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

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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)

References: Mortensen (1948), Bernasconi (1953, 1966), Barattini and Ureta (1960), Klappenbach and Scarabino (1969), Milstein *et al.* (1976), Giberto *et al.* (2004).

Leodia sexisperforata
(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 Vizcaíno (=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).

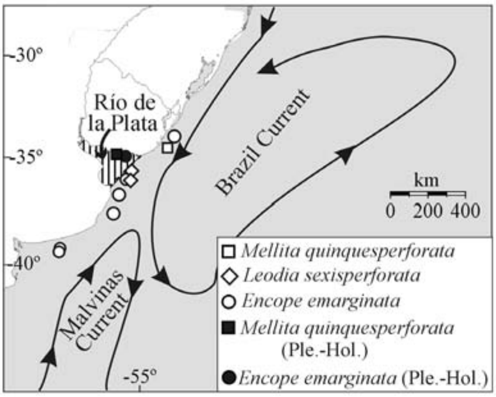

Fig. 1. Most southern records of extant representatives of *Mellita*, *Encope*, and *Leodia*, and the Pleistocene-Holocene record of *Encope* and *Mellita* in Uruguay. Occurrences in very close proximity are not resolved at this scale. Based on references given in the text and Olivier *et al.* (1968).

Fig. 1. Registros más australes de los representantes de *Mellita*, *Encope* y *Leodia*, y registro Pleistoceno-Holoceno de *Encope* y *Mellita* en Uruguay. Sitios muy próximos no son discriminados a esta escala. Basado en las referencias indicadas en el texto y en Olivier *et al.* (1968).

Monophoraster duboisi
(Cotteau, 1884) (Fig. 2.1)

References: Martínez (1994), Mooi *et al.* (2000).

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
Martínez, 1984 (Fig. 2.2)

References: Martínez (1984, 1994) (partim), Martínez and Durham (1988), Mooi *et al.* (2000).

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

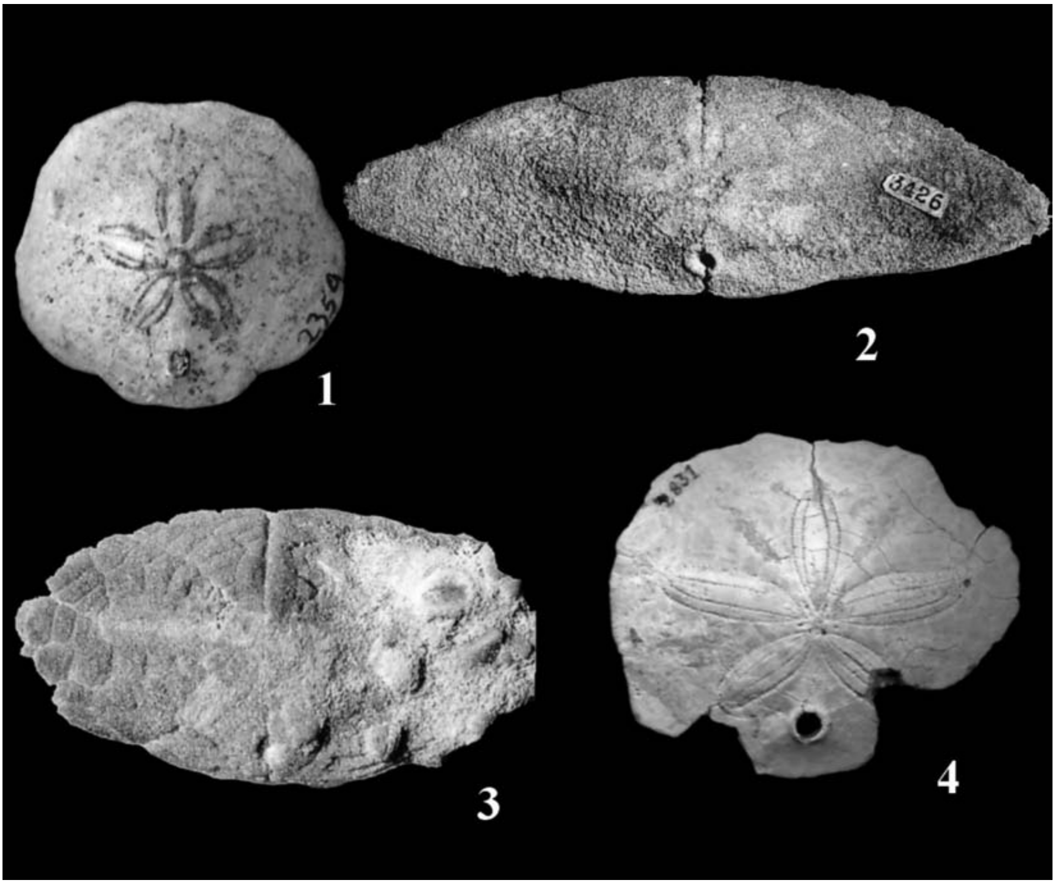

Fig. 2. Miocene sand dollars from Uruguay. 1. *Monophoraster duboisi* (x 0.5), FCDP 2359; 2. *Amplaster coloniensis* (x 0.3); holotype MNA-CPO 3426; 3. *Amplaster ellipticus* (x 0.3), paratype MNA-CPO 3425; 4. *Amplaster alatus* (x 0.5), FCDP 2831.

Fig. 2. Escudos de mar del Mioceno de Uruguay. 1. *Monophoraster duboisi* (x 0.5), FCDP 2359; 2. *Amplaster coloniensis* (x 0.3); holotype MNA-CPO 3426; 3. *Amplaster ellipticus* (x 0.3), paratype MNA-CPO 3425; 4. *Amplaster alatus* (x 0.5), FCDP 2831.

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 Río 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. 43º S and ca. 28º S, Scarabino 1977, Boschi 2000). However, to some authors it could be a true "Provinciatone" between the Magellanic and Brazilian Provinces (Scarabino 1977, Martínez and del Río 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 Monophorasteridae are included in the Late Miocene Paranaian Province established on the basis of molluscs by Martínez and del Río (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

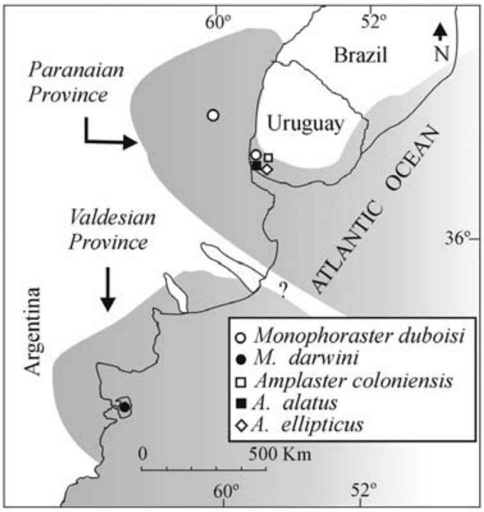

Fig. 3. Location of Miocene Uruguayan sand dollars, and their distribution outside the country.

Fig. 3. Ubicación geográfica de los escudos de mar del Mioceno de Uruguay, y su distribución fuera del país.

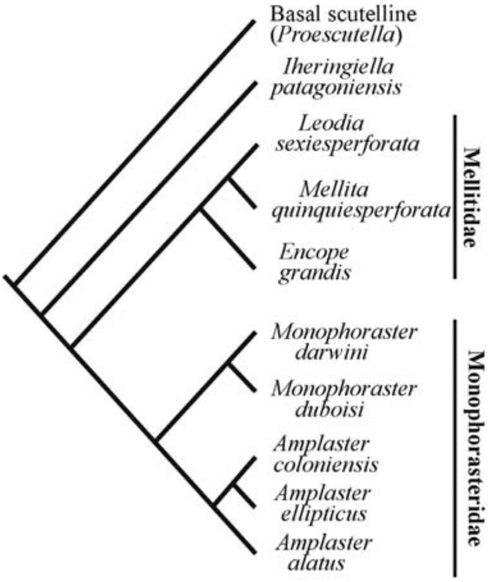

Fig. 4. Phylogenetic tree showing the relationship of mellitids and monophorasterids (based on Mooi *et al.* 2000).

Fig. 4. Arbol filogenético mostrando las relaciones entre melítidos y monoforastéridos (basado en Mooi *et al.* 2000).

more northern occurrences of members of the monophorasterid clade.

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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 (Monophorasteridae). 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 Monophorasteridae son el grupo hermano (y basal) de los Mellitidae.

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

REFERENCES

Barattini, L.P. & E.H. Ureta. 1960. La fauna de las costas uruguayas del este (invertebrados). Publicaciones de Divulgación Científica. Museo Dámaso Antonio Larrañaga. Montevideo. 195 p.

Barker, P.F. & E. Thomas. 2004. Origin, signature and palaeoclimatic influence of the Antarctic Circumpolar Current. Earth Sci. Rev. 66: 143-162.

Barker, P.F., I.A. Hill, S.D.Weaver & R.J. Pankhurst. 1982. The origin of the eastern South Scotia Ridge as an intraoceanic island arc. p. 203-211. *In* C. Craddock (ed.). Anctartic Geoscience Symposium on Anctartic Geology and Geophysics. University of Wisconsin, Madison.

Bernasconi, I. 1941. Sobre la distribución geográfica de "*Mellita sexiesperforata*" (Leske). Physis 19: 106-108.

Bernasconi, I. 1947. Una nueva especie de "*Mellita*" en la República Argentina. Physis 20: 117-118.

Bernasconi, I. 1953. Monografía de los equinoideos argentinos. An. Mus. Hist. Nat. Montevideo 6: 1-58.

Bernasconi, I. 1966. Los Equinoideos y Asteroideos colectados por el buque oceanografico R/V "Vema" frente a las costas argentinas, uruguayas y sur de Chile. Rev. Mus. Arg. Cienc. Nat. "Bernardino Rivadavia" 9: 147-175.

Boltovskoy, E. 1966. La zona de convergencia subtropical/subantártica en el Océano Atlántico (parte occidental) (un estudio con base en la investigación de Foraminíferos - indicadores). Argentina, Serv. Hidrogr. Nav., H. 640. 69 p.

Boschi, E.E. 2000. Species of decapod crustaceans and their distribution in the American marine zoogeographic provinces. Rev. Invest. Des. Pesq. 13: 7-136.

Cotteau, M.G. 1884. Echinides nouveaux ou peu connus. Bull. Soc. Zool. France 7: 1-185.

Figueiras, A. 1962. Sobre nuevos hallazgos de moluscos subfósiles de la Transgresión Querandina. Com. Soc. Malac. Uruguay 1: 53-68.

Figueiras, A. & J. Broggi. 1967. Estado actual de nuestros conocimientos sobre los moluscos fósiles del Uruguay. I. Com. Soc. Malac. Uruguay 2: 147-186.

Figueiras A. & J. Broggi. 1971. Estado actual de nuestros conocimientos sobre los moluscos fósiles del Uruguay. III. Com. Soc. Malac. Uruguay 3: 131-154.

Giberto, D.A., C.S. Bremec, E.M. Acha & H. Mianzan. 2004. Large-scale spatial patterns of benthic assemblages in the SW Atlantic: the Rio de la Plata estuary and adjacent shelf waters. Est. Coast. Shelf Sci. 61: 1-13.

González-Silvera A., E. Santamaria-del-Angel, V.M.T. Garcia, C.A.E. Garcia, R. Millán-Núñez & F. Muller-Karger. 2004. Biogeographical regions of the tropical and subtropical Atlantic Ocean off South America: classification based on pigment (CZCS) and chlorophyll-a (SeaWiFS) variability. Continental Shelf Research 24: 983–1000.

Goso, H. & J. C. Bossi. 1966. Cenozoico, p. 259-305. *In* J.C. Bossi (ed.). Geología del Uruguay. Universidad de la República, Montevideo.

Klappenbach, M.A. & V. Scarabino. 1969. El borde del mar. Nuestra Tierra, Montevideo. 68 p.

Lentini, C.A.D., E.J.D. Campos & G.G. Podestá. 2000. The annual cycle of satellite derived sea surface temperature on the western South Atlantic shelf. Rev. Bras. Oceanogr. 48: 93-105.

Leske, N.G. 1778. Additamenta ad Jacobi Theodori Klein naturalem dispositionem Echinodermatum et lucubratiunculam de aculeis echinorum marinorum. Lipsiae, Leipzig. 278 p.

Martínez, S. 1984. *Amplaster coloniensis* n.g. n.sp. (Echinoidea: Monophorasteridae) del Mioceno de Uruguay. Memorias del III Congreso Latinoamericano de Paleontología, México, pp. 505-508.

Martínez, S. 1990. Taphonomy and paleoecology of Holocene mollusks from the western margin of the Merin Lagoon (Villa Soriano Fm., Uruguay). Quat. South Am. & Ant. Pen. 7: 121-135.

Martínez, S. 1994. Bioestratigrafía (Invertebrados) de la Formación Camacho (Mioceno, Uruguay). Tesis de Doctorado, Universidad de Buenos Aires, Argentina. 346 p.

Martínez, S. & J.W. Durham. 1988. La cara oral de *Amplaster coloniensis* (Echinoidea: Monophorasteridae) (Mioceno Superior, Uruguay). Ameghiniana 25: 185-186.

Martínez, S. & C.J. del Río. 2002a. Late Miocene molluscs from the Southwestern Atlantic Ocean (Argentina and Uruguay): a palaeobiogeographic analysis. Palaeogeogr., Palaeoclimat., Palaeoecol. 188: 167-187.

Martínez, S. & C.J. del Río. 2002b. Las provincias malacológicas Miocenas y Recientes del Atlántico Sudoccidental. An. Biol. 24: 121-130.

Martínez, S., M. Ubilla, M. Verde, D. Perea, A. Rojas, R. Guérèquiz & G. Piñeiro. 2001. Paleoecology and Geochronology of Uruguayan Coastal Marine Pleistocene Deposits. Quat. Res. 55: 246-254.

Milstein, A., M. Juanicó & J. Olazarri. 1976. Algunas asociaciones bentónicas frente a las costas de Rocha, Uruguay. Resultados de la campaña del R/V "Hero", viaje 72-3ª. Com. Soc. Malac. Uruguay IV: 143-164.

Mooi, R. & D. Peterson. 2000. A new species of *Leodia* (Clypeasteroida: Echinoida) from the Neogene of Venezuela and its importance in the phylogeny of mellitid sand dollars. J. Paleont. 74: 1083-1092.

Mooi, R., S. Martínez & S.G. Parma. 2000. Phylogenetic systematics of Tertiary monophorasterid sand dollars (Clypeasteroida: Echinoidea) from South America. J. Paleont. 74: 263-281.

Mortensen, T. 1948. A Monograph of the Echinoidea, 2(4), Clypeasteroida. C.A. Reitzel, Copenhagen. 471 p.

Olivier, S.R., R. Bastida & M.R. Torti. 1968. Resultados de las campañas oceanográficas Mar del Plata I-V. Contribución al trazado de una carta bionómica del área de Mar del Plata. Las Asociaciones del Sistema Litoral entre 12 y 79 metros de profundidad. Bol. Inst. Biol. Mar. Mar del Plata 16: 3-85.

Olson, D.B., G.P. Podestá, R.H. Evans & O.T. Brown. 1988. Temporal variations in the separation of Brazil and Malvinas Currents. Deep-Sea Res. 35: 1971-1990.

Petuch, E.J. 1988. Neogene History of Tropical American Mollusks. Coastal Found., Charlottesville. 217 p.

Piola, A.R., E.J.D. Campos, O.O. Möller Jr., M. Charo & C. Martínez. 2000. Subtropical shelf off eastern South America. J. Geophys. Res. 105: 6565-6578.

Podestá, G.P., O.B. Brown & E.H. Evans. 1991. The annual cycle of satellite-derived sea surface temperature in the southwestern Atlantic Ocean. J. Clim. 4: 457-467.

Rossi de García, E. & R. Levy. 1989. Presencia de *Amplaster* n.sp. (Echinodermata: Clypeasteroidea) en el Terciario de Patagonia. Actas IV Congr. Arg. Paleont. Bioest., Mendoza 4: 89-92.

Scarabino, V. 1977. Moluscos del Golfo San Matías (Provincia de Río Negro, República Argentina). Inventario y claves para su identificación. Com. Soc. Malac. Uruguay 4: 177-285.

Scasso, R.A., L.N Castro & O.R. Tófalo. 2000. Phosphogenesis, sequence-stratigraphy and paleoceanography in Gaiman Formation phosphates, Argentina. 31th International Geological Congress, Rio de Janeiro. Abstract 2344 (CD-ROM).

Seilacher, A. 1979. Constructional morphology of sand dollars. Paleobiology 5: 191-221.

Telford, M. 1990. Computer simulation of deposit-feeding by sand dollars and sea biscuits (Echinoidea: Clypeasteroida). J. Exp. Mar. Biol. Ecol. 142:75-90.

Telford, M. & R. Mooi. 1986. Resource partitioning by sand dollars in carbonate and siliceous sediments: Evidence from podial and particle dimensions. Biol. Bull. 171:197-207.