Extinct and extant sand dollars (Clypeasteroida: Echinoidea) from Uruguay

Sergio Martínez1 & Rich Mooi2

1 Departamento de Evolución de Cuencas, Facultad de Ciencias, Iguá 4225, 11400 Montevideo, Uruguay; smart@fcien.edu.uy
2 California Academy of Sciences, Golden Gate Park, San Francisco, 94118-4599 California, USA; rmooi@calacademy.org


Abstract: We summarize information concerning Recent and Pleistocene-Holocene Uruguayan sand dollars (Mellitidae), as well as Miocene taxa (Monophorasteridae). Recent and Pleistocene-Holocene species (Encope emarginata, Mellita quinquiesperforata, and Leodia sexisperforata) are at their southernmost limits of distribution, with only E. emarginata recorded further south than Uruguay. Lower temperatures to the south, and/or the Rio de la Plata salinity barrier are suggested as controlling factors of these distributions. During the Miocene, the sea temperatures were notably higher than at present, and it was at this time that the extinct genera Monophoraster and Amplaster reached their maximum diversity in Uruguay. The family Monophorasteridae is the basal sister group of the Mellitidae. Rev. Biol. Trop. 53(Suppl. 3): 1-7. Epub 2006 Jan 30.

Key words: Echinoidea, Monophorasteridae, Mellitidae, Tertiary, Uruguay.

Uruguay has only about 500 km of coastline. Of that, the eastern 220 km are considered marine (salinities around 30-35‰), thereby excluding the Río de la Plata estuary. Even in this region, salinity fluctuations are produced by proximity to the estuary (Piola et al. 2000, and references therein). Perhaps not surprisingly, given the overall dominance of tropical or subtropical species in the Clypeasteroida, this region, being situated in the temperate zone of the southwestern Atlantic Ocean, is today populated by only three species of sand dollars. However, the geographic setting of Uruguay provides several points of interest, since it is situated in the confluence zone between the warm N-S Brazilian current, and the cold, S-N Malvinas (Falkland) current (Boltovskoy 1966, Podestá et al. 1991, Lentini et al. 2000) (Fig. 1). Also, the Uruguayan region has a very interesting and diverse record of the extinct family Monophorasteridae, the sister group to the mellitid sand dollars to which the extant species belong. The goal of this paper is to present and discuss the data concerning fossil and extant Uruguayan sand dollars. We review their past and present geographic distribution, related restricting environmental factors, and the phylogenetic relationships of major taxa.

MATERIAL AND METHODS

Data used in this paper were taken from a critical review of bibliography (see references in the text), and the paleontological collection of the Facultad de Ciencias, Montevideo (FCDP).

RESULTS

The Recent species

The three species of sand dollars that reach Uruguay are listed below. References are limited to literature recording the presence of...
the species in the area, and do not constitute a synonymy. According to these authors, the three species have their southern distribution limits at latitudes opposite the Uruguayan coast, or nearly so (i.e. Mar del Plata, Argentina, see Fig. 1). Some references to specimens recovered from deep water (more than 1000 meters) mentioned by Bernasconi (1953) are not considered legitimate autochthonous occurrences, because these undoubtedly represent specimens that were transported post-mortem from shallower waters.

**Mellita quinquesperforata**

(Leske, 1778)

References: Mortensen (1948), Bernasconi (1953), Barattini and Ureta (1960), Klappenbach and Scarabino (1969), Milstein et al. (1976).

**Encope emarginata**

(Leske, 1778)


**Leodia seisisperforata**

(Leske, 1778)

References: Bernasconi (1941), Bernasconi (1947, 1953) (as Mellita platensis), Mortensen (1948).

**The Pleistocene-Holocene species**

Figueiras (1962) and Figueiras and Broggi (1967) recorded the presence of *Mellita* from the Pleistocene-Holocene Vizcaino (=Villa Soriano) Formation, up to the present, with an uncertain age within this period. The senior author has also found specimens of *Encope* (FCDP 2126, 4181, 4182) in transgressive Pleistocene-Holocene deposits.

**The Miocene species**

As in the section concerning the Recent species, the references are for occurrences in Uruguay, not a synonymy. All the species are found in the Late Miocene Camacho Formation, deposited under shallow marginal-marine depositional conditions (see Mooi et al. 2000 and references therein, for more information).

**Monophoraster duboisi**

(Cotteau, 1884) (Fig. 2.1)


Comments: Prior to these records, all authors (e.g., Goso and Bossi 1966, Figueiras and Broggi 1971) mentioned the presence of *Monophoraster darwini* in Uruguay. In fact, this species is not present in the Miocene of Uruguay and all the known specimens are referable to *M. duboisi*. The species was originally described from the contemporaneous Paraná Formation of Argentina (Cotteau 1884, Mooi et al. 2000).

**Amplaster coloniensis**

Martinez, 1984 (Fig. 2.2)

Comments: This species is endemic to Uruguay.

*Amplaster ellipticus*
Mooi, Martínez and Parma, 2000 (Fig. 2.3)
References: Mooi et al. (2000).
Comments: This species is endemic to Uruguay.

*Amplaster alatus*
(Rossi de Garcia and Levy, 1989) (Fig. 2.4)
References: Mooi et al. (2000).
Comments: This species was described from the “Patagoniense” strata from Chubut Province (Rossi de Garcia and Levy 1989), but with a controversial age assignment ranging from the ?Middle Eocene to the ?Late Oligocene-Early Miocene (see Mooi et al. 2000 and del Río and Martínez in prep.).

**DISCUSSION**

**Biogeography of extant Uruguayan sand dollars**

It might not be by chance that the three species that reach Uruguayan waters are at
the southern limits of their distributions. Two main factors are important to consider at this latitude: i) the confluence of the cold Malvinas (Falkland) Current and the warm Brazilian Current (known as Subtropical Confluence Zone, 30 to 45ºS, according to different authors - see Boltovskoy 1966 for example); and ii) the strong influence of the Rio de la Plata basin fresh water discharge, and the consequent lowering of salinity and raising of turbidity in its proximity (Piola et al. 2000, González-Silvera et al. 2004). This situation leads to a marked variability in temperature and salinity, a widely recognized and complex situation in which seasonality, wind, topography, and even ENSO phenomena play a role (Olson et al. 1988, Podestá et al. 1991, Lentini et al. 2000). Both temperature and salinity factors could be acting separately or together in truncating the distribution of the sand dollars.

At the same time, it must be remembered that mellitid clypeasteroids are demonstrably sensitive to changes in ambient particle size ranges. Their feeding mechanisms are tightly integrated with the type and size of particles in the substrates they inhabit (Telford and Mooi 1986). The turbidity of the Rio de la Plata has a powerful influence on the substrate, creating finer-grained deposits that are not suitable for sand dollars, particularly members of the mellitid clade, which has been shown to have podial and spine configurations closely configured to optimize on ambient particle size ranges (Telford 1990). Giberto et al. (2004), in a large-scale study of benthic assemblages in the Rio de la Plata and adjacent shelf waters, found Encope emarginata to be a characteristic species of the sandy Argentinean shelf coast, in contrast with the more muddy and shelly Uruguayan coast.

With respect to other groups, such as molluscs or crustacean decapods, the area is recognized as a core part of a separate Province (Argentinean or Patagonian Province, ca. 43ºS and ca. 28ºS, Scarabino 1977, Boschi 2000). However, to some authors it could be a true “Provinciate” between the Magellanic and Brazilian Provinces (Scarabino 1977, Martínez and del Rio 2002a). Moreover, Scarabino (1977) stressed the faunistic complexity of the area, emphasizing the role of the Rio de la Plata as a barrier for some supra- to infralittoral communities. As seen in Fig. 1, only Encope emarginata passes through this barrier. Although this would favor the salinity factor as predominant, studies on mollusks show that during the Pleistocene-Holocene transgressions, temperatures higher than present were recorded (Martínez 1990, Martínez et al. 2001).

During the Pleistocene-Holocene, representatives of the extant genera Mellita and Encope reached locations more to the west than today, to localities well within the present Rio de la Plata estuary. This was a consequence of a marine transgression of warmer waters than present that placed the marine front about 300 km farther to the northwest than it is today (Martínez et al. in prep.).

The Late Miocene Uruguayan Monopho-rasteridae are included in the Late Miocene Paranaian Province established on the basis of molluscs by Martínez and del Rio (2002a, b) (Fig. 3). The sea was warmer than at present and than during the Pleistocene-Holocene. The Paranaian Province includes assemblages contained in the Paraná (Argentina) and Camacho (Uruguay) Formations, and coeval with fossiliferous deposits recovered from wells in Southern Brazil and Buenos Aires. During Late Miocene times, the cold Malvinas (Falkland) Current still had very little influence in the area, perhaps due to the presence of continental fragments, and the formation of an old volcanic arc at the present location of the South Sandwich Islands that followed the opening of the Drake Passage (Barker et al. 1982, Barker and Thomas 2004).

The presence of these obstacles could have restricted the free circulation of the Antarctic Circumpolar Current (ACC) between 17 and 8 MY, deflecting the proto-Malvinas (Falkland) Current to the east (Scasso et al. 2000 and pers. comm. july 2001), allowing “paratropical” (in the sense of Petuch 1988) faunas to develop along the Southwestern Atlantic littoral, where recorded temperatures were higher
than at the present. Once the ACC circulation and proto-Malvinas Current strengthened again, this fauna became extinct in the region or withdrew northwards. Although the family is present also in Argentina, maximum diversity of the Monophorasteridae is reached in Uruguay. The family has not been reliably reported to occur anywhere else or at any time since the Miocene.

**Fossil species and the phylogeny of mellitid sand dollars**

This subject has been reviewed by Mooi et al. (2000). Their conclusions are summarized in the phylogeny in Fig. 4, a tree that reflects the importance of the southern clade of monophorasterids in the phylogeny of Recent sand dollars. According to these authors the Monophorasteridae is the sister group of the Mellitidae. This group was consequently used to root trees exploring the relationships among taxa within the latter family (Mooi and Peterson 2000). The monophorasterids possess some synapomorphies that justify this situation, among them the absence of ambulacral lunules, lack of a wall between the intestine and the Aristotle’s lantern, a periproct that never contacts the interambulacral basicoronal, continuous interambulacra, and lack of a pressure drainage channel around the anal lunule. In addition, the presence of ambulacral indentations in Monophoraster is probably a precursor to the ambulacral notches of the earliest mellitids, although the character distributions do not yet permit an unequivocal assertion that this is the case.

In any case, biogeographic hypotheses about sand dollars must consider this “southern connection” with key Uruguayan forms. These considerations will undoubtedly be seen as an appropriate challenge the supposed northern origin (i.e. Seilacher 1979) and later southern “expansion” of extant mellitids. In the context of the presently accepted phylogeny, a southerly origin of basal mellitids would only be falsified by the discovery of much more.
more northern occurrences of members of the monophorasterid clade.

ACKNOWLEDGMENTS

Claudia del Río and Sergio Monterroso kindly helped with the bibliography. S. Martínez thanks CSIC (Uruguay) for partial funding.

RESUMEN

Se resume la información concerniente a los escudos de mar presentes en aguas uruguayas actualmente y en el Pleistoceno-Holoceno (Mellitidae), así como en el Mioceno (Monophasteridae). Las especies actuales y del Pleistoceno-Holoceno (Encope emarginata, Mellita quinquesperforata y Leodia sexisperforata) se encuentran en su límite de distribución sur, superando en esa dirección la latitud de Uruguay solamente E. emarginata. Tanto la temperatura más fría como la barrera de salinidad que forma el Río de la Plata pueden estar influyendo en esta situación. En el Mioceno vivieron en un mar sensiblemente más cálido que el actual representantes de los géneros extintos Monophoraster y Amplaster, alcanzando en Uruguay su máxima diversidad. Los Monophasteridae son el grupo hermano (y basal) de los Mellitidae.

Palabras claves: Echinoidea, Monophasteridae, Mellitidae, Terciario, Uruguay.

REFERENCES


