Zootaxa 4369 (3): 301–326
http://www.mapress.com/j/zt/

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

https://doi.org/10.11646/zootaxa.4369.3.1
http://zoobank.org/urn:lsid:zoobank.org:pub:97CAA2FC-F3CC-407B-8768-2BB9DE037C86

Late Oligocene–Miocene non-lunulate sand dollars of South America: Revision of abertellid taxa and descriptions of two new families, two new genera, and a new species

RICH MOOI[1,5], SERGIO A. MARTÍNEZ[2], CLAUDIA J. DEL RÍO[3] & MARIA INÊS FEIJÓ RAMOS[4]

[1] *California Academy of Sciences, Department of Invertebrate Zoology and Geology, 55 Music Concourse Drive, San Francisco, California 94118, USA*

[2] *Departamento de Paleontología, Facultad de Ciencias,Universidad de la República, Iguá 4225,11400 Montevideo, Uruguay. E-mail: smart@fcien.edu.uy*

[3] *Museo Argentino de Ciencias Naturales Bernardino Rivadavia, División Paleoinvertebrados, Angel Gallardo 470, (C1405DJR) Buenos Aires, Argentina. E-mail: claudiajdelrio@gmail.com*

[4] *Museu Paraense Emílio Goeldi, Coordenação de Ciências da Terra e Ecologia, Av. Presidente Tancredo Neves 1901, CEP 66077-530, PA, Brazil. E-mail: mramos@museu-goeldi.br*

[5] *Corresponding author. E-mail: rmooi@calacademy.org*

Abstract

Material for all seven South American species of late Oligocene and Miocene scutelliform, non-lunulate sand dollars (Echinoidea: Clypeasteroida) was examined, resulting in revision of several taxa, and description of a new family, Placatenellidae **n. fam.**, to house *Placatenella* **n. gen.** and *Camachoaster* **n. gen.** Known only from the state of Pará, Brazil, and previously described as a member of *Abertella* Durham, 1953, *A. complanata* Brito, 1981 is redescribed on the basis of analysis of the holotype and subsequently described material from the same region. *A. complanata* is removed from synonymy with *A. pirabensis* (Marchesini Santos, 1958), and transferred as the type species of *Placatenella* **n. gen.** A new taxon, *Camachoaster* **n. gen.**, is described to hold *C. maquedensis* **n. sp.** The Abertellidae Durham, 1955 is revised and the concept of the genus *Abertella* restricted to include only those forms with a posterior notch and all interambulacra discontinuous, including *A. pirabensis*, which is redescribed from the only known specimen, confirming that this species lacks any trace of an anal lunule but possesses features fully congruent with its placement in *Abertella*. Iheringiellidae **n. fam**. is established to house the common but taxonomically challenging taxon, *Iheringiella* Berg, 1898. New data on the occurrence and location of the types of *Iheringiella* are discussed, and comments on the status of *Eoscutella mirandae* Parma, 1985 provided. A tabular key to all seven South American non-lunulates is given, along with discussion of the relationship between the posterior notch and the anal lunule.

Key words: Clypeasteroida, Abertellidae, sand dollars, new family, new genus, new species, Argentina, Patagonia, Oligocene, Miocene

Introduction

Fossil clypeasteroids (sea biscuits, sand dollars, keyhole urchins, and allied forms) have been reported from all major land masses on Earth, including Antarctica. Only a few decades ago, the diversity of fossil clypeasteroids found in South America was considered to be low relative to regions such as North America and Europe. South America's clypeasteroid fossil faunas remain relatively unknown, but knowledge continues to grow concerning scutelliform (*sensu* Kroh & Smith 2010) clypeasteroids in particular.

Scutelliforms are sometimes referred to as "true" sand dollars, distinguishing them from clypeasterine or laganiform taxa that, in some cases, also adopt features of the "sand dollar paradigm" (Seilacher 1979). One of the major features of such "true" sand dollars that is seldom, if ever, found outside the scutelliform clade is the presence of a hole or holes through the coronal skeleton (or test). Known as lunules, these holes can occur in any of the five ambulacral regions distal to the petals (specialized regions of respiratory tube feet arranged along each ray

Accepted by A. Kroh: 3 Nov. 2017; published: 5 Jan. 2018

on the top of a sand dollar), as well as in the posterior interambulacrum. In some forms, the hole is positioned sufficiently close to the ambitus that it is expressed as a notch, but these are demonstrably homologous to the closed lunules in closely related species.

The lunule that occurs in the posterior interambulacrum is also known as the anal lunule due to its occurrence just anterior (proximal) to the periproct (which contains the anal opening). The anal lunule is not homologous with the ambulacral lunules (Mooi *et al.* 2000). Presence of an anal lunule is a synapomorphy for a large and diverse lunulate sand dollar clade found on both Atlantic and Pacific sides of the tropical and subtropical Americas (Mooi *et al.* 2000). Although several scutelliform taxa possess a posterior notch, the plate patterns and ontogeny of this notch strongly support the hypothesis that it is not in any way related to the origins of, nor is it homologous with the anal lunule (see Discussion, below).

In Durham's (1955, 1966) revisionary works, only two species of lunulate taxa had been recorded from the Neogene of South America, both of them supposedly characterized by an anal lunule. The taxonomic status of one of these, *Karlaster* Marchesini Santos, 1958, was compromised by a lack of data concerning the type and only specimen, which was sufficiently broken along the posterior edge to raise doubts about the presence or absence of features crucial to determining the affinities of this form (see below). Only a single South American species lacking lunules, hereafter referred to as non-lunulates, was recognized by Durham (1966). At that time, supposed diagnoses of supraspecific taxa, and even the species themselves, listed many features that were not unique, and therefore did not actually diagnose the forms under consideration. Insufficient characterization prevented unequivocal allocation to described families.

Recent efforts have attempted to generate data that could help rectify this situation. New approaches to examination of type material and the study of newly discovered specimens have revealed a sand dollar fauna that can tell us much about its evolution in the region, particularly in the Miocene (Martínez 1984; Rossi de García & Levy 1986; Martínez & Mooi 1997, 2005; Mooi *et al*. 2000, 2016; Mooi *et al*. 2016). These works focused on lunulate clypeasteroids, notably South American monophorasterids thought to figure prominently in the origins of mellitid, lunulate taxa distributed today along the shores of southeastern North America, the Caribbean, Gulf of Mexico, and on both the Atlantic and Pacific coasts of Central and South America.

In contrast, non-lunulate species have received very little attention, perhaps because they lack diagnostic features such as lunules to place them unequivocally among known genera or families. Only a handful of works since 1966 have taken a more focused look at the systematics of non-lunulate forms (Brito 1979, 1981, 1986; Parma 1985; Martínez *et al*. 2005; Kroh *et al*. 2013). The Abertellidae Durham, 1955, once thought to occur only in Miocene deposits in the United States and Mexico, has received the most recent attention in works on the South American Miocene. The documented presence of this group in South America (Fig. 1) has greatly expanded the known ranges of the family, as well as our knowledge of the evolution of this extinct but important group now known to occur in all the Americas (Kroh *et al*. 2013).

The present study was compelled by the discovery of a new species of non-lunulate scutelliform that was collected alongside a recently described new species of monophorasterid lunulate (Mooi *et al.* 2016) from the Punta Maqueda region in Santa Cruz Province, Argentina. Preliminary analysis suggested that the undescribed non-lunulate was not clearly related to any known group of scutelliforms. Attempts to compare the new species with other non-lunulates from throughout the Americas revealed the inadequate state of our knowledge of several enigmatic forms. These had previously been set aside for further analysis until the types had been reassessed, and new fossils had come to light.

Such taxa included the aforementioned *Karlaster*, which was considered by Marchesini Santos (1958), and even by some later workers (*e.g.* Durham 1966), to be a lunulate monophorasterid, an assertion disputed by Martínez & Mooi (1997) and Mooi *et al.* (2000). The latter authors questioned that the type and only known specimen of *Karlaster pirabensis* Marchesini Santos, 1958 had an anal lunule, and used data from what could be observed of the oral plate patterns to compare that species with *Abertella complanata* Brito, 1981. Mooi *et al.* (2000) reviewed the situation, and came to the conclusion that much as in *A. complanata*, *K. pirabensis* probably did not have an anal lunule. It was, in part, this feature that convinced Mooi *et al*. (2000) that *Karlaster pirabensis* was a member of the Abertellidae, and they placed it in the genus *Abertella* Durham, 1953.

One of the features that continues to exert strong influence on placement of certain South American non-lunulate sand dollars into the Abertellidae is the presence of a posterior notch, an indentation along the interradial suture of the posterior interambulacrum where it meets the edge of the test (ambitus). The development of this notch (essentially an interradial region that stops growing outward at the ambitus) can result in the formation of a conspicuous pair of lobes on either side of the posterior interambulacrum at the ambitus. The way in which the plates of the posterior interambulacrum were usually reduced in size, and the patterns in which the ambital plates of adjacent ambulacra curved anteriorly around the ends of these lobes and into the notch, are distinctive of the posterior notch. In some cases, notably in *A. pirabensis* and some of the North American species of *Abertella*, the posterior notch can be very deep. It can sometimes be slit-like, as in *A. complanata*. In other taxa, such as the South American *A. gualichensis* Martínez *et al*., 2005 and *A. miskellyi* Kroh *et al*., 2013, and even in the eastern North American type species of the genus, *A. aberti* (Conrad, 1842), the notch is much more poorly developed. Such variation in the degree to which the posterior notch is developed raises questions concerning how it forms, and its significance as a diagnostic feature. Here we initiate some of these investigations, including its usefulness as part of the basis for establishing *Abertella* as monophyletic.

An important way in which clypeasteroid systematics has progressed is illustrated by Durham's (1955, 1966) ground-breaking investigations of sand dollar plate architecture. These analyses are most often done through the mapping of plate sutures on both the aboral (top) and oral (bottom) surfaces of the echinoid (*e.g.* Mooi 1989). Such studies are especially crucial for fossil taxa, in which other types of data (spination, internal structure, DNA) are almost impossible to obtain in sufficient quantity to resolve taxonomic challenges. Examination of plate maps can result in substantive phylogenetic data critical to establishing major clypeasteroid clades (Mooi 1990). These data are now starting to come to light concerning South American non-lunulates. Preliminary work suggested that an approach combining plate maps, particularly of the oral surface, with other types of morphological information would be central in determining affinities of enigmatic forms occurring in Miocene strata, including the newly discovered non-lunulate from Punta Maqueda.

There are two main types of plates distinguished along both ambulacral and interambulacral plate columns on the oral surface of a clypeasteroid. In a circlet surrounding the peristome (mouth region), there are five pairs of ambulacral plates alternating with five single, interambulacral plates. These comprise the basicoronal plates. The second type, the postbasicoronal plates, comprises all the rest of the plates in the column leading across the oral surface, around the ambitus, and onto the aboral surface. Arguably the most conspicuous characteristic of the oral plate architecture of abertellids is that in adults, all the interambulacral columns are discontinuous (or disjunct) due to the meeting up of adjacent ambulacral postbasicoronals along the interradius. The expansion of ambulacral postbasicoronals interrupts the sutural connection between the interambulacral basicoronals and the corresponding first interambulacral postbasicoronals (see Durham 1966 and Mooi 1989 for further explanation, examples, and illustrations). This characteristic is apparent even in some of the earliest images of the oral surface of *A. aberti* (*e.g.*, Clark & Twitchell, 1915: pl. 87), and has been used as an important diagnostic feature for the genus and family by workers such as Durham (1966), Martínez *et al*. (2005) and Kroh *et al*. (2013). It is important to note that several other genera of non-lunulate, scutelliform sand dollars (*e.g. Dendraster* L. Agassiz in Agassiz & Desor, 1847; *Scaphechinus* A. Agassiz, 1864; *Vaquerosella* Durham, 1955) also have all interambulacra discontinuous in a manner similar to that of *Abertella*. However, unlike *Abertella*, none combines this feature with the presence of a posterior notch.

These important aspects of plate architecture and test form in both *Abertella pirabensis* and *A. complanata* remain poorly corroborated. A thorough revision of all these non-lunulate taxa was made possible by examination of type material—something that had not been done since their original descriptions. This was required in order to evaluate the taxonomic status of the new material from Punta Maqueda. Initial examination suggested that this new non-lunulate was similar to species in the genus *Abertella*, notably *A. gualichensis*, largely due to the presence of a shallow posterior notch. However, studies of the plate architecture on the oral surface contested this idea, necessitating comparisons with all known non-lunulate sand dollar taxa found in South America, and not just those assigned to *Abertella*. This in turn compelled us to provide a more thorough and restrictive diagnosis of the genus. Our analyses also illustrated that *Abertella complanata* did not have oral plate morphology supporting its placement in the abertellids, let alone in *Abertella*. Surprisingly, features of the type specimen of "*Karlaster*" *pirabensis* agreed with the diagnosis of *Abertella*, but those of the type of "*Abertella*" *complanata* did not.

The outcome of these investigations indicated the need to name a new family, in part to house the new genus and species from Punta Maqueda, and in part to accommodate a new genus in which to place the reassigned "*Abertella*" *complanata*. In the process, we assessed what was known of all Miocene lunulates reported to occur in South America, including the relatively well-known *Iheringiella* Berg, 1898. It turned out that *Iheringiella* is very different from any other non-lunulates, not only in South America, but from anywhere else in the Americas, suggesting that it is best placed in a family of its own until further analysis can provide a phylogenetic framework. We note here that *Iheringiella* is at least as distinct as other monotypic families erected by Durham (1955, 1966). Until such time as a global phylogenetic analysis of all scutelline clypeasteroids is able to determine which of the known families can be considered monophyletic, we here place *Iheringiella* into a family of its own to highlight its distinctiveness and need for continuing analyses of all South American scutellines.

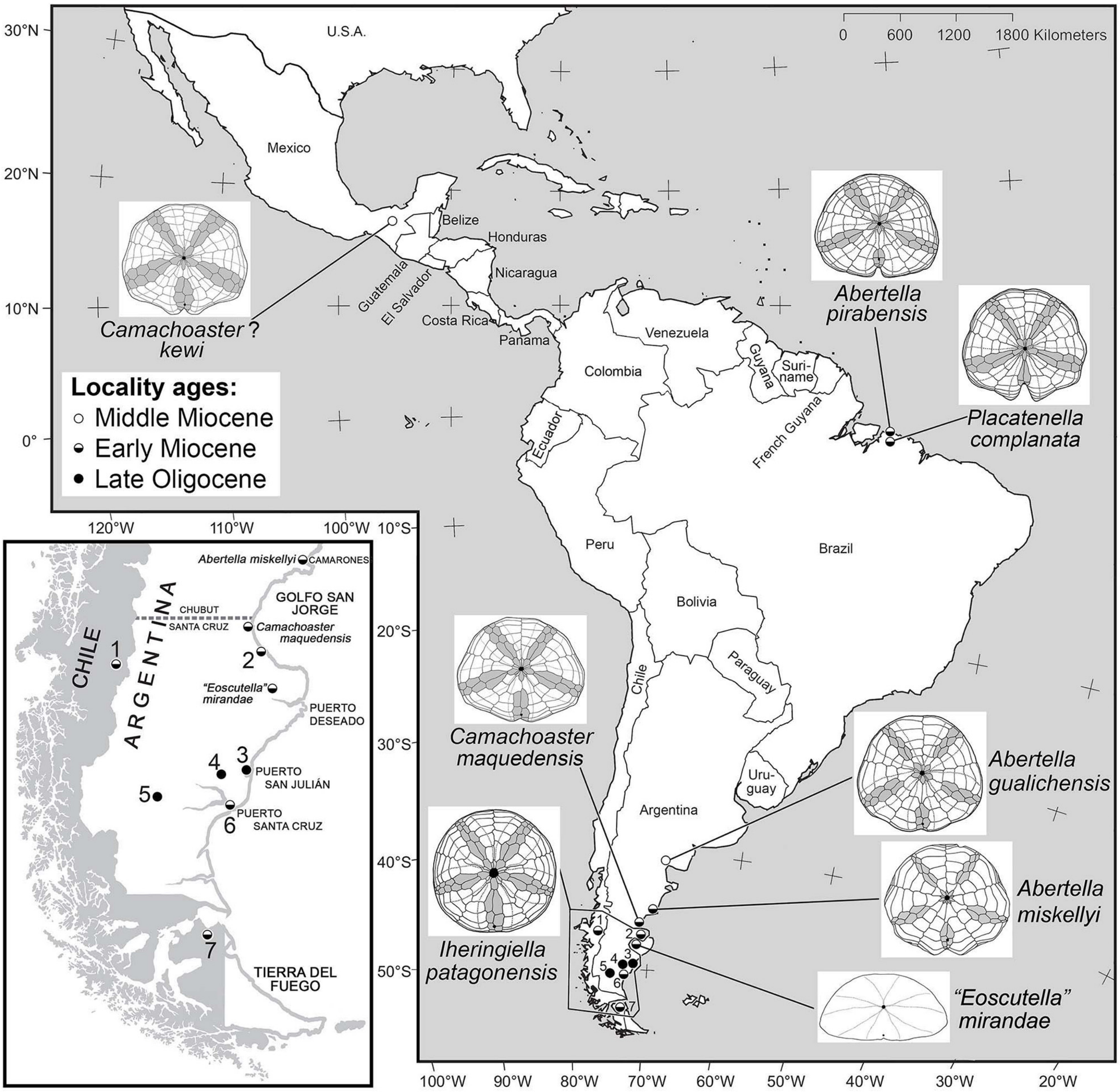


FIGURE 1. Localities for taxa discussed in the text. Inset at lower left centers on the Santa Cruz region of Patagonia. Numbered occurrences correspond to unequivocal *Iheringiella patagonensis* localities (inside boxed region in main map): 1. Pampa Castillo, Chile (Andre Wyss, pers. comm.); 2. Cañadón El Lobo, Santa Cruz, Argentina (CPBA 16493-95); 3. Oven Point/Sholl's Tomb, Santa Cruz, Argentina (Ortmann 1902), Punta Cuevas, Santa Cruz, Argentina (MACN 4586 and Cuitiño 2011), Playa La Mina, Santa Cruz, Argentina (Cuitiño 2011); 4. Meseta Chica, Bajo de San Julián, Santa Cruz, Argentina (MACN 5144 and Cuitiño 2011); 5. Upper Rio Chalia, Santa Cruz, Argentina (Ortmann 1902); 6. Puerto Santa Cruz, Santa Cruz, Argentina (ROM 5433M, 5468M, 5469M); 7. Sector Flamenco, Tierra del Fuego, Chile (Larrain 1984)—reported to be from Eocene strata, but this is questionable (Mooi *et al*. 2000).

Status of Eoscutellidae Durham, 1955 in South America—The Eoscutellidae is allegedly represented in South America by a single named species, *Eoscutella mirandae* Parma, 1985, from the Monte León Formation of Santa Cruz Province, Argentina (Fig. 1). *Eoscutella* Grant & Hertlein, 1938, is a genus of non-lunate sand dollars otherwise found only in the northern Pacific region. The type species of the genus, *E. coosensis* Kew, 1920, is known only from the Eocene of Oregon. Another described *Eoscutella* from the Kamchatka region, *E. kamtschatika* Shmidt, 1975, is similarly known only from the Eocene. At least two other as yet unnamed Eocene species from California represent the hitherto undocumented diversity of the genus suggested by Durham (1955). All known specimens of *Eoscutella* from the northern hemisphere possess continuous interambulacra, the basicoronals broadly in contact with the first postbasicoronals. Recent observations made by R.M. and S.M. on type specimens 12901 and 12902 at the Cátedra de Paleontología de la Universidad de Buenos Aires, Argentina strongly suggest that at least some of the interambulacra of *E. mirandae* are discontinuous. Resemblance of *E. mirandae* to North American *Eoscutella* is superficial, consisting almost entirely of extreme widening of the test, but little else. Such widening is known to occur convergently in several other unrelated scutelliforms. Re-examination of *Eoscutella* in South America is much needed in the light of new data from North American forms before any more can be said of the genus- and family-level assignment of Parma's (1985) specimens. Therefore, these are considered only briefly in the treatments below.

Material and methods

Studied material of the new species was collected from shoreline deposits in southern Argentina, about 2 km south of Punta Maqueda, Santa Cruz Province (Mooi *et al.*, 2016). Specimens of all other taxa considered in this revision were studied at the indicated institutions. Newly collected material was prepared and cleaned using fine picks and sonication. All studied specimens were photographed under a variety of light conditions to reveal surface detail and test plate patterns. When it was necessary to enhance visibility of suture lines for the production of plate maps, selected specimens from the new species were polished using a graded series of waterproof sand papers.

Abbreviations:

CPBA	Cátedra de Paleontología de la Universidad de Buenos Aires, Argentina
DNPM	Departamento Nacional de Produção Mineral (former name of the Brazilian Geological Survey)
MACN	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina
MB	Museum für Naturkunde, Berlin, Germany
MNRJ	Museu Nacional, Rio de Janeiro, Brazil
MPEG	Museu Paraense Emílio Goeldi, Belém, Brazil
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, USA
ROM	Royal Ontario Museum, Toronto, Canada
TL	Test length
UCMP	University of California Museum of Paleontology, Berkeley, California, USA

Systematic part

Class Echinoidea Leske, 1778

Irregularia Latreille, 1825

Order Clypeasteroida A. Agassiz, 1872

Suborder Scutellina Haeckel, 1896

Infraorder Scutelliformes Haeckel, 1896

Family Placatenellidae n. fam.

Diagnosis. Scutelline sand dollars with a slight to very pronounced posterior notch; paired oral interambulacra continuous; first postbasicoronal plates in paired oral interambulacra greatly elongated along the interradius, at least four times longer than wide and at least two to three times the length of any other postbasicoronal in the paired columns.

Etymology. The genus group name represents a combination of the term "*placa*", from the Latin for "plate", and the term "*catena*", Greek for "chain", signifying continuity of the paired oral interambulacra. There is also an implicit double meaning in the combination, as the first seven letters of the name form the word "placate", suggesting our attempt to put at peace the many problems associated with this, and related problematic South American taxa.

Type genus. *Placatenella* **n. gen.**

Remarks. In general, morphological disparity among scutelliform taxa, particularly the extinct forms, often leads to either monotypic families, or those containing only a very few species. The description of the Placatenellidae **n. fam.** is no exception, in that it contains only two genera, each of which is monotypic. However, this action steers a course between lumping these taxa with the Abertellidae, which is undesirable given how wide and intractable the diagnosis of the latter would then become, and describing not one, but two new families, one for *Placatenella* **n. gen.**, and the other for *Camachoaster* **n. gen.** These two genera are very similar except in the nature of the posterior interambulacrum (see below), and it is here considered inconsistent with current practice in scutelliform taxonomy to designate a new family for each on the basis of these features alone, when the two genera have so much in common to the exclusion of all other scutelliforms. Pending full phylogenetic revision of all these taxa, including those occurring outside of South America, this leaves open the possibility of maintaining a simplified diagnosis of the Abertellidae, and avoids over-extending the concept of this important family.

Genus *Placatenella* n. gen.

Diagnosis. As for the family, but with interambulacrum 5 continuous, basicoronal 5 contiguous with both postbasicoronals; postbasicoronals in interambulacrum 5 greatly elongated and arrow-shaped, at least three times the length of more distal oral postbasicoronals in the same interambulacrum; periproct marginal inside posterior notch.

Type species. *Abertella complanata* Brito, 1981.

Placatenella complanata (Brito, 1981)

Figures 1–4.

1981 *Abertella complanata* Brito: 3–4, figs 1–2.
2000 *Abertella pirabensis* Marchesini Santos—Mooi *et al.*: 266, in part.

Diagnosis. As for the genus, which is emended from Brito's (1981: 3) original diagnosis or description (it is not stated which). Brito's information does not diagnose the species because it does not distinguish it from other members of the genus *Abertella* to which it was originally assigned (translated from the Portuguese): "Test flattened, flat on the oral and convex on the aboral surface, with a semicircular outline, and a marked anal indentation, a small but sharp indentation in the anterior ambulacrum, and only a sinuosity in the paired ambulacra. Petals closed, measuring approximately two-thirds of the test radius with the poriferous zones slightly narrower than the interporiferous. Central peristome, from which extend five food grooves that soon fork. Periproct ventral in the posterior indentation."

Type and other material studied. The holotype, MNRJ 5460-I, is the only originally described specimen, and is housed at the Museu Nacional, Rio de Janeiro, Brazil. We also examined other specimens assigned to this species by Brito (1986), including MNRJ 5536-I, MPEG-886-I, MPEG 1753-I, MPEG 2405-I, and DNPM 6217. These are generally of higher quality than the holotype, revealing new information concerning the species.

Description. Brito (1986: 2) expanded upon the original description/diagnosis of the species based on new material, adding that there were five distinct genital pores. This is evidently an error, as Brito's (1986) own photos and original description indicate four gonopores. Our emended description is as follows.

Holotype (Fig. 2A, B) approximately 25 mm TL (measured as described in Table 1, from junction of perradial suture of ambulacrum III with anterior edge of test to junction of interradial suture of interambulacrum 5 with posterior edge of test [*i.e.* inside notch]). Largest known specimen (Brito 1986: Fig. 1) approximately 45 mm TL, almost 55 mm in test width at widest point. Best preserved specimen (MNRJ 5536-I, Fig. 2C, D) approximately 38 mm TL (Fig. 2C, D), 57 mm test width. Ratio of width to length including lobes on either side of notch 1.17. All ensuing percentage calculations for species are from MNRJ 5536-I (Fig, 2C, D). Aboral surface slightly domed, oral surface flat. Highest point of test approximately 17% TL, located at apical system. Very sharply defined, parallel-sided, narrow posterior notch in largest specimens, depth just over 25% TL, width 10% TL, notch slightly widening near ambitus in holotype (Fig. 2A, B). Broad but shallow marginal indentations present where perradial suture meets ambitus in each ambulacrum, particularly in posterior paired ambulacra.

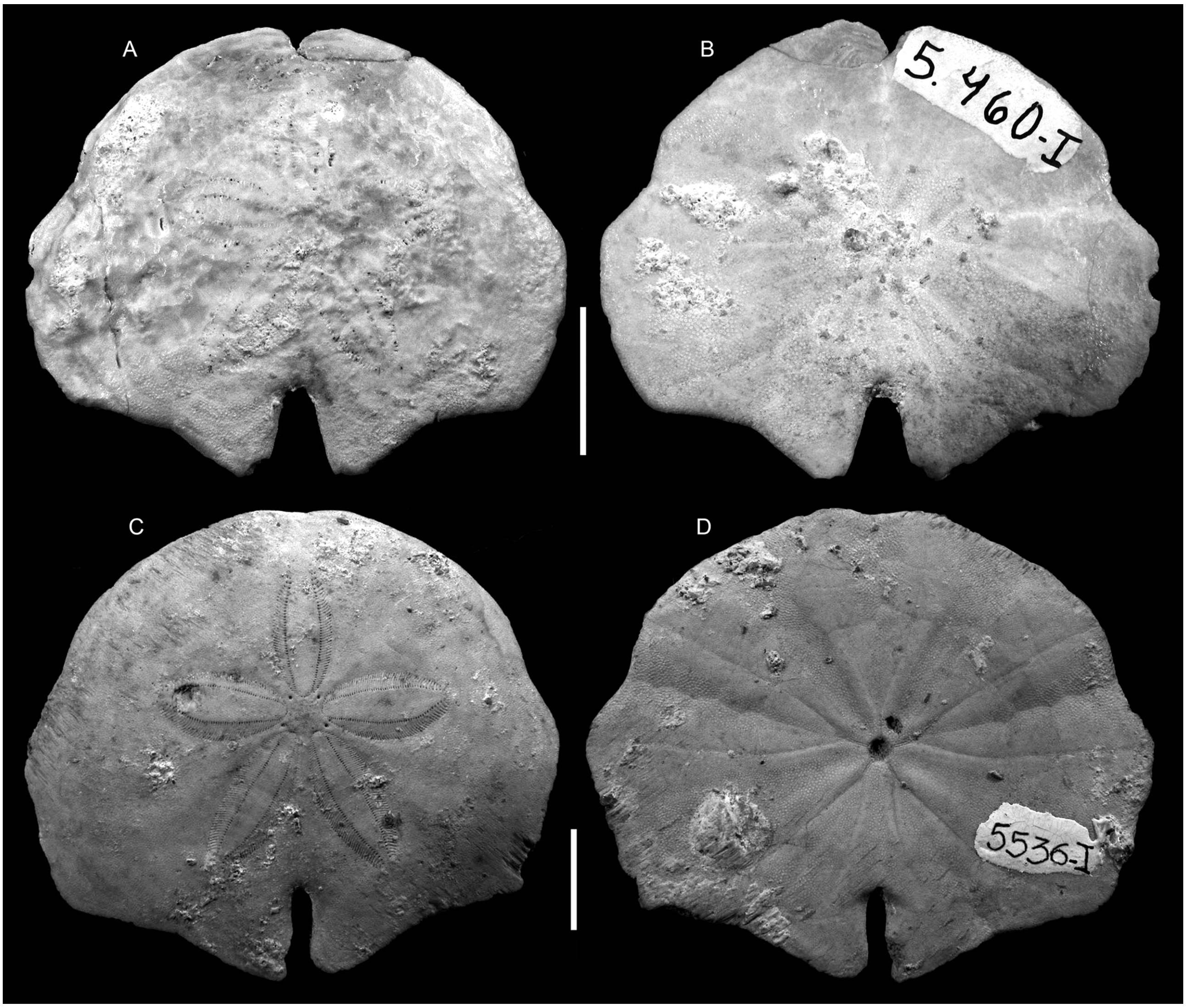


FIGURE 2. *Placatenella complanata* (Brito, 1981), photographs. A: Aboral surface of holotype, MNRJ 5460-I. B: Oral surface of holotype, MNRJ 5460-I. C: Aboral surface of MNRJ 5536-I, with deep, narrow posterior notch. D: Oral surface of MNRJ 5536-I. Scale bars 10 mm in length.

Apical system monobasal, pentagonal (not star-shaped), 49% TL from ocular III to anterior edge of test, length 11% TL, numerous hydropores scattered over madreporic plate. Four gonopores, one in each of paired interambulacra and located at suture between madreporic plate and first adapical plates of interambulacral column.

Ambulacra petaloid adapically. Posterior paired petals (I and V) noticeably longest, each extending 67% of corresponding test radius, but 39% TL; anterior paired petals (II and IV) 59% of corresponding test radius, but 33%

TL; anterior unpaired (III) shortest, 68% of corresponding test radius, but 31% TL. Petal V width at widest point 16% TL, interporiferous zone 7% TL; petal IV width 18% TL, interporiferous zone 10% TL; petal III width 16% TL, interporiferous zone 9% TL. Petals lyrate, almost closed distally, with four or five trailing tube feet (*sensu* Mooi 1989) at distal end of each column of respiratory tube feet (Fig. 3A). Respiratory tube foot pore pairs strongly conjugated, inner pore slightly elongate or almost circular, outer pore extremely elongated, comprising about half length of pore pair, apparently subdivided by stereom septae. Four or five occluded plates present at tips of petals. At ambitus, ambulacra strongly widened, forming strip-like ambital plates that follow contour of shallow indentation at each perradius, and curving strongly adapically to form test wall along each side of posterior notch (Fig. 4). Ambulacra all in agreement with Lovén's Rule (*sensu* David *et al.* 1996). Ambulacral basicoronal plates all similar, narrow and straight with almost parallel radial sutures on each side (Fig. 4).

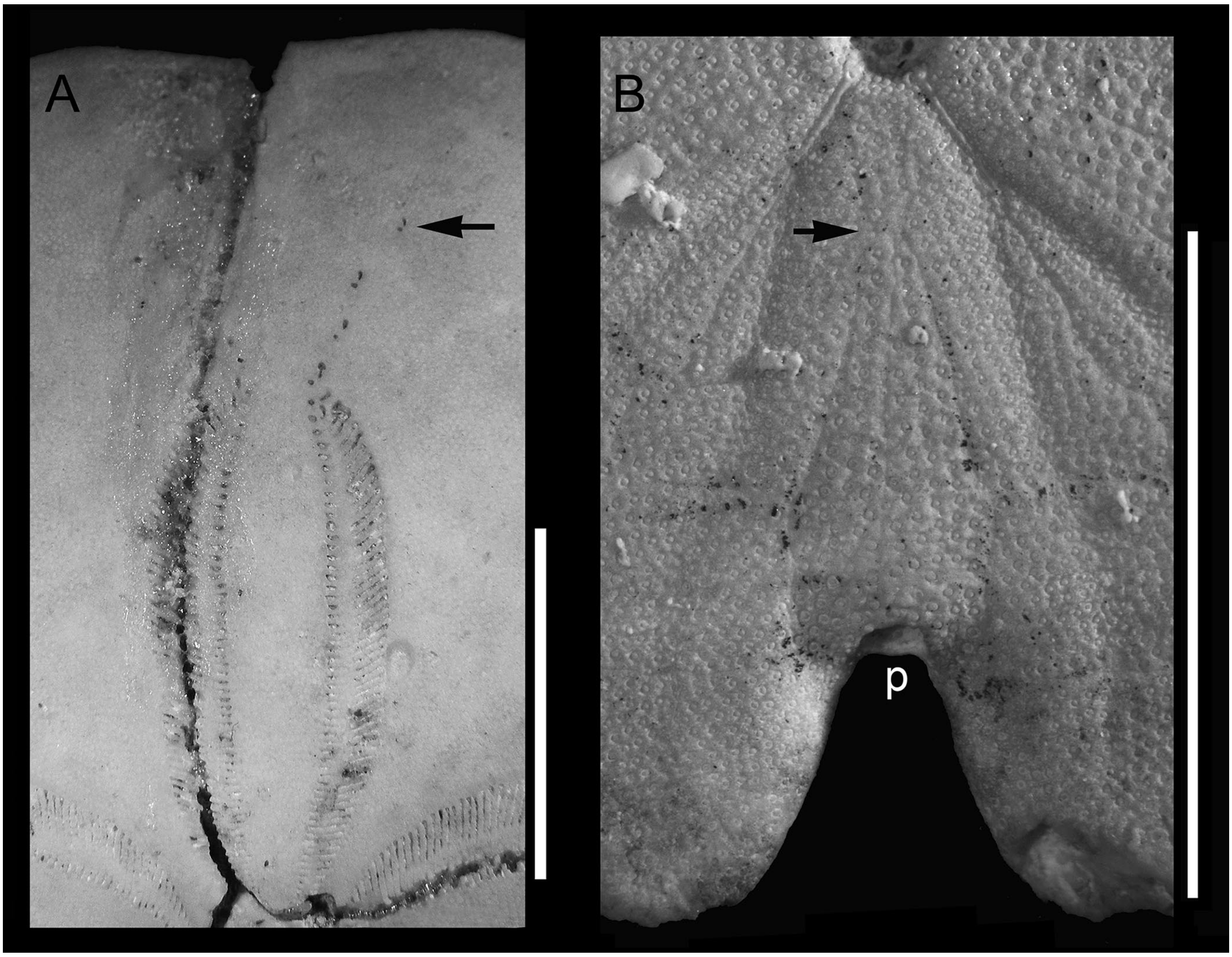
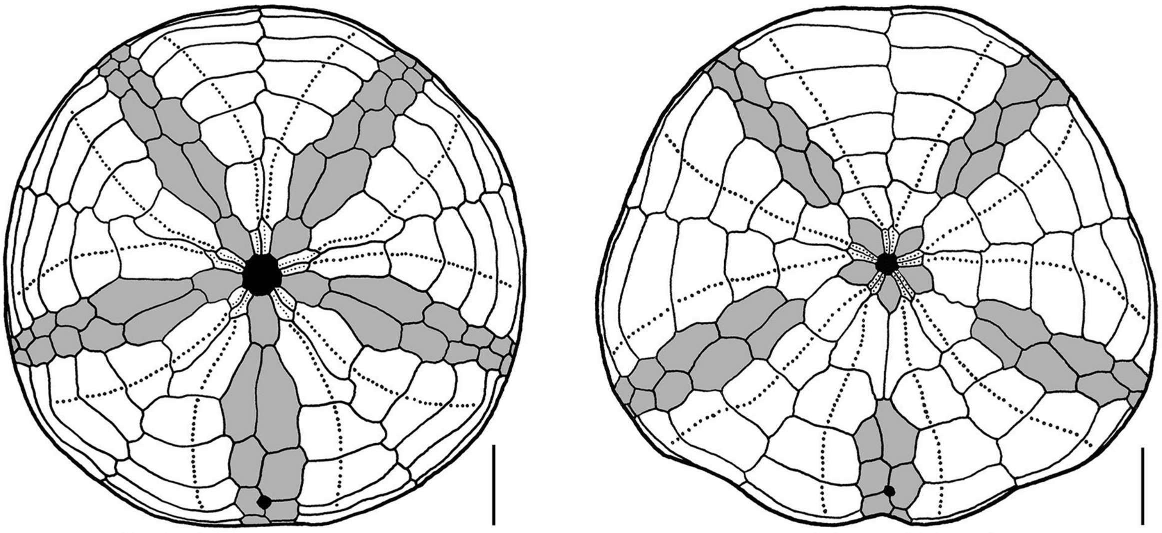
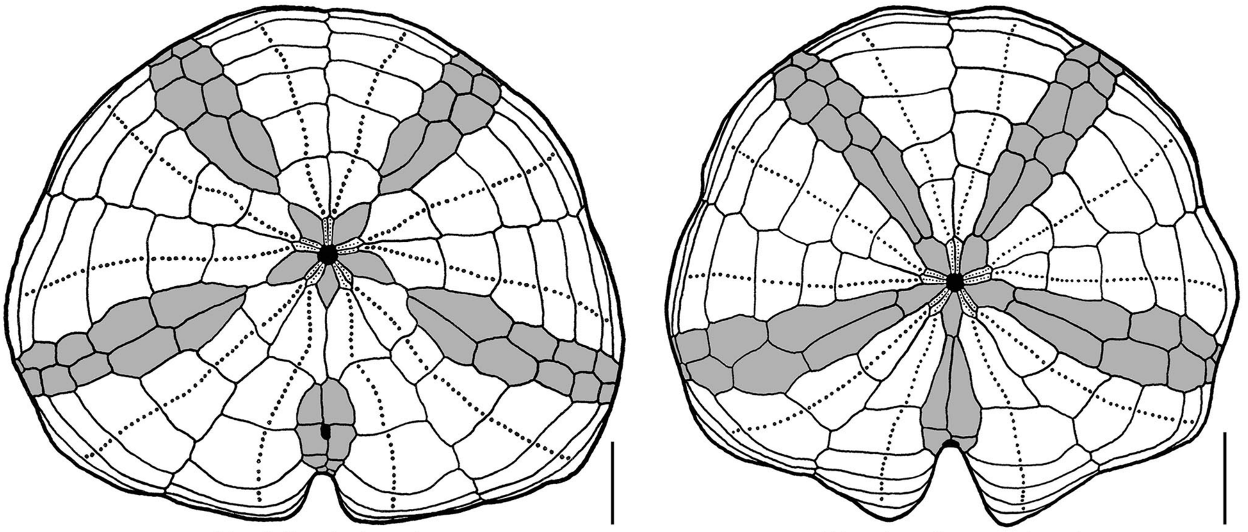


FIGURE 3. *Placatenella complanata* (Brito, 1981), photographs. A: Detail of petal in ambulacrum III of MPEG 886-I showing pores of trailing tube feet (arrow indicating most distal pore pair). B: Detail of oral surface near posterior edge of MPEG 2405-I showing periproct at margin, inside notch (p), and continuity of posterior interambulacral post-basicoronals with basicoronal 1 (arrow). Scale bars 10 mm in length.

Interambulacra narrow and straight on oral surface, narrowing towards ambitus, but containing paired, zig-zag plates right up to madreporic plate. On oral surface, two postbasicoronal plates in each half-interambulacrum in interambulacrum 5, about four in interambulacra 1 and 4, and about five in interambulacra 2 and 3. Widest point of each interambulacrum about two thirds of way from basicoronal to ambitus, narrowing distally to about half that width so that paired interambulacra only about 14% width of adjacent ambulacra at ambitus. In each paired interambulacrum, first postbasicoronal greatly elongated, nearly five times as long as wide, about twice length of corresponding second postbasicoronal. Unpaired posterior interambulacrum 5 very narrow near basicoronal, widening distally, then narrowing as it approaches ambitus inside notch (Fig. 4). All interambulacral basicoronals broadly in contact with both corresponding first postbasicoronals.



Iheringiella patagonensis　*Abertella gualichensis*



Abertella pirabensis　*Placatenella complanata*

FIGURE 4. Comparison of oral plate architecture of *Iheringiella patagonensis* (Desor, 1847) (based on ROM 5433M), *Abertella gualichensis* Martínez *et al.*, 2005 (based on the holotype, MACN-Pi 4706), *Abertella pirabensis* (Marchesini Santos, 1958) (reconstruction based on the holotype and only known specimen, DNPM 4493, details of interambulcrum 2 inferred by comparison with interambulacrum 4, and of ambulacrum V by comparison with ambulacrum I), and *Placatenella complanata* (Brito, 1981) (based on the holotype, MNRJ 5460-I, as well as MNRJ 5536-I, MPEG 886-I, MPEG 2405-I). Food grooves indicated by dotted lines, peristome and periproct in solid black, interambulacra shaded, scale bars 10 mm in length.

Peristome circular, relatively small, about 4% TL, with distinct perradial process in each ambulacrum extending into peristome beyond slight bulge containing sphaeridium (Fig. 3B). Anterior edge of peristome 60% TL from anterior edge of test. Periproct small, about 4% TL, situated at ambitus in anterior wall of posterior notch, between second and third pair of postbasicoronals.

Aboral tuberculation homogeneous. Very slight enlargement of tubercles in oral interambulacral regions relative to those in ambulacral regions. In specimens with best preservation of surface detail, distinct tube foot pores visible in food grooves.

Food grooves well developed (Figs. 2, 3, 4), restricted to oral surface, with primary bifurcation near adapical ends of ambulacral basicoronal plates. After this branch point, food grooves continuously diverging as they approach ambitus. Secondary branching faint in all specimens, apparently poorly developed. Slight depressions along perradial sutures on oral surface forming extremely shallow channels reminiscent of rudimentary pressure drainage channels.

Occurrence. Known from the holotype collected from the early Miocene Pirabas Formation in the town of Castelo on the island of Fortaleza, State of Pará, Brazil, and from several additional specimens from the same formation, 5 km north of Capanema, near Colônia Pedro Teixeira, Pará, Brazil.

Remarks. See the description of the family for etymology of the genus name. None of Brito's (1981, 1986) descriptions illustrates oral plate patterns, but these are crucial to interpreting the taxonomic placement of *Placatenella complanata*. Our investigations indicate that *Placatenella* is very different in many respects from *Abertella pirabensis*. Although these two taxa are found near each other in similar stratigraphic circumstances, it is clear that Mooi *et al*. 2005 were incorrect in assuming that *P. complanata* and *A. pirabensis* were conspecific, and that examination of Brito's (1986) additional material of the former was not going to shed light on the morphology of the latter. It was only through re-examination of the type material of both taxa that the major differences became apparent, particularly in oral view. For example, the periproct is on the oral surface in *A. pirabensis* (see below), not marginal as in *Placatenella*.

The interambulacra of *A. pirabensis* are all discontinuous (Fig. 4), as is typical for all adult specimens of any species of *Abertella*. In all specimens of *Placatenella* in which plate patterns can be discerned either completely (Fig. 4), or in part (including the holotype), all interambulacra are continuous. Unusual among scutelliforms, and perhaps unlike any known species of abertellid, *P. complanata* typically has more oral postbasicoronal plates in the anterior paired interambulacra than in the posterior paired interambulacra. In addition, the oral tuberculation of *Placatenella* is more strongly differentiated in the interambulacral and ambulacral regions, and the regions between the branches of the food grooves are more depressed along the perradial suture, than in *Abertella*. In *A. pirabensis*, tuberculation of the oral surface is very uniform, and the surface itself is nearly planar, without significant perradial depressions. *Placatanella* also differs from *A. pirabensis* in petal shape. In the former, the petals are more lyrate, whereas in the latter, the two columns of pore pairs are more parallel, and remain so for a great portion of the petals' lengths. In addition, the petals of *A. pirabensis* vary less in length, are distinctly narrower relative to test length, and have narrower interporiferous zones than in *Placatenella*.

The posterior notch of *Placatenella* is remarkable for its depth and narrowness. This condition is unmatched in other South American non-lunulates, including the abertellids and the other genus of placatenellid, *Camachoaster*. The only species in the Americas that has a posterior notch similar to that of *P. complanata* is *Abertella palmeri* Durham, 1957, which stands out in this respect even among the abertellids. However, *A. palmeri* is easily assigned to the genus *Abertella*, having all interambulacra markedly discontinuous, and the periproct on the oral surface. The test outline of *A. palmeri* is also much more strongly alate (*sensu* Mooi *et al.* 2000) than in *P. complanata*. There can be little question that these two forms are not closely related.

Genus *Camachoaster* n. gen.

Diagnosis. As for the family, but with interambulacrum 5 discontinuous, the basicoronal widely separated from the first postbasicoronals by adjacent first postbasicoronal plates I and V.

Etymology. Named in recognition of Dr. Horacio Homero Camacho (1922-2015), the first geologist and paleontologist to revisit the early 20th century work of H. von Ihering on Patagonian Mesozoic and Cenozoic faunas. Camacho worked and taught at the University of Buenos Aires for over 65 years, and was among the first to recognize the importance of the study of Patagonian echinoids in stratigraphic correlation and paleoenvironmental reconstruction.

Type species. *Camachoaster maquedensis* **n. sp.**

Camachoaster maquedensis n. sp.

Figures 1, 5–8.

Diagnosis. As for the genus.

Etymology. Named for the type locality of Punta Maqueda, Santa Cruz Province, Argentina, where the sand dollars occur in the Chenque Formation, which is exposed about 2 km south of the point.

Type material studied. Material is housed at the Museo Argentino de Ciencias Naturales Bernardino

Rivadavia (MACN). Holotype is MACN-Pi 5809, from shoreline deposits about 2 km south of Punta Maqueda, Santa Cruz Province, southern Argentina. These deposits form part of the Chenque Formation, lower Miocene. There are two paratypes, MACN-Pi 5859 and MACN-Pi 5860. These have the same provenience as the holotype.

Description. Holotype and largest specimen (Fig. 5) 59.3 mm TL. Measurements for all known specimens given in Table 1. All ensuing percentages, calculated to facilitate comparisons with other descriptions herein, are from holotype. Aboral surface slightly domed, oral surface flat. Highest point of test 11% TL, located at apical system. Very shallow but distinct posterior notch, depth just over 5% TL, width 16% TL, notch widening significantly near ambitus. Broad, shallow marginal indentations present where perradial suture meets ambitus in each ambulacrum.

Apical system monobasal, pentagonal (not star-shaped), 49% TL from ocular III to anterior edge of test, length 8% TL, numerous hydropores scattered over madreporic plate. Four gonopores, one in each of paired interambulacra and located at suture between madreporic plate and first adapical plates of interambulacral column (Fig. 8A).

Ambulacra petaloid adapically. Posterior paired petals (I and V) not noticeably longer than any other petals, each extending 56% of corresponding test radius, but 30% TL; anterior paired petals (II and IV) 51% of corresponding test radius, but 29% TL; anterior unpaired (III) 56% of corresponding test radius, but 29% TL. Petal V width at widest point 12% TL, interporiferous zone 4% TL; petal IV width 12% TL, interporiferous zone 5% TL; petal III width 13% TL, interporiferous zone 6% TL. Petals lyrate, almost closed distally (Figs. 5, 8A, B), with two or perhaps as many as three trailing tube feet (*sensu* Mooi 1989) at distal end of each column of respiratory tube feet (Fig. 8A). Respiratory tube foot pore pairs strongly conjugated, inner pore slightly elongated, outer pore extremely elongated, comprising about half length of pore pair, apparently subdivided by stereom septae (Fig. 8A, B). Five or six occluded plates present at tips of petals (Fig. 8A). At ambitus, ambulacra greatly widened, forming strip-like ambital plates that follow contour of shallow indentation at each perradius, and curving adapically to form test wall along each side of posterior notch (Fig. 7). Ambulacra all in agreement with Lovén's Rule (*sensu* David *et al*. 1996). Ambulacral basicoronal plates all similar, narrow and straight with almost parallel radial sutures on each side (Figs. 6, 7).

Interambulacra narrow and straight on oral surface, narrowing towards ambitus, but containing paired, zig-zag plates right up to madreporic plate. On oral surface, three or four postbasicoronal plates in each half-interambulacrum in interambulacrum 5, four or five in in other interambulacra. Widest point of each interambulacrum about one third of way from basicoronal to ambitus, narrowing distally so that paired interambulacra about 22% width of adjacent ambulacra at ambitus. In each paired interambulacrum, first postbasicoronal greatly elongated, about four times as long as wide, about twice length of corresponding second postbasicoronal. In interambulacra 1 to 4, basicoronals broadly in contact with both corresponding first postbasicoronals. Unpaired, posterior interambulacrum 5 discontinuous, separated from basicoronal by adjacent ambulacral postbasicoronals (Figs. 6, 7).

Peristome circular, relatively small, about 5% TL, with distinct perradial process in each ambulacrum extending into peristome beyond slight bulge containing sphaeridium (Fig. 8C). Anterior edge of peristome 51% TL from anterior edge of test. Periproct small, about 3% TL, on oral surface between second and third pair of postbasicoronals.

Aboral tuberculation homogeneous. Very slight enlargement of tubercles in oral interambulacral regions relative to those in ambulacral regions. In specimens with best preservation of surface detail, distinct tube foot pores visible in food grooves (Fig. 8C).

Food grooves well developed (Figs. 5, 7, 8C), restricted to oral surface, with primary bifurcation near adapical ends of ambulacral basicoronal plates. After this branch point, food grooves continuously diverging as they approach ambitus. Secondary branching well developed (Fig. 5). Extremely shallow depressions along perradial sutures on oral surface.

Occurrence. Known only from the type locality.

Geologic setting. The shallow marine deposits in which the new species was found have been described in Mooi *et al.* (2016). In summary, the rocks of the Chenque Formation in the Golfo San Jorge Basin (Chubut and Santa Cruz Provinces, Argentina) exposed near Punta Maqueda have been described as early Miocene (del Río 2004). The type specimens of *Monophoraster telfordi* Mooi *et al.*, 2016 were collected from the same thin bed (up to 15 cm thick) of fine-grained sandstones from which the new species of non-lunulate was recovered.

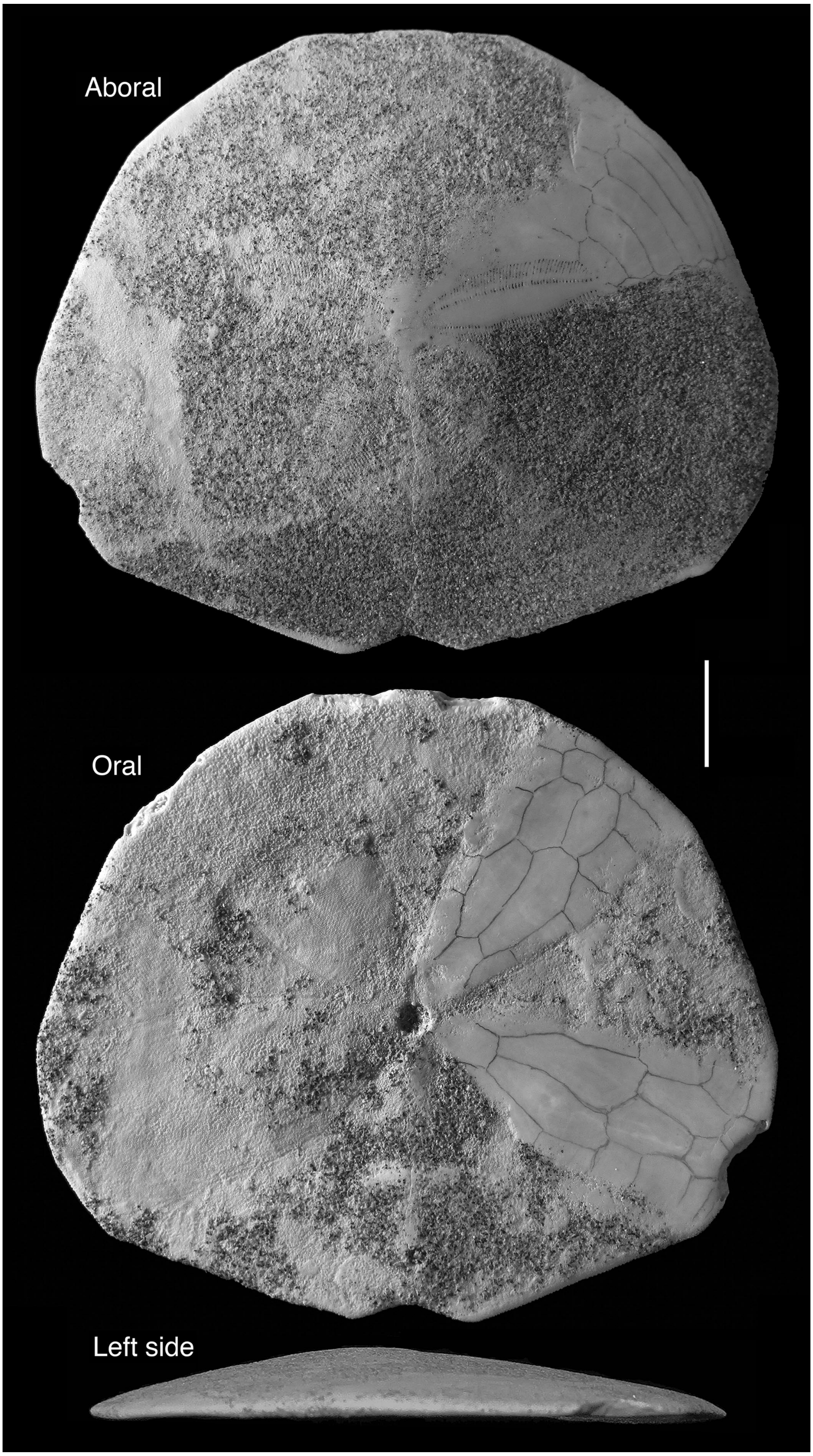


FIGURE 5. *Camachoaster maquedensis* **n. sp.**, photographs of the holotype MACN-Pi 5809. Oral surface shows pencil marks indicating some of the plate architecture. Scale bar 10 mm in length.

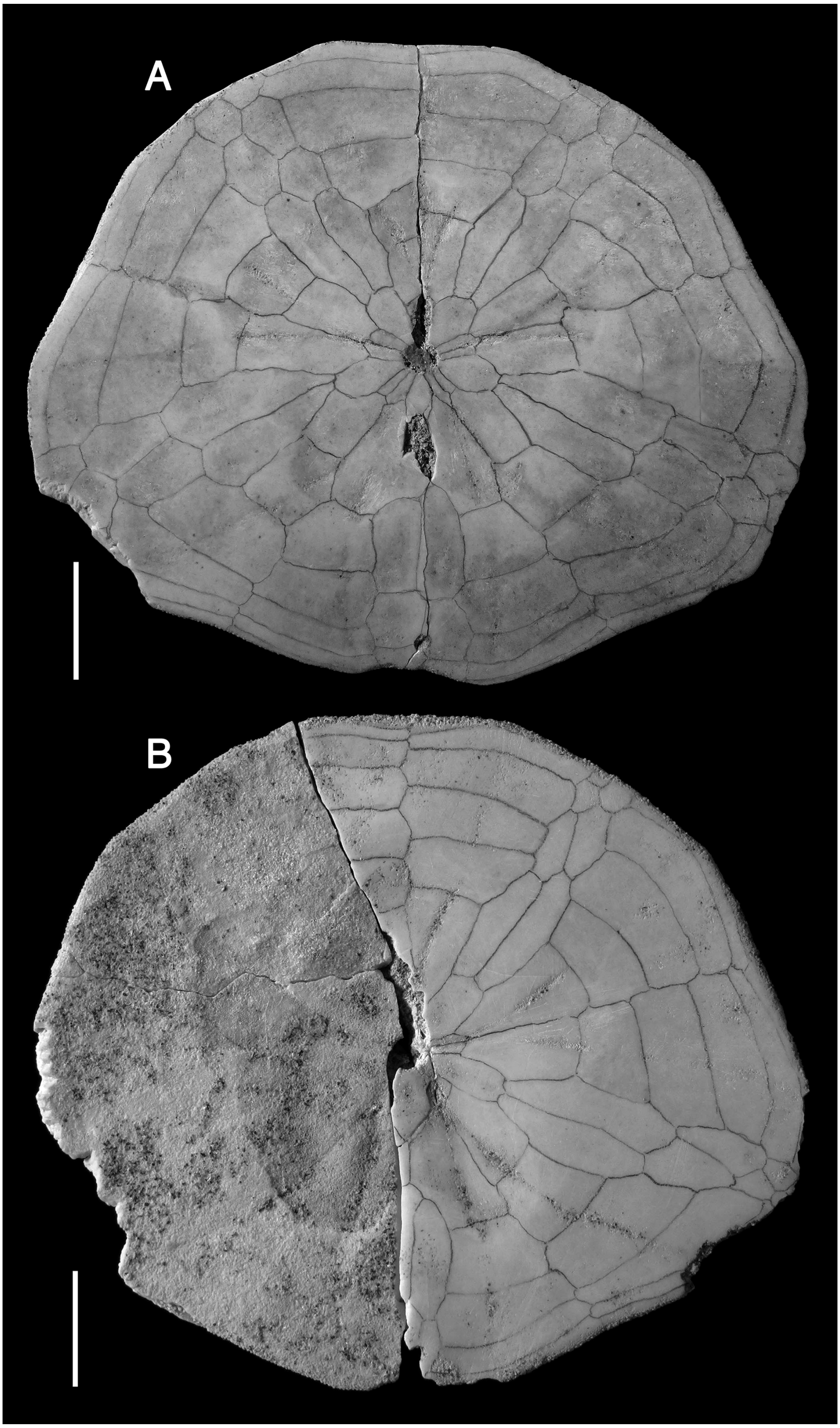


FIGURE 6. *Camachoaster maquedensis* **n. sp.**, photographs of the oral surfaces of paratypes. A: MACN-Pi 5859, prepared specimen with pencil marks indicating plate architecture. B: MACN-Pi 5860, partially prepared specimen with pencil marks indicating plate architecture, faint tuberculation, and main branches of food grooves. Scale bars 10 mm in length.

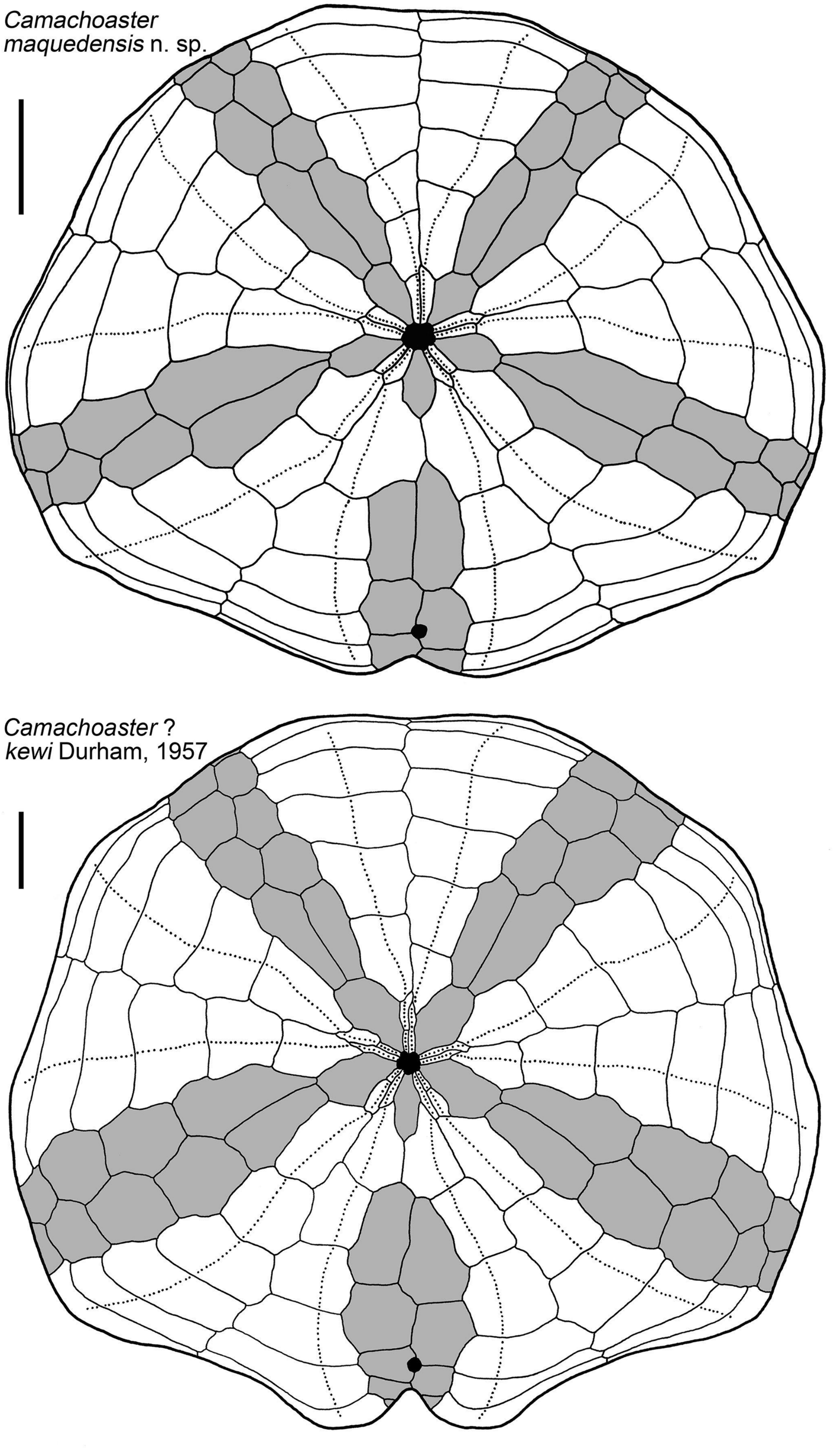


FIGURE 7. Comparison of oral plate architecture of *Camachoaster maquedensis* **n. sp.** (based on paratypes MACN-Pi 5859 and 5860) and *Camachoaster* ? *kewi* (= *Abertella kewi* Durham, 1957) (based on specimens from UCMP locality B8562, Chiapas, Mexico). Food grooves indicated by dotted lines, peristome and periproct in solid black, interambulacra shaded, scale bars 10 mm in length.

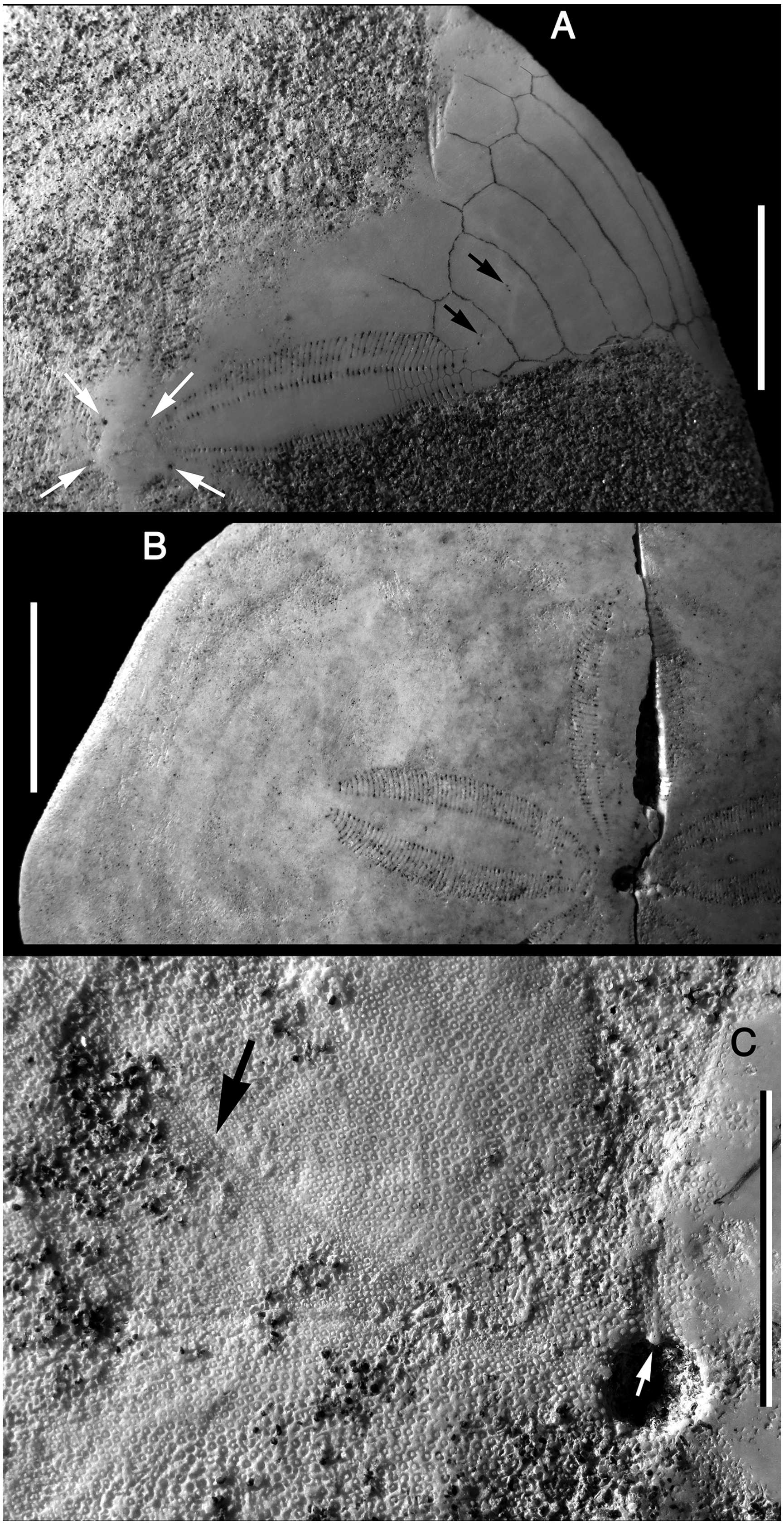


FIGURE 8. *Camachoaster maquedensis* **n. sp.**, details of test features. A: Holotype MACN-Pi 5809, pencil marks indicating partial aboral plate architecture in region within and around petal in ambulacrum II, gonopores indicated by white arrows, pores of trailing tube feet by black arrows. B: Paratype MACN-Pi 5859, complete aboral ambulacrum IV showing shape of petal. C: Holotype MACN-Pi 5809, details of tuberculation, food groove (black arrow), and peristome (peristomial projection indicated by white arrow). All scale bars 10 mm in length.

Remarks. Although *Camachoaster maquedensis* **n. sp.** is found in the same strata as *Monophoraster telfordi* Mooi *et al*., 2016, the former is immediately recognizable as a different species, as well as representing a different major scutelliform clade, by its complete lack of an anal lunule. *Camachoaster* resembles the Abertellidae only in the possession of a shallow notch, and in the discontinuity of the posterior interambulacrum. However, the continuity of the paired interambulacra immediately invites favorable comparison with *Placatenella*, as do the similar shapes and dimensions of the petals.

Nevertheless, *Camachoaster* differs from *Placatenella* in having the posterior interambulacrum discontinuous. *Camachoaster*'s combination of continuous paired interambulacra with a discontinuous posterior, unpaired interambulacrum, is unique among South American forms. A small species of *Vaquerosella* from California seems to have a similar oral plate pattern. However, among large scutelliforms with a posterior notch, this condition seems to be shared only with a Mexican species previously ascribed to *Abertella*, *A. kewi* Durham, 1957. The original description of *A. kewi* lacks figures of, or any reference to, oral plate architecture, likely due to the condition of the specimens. However, access to material from UCMP locality B8562, collected from the same locality as the types (Simojovel, Chiapas, Mexico) allows reconstruction of this architecture for comparison with *Camachoaster maquedensis* **n. sp.** (Fig. 7). This suggests that *A. kewi* is not an *Abertella*. Aspects of the oral plate pattern are reminiscent of some abertellid species, notably *Abertella miskellyi* Kroh *et al.*, 2013, such as the periproct placement, the reduced posterior interambulacral basicoronal, and discontinuity of the posterior interambulacrum. However, *A. kewi* is unlike any abertellid in the continuity of the paired interambulacra, and the insertion of very small first postbasicoronals in either the "a" or the "b" column of each of the ambulacra. The latter situation is seen in the Pliocene *Scutellaster* Cragin, 1895, the Miocene and Pliocene *Kewia* Nisiyama, 1935, and in the Eocene *Eoscutella*, all from the northwest Pacific coasts of North America. The occurrence of these small postbasicoronals has not yet been analyzed in a phylogenetic context in order to determine its overall significance. The aforementioned differences between *Camachoaster maquedensis* **n. sp.** and *A. kewi* might suggest that they are not congeneric, but we here provisionally place *A. kewi* in *Camachoaster* as *Camachoaster* ? *kewi* pending full revision of all the relevant North American taxa associated with the Abertellidae and Placatenellidae.

Family Abertellidae Durham, 1955

Emended diagnosis. Scutelliforms with shallow to very deep, usually well-defined notch at ambitus in posterior interambulacrum; all oral interambulacra discontinuous, sometimes widely disjunct; interambulacral basicoronals large, usually more than twice length of ambulacrals. In addition, the following plesiomorphic features that are useful in that they are found in virtually all members of the family: two to five distinct trailing tube feet at end of each column of respiratory tube feet; pressure drainage channels absent, but ambulacral regions between main branches of food grooves populated by spines slightly shorter than interambulacral basicoronals; posterior interambulacral column typically narrowing towards ambitus and into posterior notch; periproct on oral surface between second, or second and third postbasicoronals.

Description and remarks. Previous diagnoses of the family (Durham 1953, 1955, 1966) relied on combinations of easily discerned features otherwise not unique within the scutellines. Durham (1955) provided the following description for his new family: "Medium-sized to large, flattened; internal supports well developed; with broad ambulacral and anal indentations of margin; petals well defined, nearly closed; outer member of pore-pair greatly elongated, few primary pore-pairs outside petals; all interambulacra discontinuous on oral surface; basicoronal interambulacral plates considerably larger than ambulacral plates; periproct on oral surface; ambulacral food grooves bifurcating just outside basicoronal row; 4 genital pores." Unfortunately, not a single one of these features, taken on their own, is unique to the Abertellidae, and do not provide an unequivocal diagnosis in the modern concept of a diagnosis, which should consist of autapomorphies and, in some cases, distinctive plesiomorphic features unique to the taxon being diagnosed. In part because it is an entirely extinct group, this remains a challenge for the Abertellidae, and even the diagnosis provided above does not contain synapomorphies entirely unique to the abertellids.

However, when all these features are taken in combination, the family is well circumscribed. Durham (1955) noted both the discontinuous oral interambulacra and the pronounced posterior notch. Some other South American non-lunulate taxa possess this notch as well, but are not like abertellids in other ways, including the pattern of interambulacral discontinuity. Therefore, in considering such taxa, we are left with a choice of considerably broadening the concept of the Abertellidae to include these species, or establish new supraspecific taxa. We decided to restrict the concept of the Abertellidae to include only those forms that have all the oral interambulacra discontinuous, as discussed above in the sections dealing with the excluded forms such as *Placatenella* and *Camachoaster*.

The diagnosis of Abertellidae is therefore emended here to include scutellines with a shallow to very deep notch at the ambitus in the posterior interambulacrum, in combination with having all oral interambulacra strongly discontinuous in all adult specimens. Studies of specimens of the type species, *A. aberti*, from the Smithsonian Institution (NMNH 438168, 438169) permits inclusion of characters concerning spine morphology and distribution that seem unique to the family. Although the spines are differentiated and distributed in fields of aboral club-shaped and miliary types as in most scutelliforms, the oral surface is populated by fields of locomotory and geniculate spine types similar to those seen in mellitids, but not as strongly differentiated. There are no well-differentiated pressure drainage channels, but ambulacral regions between the main branches of the food grooves are populated by spines slightly shorter than interambulacral basicoronals. Each main branch of the food grooves beyond the primary bifurcation at the ends of the ambulacral basicoronals is always strongly developed in abertellids, but the degree of secondary branching is variable. The periproct is always situated distinctly on the flat portion of the oral surface, surrounded by the second pair of postbasicoronal interambulacral plates, or sometimes in contact with one (rarely both) of the third postbasicoronals. Features of the petals, which are lyrate, almost closed, but large (one half to three-quarters the length of the corresponding aboral ambulacrum), do not serve to distinguish abertellids from other scutelliforms. Trailing tube feet at the end of each column of respiratory tube feet are always large and distinct in abertellids, and can number up to five, but this also does not separate abertellids from other forms. The type species, *A. aberti*, can attain a TL of well over 150 mm, but the smallest known species, such as *A. palmeri*, are not known to exceed 60 mm TL. As noted and figured by Clark & Twitchell (1915), the microcanal system is well developed, as it is in several other scutelliform groups including lunulates such as the monophorasterids.

Type genus. *Abertella* Durham, 1953

Genus *Abertella* Durham, 1953

1958 *Karlaster* Marchesini Santos, 1958, p. 16

Emended diagnosis. As for the family, see above.

Type species. *Scutella aberti* Conrad, 1842, by original designation (Durham 1953, p. 350).

Included species. *A. aberti* (Conrad, 1842); *A. cazonesensis* Kew in Dickerson & Kew, 1917; *A.*? *habanensis* (Sánchez-Roig, 1949); *A. palmeri* Durham, 1957; *A. pirabensis* (Marchesini Santos, 1958); *A. gualichensis* Martínez *et al.*, 2005; *A. dengleri* Osborn & Ciampaglio, 2010; *A. miskellyi* Kroh *et al.*, 2013.

Remarks. Of the above included species, only *A. pirabensis*, *A. gualichensis*, and *A. miskellyi* are known to occur in South American outcrops. *Abertella*? *habanensis* is provisionally listed as an *Abertella* until further information comes to light on this species. *Abertella kewi* Durham, 1957, as listed by Kroh *et al*. (2013), is hereby formally removed from *Abertella* and moved provisionally to *Camachoaster* as *Camachoaster* ? *kewi*, as it no longer satisfies the emended diagnosis provided in this paper.

Abertella gualichensis Martínez *et al.*, 2005

Figures 1, 4.

2005 *Abertella gualichensis* Martínez *et al.*: 1230–1232, figs. 2–3.

Diagnosis. *Abertella* with pronounced, marginally-directed, curved extensions of oral ambulacral plates joining proximal edges of first interambulacral postbasicoronal plates in posterior interambulacrum; posterior notch shallow but acute; paired interambulacra narrower, than in other *Abertella*, not narrowing near the ambitus.

Type material studied. Holotype MACN-Pi 4714, paratypes MACN-Pi 4705, 4706, 4709.

Description. See Martínez *et al.* (2005).

Occurrence. *A. gualichensis* is recorded only from the earliest middle Miocene of Salina del Gualicho, Río Negro Province, Argentina in the lower part of the Gran Bajo del Gualicho Formation (Fig. 1).

Remarks. In the original description, *A. gualichensis* was distinguished from other *Abertella* largely by its broad but shallow posterior notch and its relatively narrow, non-alate test compared to other members of the genus. In addition, the separation of the oral interambulacral postbasicoronals from the basicoronal plates is less pronounced in *A. gualichensis* than in most other *Abertella*, with the exception of *A. pirabensis*, and the oral interambulacra of *A. gualichensis* do not widen and then markedly attenuate as they approach the ambitus.

Abertella miskellyi Kroh *et al.*, 2013

2013 *Abertella miskellyi* Kroh *et al.*: 371–376, figs. 2–6.

Diagnosis. *Abertella* with strongly heterogeneous interambulacral basicoronal plates (small in interambulacrum 5, largest in interambulacra 2 and 3); oral interambulacra discontinuous by involvement of two adjacent ambulacral plates (rather than one as in other *Abertella*) in at least one of the oral interambulacra; apparent "violation" of Lovén's Rule in oral ambulacrum III.

Type material studied. Holotype MB E.7463, paratype MB E.7462.

Description. See Kroh *et al.* (2013).

Occurrence. *A. miskellyi* is recorded only from the (possibly early) Miocene of Chubut Province, southern Argentina in the Camarones Formation (Fig. 1).

Remarks. This species is unique among *Abertella* in that the posterior interambulacral basicoronal plate is much smaller than that in each of the paired interambulacral basicoronals. It is also the only *Abertella* in which specimens are known to have a discontinuity involving more than one postbasicoronal plate in a given half-ambulacrum. An unusual feature of one of the known specimens of *A. miskellyi* is that ambulacral basicoronal III at first seemed longer in the "a" column than in the "b" column, suggesting violation of Lovén's Rule (*sensu* David *et al.* 1996) until a small plate was detected, wedged between the basicoronal plates of ambulacrum III to re-establish the Lovénian pattern (Kroh *et al.* 2013).

Abertella pirabensis (Marchesini Santos, 1958)

Figures 1, 4, 9.

1958 *Karlaster pirabensis* Marchesini Santos: 16–19, pl. 5: figs. 1–3.
1979 *Karlaster pirabensis* Santos—Brito: 736–738, pl. 3: fig. 1, pl. 4: fig. 6.
1997 *Abertella pirabensis* (Marchesini Santos)—Martínez & Mooi: 61.
2000 *Abertella pirabensis* (Marchesini Santos) (as senior synonym of *Abertella complanata* Brito 1986)—Mooi *et al.*: 266.

Diagnosis. An *Abertella* in which the posterior notch is deep and sharply defined, the periproct just barely between the second pair of posterior interambulacral postbasicoronals, and the length of the disjunction between the interambulacral basicoronal and first postbasicoronals much less than half the length of the corresponding basicoronal in paired interambulacra.

Type material studied. The holotype, DNPM 4493, is the only known specimen.

Description. In general, the original description by Marchesini Santos (1958) is accurate and detailed, except for the instances discussed below. Her images do not satisfy modern standards, and we provide additional images of both surfaces, detailed views of the oral surface and wall of the notch, and a reconstructed plate map (Figs. 4, 9). The following description is of the same format as for placatenellid species discussed above, to facilitate comparisons.

Holotype (Fig. 9A, B) approximately 51 mm TL (as defined in Table 1). Ratio of width to length including lobes on either side of notch 1.21. Aboral surface slightly domed, oral surface extremely flat, nearly planar and without significant sculpting or radial depressions. Highest point of test approximately 11% TL, located at apical system. Well-defined posterior notch, depth estimated to be approximately 11% TL, width approximately 10% TL at ambitus, notch widening near ambitus. Marginal indentations extremely shallow where perradial suture meets ambitus in posterior paired ambulacra, nearly absent in anterior paired ambulacra.

Apical system monobasal, star-shaped, 54% TL from ocular III to anterior edge of test, length 9% TL, numerous hydropores scattered over madreporic plate. Four gonopores, one in each of paired interambulacra and located at suture between madreporic plate and first adapical plates of interambulacral column.

Ambulacra petaloid adapically. Posterior paired petals (I and V) longest, but only slightly so, each extending 65% of corresponding test radius, but 34% TL; anterior paired petals (II and IV) 62% of corresponding test radius, but 33% TL; anterior unpaired (III) shortest, 61% of corresponding test radius, but 32% TL. Petal V width at widest point 13% TL, interporiferous zone 4% TL; petal IV width 13% TL, interporiferous zone 5% TL; petal III width 15% TL, interporiferous zone 6% TL. Petals not obviously lyrate, but have outer edges of each pore pair column in a given petal parallel for most of its length, petals almost closed distally, with three or four trailing tube feet at distal end of each column of respiratory tube feet. Respiratory tube foot pore pairs strongly conjugated, inner pore slightly elongate or almost circular, outer pore extremely elongated, comprising about two thirds length of pore pair, apparently subdivided by stereom septae. Five or six occluded plates present at tips of petals. At ambitus, ambulacra greatly widened, forming strip-like ambital plates, curving strongly adapically to form test wall along each side of posterior notch (Figs. 4, 9C, D). Ambulacra all in agreement with Lovén's Rule (*sensu* David *et al.* 1996). Ambulacral basicoronal plates all similar, narrow and straight with almost parallel radial sutures on each side (Fig. 4).

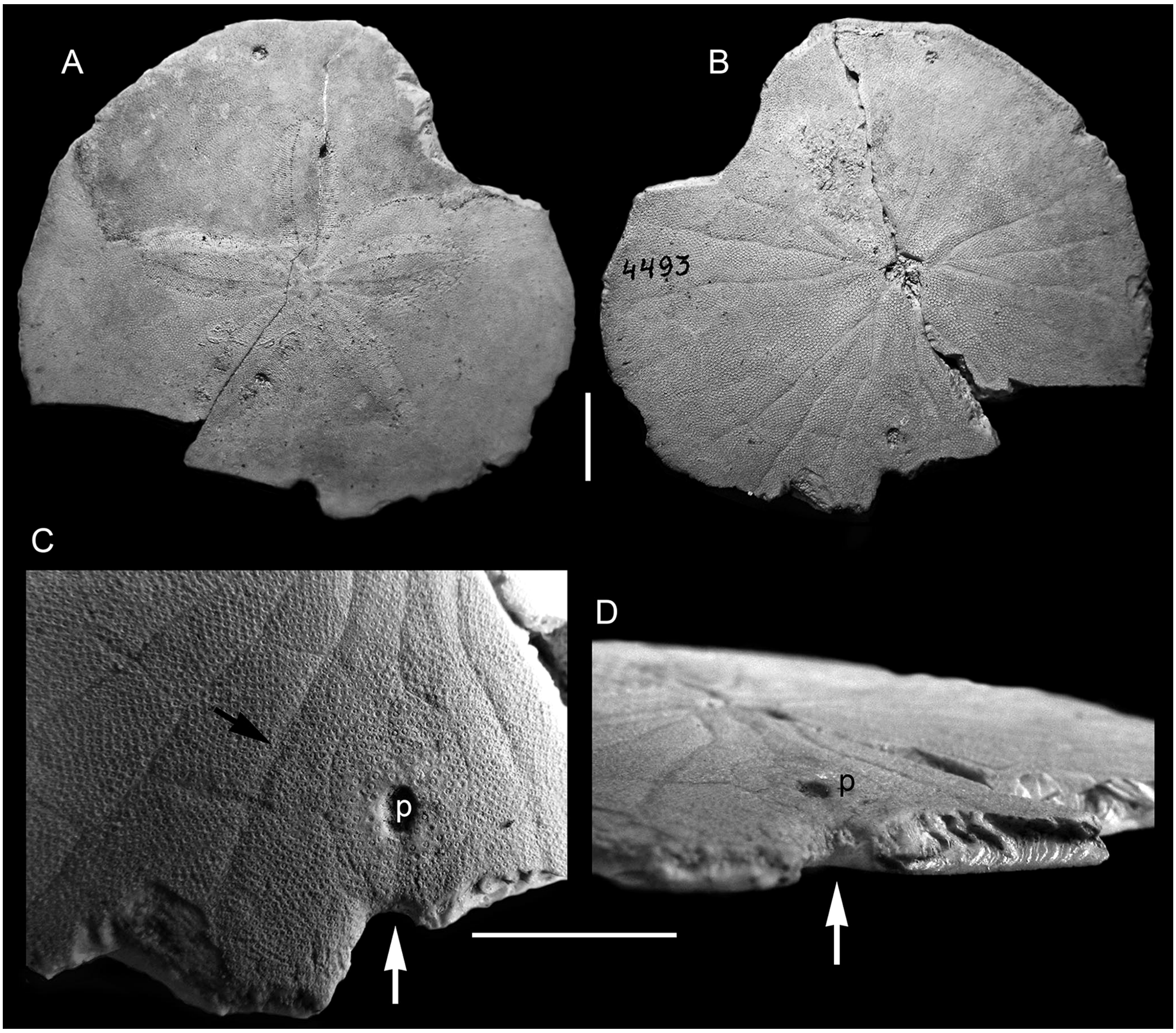


FIGURE 9. *Abertella pirabensis* (Marchesini Santos, 1958), photographs of the holotype, DNPM 4493. A: Aboral surface. B: Oral surface. C. Strongly side-lighted detail of posterior edge showing notch (white arrow), food groove (black arrow), tuberculation, and periproct (p). D. Oblique, nearly edge-on view of posterior edge showing notch (white arrow) and periproct (p). Scale bars 10 mm in length.

TABLE 1. *Camachoaster maquedensis* **n. gen.**, **n. sp.**: measurements (in mm) of holotype and both paratypes from the Chenque Formation, Punta Maqueda, Santa Cruz Province, Argentina.

	Holotype (MACN-Pi 5809)	**Paratype 1** (MACN-Pi 5859)	**Paratype 2** (MACN-Pi 5860)
Test length (from junction of perradial suture of ambulacrum III with anterior edge of test to junction of interradial suture of interambulacrum 5 with posterior edge of test [inside notch])	59.3	55.3	57.9
Test width (maximum, estimated for second paratype by doubling width of left side of test to center of peristome)	72.2	67.8	68.8
Test height (at apical system)	6.4	5.2	6.4
Ratio of test width to length	1.22	1.23	1.19
Depth of posterior notch (from junction of interradial suture of interambulacrum 5 to a line drawn between the posteriormost extensions of the lobes adjacent to the notch)	0.2	0.2	0.2
Apex position (from anterior edge of test to anterior edge of madreporic plate)	29.3	26.5	27.1
Ambulacrum I length (from corresponding ocular to intersection of perradial suture and ambitus)	31.8	27.7	28.9
Ambulacrum II length (from corresponding ocular to intersection of perradial suture and ambitus)	32.5	29.8	30.7
Ambulacrum III length (from corresponding ocular to intersection of perradial suture and ambitus)	29.3	26.5	27.1
Petaloid I length (from corresponding ocular to point at which trailing tube feet start)	17.8	15.4	17.3
Petaloid I width (at widest point)	7.3	5.9	6.4
Petaloid I interporiferous zone width (at widest point)	2.5	2.3	3.0
Petaloid II length (from corresponding ocular to point at which trailing tube feet start)	16.5	15.4	15.5
Petaloid II width (at widest point)	7.2	5.8	6.9
Petaloid II interporiferous zone width (at widest point)	2.7	2.3	3.4
Petaloid III length (from corresponding ocular to point at which trailing tube feet start)	16.5	14.1	16.4
Petaloid III width (at widest point)	7.5	6.2	7.1
Petaloid III interporiferous zone width (at widest point)	3.4	3.1	3.7
Peristome length	2.8	2.8	2.6
Peristome position (anterior edge of test to anterior edge of peristome)	30.5	27.0	28.2
Periproct length	1.5	1.2	1.3
Periproct position (anterior edge of test to anterior edge of periproct)	53.5	52.1	54.2

Interambulacra narrow and straight on oral surface, narrowing towards ambitus, but containing paired, zig-zag plates right up to madreporic plate. On oral surface, three or four postbasicoronal plates in each half-interambulacrum in interambulacrum 5, four or five in the other interambulacra. Widest point of interambulacra 1 and 4 at first or second postbasicoronals, about one third of way to ambitus, narrowing distally to about two thirds that width so that paired interambulacra about 21% width of adjacent ambulacra at ambitus. In each paired interambulacrum, first postbasicoronal slightly elongated, two to three times as long as wide in posterior paired interambulacra, three to four times as long as wide in anterior paired interambulacra. Unpaired, posterior interambulacrum narrowing as it approaches ambitus inside notch (Fig. 4). All interambulacral basicoronals discontinuous, separated from first postbasicoronals by adjacent ambulacral first postbasicoronals, very widely so in interambulacrum 5 (Fig.4), but by far less than half length of a corresponding basicoronal in paired interambulacra.

Peristome circular, relatively small, about 4% TL, with distinct perradial process in each ambulacrum extending into peristome beyond slight bulge containing sphaeridium. Anterior edge of peristome 54% TL from anterior edge of test. Periproct small, about 4% TL, situated 90% TL from anterior edge of test, just barely between second pair of postbasicoronals, with slight apparent contact with one of the first pair of postbasicoronals (Fig. 4).

Aboral tuberculation homogeneous, oral tuberculation nearly so, without discernible enlargement of tubercles in oral interambulacral regions. Tube foot pores visible in food grooves (Fig. 9C).

Food grooves well developed (Figs. 4, 9B, C), restricted to oral surface, with primary bifurcation near adapical ends of ambulacral basicoronal plates. After this branch point, food grooves continuously diverging as they approach ambitus. Secondary branching faint or non-existent. No significant depressions along perradial sutures on oral surface, no evidence of pressure drainage channels.

Occurrence. *A. pirabensis* is known only from the early Miocene Pirabas Formation, Ponta de Pirabas, Ilha de Fortaleza, State of Pará, Brazil.

Remarks. We suggest that all previous attempts to allocate this taxon to a genus were incorrect to some degree. We were able to confirm the original suggestion, indicated by the figures of Marchesini Santos (1958) and Brito (1979), that all interambulacra are discontinuous. This alone suggests that the attempts to place *A. pirabensis* in the Monophorasteridae Lahille, 1896 are misguided because all the interambulacra of all species in that family are broadly continuous, both postbasicoronal plates being in contact with the basicoronal, with a minor exception in a specimen of *M. telfordi* (see Mooi *et al.* 2016). Martínez and Mooi (1997) and Mooi *et al.* (2000) compared *A. pirabensis* with what was then known as *Abertella complanata* (here placed in the new genus *Placatenella*), and became convinced that *A. complanata* was a junior synonym of *A. pirabensis*. However, this was before the oral surface plate pattern of *A. pirabensis* could be confirmed to be of the *Abertella* configuration. Moreover, the hitherto unknown plate architecture of the oral surface of what we here recognize as *Placatenella complanata* has turned out to be unique among all taxa with a posterior notch because all the oral interambulacra are continuous. This is clearly unlike any *Abertella*, and undermines any relation between *A. pirabensis* and *P. complanata*.

The conclusion is that the only known specimen of *A. pirabensis* is the holotype, described as the type specimen of a new genus, *Karlaster*, by Marchesini Santos (1958). *Karlaster* Marchesini Santos (1958) is not recognized by the present revision, and in this respect, we follow the work of Mooi *et al.* (2000) in regarding *Karlaster* a junior synonym of *Abertella*.

We have been unable to support the assertion by Marchesini Santos (1958) that *A. pirabensis* possessed an anal lunule. Breakage along the posterior edge of the only known specimen would have rendered it impossible to make the determination that the distal parts of the lobes meet again at the ambitus. However, the curvature of the ambulacral plate sutures on either side of the posterior indentation is not consistent with that observed in all other scutelliforms that possess an anal lunule. The anal lunule of all mellitids and monophorasterids possesses walls constructed of interambulacral plates in the cross-linked pattern (*sensu* Seilacher 1979: Fig. 8B, Mooi *et al.* 2000: Fig. 4.4), a situation than can be considered diagnostic for the anal lunule. In *A. pirabensis*, there are no traces of the cross-linked pattern, leading us to reconstruct *A. pirabensis* with a notch of moderate depth through extrapolation of the aforementioned ambulacral plate curvatures (Fig. 4).

Examination of the anterior wall of the notch reveals no evidence for the existence of an opening that could be interpreted as a periproct (Fig. 9D). Marchesini Santos (1958) appears to have been correct in interpreting the aperture on the oral surface as the periproct. It is neither a trace of an anal lunule, nor damage to the fossil. However, there does appear to be some damage to the test around the edges of the aperture, causing enlargement that could explain why the periproct appears to be in slight contact with the first interambulacral postbasicoronals (Fig. 9C). The periproct of *A. pirabensis* is between the second pair of interambulacral postbasicoronals, not solely enclosed within the first pair as in all monophorasterids. Therefore, the periproct position of *A. pirabensis* is like that of abertellids, but not of monophorasterids. The unequal development of the interambulacral basicoronals is also very similar to the condition seen in other *Abertella*, notably *A. miskellyi*, further undermining placement of *A. pirabensis* in the monophorasterids.

Family Iheringiellidae n. fam.

Diagnosis. Basicoronal plates very wide, broadly in contact with first postbasicoronals so that all oral interambulacra are continuous; interambulacral columns narrow markedly towards ambitus, particularly on aboral surface; peristome large, almost as long as a paired interambulacral basicoronal plate; periproct between second and third postbasicoronals in interambulacrum 5; at least 6 trailing tube foot pores distal to petal in each half-ambulacrum.

Type genus. *Iheringiella* Berg, 1898.

Remarks. Iheringiellids are distinct from other non-lunulate forms in which all oral interambulacra are continuous because of the extreme narrowing of the interambulacral columns near the ambitus. The lack of a posterior notch or anal lunule also prevents placement of *Iheringiella* within any of the other known families in South America. The genus *Iheringiella* had most recently been considered a member of the Monophorasteridae (see Durham 1955, 1966), but was removed from that family by Mooi *et al.* (2000) pending further analysis of all scutelliforms. As long as it remains *incertae sedis*, consideration of an important South American form such as *Iheringiella* will continue to be overlooked by studies focusing on family-level analyses, such as Kroh and Smith (2010). Given that the Iheringiellidae can be diagnosed unequivocally and uniquely, the new family is here proposed to accept *Iheringiella*.

Genus *Iheringiella* Berg, 1898

1898 *Iheringia* Lahille: 437.
1898 *Iheringiella* Berg: 16.
1898 *Iheringiana* Berg: 41.
1899 *Iheringina* Lahille: 395.

Diagnosis. As for the family.

Type species. *Scutella patagonensis* Desor in Agassiz & Desor, 1847, by original designation (Desor 1847: 135).

Material studied. Holotype of *Echinarachnius juliensis* Desor in Agassiz & Desor, 1847, MCZ 102431, plus specimens attributed to *I. patagonensis*, including CPBA 16493-95, MACN-Pi 4586, MACN-Pi 5144, ROM 5433M, 5468M, 5469M, and two specimens sent to R.M. for identification by A. Wyss (University of California, Santa Barbara).

Iheringiella patagonensis (Desor in Agassiz & Desor, 1847)

Figures 1, 4.

Diagnosis. As for the family and genus. We note, in addition, that *I. patagonensis* is the only South American scutelliform clypeasteroid in which test length and width are nearly equal (all other such species being significantly wider than long).

Occurrence. Arguably the most commonly encountered species of clypeasteroid in South America, *I. patagonensis* was evidently widespread during the late Oligocene and early Miocene in the southern Patagonian region of Argentina from the southern edge of Golfo San Jorge south to the northern edge of Tierra del Fuego (Fig. 1, inset). The recent discovery of specimens from the early Miocene Guadal Formation extends the known range of *I. patagonensis* westward to the Pampa Castillo region of southern Chile (Frassinetti & Covacevich, 1999; Andre Wyss, pers. comm.).

Remarks. We recommend usage of the original spelling of the species name used in Desor (1847) and Agassiz & Desor (1847). Desor (1847) only listed names of taxa from Patagonia, without accompanying figures or descriptions, and these names are therefore here considered *nomina nuda*. In the same year, Desor (in Agassiz & Desor, 1847) provided cursory, but valid descriptions of two taxa, with locality information from the Patagonian region. Lacking figures, these descriptions have been the source of great confusion ever since. The type of one of these forms, *Echinarachnius juliensis*, from "Port Saint Julien" (Desor in Agassiz & Desor, 1847: 134), is known to exist in the collections of the Museum of Comparative Zoology, in Cambridge, Massachusetts. All known specimens presently identified as *Iheringiella patagonensis* compare favorably with this type. The types of the second form, *Scutella patagonensis*, reported to be from "Port Desire" (Desor in Agassiz & Desor, 1847: 135), have not been yet been found.

The situation is made more difficult by our inability to locate the original material upon which Lahille (1898) based his revision. Given the complex taxonomic history of the species involved, along with the provenance of the material, a full revision of the nomenclature is warranted and pending. For comparison with other taxa described herein, we provide a map of plate architecture of the oral surface of a typical specimen from the Puerto Santa Cruz region of Argentina. This specimen compares most favorably with the type of *Scutella juliensis*. However, as is common for all such material, it is identified as *Iheringiella patagonensis* until the situation concerning the relationship between the types of *S. juliensis* and *I. patagonensis* can be resolved. What seems clear from the present evidence is that these two named entities are congeneric. *Iheringiella* does not have any indication of a posterior notch, making it the only described species of South American scutelliform to lack this feature.

Discussion

With the description of *Camachoaster maquedensis* **n. sp.**, the number of scutelliform species in South America rises to 13, seven of which are non-lunulates. Table 2 presents a tabular key to these seven non-lunulate species. All of these taxa have been found in strata dating from the late Oligocene to the middle Miocene. The fact that these strata are widely distributed in very different parts of South America strongly suggests that other scutelliforms will be found in South America. For example, a specimen of clypeasteroid from the Miocene of Chile ascribed to *Philipaster* by Kutscher *et al.* (2004) is most likely to be a taxon of miniaturized scutelliform, based on preliminary examination by R.M. The senior author is also in possession of material representing an undescribed non-lunulate from the Miocene of Peru. These pending analyses indicate the need for the present revision, which is intended to provide a statement of knowledge of these forms upon which further work can be based.

For example, it seems most likely, in light of its very different stratigraphic and biogeographic occurrence, that the Miocene *Eoscutella mirandae* Parma, 1985 of Argentina is not a member of the Eocene Eoscutellidae from the Pacific Northwest and Kamchatka. The plate architecture of *E. mirandae* remains poorly known but in any case, will need to be analyzed in the context of the taxonomy presented in the present revision. Preliminary examination of the type material (CPBA 12901, 12902) suggests discontinuity in at least some of the oral interambulacra. This alone indicates that removal from the Eoscutellidae is warranted while raising the interesting possibility that this species is another member of one of the groups described herein, such as the Abertellidae. Furthermore, the existence of a posterior notch in *E. mirandae* underscores the need for a new study of that taxon.

Our analyses also suggest that further study of the evolution of the posterior notch found in North American abertellids, as well as in the other non-lunulate taxa described herein, is necessary. It is possible that the posterior notch represents a synapomorphy for the Abertellidae and Placatenellidae **n. fam.** If this is the case, then lability in the oral plate architecture and periproct position, although apparently conservative within genera, would be similar to that seen in other families of scutelliforms.

It is tempting to hypothesize that the anal lunule of monophorasterids and mellitids evolved from taxa that had a deep posterior notch, such as in some abertellids, and especially in *Placatenella*. However, there is nothing in the present study to suggest that the posterior notch is somehow related to the origin of the anal lunule. The walls of the anal lunule are characterized by a cross-linked plating structure that is very different from anything seen along the ambitus of any scutelliform, including within the posterior notch. The anal lunule's ontogeny is very different from that of any other lunule type (except, perhaps the cross-linked ambulacral lunules of astriclypeids), and forms only by direct perforation of the test. This occurs through differential growth of interambulacral plates well inward from the ambitus (Telford 1988). The formation of the anal lunule is not preceded by notching or any other involvement of the ambitus where it intersects with the interradial suture. The sister group of the clade containing monophorasterids and mellitids remains elusive, but it is clear that the posterior notch is not a precursor homologous with the anal lunule.

TABLE 2. Tabular key to the species of early Oligocene–middle Miocene non-lunulate scutelliforms recorded from South America.

Species	Test width/ length	Periproct position	Discontinuous oral interambulacra	Posterior notch	Relative size of posterior basicoronal
Placatenella complanata	<1.5	marginal	None	deep, >20% TL	greatly reduced
Camachoaster maquedensis	<1.5	oral	Paired only	shallow, <10% TL	about equal
Abertella gualichensis	<1.5	oral	All	shallow, <10% TL	about equal
Abertella miskellyi	<1.5	oral	All	shallow, <10% TL	greatly reduced
Abertella pirabensis	<1.5	oral	All	10–15% TL	greatly reduced
Iheringiella patagonensis	<1.5	oral	None	absent	about equal
Eoscutella mirandae	>1.7	oral	?	shallow, <10% TL	about equal

Acknowledgements

We are grateful to Antonio Carlos Sequeira Fernandes, Museu Nacional-UFRJ, Brazil; Rodrigo Da Rocha Machado, Museu de Ciéncias da Terra, Departamento Nacional de Produção Mineral, Brazil; and Marian Tanuz, Catedra de Paleontología Universidad de Buenos Aires, Argentina for help with and access to collections in their care. Andre Wyss, University of California, Santa Barbara, kindly made available specimens collected during his Chilean expeditions. Adam Osborn, Louis Zachos, James Nebelsick, and Andreas Kroh made insightful comments that greatly improved the manuscript. The work described in this paper was supported by ANPCyT PICT-57 and CONICET PIP 320 to C.d.R., CSIC-UdelaR to S.M., and Museu Paraense Emílio Goeldi and CNPq, Brazil to M.I.F.R. and S.M. This paper is dedicated to the memory of Dr. Horacio H. Camacho.

References

Agassiz, L. & Desor, P.J.E. (1847) Catalogue raisonné des espèces, des genres, et des familles d'échinides. *Annales des Sciences Naturelles, Troisième Série, Zoologie*, 7, 129–168.

Agassiz, A. (1864) Synopsis of the echinoids collected by Dr. W. Stimpson on the North Pacific Exploring Expedition under the command of Captains Ringgold and Rodgers. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 15, 352–361.

Agassiz, A. (1872–1874) Revision of the Echini. *Illustrated Catalogue of the Museum of Comparative Zoölogy at Harvard College*, 7, (pt. 1–2, 3 & 4) i–xii, 1–378, pls. 1–49 (1872); 379–628 +1, pls. 50–77 (1873) & 629–762, pls. 78–94 (1874).

Berg, A. (1898) Substitución de nombres genéricos. *Comunicaciones del Museo Nacional de Buenos Aires*, 1, 16.

Brito, I.M. (1979) Clipeasteróides Cenozóicos do Brasil (Echinodermata, Echinoidea). *Anais da Academia Brasileira de Ciências*, 54, 729–740.

Brito, I.M. (1981) Contribuição à paleontologia do Estado do Pará. A ocorrência de *Abertella* (Echinoidea, Clypeasteroidea) na Formação Pirabas. *Boletim do Museu Paraense Emílio Goeldi, Nova Série, Geologia*, 23, 1–8.

Brito, I.M. (1986) *Abertella complanata* Brito (Echinoidea, Clypeasteroida) da Formaçâo Pirabas (Pará, Brasil). *Boletim do Museu Paraense Emílio Goeldi, Nova Série, Geologia*, 28, 1–4.

Clark, H.L. & Twitchell, M.W. (1915) The Mesozoic and Cenozoic Echinodermata of the United States. *United States Geological Survey Monograph*, 54, 1–341.

Conrad, T.A. (1842) Observations on a portion of the Atlantic Tertiary region, with a description of a new species of organic remains. *Proceedings of the National Institute for the Promotion of Science*, 2, 171–194.

Cragin, F.W. (1895) A new Cretaceous genus of Clypeasteridae. *American Geologist*, 15, 90–91.

Cuitiño, J.I. (2011) *Registro sedimentológico e isotópico de paleoambientes marinos y transicionales en el Patagoniano (Mioceno) del Lago Argentino*. Unpublished Ph.D. dissertation, Buenos Aires University, Buenos Aires 263 pp.

David, B., Mooi, R. & Telford, M. (1996) The ontogenetic basis of Lovén's Rule clarifies homologies of the echinoid peristome. *In*: Emson, R., Smith, A.B. & Campbell, A. (Eds.), *Echinoderm Research 1995.* A. A. Balkema, Rotterdam, pp. 155–164.

del Río, C.J. (2004) Tertiary marine molluscan assemblages of eastern Patagonia (Argentina): a biostratigraphic analysis. *Journal of Paleontology*, 78, 1097–1122.
https://doi.org/10.1017/S0022336000043912

Desor, E. (1847) Sur quelques oursins fossiles de la Patagonie. *Bulletin de la Société Géologique de France*, Series 2, 4, 287–

288.

Dickerson, R.E. & Kew, W.S.W. (1917) The fauna of a medial Tertiary formation and the associated horizons of northeastern Mexico. *Proceedings of the California Academy of Sciences*, Series 4, 7, 125–156.

Durham, J.W. (1953) Type species of *Scutella*. *Journal of Paleontology*, 27, 347–352.

Durham, J.W. (1955) Classification of clypeasteroid echinoids. *California University Publications in Geological Science*, 31, 73–198.

Durham, J.W. (1957) Notes on echinoids. *Journal of Paleontology*, 31 (3), 625–631.

Durham, J.W. (1966) Clypeasteroids. *In*: Moore, R.C. (Ed.), *Treatise on Invertebrate Paleontology, Part U. Echinodermata. 3 (2)*. Geological Society of America and The University of Kansas Press, Boulder, CO & Lawrence, KS, pp. 450–491. [pp. U450–U491]

Frassinetti, D. & Covacevich, V. (1999) Invertebrados fósiles marinos de la Formación Guadal (Oligoceno Superior-Mioceno Inferior) en Pampa Castillo, Región de Aisén, Chile. *Servicio Nacional de Geología y Minería, Chile, Boletín*, 51, 1–96.

Grant, U.S. IV & Hertlein, L.G. (1938) The West American Cenozoic Echinoidea. *Publications of the University of California at Los Angeles in Mathematical and Physical Sciences*, 2, 1–225.

Haeckel, E.H.P.A. (1896) *Systematische Phylogenie der Wirbellosen Thiere (Invertebrata). Zweiter Theil des Entwurfs einer systematischen Stammesgeschichte*. Reimer, Berlin, 720 pp.
https://doi.org/10.1515/9783111443935

Kew, W.S.W. (1920) Cretaceous and Cenozoic Echinoidea of the Pacific Coast of North America. *University of California Publications in Geology*, 12 (2), 23–236.

Kroh, A. & Smith, A.B. (2010) The phylogeny and classification of post-Palaeozoic echinoids. *Journal of Systematic Palaeontology*, 8, 147–212.
https://doi.org/10.1080/14772011003603556

Kroh, A., Mooi, R., del Río, C. & Neumann, C. (2013) A new late Cenozoic species of *Abertella* (Echinoidea: Clypeasteroida) from Patagonia. *Zootaxa*, 3608 (5), 369–378.
https://doi.org/10.11646/zootaxa.3608.5.5

Kutscher, M., Neumann, C., Nielsen, S., Reich, M. & Villier, L. (2004) Echinoderms from the Miocene of Chile. *In*: Heinzeller, T. & Nebelsick, J. (Eds.), *Echinoderms: München.* A. A. Balkema, Leiden, pp. 453–456.

Lahille, F. (1896) Variabilité et affinités du *Monophora darwini*. *Revista del Museo de La Plata*, 7, 411–444.

Lahille, F. (1898) Notes sur le nouveau genre *Iheringia*. *Revista del Museo de la Plata*, 8, 439–451.

Lahille, F. (1899) New name for *Iheringia* Lahille. *Revista del Museo de la Plata*, 9, 395.

Larrain, A. (1984) The fossil and Recent shallow water irregular echinoids from Chile. Unpublished Ph.D. dissertation, University of Southern California, Los Angeles, 235 pp.

Latreille, P.A. (1825) *Familles naturelles du règne animal*. Baillière, Paris, 570 pp.

Leske, N.G. (1778) *Jacobi Theodori Klein naturalis dispositio echinodermatum . . ., edita et descriptionibus novisque inventis et synonomis auctorem aucta. Addimenta ad I. T. Klein naturalem dispositionem Echinodermatum*. G. E. Beer, Leipzig, xxii + 278 pp.

Marchesini Santos, M.E. (1958) Equinóides Miocénicos da Formação Pirabas. *Departamento Nacional da Produção Mineral, Divisão de Geologia e Mineralogia, Boletim*, 179, 1–24.

Martínez, S. (1984) *Amplaster coloniensis* n. g. n. sp. (Echinoidea: Monophorasteridae) del Mioceno de Uruguay. *In*: del Carmen, P.M. (Ed.), *Memoria III Congreso Latinoamericano de* Paleontologia Instituto de Geologia de la UNAM, Mexico, D.F., pp. 505–508.

Martínez, S. & Mooi, R. (1997) "*Karlaster" pirabensis* from the Brazilian Miocene is a species of *Abertella* (Scutellina, Echinoidea), not a monophorasterid. *158 Congresso Brasileiro de Paleontologia, São Paulo*, 1997, 61.

Martínez, S. & Mooi, R. (2005) Extinct and extant sand dollars (Clypeasteroida: Echinoidea) from Uruguay. *Revista de Biología Tropical*, 53 (3), 1–7.

Martínez, S., Reichler, V. & Mooi, R. (2005) A new species of *Abertella* (Echinoidea: Scutellina) from the Gran Bajo del Gualicho Formation (Late Early Miocene-Early Middle Miocene), Río Negro Province, Argentina. *Journal of Paleontology*, 79 (6), 1229–1233.
https://doi.org/10.1666/0022-3360(2005)079[1229:ANSOAE]2.0.CO;2

Mooi, R. (1989) Living and fossil genera of the Clypeasteroida (Echinoidea: Echinodermata): An illustrated key and annotated checklist. *Smithsonian Contributions to Zoology*, 488, 1–51.
https://doi.org/10.5479/si.00810282.488

Mooi, R. (1990) Paedomorphosis, Aristotle's lantern, and the origin of the sand dollars (Echinodermata: Clypeasteroida). *Paleobiology*, 16 (1), 25–48.
https://doi.org/10.1017/S0094837300009714

Mooi, R., Martínez, S. & Parma, S.G. (2000) Phylogenetic systematics of Tertiary monophorasterid sand dollars (Clypeasteroida: Echinoidea) from South America. *Journal of Paleontology*, 74 (2), 263–281.
https://doi.org/10.1017/S0022336000031486

Mooi, R., Martínez, S. & del Río, C.J. (2016) A new South American Miocene species of 'one-holed' sand dollar (Echinoidea: Clypeasteroida: Monophorasteridae). *Zootaxa*, 4173 (1), 45–54.
https://doi.org/10.11646/zootaxa.4173.1.4

Nisiyama, S. (1968) The echinoid fauna from Japan and adjacent regions. Part II. *Palaeontological Society of Japan Special Papers*, 13, 1–491.

Ortmann, A.E. (1902) Tertiary invertebrates. *Princeton University Expedition to Patagonia, Reports*, 4 (2), 45–332.

Osborn, A.S. & Ciampaglio, C.N. (2010) A new species of *Abertella* (Echinoidea, Scutellina) from the Late Miocene (Tortonian) Peace River Formation of Hardee County, Florida. *Southeastern Geology*, 47, 207–218.

Parma, S.G. (1985) *Eoscutella* Grant y Hertlein (Echinodermata: Clypeasteroida) en el Patagoniano (Terciario inferior) de la Provincia de Santa Cruz, República Argetina. *Ameghiniana*, 22, 35–41.

Sánchez Roig, M. (1949) Los equinodermos fosiles de Cuba. *Paleontologia Cubana*, 1, 1–302.

Shmidt, O.I. (1975) [On the new subgenus of the family Eoscutellidae Durham in the Paleogene of Kamchatka (Yuzhno Sakhalinsk)]. *Trudy Sachalinskij Kompleksnyj Nauèno-Issledovatel'skij Institut,* 36, 29–31.

Seilacher, A. (1979) Constructional morphology of sand dollars. *Paleobiology*, 5, 191–221.
https://doi.org/10.1017/S0094837300006527

Telford, M. (1988) Ontogenetic regulatory mechanisms and evolution of mellitid lunules (Echinoidea, Clypeasteroida). *Paleobiology*, 14, 52–63.
https://doi.org/10.1017/S0094837300011799