation; therefore, they became extinct during the last few million years. The changing environment and its conditions led to extinction of other invertebrate groups (Johnson 1995; Aguilera et al. 2010; O'Dea et al. 2007; Todd et al. 2001). The genus *Prionocidaris* experienced a shift of its distribution pattern from the Mediterranean and Caribbean regions, from where the fossils of this genus are known, to the Indian and Pacific Oceans, where the extant species of this genus occur (Mortensen 1928). The route and the exact time of the shift are unknown. Thus, the genus could have spread to the Pacific before the closure of the Central American Isthmus or moved to the Indian Ocean before the separation of the Mediter-

anean Sea and the Indian Ocean due to a drift of the African continent. The present radiation of *Prionocidaris* may be a consequence of both processes (Cutress 1980).

Diversity Analyses of Venezuelan and All Caribbean Fossil Echinoids

Echinoid fossils from Venezuela have been repeatedly reported during the last decades. Most of the material is from the Cenozoic era (Jeannet 1928; Cooke 1941; Von der Osten 1957; Cooke 1961; Anisgard 1954; Weisbord 1969; Mooi and Peterson 2000), but there are nine genera known from the Early Cretaceous (Cooke 1961; Cutress 1980) and one record dates back to the Permian (Hoover 1981).

Together with our new records, the previously reported Venezuelan echinoid fossils presented in this work include 38 genera collected mostly from the northern half of the country, especially from Falcón State (Figure 9, Table 2). Since Venezuela,

TABLE 2. The Venezuelan fossil record.

| Genus | Species | Author that reported the sp. in Venezuela | Locality | Formation or unit referred to in original publication | Age |
|---|-----------------------|---|--|--|--|
| <i>Agassizia</i> | <i>scrobiculata</i> | Cooke, 1961 | Rio Seco area, Falcón State | San Gregorio | Pliocene |
| <i>Agassizia</i> | <i>clevei</i> | Jeannet, 1928 | Entre Taratara et La Vela, Falcón State | La Vela | Middle Miocene |
| <i>Agassizia</i> | <i>excentrica</i> | this work | Rio Seco area, Falcón State | San Gregorio | Late Pliocene, Early Pleistocene |
| <i>Antillaster</i> | <i>lamberti</i> | Cooke, 1961; Jeannet, 1928 | Sabanas Altas, Falcón State El Vigía, Falcón State Cerro La Luz, Falcón State | upper part of the "couches d'Ojo de Agua"; La Vela | Middle Miocene, Late Miocene |
| <i>Arbacia</i> | <i>punctulata</i> | this work | Rio Seco area, Falcón State | San Gregorio | Late Pliocene, Early Pleistocene |
| <i>Brissoma</i> | <i>vonderschmitti</i> | Jeannet, 1928 | Entre Puerto Escandido et Aguide, Falcón State | superior series of d'Agua Salada | Early Miocene |
| <i>Brissopsis</i> | <i>antillarum</i> | Cooke, 1961 | Pueblo Nuevo, Falcón State | La Vela; Anguilla; Paraguana | Middle Miocene, Late Miocene |
| <i>Brissopsis</i> | cf. <i>atlantica</i> | Weisbord, 1969 | Cabo Blanco area | "Cabo Blanco Group" | Pliocene - Recent |
| <i>Cassidulus</i> (<i>Cassidulus</i>) | <i>falconensis</i> | Cooke, 1961 | San Jose de la Costa, Falcón State | upper part of the "couches d'Ojo de Agua"; Punta Gavilan | Middle Miocene |
| <i>Cidaroida</i> | indet. | Hoover, 1981 | Mérida State | Palmarito | Permian |
| <i>Clypeaster</i> | sp. | Jeannet, 1928 | Region de Capadare, Falcón State | "Damsite series" | Middle Miocene |
| <i>Clypeaster</i> | <i>rosaceus</i> | Cooke, 1961; this work | Rio Motoruco, Falcón State Rio Coro, SW Cumarebo field, Falcón State playa de Taratara, Falcón State Goajira Peninsula, Zulia State Isla Margarita, Nueva Esparta Stat | La Vela | Miocene - Recent, Late Miocene, Pliocene |
| <i>Clypeaster</i> | <i>kugleri</i> | Jeannet, 1928 | Puerto Leon, entre Taratara et La Vela, Falcón State | upper part of "Damsite Series" | Middle Miocene |
| <i>Clypeaster</i> | <i>subdepressus</i> | this work | playa de Taratara, Falcón State | La Vela | Late Miocene, Pliocene |
| <i>Echinolampas</i> | sp. | Jeannet, 1928 | Caño Leon, Falcón State | "Damsite series" | Middle Miocene |
| <i>Echinolampas</i> | <i>lycopersicus</i> | Cooke, 1961 | Bejuco, Araurima Valley, Falcón State | ? | Middle Miocene |
| ? <i>Echinolampas</i> | sp. | Weisbord, 1969 | Cabo Blanco area | "Cabo Blanco Group" | ? |
| <i>Echinometra</i> | <i>lucunter</i> | Weisbord, 1969 | Cabo Blanco area | ? | Late Miocene - Recent |
| <i>Encope</i> | sp.A | Jeannet, 1928 | Entre La Caridad et Mirimiri, Falcón State | "Unt. Pectenbeds" | Middle Miocene |
| <i>Encope</i> | sp.B | Jeannet, 1928 | Entre La Caridad et Mirimiri, Falcón State | "Unt. Pectenbeds" | Middle Miocene |
| <i>Encope</i> | sp.C | Jeannet, 1928 | Entre La Caridad et Mirimiri, Falcón State | "Unt. Pectenbeds" | Middle Miocene |
| <i>Encope</i> | sp.D | Jeannet, 1928 | Boca de Hueque, Falcón State | "Couches d'Ojo de Agua" | Middle Miocene |

TABLE 2 (continued).

| Genus | Species | Author that reported the sp. in Venezuela | Locality | Formation or unit referred to in original publication | Age |
|--|-----------------------|---|--|---|--|
| <i>Encope</i> | sp.E | Jeannet, 1928 | Boca de Hueque, Falcón State | "Couches d'Ojo de Agua" | Middle Miocene |
| <i>Encope</i> | michelini | Cooke, 1961 | Bocade Hueque, Falcón State Cumana, Sucre State | San Gregorio; "Couches d'Ojo de Agua" | Miocene - Recent, Middle Miocene, Pliocene |
| <i>Encope</i> | kugleri | Cooke, 1961, Jeannet, 1928 | La Jovita de Candado, Falcón State Rio Seco Area, Falcón State E. de Corrocorote, Falcón State | Capadare limestone; Chiguaje Member; San Gregorio | Middle Miocene, Late Miocene |
| <i>Encope</i> | wiedermayeri | Jeannet, 1928 | Boca de Hueque, Falcón State | "Couches d'Ojo de Agua" | Middle Miocene |
| <i>Encope</i> | vonderschmitti | Jeannet, 1928 | Boca de Hueque, Falcón State | "Couches d'Ojo de Agua" | Middle Miocene |
| <i>Encope</i> | emarginata | Weisbord, 1969; this work | Rio Seco area, Falcón State Cabo Blanco area | San Gregorio; "Cabo Blanco Group" | Late Miocene, Late Pliocene, Early Pleistocene - Recent |
| <i>Encope</i> | secoensis | Cooke, 1961; this work | Rio Seco area, Falcón State Cabo Blanco area | San Gregorio | Middle Miocene, Pliocene, Late Pliocene, Early Plesistocene |
| <i>Epiaster</i> | whitei | Cooke, 1961 | Rio Caripe, Monagas State | ? | Early Cretaceous |
| <i>Eucidaris</i> | tribuloides | Weisbord, 1969; Cutress, 1980 | Cabo Blanco area Isla Margarita, Nueva Esparta State Araya, Sucre State | Abisinia; "Cabo Blanco" | Oligocene? - Recent |
| <i>Eupatagus</i> | sp. | Anisgard, 1954 | Montatan, Trujillo State | Misoa | Late Eocene |
| <i>Eupatagus</i> | clevei | Cooke, 1961 | San Mateo, Lara State | ? | Late Eocene |
| <i>Eurhodia</i> | falconensis | Jeannet, 1928 | La Guarava - Sta Clara, Falcón State | upper part of the "couches d'Ojo de Agua"; La Vela | Middle Miocene |
| <i>Hemiaster</i> | sp. | Cooke, 1961 | Monagas State | ? | Early Cretaceous |
| <i>Heteraster</i> (<i>Washitaster</i>) | bravoensis | Cooke, 1961 | Rio Socuy, Zulia State | Cogollo limestone | Early Cretaceous (late Albian) |
| <i>Heteroclypeus</i> | wiedermayeri | Jeannet, 1928 | Cerro de Chichiriviche, Falcón State | Calcaire de Capadare | Middle Miocene |
| <i>Holectypus</i> (<i>Coenholectypus</i>) | planatus aponensis | Cooke, 1961 | Rio Apon, Zulia State | Capacho | Early Cretaceous (Middle Albian to Vraconian) |
| <i>Leoida</i> | divinata | Mooi & Peterson, 2000 | Cabo Blanco area | "Cabo Blanco Group" | Early Pliocene |
| <i>Lovenia</i> | cf. <i>dumblei</i> | Cooke, 1961 | San Jose de la Costa, Falcón State | Punta Gavilan | Miocene |
| <i>Lytechinus</i> | cf. <i>euerces</i> | this work | playa de Taratara, Falcón State | La Vela | Late Miocene, Pliocene |
| <i>Lytechnus</i> | variegatus | Cooke, 1961 | Rio Seco area, Falcón State | San Gregorio | Pliocene |

TABLE 2 (continued).

| Genus | Species | Author that reported the sp. in Venezuela | Locality | Formation or unit referred to in original publication | Age |
|-----------------------|-------------|---|--|---|--|
| <i>Mellitella</i> | falconensis | Cooke, 1961; this work | Rio Seco area, Falcón State | Chiguaje Member; San Gregorio | Late Miocene, Pliocene, Late Pliocene, Early Pleistocene |
| <i>Moira</i> | antropos | Cooke, 1961, Weisbord, 1969; this work | Rio Seco area, Falcón State Cabo Blanco area | San Gregorio; "Cabo Blanco Group" | Pliocene, Late Pliocene, Early Pleistocene |
| <i>Oligopygus</i> | rotundus | Cooke, 1961 | Bolivar, Zulia State Alta Casa Nueva, Guárico | Tinajitas | Late Eocene |
| <i>Oligopygus</i> | christi | Jeannet, 1928 | Rio Calderas pres de Los Baños, Barinas | ? | Late Eocene |
| <i>Oligopygus</i> | nancei | Cooke, 1961, 1941 | Rio amana, Monagas State | Tinajitas | Late Eocene |
| <i>Opissaster</i> | sp. | Jeannet, 1928 | Aguide-Escondido; Falcón State | upper part of the d'Agua Salada | Early Miocene |
| <i>Opissaster</i> | kugleri | Jeannet, 1928 | Aguide-Escondido; Falcón State | upper part of the d'Agua Salada | Early Miocene |
| <i>Pauropygus</i> | sp. | Jeannet, 1928 | Rio Calderas, Barinas | ? | Late Eocene |
| <i>Pericosmus</i> | sp. | Jeannet, 1928 | Environs de Capadare; Falcón State | "Damsite series" | Middle Miocene |
| <i>Pericosmus</i> | stehlini | Cooke, 1961; Jeannet, 1928 | Coro, Falcón; El Vigía, Falcón State | "Damsite series"; La Vela; Paraguana | Middle Miocene?, Late Miocene |
| <i>Phyllobrissus</i> | zulianus | Cooke, 1961 | Roas Island, Zulia State | Apón | Early Cretaceous (Aptian) |
| <i>Plagiobrissus</i> | grandis | Cooke, 1961 | Paraguana Peninsula, Falcón State | Paraguana | Miocene? |
| <i>Plagiobrissus</i> | lamberti | Jeannet, 1928 | Chemin de Guaidima a Riecito, Falcón State | "Couches d'Ojo de Agua" | Middle Miocene |
| <i>Prionocidaris</i> | sp. | this work | playa de Taratara, Falcón State | La Vela | Late Miocene, Pliocene |
| <i>Pseudananchys</i> | sp. | Cooke, 1961 | Island of Chimana Grande, Anzoátegui State | Chimana | Early Cretaceous (early to middle Albian) |
| <i>Rhynobrissus</i> | rostratus | Cooke, 1961 | San Jose de la Costa, Falcón State | Punta Gavilan | Miocene? |
| <i>Schizaster</i> | eurynotus | Jeannet, 1928 | Punta de los Zamuros pres San Jose de la Costa, Falcón State | Punta Gavilan | Middle Miocene |
| <i>Stereocidaris?</i> | sp. | Von der Osten, 1957 | Bahia de Santa Fe, Sucre State | Barranquin | Early Cretaceous |
| <i>Tetragramma</i> | sp. | Cooke, 1961 | El Pao, Cojedes State | ? | Early Cretaceous (Late Albian) |
| <i>Tripneustes</i> | tobleri | Jeannet, 1928 | Punta de los Zamuros pres San Jose de la Costa, Falcón State | Punta Gavilan | Middle Miocene |
| <i>Tylocidaris?</i> | sp. | Von der Osten, 1957 | Bahia de Santa Fe, Sucre State | Barranquin | Early Cretaceous |

Trinidad and Tobago together with part of the Dutch Antilles off the coast (Aruba, Curacao and Bonaire) can be considered as a geographical unit, echinoid fossil diversity in these regions was analysed as a whole. This region holds a total of 51 genera. In the following, we will refer to this whole region when we discuss the diversity of Venezuela.

For the diversity analyses, we applied several methods: we calculated the mean standing diversity with or without singletons and counted boundary crossers. The mean standing diversity approach turned out to be a reasonable estimate of the fossil record diversity through time, since it deals well with long ranging taxa and turnovers (origination and extinction) within certain time interval (Hammer and Harper 2005). To be able to better understand the echinoid evolutionary patterns in the Caribbean, the same diversity analyses were applied to echinoid faunas of other Caribbean regions: Central America, Lesser Antilles and Great Antilles (Appendix). Echinoid fossil records of all mentioned regions were also analyzed together to obtain the general echinoid diversity patterns for the whole Caribbean (Figure 10). Since Jamaica and Cuba have a rich echinoid fossil record they were analyzed separately. We are aware of a potential bias within the Cuban fossil record and its need of revision. Furthermore, the irregular echinoids clearly outnumber the regular ones, probably due to a more rigid test that facilitates preservation (Kier 1963b; Donovan 2001). Due to the lower preservation potential of regular echinoids fossils and of the lack of thorough systematic collecting of echinoid fossils, the number of known taxa is most probably far from reflecting complete sampling.

Three diversity decreases are recognizable in the overall pattern of Venezuelan echinoids (Figure 10, Table. 3): at the end of the Early Cretaceous, around the Eocene-Oligocene boundary and after the diversity peak in the Middle Miocene. The gap in the fossil record between the Early Cretaceous and the Late Eocene is most probably an artifact of biased sampling rather than of an extinction event. All of the analyzed regions show a diversity decrease either in the beginning or at the end of the Late Cretaceous. It is not clear if this is as well an artifact of biased sampling or some other unknown event. The Eocene-Oligocene boundary extinction event, caused by severe cooling and changes in oceanographic currents, is well documented (Prothero 1989; Berggren and Prothero 1992). The extinction of echinoid taxa at the Eocene-Oligocene boundary is also documented

from other Caribbean echinoid faunas (McKinney et al. 1992; Dixon and Donovan 1994), and our review of the data suggests this extinction event for the first time for Venezuela. Due to different results of our diversity analyses, it is not clear, however, whether this diversity decrease in Venezuela happened exactly on the Eocene-Oligocene Boundary or somewhat later at the end of the Early Oligocene. Other Caribbean echinoid fossil records show even earlier diversity decreases, starting already at the end of the Middle Eocene (Figure 10). The third diversity decrease occurred after the beginning of the closure of the Central American Isthmus, 14 m.y.a. (Lessios 2008). As previously mentioned, the gradual closure of the Central American Isthmus was accompanied with significant environmental changes that probably triggered the extinction of some echinoid taxa. However, extinctions of other invertebrate faunas are reported closer to the end of the closure (Johnson 1995; Budd et al. 1996; Todd 2001) rather than to the beginning, in contrast to the Venezuelan and all other analyzed Caribbean echinoid fossil records, except the Lesser Antilles. This diversity decrease continues until today in Venezuela, Cuba and Central America, but not in the Lesser Antilles and Jamaica where we observe a slight diversity increase in the Early Pleistocene. Unfortunately, the complete record of the Recent Caribbean echinoids is not available (Penchaszadeh 2003; Schultz 2006; Francisco and Pauls 2008). The knowledge of this information would bring better resolution of the evolutionary patterns in last few million years.

The highest diversity peak of Venezuelan echinoids was in the Middle Miocene in contrast to other studies of Caribbean echinoid faunas that documented the highest diversity peak in the Eocene (Kier 1977; McKinney et al. 1992; Donovan 2001). This difference may be due the poor diversity data on Venezuelan Eocene echinoids.

When comparing Venezuelan echinoid diversity patterns with other Caribbean regions, one has to be aware that northern Venezuela experiences upwelling events caused by trade wind from February to April (Gilbes and Armstrong 2004). This upwelling phenomenon in Venezuela is not restricted to today but has been shown to exist with intensity variations since the Early Miocene, i.e., upwelling events occurred both before and after the closure of the Central American Isthmus (Aguilera and Aguilera 2001). Considering that this major geological event was accompanied by changes in ocean currents and that there are two other nutri-

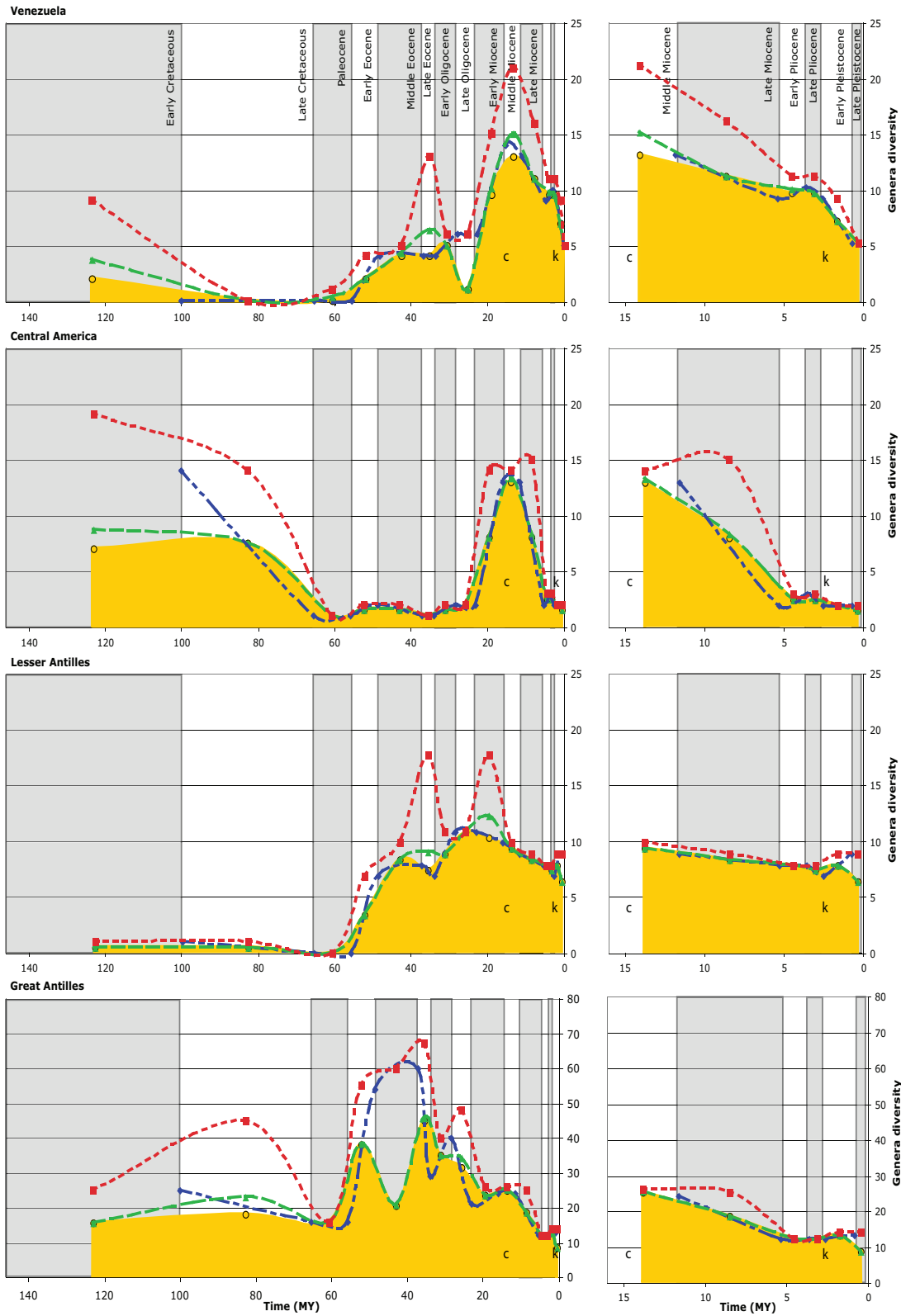


FIGURE 10. Diversity curves obtained by calculating the mean standing diversity with and without singletons and by counting boundary crossers of echnoids from different Caribbean regions.

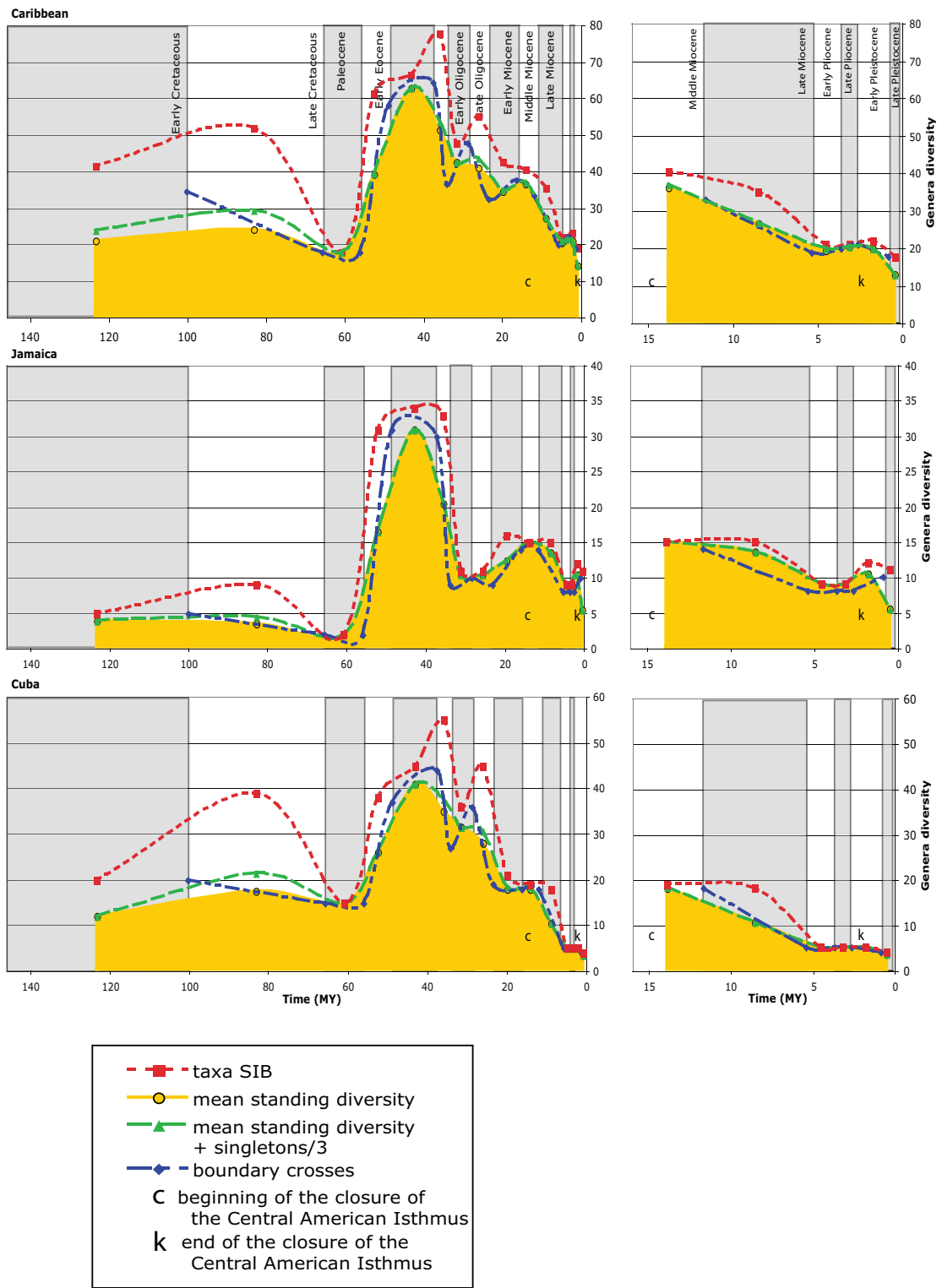


FIGURE 10 (continued).

TABLE 3. Diversity analyses of the Venezuelan and the Caribbean echinoid fossil record. ABBREVIATIONS: N – absolute number of genera; MDS – mean standing diversity without singletons; MDS+s – mean standing diversity with singletons; BC – boundary crossers.

| | Venezuela | | Caribbean | | Greater Antilles | | Cuba | | Jamaica | | Lesser Antilles | | Central America | | | | | | | | | | | | | | | | |
|-------------------|-----------|-----|-----------|----|------------------|------|-------|-----|---------|------|-----------------|----|-----------------|------|-------|----|-----|------|-------|----|-----|------|------|----|-----|-----|-------|----|--|
| | N | MDS | B | C | N | MDS | +s | N | MDS | +s | B | N | MDS | +s | B | | | | | | | | | | | | | | |
| Early Cretaceous | 9 | 2 | 3.67 | 0 | 41 | 21 | 23.67 | 34 | 25 | 15.5 | 15.5 | 25 | 20 | 12 | 12 | 20 | 5 | 4 | 4 | 5 | 1 | 0.5 | 0.5 | 1 | 19 | 7 | 8.67 | 14 | |
| Late Cretaceous | 0 | 0 | 0 | 0 | 51 | 24 | 29 | 18 | 45 | 18 | 23 | 16 | 39 | 17.5 | 21.5 | 15 | 9 | 3.5 | 4.5 | 2 | 1 | 0.5 | 0.5 | 0 | 14 | 7.5 | 7.5 | 1 | |
| Paleocene | 1 | 0 | 0.33 | 0 | 18 | 18 | 18 | 16 | 16 | 16 | 16 | 16 | 15 | 15 | 15 | 15 | 2 | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | |
| Early Eocene | 4 | 2 | 2 | 4 | 60 | 38.5 | 38.83 | 57 | 55 | 38 | 38.33 | 54 | 38 | 26 | 26.33 | 37 | 31 | 16.5 | 16.5 | 31 | 7 | 3.5 | 3.5 | 7 | 2 | 1.5 | 1.5 | 2 | |
| Middle Eocene | 5 | 4 | 4.33 | 4 | 65 | 61.5 | 61.5 | 63 | 60 | 20.5 | 20.83 | 60 | 45 | 41 | 41 | 44 | 34 | 31 | 31 | 30 | 10 | 8.5 | 8.5 | 8 | 2 | 1.5 | 1.5 | 1 | |
| Late Eocene | 13 | 4 | 6.33 | 4 | 76 | 50.5 | 52.83 | 36 | 67 | 45 | 45.67 | 29 | 55 | 35 | 37.67 | 27 | 33 | 20.5 | 20.83 | 9 | 18 | 7.5 | 9.17 | 7 | 1 | 1 | 1 | 1 | |
| Early Oligocene | 6 | 5 | 5 | 6 | 47 | 42 | 42 | 47 | 40 | 35 | 35 | 40 | 36 | 31.5 | 31.5 | 36 | 11 | 10.5 | 10.5 | 10 | 11 | 9 | 9 | 11 | 2 | 1.5 | 1.5 | 2 | |
| Late Oligocene | 6 | 1 | 1 | 6 | 54 | 40.5 | 42.83 | 32 | 48 | 31.5 | 34.17 | 21 | 45 | 28 | 30.67 | 19 | 11 | 10.5 | 10.5 | 9 | 11 | 11 | 11 | 11 | 2 | 2 | 2 | 2 | |
| Early Miocene | 15 | 9.5 | 10.17 | 14 | 42 | 34 | 34.67 | 37 | 26 | 23.5 | 23.5 | 24 | 21 | 18 | 18.33 | 18 | 16 | 12.5 | 12.5 | 14 | 18 | 10.5 | 12.5 | 10 | 14 | 8 | 8 | 13 | |
| Middle Miocene | 21 | 13 | 15 | 13 | 40 | 36 | 36.67 | 33 | 26 | 25 | 25.33 | 24 | 19 | 18 | 18.33 | 18 | 15 | 15 | 15 | 14 | 10 | 9.5 | 9.5 | 9 | 14 | 13 | 13.33 | 13 | |
| Late Miocene | 16 | 11 | 11 | 9 | 35 | 27 | 27.33 | 20 | 25 | 18.5 | 18.5 | 12 | 18 | 10.5 | 10.5 | 5 | 15 | 13.5 | 13.5 | 8 | 9 | 8.5 | 8.5 | 8 | 15 | 8 | 8.33 | 2 | |
| Early Pliocene | 11 | 9.5 | 9.83 | 10 | 22 | 20.5 | 20.83 | 21 | 12 | 12 | 12 | 12 | 5 | 5 | 5 | 5 | 9 | 9 | 9 | 8 | 8 | 8 | 8 | 8 | 3 | 2.5 | 2.5 | 3 | |
| Late Pliocene | 11 | 9.5 | 9.5 | 9 | 22 | 21.5 | 21.5 | 22 | 12 | 12 | 12 | 12 | 5 | 5 | 5 | 5 | 9 | 9 | 9 | 8 | 8 | 7.5 | 7.5 | 7 | 3 | 2.5 | 2.5 | 2 | |
| Early Pleistocene | 9 | 7 | 7 | 5 | 23 | 21 | 21 | 19 | 14 | 13 | 13 | 13 | 5 | 5 | 5 | 4 | 12 | 10.5 | 10.5 | 10 | 9 | 8 | 8 | 9 | 2 | 2 | 2 | 2 | |
| Late Pleistocene | 5 | 5 | 5 | 5 | 19 | 14.5 | 14.5 | 14 | 8.5 | 8.5 | 8.5 | 4 | 3.5 | 3.5 | 3.5 | 11 | 5.5 | 5.5 | 5.5 | 9 | 6.5 | 6.5 | 6.5 | 2 | 1.5 | 1.5 | 1.5 | | |
| Total Genera | 51 | | | | 157 | | | 122 | | 102 | | 54 | | 36 | | 38 | | | | | | | | | | | | | |

ent rich intrusions in the Caribbean (intrusions from Orinoco and Amazon River), it is possible that these nutrient rich waters may have reached wider parts of the Caribbean and not only the Lesser Antilles as they do today (Aguilera et al. 2010; Gilbes and Armstrong 2004). Since it is known that a combination of upwelling events and nutrient-rich intrusions have an effect on both echinoid larvae and adults, it is fair to assume that they also influence species assemblages and diversity. It would therefore be of great importance to further explore the potential of paleontological data in revealing these complex temporal and spatial nutrient patterns in the Caribbean (McAlister 2008; Smith and Stockley 2005).

CONCLUSIONS

The Venezuelan fossil echinoids have been sporadically reported before by several authors, but no diversity analyses were available until now. In spite of the omnipresent issues of sampling and preservation biases, chronostratigraphical uncertainty, taxonomical confusion and choice of time interval played the role in this diversity analysis, it still enables us to observe echinoid diversity patterns through time. The major difference between the Venezuelan fossil record and other Caribbean echinoid faunas is the time of the highest diversity, which is recorded in Venezuela in the Middle Miocene and not in the Eocene as reported from most other Caribbean echinoid faunas. However, the diversity decrease around the Eocene-Oligocene boundary and one after the Middle Miocene diversity peak appears to be common for both Venezuelan and Caribbean echinoids. The gap in the Venezuelan echinoid fossil record from the end of the Early Cretaceous to the beginning of the Late Eocene unfolds an area of possible future research. A complete record of the Recent Caribbean echinoids would bring new and valuable information for better understanding the Quaternary echinoid diversity patterns in the Caribbean. The Caribbean region, experiencing the closure of the Central American Isthmus and its accompanied effects, has undergone major geographical and ecological changes in the last 12 m.y. Although the Venezuelan coast has somewhat different characteristics than other Caribbean regions, the knowledge about its fossil and extant fauna is still essential for understanding the evolutionary patterns in this region.

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APPENDIX

Data sources for the diversity analysis.

| Genus | Author | Country | |
|----------------------|---------------------------|------------------------|-----------|
| <i>Abertella</i> | Durham 1957 | Guatemala | |
| <i>Agassizia</i> | Donovan 1993 | Anguilla | |
| | Donovan et al. 2005 | Costa Rica | |
| | Fischer 1985 | Cuba | |
| | Jackson 1922 | Jamaica | |
| | Linkimer and Aguilar 2000 | Puerto Rico | |
| | Sanchez Roig 1949 | St.Bartholomew | |
| | Sanchez Roig 1951 | Trinidad | |
| | Sanchez Roig 1952a | | |
| | Sanchez Roig 1953a | | |
| <i>Aguayoaster</i> | Weisbord 1934 | | |
| | Kier 1984 | Cuba | |
| <i>Amblypneustes</i> | Sanchez Roig 1952b | | |
| | Sanchez Roig 1949 | Cuba | |
| <i>Amblypygus</i> | Donovan 1993 | Cuba | |
| | Jackson 1922 | Jamaica | |
| | Sanchez Roig 1949 | | |
| | Sanchez Roig 1953a | | |
| <i>Anisopetalus</i> | Arnold and Clark 1927 | British West Indies | |
| | | Jamaica | |
| <i>Anorthopygus</i> | Sanchez Roig 1949 | Cuba | |
| <i>Antillaster</i> | Arnold and Clark 1927 | Costa Rica | |
| | Donovan 1993 | Cuba | |
| | Fischer 1985 | Dutch West Indies | |
| | Kier 1984 | Jamaica | |
| | Pijpers 1933 | | |
| | Sanchez Roig 1949 | | |
| | Sanchez Roig 1951 | | |
| | Sanchez Roig 1952a | | |
| | Sanchez Roig 1952b | | |
| | Sanchez Roig 1953b | | |
| | <i>Arnaudaster</i> | Cooke 1955 | Columbia |
| | | Donovan 1991 | Cuba |
| | <i>Asterostoma</i> | Donovan and Lewis 1993 | Jamaica |
| Jackson 1922 | | St.Bartholomew | |
| Kier 1966 | | | |
| Kier 1984 | | | |
| Sanchez Roig 1949 | | | |
| Sanchez Roig 1952a | | | |
| Sanchez Roig 1952b | | | |
| <i>Australanthus</i> | | Sanchez Roig 1949 | Cuba |
| | | | |
| <i>Barnumia</i> | | Cooke 1953 | Guatemala |
| <i>Bonaireaster</i> | Pijpers 1933 | Dutch West Indies | |
| <i>Breynia</i> | Jackson 1922 | Cuba | |
| | Sanchez Roig 1953a | | |

| Genus | Author | Country |
|------------------------|------------------------------|---------------------|
| <i>Brissolampas</i> | Sanchez Roig 1949 | Cuba |
| <i>Brissopatagus</i> | Sanchez Roig 1951 | Cuba |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| <i>Brissopsis</i> | Donovan et al. 2005 | Anguilla |
| | Durham 1961 | Costa Rica |
| | Jackson 1922 | Cuba |
| | Kier 1984 | Dominican Republic |
| | Sanchez Roig 1949 | Trinidad |
| <i>Brissus</i> | Cooke 1961 | Anguilla |
| | Donovan et al. 2005 | Barbados |
| | Jackson 1922 | Cuba |
| | Kier 1984 | Guadeloupe |
| | Sanchez Roig 1952b | Jamaica |
| | Sanchez Roig 1953a | Trinidad |
| | Weisbord 1934 | |
| <i>Cardiaster</i> | Jackson 1922 | Cuba |
| | Sanchez Roig 1949 | |
| <i>Caribbaster</i> | Donovan 1991 | Jamaica |
| | Donovan and Lewis 1993 | |
| <i>Cassidulus</i> | Alvarado et al. 2006 | Barbados |
| | Arnold and Clark 1934 | British West Indies |
| | Donovan and Lewis 1993 | Costa Rica |
| | Kier 1966 | Cuba |
| | Sanchez Roig 1953a | Jamaica |
| | Weisbord 1934 | Lesser Antilles |
| <i>Catopygus</i> | Lambert 1931 | Costa Rica |
| | Sanchez Roig 1926 | Cuba |
| | Sanchez Roig 1952c | |
| | Seyfreid and Sprechmann 1986 | |
| <i>Centrostephanus</i> | Bernasconi 1955 | Trinidad |
| <i>Cidaris</i> | Arnold and Clark 1927 | Anguilla |
| | Donovan 1993 | Barbados |
| | Donovan et al. 1994 | Cuba |
| | Donovan et al. 2005 | Dominican Republic |
| | Jackson 1922 | Jamaica |
| | Lambert 1931 | Puerto Rico |
| | Sanchez Roig 1926 | St. Bartholomew |
| | Sanchez Roig 1949 | Trinidad |
| | Sanchez Roig 1952a | |

| Genus | Author | Country |
|-----------------------|------------------------------|---------------------|
| <i>Clypeaster</i> | Arnold and Clark 1934 | Anguilla |
| | Carballo and Fischer 1978 | Antigua |
| | Clark 1941 | British West Indies |
| | Donovan 1993 | Costa Rica |
| | Donovan et al. 1994 | Cuba |
| | Donovan and Portell 1996 | Dominican Republic |
| | Donovan et al. 2005 | Guadeloupe |
| | Donovan and Lewis 1993 | Jamaica |
| | Durham 1961 | Puerto Rico |
| | Fischer 1985 | |
| | Jackson 1922 | |
| | Mortensen 1948 | |
| | Roman 1952 | |
| | Sanchez Roig 1926 | |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1952a | |
| Sanchez Roig 1952d | | |
| Sanchez Roig 1953a | | |
| Sanchez Roig 1953b | | |
| <i>Clypeolampas</i> | Sanchez Roig 1952c | Cuba |
| <i>Clypeopygus</i> | Sanchez Roig 1952 | Cuba |
| | Weisbord 1934 | |
| <i>Codiopsis</i> | Jackson 1922 | Cuba |
| <i>Conoclypus</i> | Sanchez Roig 1949 | Cuba |
| <i>Conulus</i> | Jackson 1922 | Costa Rica |
| | Sanchez Roig 1949 | Cuba |
| | Seyfreid and Sprechmann 1986 | |
| <i>Coraster</i> | Sanchez Roig 1952e | Cuba |
| <i>Crucibrissus</i> | Sanchez Roig 1953b | Cuba |
| <i>Cubanaster</i> | Donovan 1993 | Cuba |
| | Sanchez Roig 1952e | Jamaica |
| <i>Cyclaster</i> | Arnold and Clark 1934 | Costa Rica |
| | Kier 1984 | Cuba |
| | Sanchez Roig 1926 | Jamaica |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1952b | |
| <i>Diadema</i> | Donovan 1991 | Cuba |
| | Donovan et al. 1994 | Jamaica |
| | Weisbord 1934 | |
| <i>Diplopodia</i> | Sanchez Roig 1949 | Cuba |
| <i>Discoides</i> | Jackson 1922 | Cuba |
| <i>Echinarachnius</i> | Jackson 1922 | Puerto Rico |
| <i>Echinocorys</i> | Donovan 2004 | Belize |
| | Sanchez Roig 1926 | Cuba |
| | Sanchez Roig 1949 | |
| <i>Echinocyamus</i> | Lambert 1931 | Barbados |
| | Kier 1966 | Cuba |
| | | Lesser Antilles |

| Genus | Author | Country |
|---------------------|---------------------------|---------------------|
| <i>Echinolampas</i> | Arnold and Clark 1927 | Anguilla |
| | Donovan 1993 | Antigua |
| | Donovan et al. 2005 | Barbados |
| | Donovan and Lewis 1993 | Belize |
| | Durham 1961 | British West Indies |
| | Fischer 1985 | Costa Rica |
| | Jackson 1922 | Cuba |
| | Jeannet 1959 | Jamaica |
| | Roman and Goncalves 1965 | Puerto Rico |
| | Sanchez Roig 1926 | St.Bartholomew |
| | Sanchez Roig 1949 | Trinidad |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| | Sanchez Roig 1953b | |
| Weisbord 1934 | | |
| <i>Echinometra</i> | Donovan 1993 | Anguilla |
| | Donovan et al. 1994 | Cuba |
| | Donovan 2000 | Jamaica |
| | Donovan et al. 2005 | Puerto Rico |
| | Jackson 1922 | |
| | Sanchez Roig 1949 | |
| <i>Echinoneus</i> | Donovan and Veale 1996 | Anguilla |
| | Donovan et al. 2005 | Barbados |
| | Jackson 1922 | Carriacaou |
| | Lambert 1928 | Cuba |
| | Sanchez Roig 1952a | Guadeloupe |
| | Sanchez Roig 1953a | Jamaica |
| <i>Echinopedina</i> | Jackson 1922 | Cuba |
| | | Dominican Republic |
| <i>Echinopsis</i> | Arnold and Clark 1927 | Cuba |
| | Donovan 1993 | Jamaica |
| | Donovan and Lewis 1993 | |
| | Hawkins 1924 | |
| | Sanchez Roig 1949 | |
| <i>Encope</i> | Arnold and Clark 1934 | Costa Rica |
| | Clark 1948 | Jamaica |
| | Donovan 1993 | Nicaragua |
| | Jackson 1922 | Puerto Rico |
| | Linkimer and Aguilar 2000 | |
| <i>Eucidaris</i> | Donovan 1991 | Jamaica |
| | Donovan et al. 1994 | |

| Genus | Author | Country |
|-----------------------|------------------------------|---------------------|
| <i>Eupatagus</i> | Arnold and Clark 1927 | Anguilla |
| | Donovan 1993 | Antigua |
| | Donovan et al. 2005 | Barbados |
| | Donovan and Lewis 1993 | Cuba |
| | Jackson 1922 | Jamaica |
| | Sanchez Roig 1949 | Puerto Rico |
| | Sanchez Roig 1951 | St.Bartholomew |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| | Sanchez Roig 1953b | |
| <i>Eurhodia</i> | Arnold and Clark 1927 | British West Indies |
| | Donovan and Lewis 1993 | Cuba |
| | Sanchez Roig 1951 | Jamaica |
| <i>Faujasia</i> | Cooke 1955 | Columbia |
| <i>Fellius</i> | Donovan 1991 | Jamaica |
| <i>Fernandezaster</i> | Fischer 1985 | Costa Rica |
| | Sanchez Roig 1952a | Cuba |
| <i>Fibularia</i> | Arnold and Clark 1927 | Barbados |
| | Cooke 1961 | Cuba |
| | Donovan 1993 | Jamaica |
| | Donovan and Lewis 1993 | Lesser Antilles |
| | Kier 1966 | Trinidad |
| | Sanchez Roig 1949 | |
| <i>Galeritas</i> | Seyfreid and Sprechmann 1986 | Costa Rica |
| <i>Globator</i> | Seyfreid and Sprechmann 1986 | Costa Rica |
| <i>Goniocidaris</i> | Sanchez Roig 1949 | Cuba |
| <i>Goniopygus</i> | Lambert 1931 | Cuba |
| | Hawkins 1924 | Jamaica |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | Cuba |
| <i>Gymnopatagus</i> | Arnold and Clark 1927 | Cuba |
| <i>Haimea</i> | Cooke 1961 | Jamaica |
| | Donovan 1993 | St.Bartholomew |
| | Donovan and Lewis 1993 | Trinidad |
| | Lambert 1931 | |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1952a | |
| Sanchez Roig 1953a | | |
| <i>Hemiaster</i> | Cooke 1953 | Cuba |
| | Donovan and Lewis 1993 | Guatemala |
| | Jackson 1922 | Jamaica |
| | Kier 1984 | Puerto Rico |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1953a | |
| | Weisbord 1934 | |
| <i>Hemicidaris</i> | Sanchez Roig 1949 | Cuba |
| <i>Hemipatagus</i> | Sanchez Roig 1949 | Cuba |
| <i>Hemipedina</i> | Sanchez Roig 1949 | Cuba |

| Genus | Author | Country |
|----------------------|---------------------------|----------------|
| <i>Herrera</i> | Sanchez Roig 1951 | Cuba |
| <i>Heteraster</i> | Cooke 1955 | Columbia |
| <i>Heterosalenia</i> | Donovan 1991 | Jamaica |
| | Donovan and Lewis 1993 | |
| <i>Histocidaris</i> | Donovan et al. 2005 | Cuba |
| | Mortensen 1926 | Jamaica |
| <i>Holaster</i> | Linkimer and Aguilar 2000 | Costa Rica |
| <i>Holectypus</i> | Sanchez Roig 1949 | Cuba |
| | Sanchez Roig 1953 | |
| <i>Homoeopetalus</i> | Arnold and Clark 1934 | Jamaica |
| <i>Hypselaster</i> | Arnold and Clark 1927 | Jamaica |
| <i>Hypsoclypus</i> | Sanchez Roig 1953b | Cuba |
| <i>Jacksonaster</i> | Sanchez Roig 1926 | Cuba |
| | Sanchez Roig 1949 | |
| <i>Laganum</i> | Jackson 1922 | Cuba |
| | Sanchez Roig 1949 | |
| | Weisbord 1934 | |
| <i>Lajanaster</i> | Fischer 1985 | Costa Rica |
| | Sanchez Roig 1926 | Cuba |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1953b | |
| <i>Lanieria</i> | Jackson 1922 | Costa Rica |
| | | Cuba |
| | | Guadeloupe |
| <i>Leiopedina</i> | Sanchez Roig 1949 | Cuba |
| <i>Leptarbacia</i> | Sanchez Roig 1949 | Cuba |
| <i>Linthia</i> | Arnold and Clark 1934 | Cuba |
| | Castex 1930 | Jamaica |
| | Hawkins 1924 | Trinidad |
| | Jeannet 1928 | |
| | Kier 1984 | |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1952a | |
| <i>Lovenia</i> | Donovan, 2005 | Anguilla |
| | Linkimer and Aguilar 2000 | Costa Rica |
| <i>Lytechinus</i> | Arnold and Clark 1927 | Barbados |
| | Chesher 1968a | Jamaica |
| | Donovan and Lewis 1993 | Panama |
| <i>Macraster</i> | Kier 1984 | Cuba |
| | Sanchez Roig 1949 | |
| <i>Macropneustes</i> | Arnold and Clark 1927 | Anguilla |
| | Arnold and Clark 1934 | Cuba |
| | Donovan and Lewis 1993 | Jamaica |
| | Jackson 1922 | St.Bartholomew |
| | Kier 1984 | |
| | Sanchez Roig 1953b | |
| <i>Maretia</i> | Sanchez Roig 1926 | Cuba |

| Genus | Author | Country |
|-----------------------------|---------------------------|-------------------|
| <i>Mauritanaster</i> | Sanchez Roig 1949 | Cuba |
| | Sanchez Roig 1953b | |
| <i>Mellita</i> | Clark 1940 | Costa Rica |
| | Donovan 1993 | Jamaica |
| | Donovan et al. 1994 | Trinidad |
| | Jackson 1922 | |
| | Linkimer and Aguilar 2000 | |
| <i>Meoma</i> | Chesher 1968b | Anguilla |
| | Donovan 1993 | Barbados |
| | Donovan et al. 1994 | Costa Rica |
| | Donovan et al. 2005 | Cuba |
| | Durham 1961 | Jamaica |
| | Kier 1984 | |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1952a | |
| <i>Metalia</i> | Arnold and Clark 1934 | Costa Rica |
| | Linkimer and Aguilar 2000 | Cuba |
| | Sanchez Roig 1949 | Jamaica |
| | Sanchez Roig 1953a | |
| <i>Metholectypus</i> | Donovan 1993 | Jamaica |
| <i>Micraster</i> | Linkimer and Aguilar 2000 | Costa Rica |
| | Sanchez Roig 1949 | Cuba |
| <i>Moronaster</i> | Sanchez Roig 1952b | Cuba |
| <i>Neocatopygus</i> | Sanchez Roig 1953a | Cuba |
| <i>Neolaganum cf. Dalli</i> | Arnold and Clark 1927 | Jamaica |
| | Donovan and Lewis 1993 | |
| <i>Neopatagus cubensis</i> | Sanchez Roig 1953 | Cuba |
| <i>Nucleolites</i> | Sanchez Roig 1952 | Cuba |
| | Weisbord 1934 | |
| <i>Nucleopygus</i> | Sanchez Roig 1952 | Cuba |
| <i>Nudobrissus</i> | Sanchez Roig 1949 | Cuba |
| <i>Oligopygus</i> | Arnold and Clark 1927 | Cuba |
| | Cooke 1961 | Curacao |
| | Donovan 1991 | Dutch West Indies |
| | Donovan 1993 | Jamaica |
| | Donovan et al. 2005 | Trinidad |
| | Jeannet 1928 | |
| | Lambert 1931 | |
| | Molengraaff 1929 | |
| | Sanchez Roig 1926 | |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1953a | |
| <i>Oolopygus</i> | Sanchez Roig 1953a | Cuba |
| <i>Opissaster</i> | Sanchez Roig 1926 | Cuba |
| | Sanchez Roig 1953a | |
| <i>Orthopsis</i> | Donovan and Lewis 1993 | Jamaica |
| <i>Paleolampas alta</i> | Arnold and Clark 1927 | Jamaica |

| Genus | Author | Country |
|----------------------------|------------------------------|-------------------|
| <i>Paleopneustes</i> | Chesher 1968b | Barbados |
| | Sanchez Roig 1952b | Carriacaou |
| | | Cuba |
| <i>Paralampas</i> | Sanchez Roig 1953a | Cuba |
| <i>Parapygus</i> | Jackson 1922 | Cuba |
| | | St.Bartholomew |
| <i>Pedina</i> | Donovan 1993 | Cuba |
| | Sanchez Roig 1949 | Jamaica |
| <i>Periaster elongatus</i> | Jackson 1922 | St.Bartholomew |
| <i>Pericosmus</i> | Donovan 1993 | Anguilla |
| | Donovan et al. 2005 | Costa Rica |
| | Durham 1961 | Cuba |
| | Kier 1984 | Jamaica |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| <i>Peronella</i> | Jackson 1922 | Cuba |
| | Molengraaff 1929 | Curacao |
| | Weisbord 1934 | Dutch West Indies |
| | | Trinidad |
| <i>Phyllacanthus</i> | Cutress 1980 | Cuba |
| | Donovan 1991 | Jamaica |
| | Donovan 1993 | Puero Rico |
| | Donovan and Lewis 1993 | |
| | Jackson 1922 | |
| | Sanchez Roig 1926 | |
| <i>Phymosoma</i> | Sanchez Roig 1949 | |
| | Arnold and Clark 1927 | Costa Rica |
| | Cooke 1961 | Cuba |
| | Donovan 1993 | Jamaica |
| | Jackson 1922 | Trinidad |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| <i>Plagiobrissus</i> | Seyfreid and Sprechmann 1986 | |
| | Arnold and Clark 1927 | Costa Rica |
| | Donovan 1993 | Cuba |
| | Durham 1961 | Jamaica |
| | Jackson 1922 | St.Bartholomew |
| | Sanchez Roig 1951 | |
| <i>Plesiaster</i> | Seyfreid and Sprechmann 1986 | Costa Rica |
| <i>Porocidaris</i> | Sanchez Roig 1953a | Cuba |
| <i>Prenaster</i> | Jackson 1922 | Cuba |
| | Pijpers 1933 | Dutch West Indies |
| | Sanchez Roig 1949 | St.Bartholomew |
| | | |
| <i>Prionocidaris</i> | Donovan et al. 2005 | Anguilla |
| | Donovan and Lewis 1993 | Costa Rica |
| | Linkimer and Aguilar 2000 | Jamaica |

| Genus | Author | Country |
|------------------------------|---------------------------|---------------------|
| <i>Procassidulus</i> | Sanchez Roig 1949 | Cuba |
| | Sanchez Roig 1953a | |
| <i>Progonolampas</i> | Sanchez Roig 1952a | Cuba |
| | Sanchez Roig 1953a | |
| <i>Psammechinus</i> | Donovan et al. 2005 | Anguilla |
| <i>Pseudorthopsis</i> | Sanchez Roig 1949 | Cuba |
| | Sanchez Roig 1953a | |
| <i>Pygopistes</i> | Donovan 1991 | Jamaica |
| | Donovan 1993 | |
| <i>Pygorhynchus</i> | Sanchez Roig 1949 | Cuba |
| <i>Pygurus</i> | Cooke 1955 | Columbia |
| <i>Rhabdobrissus aloysii</i> | Pijpers 1933 | Dutch West Indies |
| <i>Rhyncholampas</i> | Donovan 1993 | Cuba |
| | Sanchez Roig 1926 | Jamaica |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| <i>Rhynchopygus</i> | Arnold and Clark 1927 | British West Indies |
| | Sanchez Roig 1952c | Cuba |
| | | Jamaica |
| <i>Rhynobrissus</i> | Linkimer and Aguilar 2000 | Costa Rica |
| <i>Rumphia</i> | Sanchez Roig 1949 | Cuba |
| <i>Salenia</i> | Jackson 1922 | Cuba |
| | Sanchez Roig 1949 | |
| <i>Sanchezella</i> | Durhan 1954 | West Indies |
| <i>Schizaster</i> | Aguilar 1978 | Anguilla |
| | Arnold and Clark 1927 | Costa Rica |
| | Carballo and Fischer 1978 | Cuba |
| | Donovan 1993 | Dutch West Indies |
| | Donovan et al. 1994 | Jamaica |
| | Donovan et al. 2005 | Lesser Antilles |
| | Donovan and Lewis 1993 | Puerto Rico |
| | Durham 1961 | St.Bartholomew |
| | Engel 1961 | Trinidad |
| | Gabb 1881 | |
| | Jackson 1917 | |
| | Jackson 1922 | |
| | Kier 1984 | |
| | Linkimer and Aguilar 2000 | |
| | Pijpers 1933 | |
| | Sanchez Roig 1949 | |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1952a | |
| | Sanchez Roig 1953a | |
| | Sanchez Roig 1953c | |
| | Weisbord 1934 | |
| <i>Schizobrissus</i> | Sanchez Roig 1949 | Cuba |
| | Sanchez Roig 1951 | |
| | Sanchez Roig 1953a | |

| Genus | Author | Country |
|----------------------|--|---------------------------------------|
| <i>Scutella</i> | Sanchez Roig 1949 Weisbord 1934 | Cuba |
| <i>Sismondia</i> | Donovan et al. 2005 Jackson 1922 | Anguilla Antigua St.Bartholomew |
| <i>Sperosoma</i> | Mortensen 1934 | Barbados |
| <i>Sternopatagus</i> | Kier 1984 | Cuba |
| <i>Studeria</i> | Sanchez Roig 1953a | Cuba |
| <i>Stylocidaris</i> | Schultz 2006 | Barbados |
| <i>Temnocidaris</i> | Donovan 1993 | Jamaica |
| <i>Trachyaster</i> | Sanchez Roig 1949 | Cuba |
| <i>Triadechinus</i> | Arnold and Clark 1927 Donovan 1993 | Jamaica |
| <i>Tripneustes</i> | Donovan et al. 2005 | Anguilla |
| <i>Trochalosoma</i> | Arnold and Clark 1927 Donovan 1993 Sanchez Roig 1949 | Cuba Jamaica |
| <i>Weisbordella</i> | Cooke 1961 | Trinidad |
| <i>Wythella</i> | Donovan 1993 Durhan 1954 | Cuba Jamaica |