

An Early Cretaceous astropectinid (Echinodermata, Asteroidea) from Patagonia (Argentina): A new species and the oldest record of the family for the Southern Hemisphere

Diana E. Fernández¹, Damián E. Pérez², Leticia Luci¹, Martín A. Carrizo²

¹ Instituto de Estudios Andinos Don Pablo Groeber (IDEAN-CONICET), Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160, Pabellón 2, Ciudad Universitaria, Ciudad Autónoma de Buenos Aires, Argentina.

elizabeth@gl.fcen.uba.ar; leticialuci@gl.fcen.uba.ar

² Museo de Ciencias Naturales Bernardino Rivadavia, Ángel Gallardo 470, Ciudad Autónoma de Buenos Aires, Argentina.
dperez@macn.gov.ar; blackdisk@gmail.com

ABSTRACT. Asterozoans are free living, star-shaped echinoderms which are important components of benthic marine faunas worldwide. Their fossil record is, however, poor and fragmentary, probably due to disarticulation of ossicles. In particular, fossil asteroids are infrequent in South America. A new species of starfish is reported from the early Valanginian of the Mulichinco Formation, Neuquén Basin, in the context of a shallow-water, storm-dominated shoreface environment. The specimen belongs to the Astropectinidae, and was assigned to a new species within the genus *Tethyaster* Sladen, *T. antares* sp. nov., characterized by a R:r ratio of 2.43:1, rectangular marginals wider in the interbrachial angles, inferomarginals (28 pairs along a median arc) with slightly convex profile and flat spines (one per ossicle in the interbrachials and two per ossicle in the arms). Both the sedimentologic features of the bearing bed, and the taphonomic signature point to a rapid burial. Considering the presence of well-developed fascioles, it is likely that the specimen was already half buried at the beginning of its taphonomic pathway. This record represents the oldest finding of Astropectinidae in the Southern Hemisphere and the first record of the genus *Tethyaster* for the Lower Cretaceous of South America.

Keywords: *Astropectinidae*, *Tethyaster*; Early Cretaceous, Patagonia, Neuquén Basin, Mulichinco Formation.

RESUMEN. Un astropectínido (Echinodermata, Asteroidea) cretácico temprano de Patagonia (Argentina): Una nueva especie y el registro más antiguo de la familia para el Hemisferio Sur. Los asterozoos son echinodermos de vida libre, con forma de estrella, y componentes importantes de las faunas marinas bentónicas a nivel mundial. Su registro fósil, sin embargo, es pobre y fragmentario, probablemente debido a la desarticulación de los osículos. En particular, los asteroideos fósiles son poco frecuentes en América del Sur. Se presenta aquí una nueva especie de estrella de mar de edad valanginiana proveniente de la Formación Mulichinco (Cuenca Neuquina), en un contexto de ambiente somero de 'shoreface' dominado por tormentas. El espécimen pertenece a la Familia Astropectinidae y fue asignado al género *Tethyaster* Sladen. *T. antares* sp. nov., se caracteriza por una relación R:r de 2.43:1, marginales rectangulares más anchos en los ángulos interbraquiales, inferomarginales (28 pares a lo largo de un arco medial) con perfil ligeramente convexo y espinas planas (una por osículo en las áreas interbraquiales y dos por osículo en los brazos). Las características sedimentológicas y tafonómicas indican un enterramiento rápido. La presencia de fasciolas bien desarrolladas sugiere la posibilidad de que el espécimen se hallara parcialmente enterrado al comienzo de su ruta tafonómica. Este registro representa el hallazgo más antiguo de Astropectinidae en el Hemisferio Sur y el primer registro del género *Tethyaster* en el Cretácico Inferior de Sudamérica.

Palabras clave: *Astropectinidae*, *Tethyaster*; Cretácico Temprano, Patagonia, Cuenca Neuquina, Formación Mulichinco.

1. Introduction

Asterozoans are free living, marine echinoderms characterized by a star-shaped or pentagonal body and arms which radiate from the central disc (Twenhofel and Shrock, 1935). They present an oral side (where the mouth opens in living position this side is downwards, contacting the sea floor) and an aboral side (the opposite one). Within Asterozoa, asteroids (or starfishes) are distinguished from ophiuroids (brittle stars) by the lack of strong separation of disc from arms and other features. Body fossils of any group of starfish are seldom preserved, since the discrete skeletal elements (ossicles) of the endoskeleton most commonly disarticulate after death. Thus, fossil forms mostly comprise dissociated ossicles only (Villier *et al.*, 2004). Whole skeletons are rare and usually preserved under exceptional conditions that prevented disarticulation (Spencer and Wright, 1966).

During the Mesozoic, there was an important radiation within asteroids (Wright, 1967). A large number of these lineages have extant representatives (Blake, 1982), and fossil specimens can be morphologically very similar to the living ones (Blake, 1986). Many fossil asteroid examples, when preserved as whole specimens, are known either from one single sample or from a single bed containing more than one specimen. Even when dealing with such limited record, assignment of Mesozoic findings to extant taxa is possible if quality of preservation is good enough and certain key morphological features are preserved (Blake, 1986). Compared to the other families of asteroids, the Astropectinidae have a relatively good fossil record, due to their robust skeletal plates. Although Astropectinidae are environmentally broad ranging and numerically important in recent settings, the discovery of body fossils remains rare (Blake and Sturgeon, 1995).

Fossil asteroids in general are infrequent in South America. The oldest records are known from the Lower Devonian of Argentina and Brazil (Haude, 1995; Melo, 1988); late Mesozoic examples are from the Upper Cretaceous of Brazil (Maury, 1930; Castro Manso, 2006). In Chile, trace fossils found in the Lower Cretaceous (mid-late Hauterivian-Barremian/Aptian?) Apeleg Formation have been assigned to *Asteriacites lumbricalis* and ascribed to asteroids (Bell, 2004); however, no asteroid body fossils from

the Lower Cretaceous of South America have been reported up to this moment. The geographically closest Cretaceous record comes from the Antarctic Peninsula (Medina and Del Valle, 1983).

A new asteroid fossil specimen was found in a level of the Lower Cretaceous Mulichinco Formation, Neuquén Basin, Argentina. The aim of this study is to report the existence of this material, provide a systematic assignment and description of the specimen, present taphonomic and palaeoecological information about it, and comment on the importance and the palaeobiogeographic implications this finding has on the record of the Astropectinidae.

2. Geological setting and palaeontological frame

The Neuquén Basin (Fig. 1) is located in the west-central part of Argentina, between 34° and 41°S, spanning mainly over Northern Patagonia and Southern Cuyo regions. It contains over 7.000 m thick marine and continental deposits of Late Triassic to Paleogene age (Vergani *et al.*, 1995; Legarreta and Uliana, 1999). Most of the Jurassic and Lower Cretaceous deposits are represented by highly fossiliferous marine facies of diverse nature associated with transgressions from the Pacific Ocean (Howell *et al.*, 2005).

The Mulichinco Formation (Weaver, 1931; Mendoza Group) is a 200 to 400-m-thick mainly clastic, marine to continental succession (Schwarz, 2002) of early Valanginian age (Aguirre-Urreta *et al.*, 2005) exposed in the Neuquén province (Argentina), in the area between the Agrio River to the south and the limit with the Mendoza Province to the north. Nearby the study area, the Mulichinco Formation comprises clastic and carbonate lithologies that have been interpreted as deposited in non-deltaic, open shallow marine environments (Schwarz *et al.*, 2006). The sample was recovered from the lowermost levels of this unit, in the outcrops located along the National Road 40 at the Pampa Tril area (37°15'S, 69°47'W; Fig. 1).

The sandstone containing the studied specimen represents the top of one of several coarsening upward successions (Figs. 2-3), which present a thickness of 2.5 to 4 m. Their bases consist of massive shale beds, followed by heterolithic intervals which are in turn covered by sandstones with current, wave or combined-flow ripple lamination, or hummocky stratification. These successions

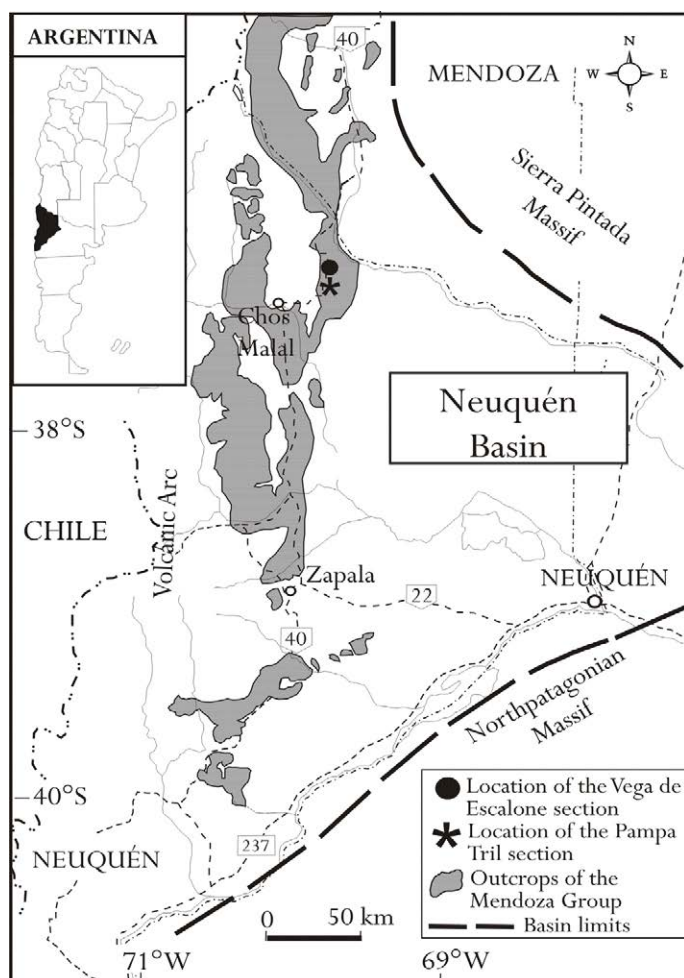


FIG. 1. Map of the Neuquén Basin, Argentina, showing location of the Pampa Tril and Vega de Escalone sections and National Road 40. Modified from Taylor *et al.* (2009).

culminate in sandstones with wave ripple lamination and abundant trace fossils assigned to *Asteriacites*, and escape structures. Very similar successions were interpreted, in the neighbouring site of Vega de Escalone (Fig. 1), as shallow-water, storm-dominated shoreface deposits (Rodríguez *et al.*, 2007). The same interpretation is valid for this facies in Pampa Tril. The bed containing the studied sample varies laterally from medium to fine-grained sandstone with wave or combined-flow ripple lamination.

Except for some internal moulds of ammonoids (*Lissonia riveroi* zone; Aguirre-Urreta and Rawson, 1999), no other body fossils are found in this particular facies. *Asteriacites* is a resting trace that has been attributed to asterozoans, both asteroids and

ophiuroids. Rodríguez *et al.* (2007) described the ones found in Vega de Escalone as *Asteriacites lumbricalis* and attributed them to ophiuroids. They are the only other evidence of asterozoans in this facies.

3. Material and Terminology

Material: The studied specimen is housed in the collection of the Área de Paleontología, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, C1428EGA, Buenos Aires, Argentina, under the repository number CPBA 16991.

Terminology: Morphological terms follow Spencer and Wright (1966) and Blake and Sturgeon (1995):

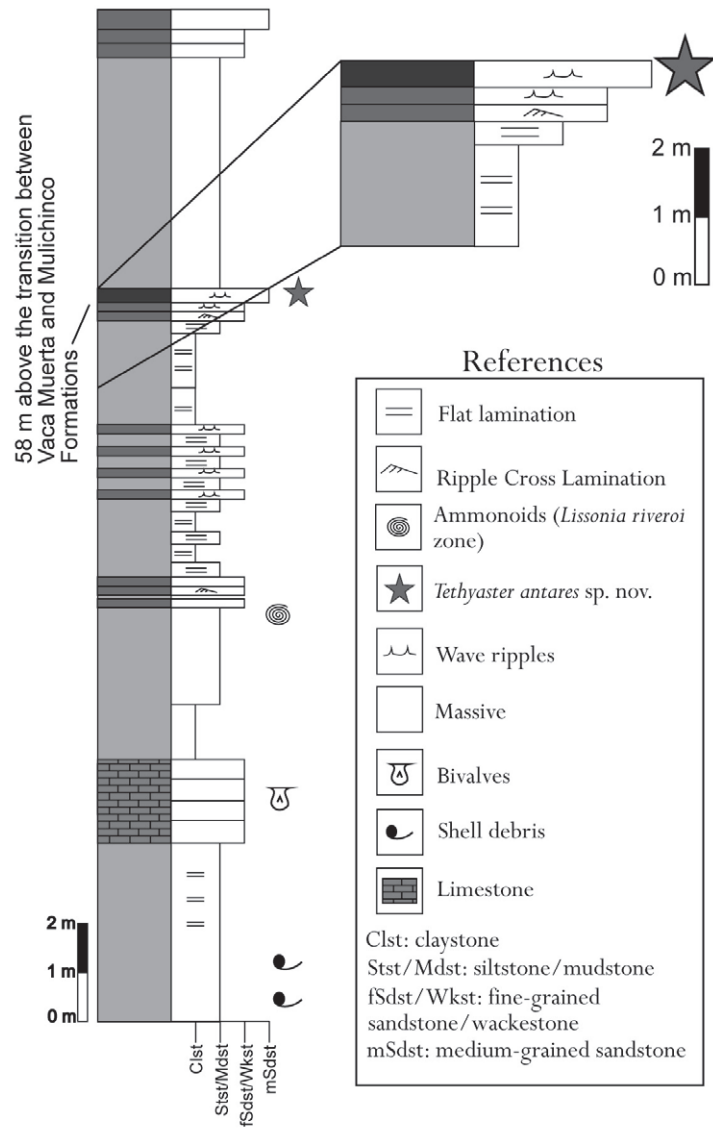


FIG. 2. Logged section of the lowermost levels of the Mulichinco Formation in the Pampa Tril area. Notice the level from which the sample was recovered, approximately 58 m above the transitional base of this unit.

‘ventral’ for the entire lower side of the specimen, ‘dorsal’ for the upper side, and ‘oral’ strictly for the area surrounding the mouth. ‘Abradial’ indicates the region of the ossicle opposite to the arm axis, the converse of ‘adradial’; ‘proximal’ means toward the centre of the disc and ‘distal’ indicates the contrary. ‘R’ is used for the length from disc centre to arm tip, and ‘r’ for the length from disc centre to inter-radial edge. Fascioles are parallel, radially directed channels between plates.

4. Systematic Palaeontology

Class Asteroidea Blainville, 1830
Subclass Neoasteroidea Gale, 1987
Order Paxillosida Perrier, 1884
Family Astropectinidae Gray, 1840

Discussion: Many members of the Astropectinidae, including extant *Tethyaster* are characteristic in presenting relatively small discs; usually elongated,

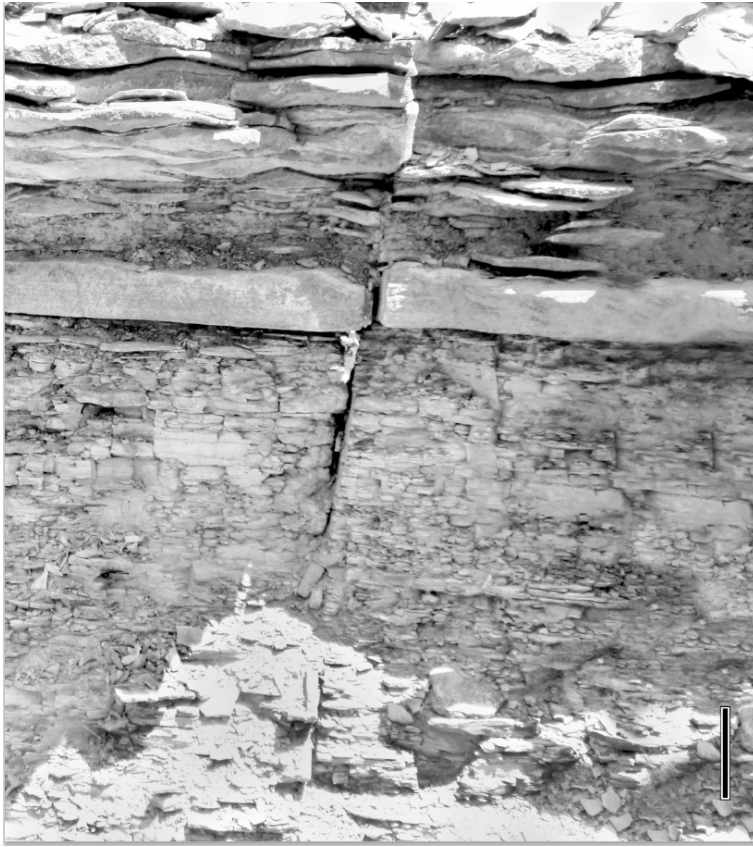


FIG. 3. Outcrop photo showing the coarsening upward succession containing the specimen bearing sandstone. Scale bar: 5 cm.

triangular, pointed, straight-sided arms; well-developed marginals with contacts facets smaller than the total length of the ossicle; fasciolate inferomarginals with spines on the outer margin of the arms in the ventral side, small actinal plates, and a bare-like oral plate (Spencer and Wright, 1966; Blake, 1981; Blake and Sturgeon, 1995). All of these features are present in this specimen. Other characteristics, such as the presence of paxillae on the dorsal surface and a large madreporite located close to the margin, can only be observed on a dorsal view, and are therefore unknown in this specimen.

Genus *Tethyaster* Sladen, 1889
***Tethyaster antares* new species**
Figs. 4-5

Diagnosis: *Tethyaster* of small size, with a R:r ratio close to 2.4:1. Arms short and triangular in outline. Marginal ossicles rectangular, with a height at least

equal to the width of the ossicle, wider in the interbrachial angles and narrower in the extremes of the arms. Inferomarginals with slightly convex profile, with approximately 28 pairs along a median arc. Marginal fascioles deep and wide. Spines of the inferomarginals large, flat and truncated; one spine per ossicle for the marginals of the interbrachial area and two spines per ossicle for the marginals of the arms.

Description: The body is rather flat, the disk is relatively large, the maximum radius (R) is 37 mm, and the minimum radius (r) is 15 mm. Arms are relatively short and have a wide base (13.5 mm wide). The specimen shows five arms; two of them are complete, one is almost complete, and two are fractured showing less than a third of their original length. The complete arms are 22.8 and 20.6 mm long. The interbrachial angles are rounded, varying from 92° to 113°. The arms are triangular in outline, pointed and straight-sided.

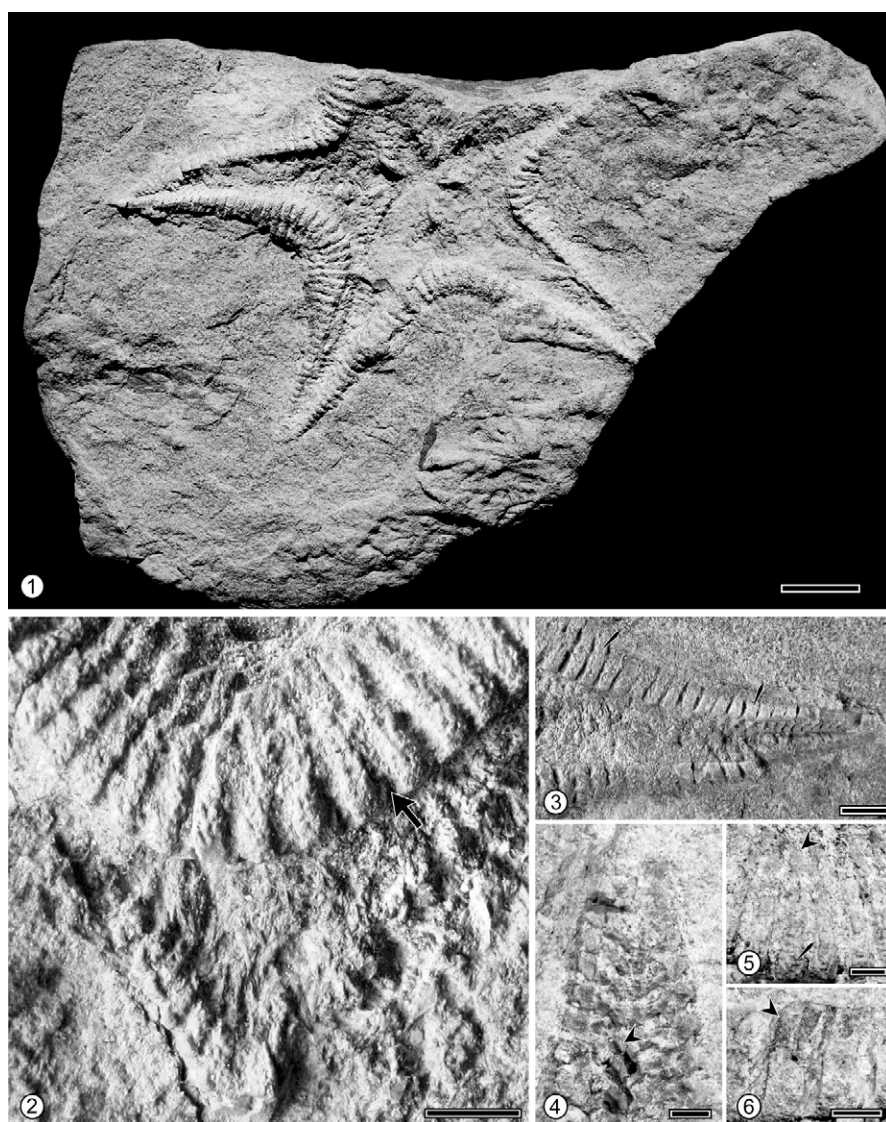


FIG. 4. *Tethyaster antares* n. sp., Mulichinco Formation, Patagonia, Early Cretaceous. Holotype (CPBA 16991). Scale bars: 1 cm in 1; 0.25 cm in 2-3; 0.1 cm in 4-6. **1.** Slab fragment bearing the starfish in oral view; **2.** Close-up of an actinal area. The arrow points the location of one fasciole; **3.** Close-up of an arm in ventral view. The lines indicate two different marginals with unequal size along the arm; **4.** Close-up of an arm tip in ventral view. The arrow points the ambulacral ossicles; **5.** Close-up of marginal ossicles in interbranchial arcs. The lines indicate the granules on marginal surface. The arrow points at the single spine per ossicle; **6.** Close-up of marginal ossicles in the arm. The arrow points at the two spines per ossicle.

Marginals are stout, rectangular, not very high, at least equal to the ossicle width, wider than long (up to four times wider than long, especially in the interbranchial angles) and narrower near the arm tips (where they are almost squared). They are orientated perpendicular to the arm axis but with the abradial extreme of every ossicle leaning to some extent

towards the distal sector of the arm; this tendency increases distally. Supermarginals and inferomarginals are equal in size. The inferomarginals are slightly convex in transverse profile, with the ventral surface covered with large and conical granules. There are approximately 28 pairs of marginals along a median arc. Interbranchial marginal ossicles are numerous.

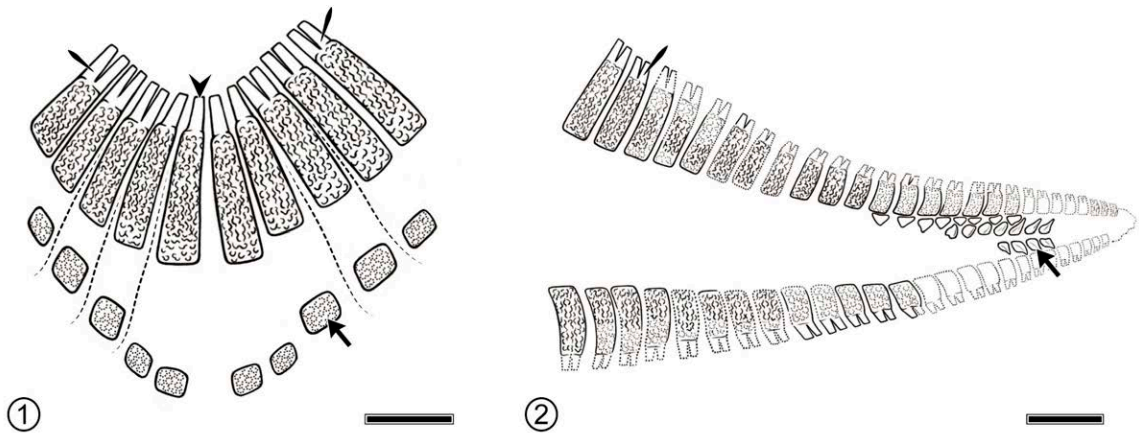


FIG. 5. Partial line drawing and reconstruction of CPBA 16991. Scale bars: 0.25 cm. **1.** Hypothetical reconstruction of an actinal area based on the entire material. Note the presence of deep and wide fascioles. The arrow head indicates the spines in the interbrachials (one per ossicle), and the lines on the upper left and right point to the spines in the arms (two per ossicle). The dotted lines mark the position of the fascioles. The arrow on the lower right points at the actinal ossicles; **2.** Line drawing of figure 4.3. The line on the upper left indicates the pair of flat spines in each inferomarginal. The arrow on the lower right points to the ambulacral ossicles.

Marginal fascioles are deep and wide. The contacts between marginals are partially covered with sediment; however, it can be distinguished that contacts are shorter than the total width of the ossicle and begin at the second third of the marginal towards the ambulacral side. Distally in the arms, these contacts are even closer to the ambulacral side. The inferomarginals bear large, rather flat spines on the abradial edge one per ossicle in the interbrachials and two per ossicle in the arms, extended distally in each arm and truncated at the ends. Intermarginal areas with short, conical spines. Terminals could not be observed. Actinal areas are large. Actinal ossicles are small, lined up in series in the intermediate actinal areas, becoming larger towards the oral sector. At least two series of actinals are extended towards the arms, reaching up to two thirds of the arm's length. Numerous small, conical spines are present over the actinal ossicles.

Ossicles of the oral frame are partially exposed. The mouth angle ossicles are rather large, keel-like and prominent.

Ambulacral ossicles are asymmetrical, with a more expanded adradial portion. Adambulacral ossicles are aligned with the ambulacral ones.

Etymology: The specific epithet derives from the giant red star Antares, of the Scorpius (scorpion) constellation, visible mainly from the Southern Hemisphere.

Holotype: CPBA 16991. It is a nearly complete specimen in ventral view.

Occurrence: Lowermost levels of the Mulichinco Formation at the Pampa Tril locality (37°15'S, 69°47'W), Neuquén Basin, Argentina.

Remarks: The genus *Tethyaster* presents: a relatively large disc for the family; rounded interbrachial angles; deep fascioles; numerous pairs of interbrachial marginals; supero- and inferomarginal ossicles of similar size, large and covered with granules; inferomarginals with flattened spines and well-developed actinal areas, with more than one line of actinals extended within the arms (Clark and Clark, 1954; Blake, 1986). This specimen presents all these features, and the proportions and body shape correspond to those typical of the genus. Next, there is a list of characteristics of the other Astropectinidae genera that allow the inclusion of this specimen within the genus *Tethyaster* and rule out the others.

Astropecten Gray, 1840 presents: a small disc; angular interbrachials; markedly reduced actinal areas; actinal ossicles restricted to the disc; subquadrangular marginals and a long spine projected horizontally from each marginal forming an edge along the whole outline of the starfish. The inferomarginals are ornamented with horseshoe shaped tubercles, which are also present in *Pentasteria* Valette, 1929 (Jurassic and Cretaceous, Europe) and in *Archastropecten*

Hess, 1955 (Jurassic and Cretaceous, Europe). *Craspidaster* Sladen, 1889 shows small and inconspicuous spines on the marginals and no actinals in the arms, as well as *Ctenopleura* Fisher, 1913, which also presents a small disc and acute interbrachial angles. *Dipsacaster* Alcock, 1893 has more quadrangular, high and stout marginals, and infero- and superomarginals of different size, like in *Astropecten*, *Ctenopleura*, *Aldebarania* Blake and Sturgeon, 1995, *Ctenophoraster* Fisher, 1906, *Patagiaster* Fisher, 1906 and *Psilaster* Sladen, 1885. *Aldebarania* (Maastrichtian, North America) presents lower inferomarginals that protrude beyond the superomarginals, and also shorter and wider arms. *Advenaster* Hess, 1955 (Jurassic and Cretaceous, Poland and India) presents a relatively small central disc, with non-rounded interbrachial angles and, as well as in *Archastropecten*, shallow fascioles and large articular contacts between marginals. *Eokainaster* Blake, 1981 (Jurassic, North America) shows a very small disc and elongated arms with no actinal ossicles, and angular interbrachial arcs. *Bathybiaster* Danielssen and Koren, 1883 is similar to *T. antares* sp. nov. in the body proportions, the presence of rounded interbrachials and subequal marginal ossicles, but the actinal areas in *Bathybiaster* are small and the spines on the marginals are inconspicuous. The interbrachial angle is not rounded in *Prothrissacanthias* Villier et al., 2007 (Berriasian, Algeria) and *Persephonaster* Wood-Mason and Alcock, 1891. *Astrocratis* Blake and Sprinkle, 1996 (Campanian, North America) shows a small disc with actinal areas reduced, subquadrangular marginals and elongated arms. *Plutonaster* Sladen, 1899 shows a similar appearance but has shallower fascioles and moderate or small actinal areas. *Coulonia* de Loriol, 1873 (Cretaceous of Spain, Switzerland and Morocco, and Tertiary of the United Kingdom) presents similar marginal and body proportions but shows only one series of actinals to each side of the ambulacrals in the arms, and no spines or granules on the inferomarginals.

Tethyaster antares sp. nov. is different from the rest of the species known for this genus. All Recent species show R:r ratios ranging from 3.2:1 to 4.8:1, and are usually larger, from 120 mm to 275 mm long (Blake, 1986). The type species, *T. subinermis* (Philippi, 1837) -Recent, Mediterranean Sea and eastern North Atlantic- is differentiated from *T. antares* sp. nov. by the presence of spines with acute tips in the inferomarginals, as well as in

T. aulaphorus (Fisher, 1911) -Recent, Philippines and Taiwan-, *T. grandis* (Verrill, 1899) -Recent, Gulf of Mexico- and *T. pacei* (Mortensen, 1925) -Recent, South Africa-. In *T. canaliculatus* (Clark, 1916) -Recent, Gulf of California- the arms are narrower and more elongated, and the inferomarginals maintain their height: width ratio along all the body margin. *T. vestitus* (Say, 1825) -Recent, western North Atlantic- and *T. grandis* bear much longer arms and proportionally smaller marginals. *T. magnificus* (Bell, 1882) -Recent, Saint Helena and Ascension Islands- has a denser cover of spines on the ventral side (Clark and Clark, 1954).

The fossil species of *Tethyaster* present R:r proportions inferior to the ones present in the Recent taxa, generally not greater than 3:1. *T. jurassicus* Blake, 1986 (Camel Formation, Jurassic, Utah, USA) is differentiated from *T. antares* sp. nov. by the presence of longer arms, conical spines and acute tips on the inferomarginals, which are of regular size along the arms and interbrachials. *?T. albertensis* Hall and Moore, 1990 (Cardium Formation, Turonian, Alberta, Canada) presents similar characteristics to *T. antares* n. sp., but equally to *T. jurassicus*, the marginals maintain a regular size along the entire margin and bear conical spines in groups of three in each inferomarginal. *T. guerangeri* Breton, 1996 (Sables et Grès du Mans Formation, Cenomanian, France) has a higher number of marginals per arm than *T. antares* n. sp. (35-40 instead of approximately 28), a higher R:r ratio (3:1) and inferomarginals with a very convex profile. The fossil species of *Tethyaster* are more similar among them than are the extant species of the genera. More research including both fossil and living species, is necessary for a better understanding of the genus.

5. Astropectinid ecology, taphonomy and palaeo-ecological inferences

Extant paxillosidans, and astropectinids in particular, live semi-infaunally on soft sandy or muddy substrates (Blake and Aronson, 1998; Jagt, 2000). They are capable of self-burial due to the presence of deep fascioles, which are deep in *Tethyaster*. *Astropecten* and *Luidia* Forbes, 1839, two common extant paxillosidan genera, are capable of self-burial, pushing sediment laterally from beneath their bodies and gradually sinking beneath the surface (Heddle, 1967); in both these genera, the presence of fascioles allows unobstructed water

flow over the animal's body surface, thereby aiding in self-burial (Blake and Aronson, 1998; Blake and Reid, 1998).

Blake and Aronson (1998) point out that asteroid self-burial evolved in the Cretaceous, and that 'the oldest clearly identified fasciole-bearing taxon is from the Early Cretaceous' (Hauterivian and Barremian; Hess and Blake 1995). The specimen reported here comes from slightly older deposits of Valanginian age, showing that well-developed fascioles (Figs. 4.2, 5) were already present at even earlier times.

Astropectinids are voracious predators that feed on molluscs and echinoderms (including other astropectinids), amongst other invertebrates, but they may also consume algae and inorganic detritus (*e.g.*, Ortega *et al.*, 2011). They actively search for prey and are able to shallowly dig into the substrate to get it (see Ortega *et al.*, 2011 and references therein). Studies on the diet of recent *Tethyaster* specimens (Penchaszadeh and Molinet, 1983) show that this taxon is the top carnivore in the food web of echinoderms and molluscs, and as it would be expected for such predators, their population density is very low.

Fossilization of articulated starfish is rare, it requires a rapid burial and thick coverage so that the body remains beyond reworking by normal biological or physical agents. Otherwise, exceptional preservation can take place on low-energy settings in which bioturbation is minimal or absent. Post-mortem collapse of starfish bodies is expected, and since ossicles are not fused to each other they are easily dispersed; recrystallization is common, especially in coarse-grained lithologies, and results in the obliteration of surface details (Jagt, 2000). Articulated remains are extremely rare, and are expected to usually happen in storm-generated beds or other kind of rapid deposition events (Hess, 1972; Goldring and Stephenson, 1972; Meyer, 1984, 1988; Jagt, 2000). For example, Blake and Reboul (2011) reported numerous specimens from Morocco at depths of 30 m or less, in a situation more similar to the case under study here, even though their material came from limestones rather than sandstones. Taking into account that seastars are a conservative group regarding general morphological features (Jagt, 2000), and particularly in the case of *Tethyaster* (according to Breton, 1996), and given that no significant change is observed in the genus since its first representatives known from the Jurassic (see below), Mesozoic *Tethyaster* specimens were most likely capable of

self-burial as well. This feature of astropectinids enhances their preservation potential (Blake and Aronson, 1998). It is possible that this specimen was already 'half buried' at the beginning of its taphonomic route. It was preserved in life position at the base of the stratum. Regarding its taphonomical properties, no sign of pre-burial disarticulation, abrasion, predation or scavenging was found. The missing fragments of some of the rays are probably due to postburial fragmentation due to sediment weight and compaction. Some recrystallization is observed. Given the sedimentological features of the bed, the taphonomical properties of the sample, and the life habit of extant astropectinids, it is inferred that burial was rapid. Even when storm-related deposits are found within this facies, sedimentary structures of this particular level do not indicate the action of storms (similarly to the case reported by Breton, 1996), but wave action is evidenced by the presence of wave ripples. Complete burial was probably post-mortem, and in this case, a mixture of a previous half-buried state, and steady sediment input favored preservation.

6. The fossil record of the Astropectinidae and palaeobiogeographical implications

According to Villier *et al.* (2004), the earliest undisputed record of the Astropectinidae dates from the Aalenian, suggesting an Early Jurassic origin of the family (see Villier *et al.*, 2004). An overview of the main record of astropectinid fossils is given by Jagt (2000). Most Jurassic records were reported from Europe, India and the USA (*e.g.*, Blake, 1981, 1986; Breton, 1997; Gale, 2011; Hess, 1973; Kutscher and Röper, 1999; Spencer and Wright, 1966; Srivastava *et al.*, 2010; Villier, 2008; Villier *et al.*, 2004).

Known Cretaceous records are mostly European, with other occurrences taking place in Canada, USA and northern Africa (*e.g.*, Blake and Reboul, 2011; Blake and Sprinkle, 1996; Blake and Sturgeon, 1995; Breton, 1996; de Loriol, 1873; Hall and Moore, 1990; Hérengrer, 1944; Hess, 1970; Hess and Blake, 1995; Jagt, 2000; Néraudeau and Breton, 1993; Neumann and Hess, 2001; Neumann and Jagt, 2011; Smith *et al.*, 1988; Spencer and Wright, 1966; Villier, 2008; Villier *et al.*, 2007; Vullo *et al.*, 2003). Regarding Lower Cretaceous records, Villier *et al.* (2007) have suggested that the sparseness of astropectinid occurrences could be more related to certain biases rather

than being a reflection of low starfish diversity. Some of these biases include unequal sampling efforts throughout the world, with findings centred mainly in Europe; likewise, literature is often restricted to very well-preserved specimens, and disarticulated ossicles are seldom given attention. Additional issues according to Villier and Kutscher (1999) and Villier *et al.* (2007) are given by the scarcity of lithofacies suitable for the preservation of starfish remains, and the problematic taxonomic scheme which was mainly constructed during the nineteenth century and requires an updated and thorough review.

Tertiary records are more widespread, with occurrences in Europe, the Antarctic Peninsula, Africa and all through America (northern, central and southern), and range from the Paleocene to the Pliocene (*e.g.*, Blake and Aronson, 1998; Breton and Vizcaíno, 1997; Brünnich Nielsen, 1926; Donovan, 2001; Donovan *et al.*, 1993, 2003, 2005; Jagt, 2000; Jagt *et al.*, 2009; Kroh and Nebelsick, 2003; Kutscher *et al.*, 2004; Oyen and Portell, 2001). The only fossil record known for the Astropectinidae in South America comes from the Miocene of Chile (Kutscher *et al.*, 2004). The specimen studied here is therefore the oldest record of the Family Astropectinidae in South America and the entire Southern Hemisphere.

At the family level, the relatively sparse record of the Astropectinidae is in contrast with their importance in Recent faunas (for example, along the South American Atlantic margin; Martínez, 2008) and their capability of surviving in a broad range of environments (Jagt, 2000). The study of ossicles as isolated elements can provide a family-level classification and, to a certain extent, genus and species classification (Villier *et al.*, 2004), but unfortunately this approach has been infrequent in studies from the Southern Hemisphere.

The genus *Tethyaster* is known from the Middle Jurassic to nowadays, with little morphological change. Blake (1986) has even regarded this genus as a 'living fossil'. Examples are known from the mid Cenomanian of France (*Tethyaster guerangeri*, Breton, 1996) and the Turonian of Canada (?*Tethyaster albertensis*, Hall and Moore, 1990), though the latter were assigned to the genus with doubts. Breton and Vizcaíno (1997) tentatively assigned disarticulated starfish ossicles, mostly marginals, to ?*Tethyaster*. In South America, Kutscher *et al.* (2004) interpreted the Miocene starfish fragments from Chile as closely related to *Tethyaster*. Therefore, the specimen of *Tethyaster* reported herein also represents the first record of the genus for the Lower Cretaceous of the Southern Hemisphere (Fig. 6).

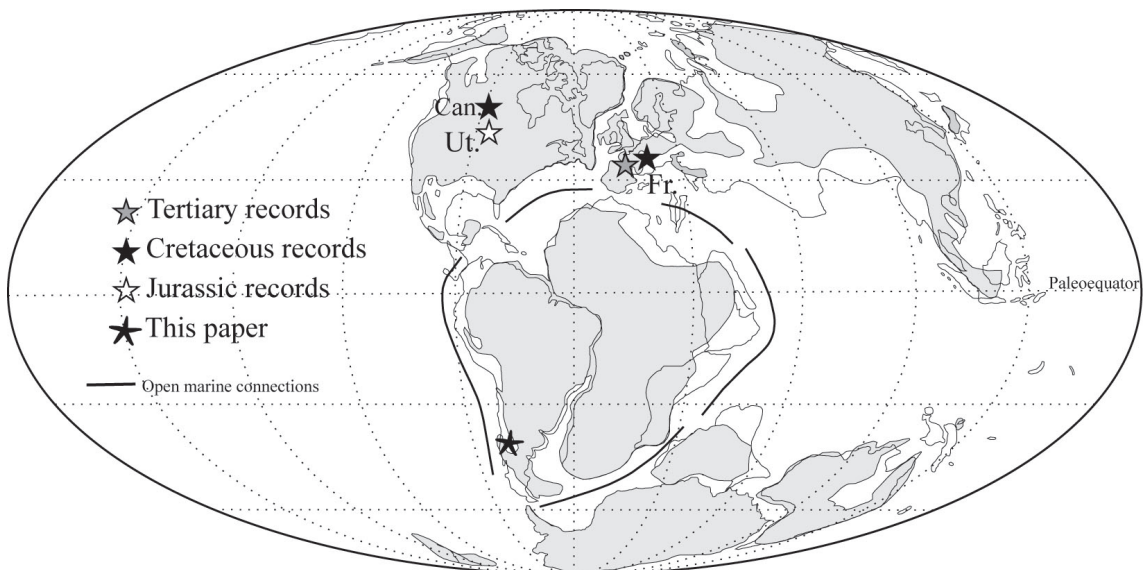


FIG. 6. Palaeogeographic reconstruction for the Lower Cretaceous (from Smith *et al.*, 1994; modified from Lazo, 2007). Note the location of the Jurassic, Cretaceous (including this new record) and Tertiary records of the genus *Tethyaster*. Can.: Canada; Fr.: France; Ut.: Utah, USA.

7. Conclusions

- For the first time a starfish is described from material coming from the lower section of the Mulichinco Formation, Neuquén Basin, Argentina. Once the presence of starfish body fossils in this basin is noticed, it is expected that more specimens will be found.
- The taxonomic analysis allows us to assign this material to the class Asteroidea, order Paxillosida, family Astropectinidae, genus *Tethyaster*. The species *T. antares* n. sp. is proposed.
- This specimen shows that well-developed fascioles were already present at early Valanginian times. It is very likely that *Tethyaster antares* n. sp. was capable of self-burial.
- This specimen expands both the palaeogeographic and temporal record of the group, since it represents: **i)** the oldest record of the Family Astropectinidae in the Southern Hemisphere; and **ii)** the first record of *Tethyaster* for the Lower Cretaceous of the Southern Hemisphere.

Acknowledgements

This study was financially supported by ANCyT (PICT-189) and CONICET (PIP 5960) given to M.B. Aguirre-Urreta. D. Lazo is thanked for sharing field work. M.B. Aguirre-Urreta, P.J. Pazos, G. Breton, C. Neumann, J.W.M. Jagt, and S. Martínez are deeply acknowledged for sharing bibliography. We are very grateful to D. Blake and L. Villier for their helpful comments as reviewers, and to L.E. Lara, for his suggestions as editor. This is contribution R-33 of the Instituto de Estudios Andinos don Pablo Groeber.

References

- Aguirre-Urreta, M.B.; Rawson, P.F. 1999. Stratigraphic position of *Valanginites*, *Lissonia* and *Acantholissonia* in the Lower Valanginian (Lower Cretaceous) ammonite sequence of the Neuquén Basin, Argentina. In *Advancing Research on Living and Fossil Cephalopods* (Olóriz, F.; Rodríguez-Tovar, F.; editors). Kluwer Academic/Plenum Publishers: 521-529. New York.
- Aguirre-Urreta, M.B.; Rawson, P.F.; Concheyro, G.A.; Bown, P.R.; Ottone, E.G. 2005. Lower Cretaceous Biostratigraphy of the Neuquén Basin. In *The Neuquén Basin: A case study in sequence stratigraphy and basin dynamics* (Veiga, G.D.; Spalletti, L.A.; Howell, J.A.; Schwarz, E.; editors). Geological Society of London, Special Publication 252: 57-81.
- Alcock, A. 1893. Natural History notes from the H.M. Indian Marine Survey Steamer Investigator 7. An account of the collection of deep-sea Asteroidea. *Annals of the Magazine of Natural History* 11 (6): 73-121.
- Bell, F.J. 1882. Description of a new species of the genus *Archaster* from St. Helena. *Annals and Magazine of Natural History, Zoology, Botany and Geology* 5 (48): 440-441.
- Bell, C.M. 2004. Asteroid and ophiuroid trace fossils from the Lower Cretaceous of Chile. *Palaeontology* 47: 51-66.
- Blake, D.B. 1981. The new Jurassic sea star genus *Eokainaster* and comments on life habits and the origins of the modern Asteroidea. *Journal of Paleontology* 55: 33-46.
- Blake, D.B. 1982. Recognition of higher taxa and phylogeny of the Asteroidea. In *Echinoderms: Proceedings of the International Conference, Tampa Bay* (Lawrence, J.M.; editor). A.A. Balkema: 105-107. Rotterdam.
- Blake, D.B. 1986. Some new post-Paleozoic sea stars (Asteroidea: Echinodermata) and comments on taxon endurance. *Journal of Paleontology* 60: 1103-1119.
- Blake, D.B.; Sturgeon, K. 1995. *Aldebarania arenitea*, a new genus and species of Astropectinidae (Asteroidea; Echinodermata) from the Maastrichtian (Upper Cretaceous) Pedee Formation of North Carolina. *Journal of Paleontology* 69: 376-380.
- Blake, D.B.; Aronson, R.B. 1998. Stelleroidea of the Late Eocene La Meseta Formation, Seymour Island, Antarctic Peninsula. *Journal of Paleontology* 72: 339-353.
- Blake, D.B.; Reid, R.III. 1998. Some Albian (Cretaceous) asteroids (Echinodermata) from Texas and their Paleobiological Implications. *Journal of Paleontology* 72: 512-532.
- Blake, D.B.; Reboul, R. 2011. A new asteroid (Echinodermata) faunule from the Early Cretaceous of Morocco. *Journal of Paleontology* 85: 1021-1034.
- Blake, D.B.; Sprinkle, J. 1996. *Astrocratis acutispina*, new genus and species, a new asteroid from the Late Cretaceous of Texas. *Eclogae Geologicae Helveticae* 89 (3): 1311-1320.
- Breton, G. 1996. *Tethyaster guerangeri* sp. nov. (Astropectinidae, Asteroidea, Echinodermata): deux spécimens d'astérides d'une conservation exceptionnelle du Cénomaniens du Mans (Sarthe, France). *Bulletin de la Société Géologique de Normandie et des Amis du Muséum du Havre, Le Havre* 82 (4): 17-29.
- Breton, G. 1997. Deux étoiles de mer du Bajocien du Nord-Ouest du Bassin de Paris (France): leurs alliés actuels sont des fossiles vivants. *Bulletin trimestriel*

- de la Société géologique de Normandie et des Amis du Muséum du Havre 84 (1): 23-34.
- Breton, G.; Vizcaíno, D. 1997. Astérides (Echinodermata) de l'Ilerdien (Yprésien) des Corbières (Aude, France): systématique, relations paléogéographiques et évolutives. Bulletin de la Société d'Études Scientifiques de l'Aude 97: 11-28.
- Brünnich Nielsen, K. 1926. Kalken paa Salholm. Danmarks Geologiske Undersøgelse 4 (1): 1-23.
- Clark, A.H. 1916. Six new starfishes from the Gulf of California and adjacent waters. Proceedings of the Biological Society of Washington 29: 51-62.
- Clark, A.M.; Clark, A.H. 1954. A revision of the sea-stars of the genus *Tethyaster*. Smithsonian Miscellaneous Collections 122 (11): 27 p.
- Danielssen, D.C.; Koren, J. 1883. Echinoderms of the Norwegian North-Atlantic Expedition. The Annals and Magazine of Natural History series 5 (11): 384-388.
- de Blainville, H.M. 1830. Zoophytes. Dictionnaire des Sciences Naturelles. F.G. Levrault: 60 p. Strasbourg.
- de Castro Manso, C.L. 2006. Primeiro registro de Goniasteridae (Echinodermata, Asteroidea) no Cretáceo do Brasil: Turoniano da Bacia Potiguar. Geociências 25: 255-260.
- de Loriol, P. 1873. Description de quelques astérides du terrain Néocomien des environs de Neuchâtel. Mémoires de la Société des sciences naturelles de Neuchâtel 5: 5-19.
- Donovan, S.K. 2001. Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils. Palaeogeography, Palaeoclimatology, Palaeoecology 166: 177-192.
- Donovan, S.K.; Gordon, C.M.; Veltkamp, C.J.; Scott, A.D. 1993. Crinoid, asteroids, and ophiuroids in the Jamaican fossil record. Geological Society of America Memoir 182: 125-130.
- Donovan, S.K.; Pickerill, R.K.; Portell, R.W.; Jackson, T.A.; Harper, D.A.T. 2003. The Miocene palaeobathymetry and palaeoenvironments of Carriacou, the Grenadines, Lesser Antilles. Lethaia 36: 255-272.
- Donovan, S.K.; Portell, R.W.; Veltkamp, C.J. 2005. Lower Miocene echinoderms of Jamaica, West Indies. Scripta Geologica 129: 91-135.
- Fisher, W.K. 1906. The starfishes of the Hawaiian islands. Bulletin of the United States Fish Commission 23: 987-1130.
- Fisher, W.K. 1911. New genera of starfishes from the Philippine Islands. Proceedings of the United States National Museum 40: 415-427.
- Fisher, W.K. 1913. Four new genera and fifty-eight new species of starfishes from the Philippine Islands, Celebes, and the Moluccas. Proceedings of the United States National Museum 43: 599-648.
- Forbes, E. 1839. On the Asteriadae of the Irish Sea. Memoirs of the Wernerian Natural History Society 8: 113-130.
- Gale, A.S. 1987. Phylogeny and classification of the Asteroidea (Echinodermata). Zoological Journal of the Linnean Society of London 89: 107-132.
- Gale, A.S. 2011. Asteroidea (Echinodermata) from the Oxfordian (Late Jurassic) of Savigna, Département du Jura, France. Swiss Journal of Palaeontology 130: 69-89.
- Goldring, R.; Stephenson, D.G. 1972. The depositional environment of three starfish beds. Neues Jahrbuch für Geologie und Paläontologie Monatshefte 10: 611-624.
- Gray, J.E. 1840. A synopsis of the genera and species of the class Hypostoma (*Asterias* Linn.). Annals of the Magazine of Natural History 6: 175-184, 275-290.
- Hall, R.L.; Moore, S. 1990. ?*Tethyaster albertensis*, a Late Cretaceous (Turonian) sea star from the Cardium Formation, Alberta, Canada. Journal of Paleontology 64: 1045-1049.
- Haude, R. 1995. Echinodermen aus dem Unter-Devon der argentinischen Praekordillere. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 197 (1): 37-86.
- Heddle, D. 1967. Versatility of movement and the origin of the asteroids. In Echinoderm Biology (Millott, N; editor). Symposium of the Zoological Society of London 20: 125-141.
- Héranger, L. 1944. Sur la présence d'Astéries (*Astropecten carthusiae* nov. sp.) dans le Valanginien de la Chartreuse (Isère). Travaux du Laboratoire de Géologie de la Faculté des Sciences de Grenoble 24: 33-47.
- Hess, H. 1955. Die fossilen Astropectiniden (Asteroidea). Neue Beobachtungen und Übersicht über die bekannten Arten. Schweizerischen Paläontologischen Abhandlungen, Birkhäuser Verlag, Basel 71: 1-113.
- Hess, H. 1970. Schlangensterne und Seesterne aus dem oberen Hauterivien 'Pierre jaune' von St-Blaise bei Neuchâtel. Eclogae geologicae Helvetiae 63 (3): 1069-1091.
- Hess, H. 1972. Eine Echinodermen-Fauna aus dem mittleren Dogger des Aargauer Juras. Schweizerische Paläontologische Abhandlungen 92: 1-86.
- Hess, H. 1973. Neue Echinodermenfunde aus dem mittleren Dogger des Aargauer Juras. Eclogae Geologicae Helvetiae 66: 625-656.

- Hess, H.; Blake, D.B. 1995. *Coulonia platispina* sp. nov., a new astropectinid sea star from the Lower Cretaceous of Morocco. *Eclogae geologicae Helvetiae* 88: 777-788.
- Howell, J.A.; Schwarz, E.; Spalletti, L.A.; Veiga, G.D. 2005. The Neuquén Basin: an overview. In *The Neuquén Basin, Argentina: A case study in sequence stratigraphy and basin dynamics* (Veiga, G.D.; Spalletti, L.A.; Howell, J.A.; Schwarz, E.; editors). Geological Society, Special Publications 252: 1-14. London.
- Jagt, J.W.M. 2000. Late Cretaceous-Early Palaeogene echinoderms and the K/T boundary in the southeast Netherlands and northeast Belgium-Part 5: Asteroids. *Scripta Geologica* 121: 377-503.
- Jagt, J.W.M.; Fraaije, R.H.B.; van Bakel, B.W.M. 2009. A late Miocene astropectinid (Echinodermata, Asteroidea) and associated ichnofossils from Liessel, province of Noord-Brabant, the Netherlands. *Netherlands Journal of Geosciences-Geologie en Mijnbouw* 88: 127-131.
- Kroh, A.; Nebelsick, J.H. 2003. Echinoid assemblages as a tool for palaeoenvironmental reconstruction: an example from the Early Miocene of Egypt. *Palaeogeography, Palaeoclimatology, Palaeoecology* 201: 157-177.
- Kutscher, M.; Röper, M. 1999. Die Asteroidea (seesterne) aus den 'Papierschiefen' von Hienheim und Ried (Malm Zeta 3, Untertithonium). *Archaeopteryx* 17: 1-13.
- Kutscher, M.; Neumann, C.; Nielsen, S.; Reich, M.; Villier, L. 2004. Echinoderms from the Miocene of Chile. In *Echinoderm* (Heinzeller, T.; Nebelsick, J.; editors). Taylor and Francis Group: 453-456. London.
- Lazo, D.G. 2007. The bivalve *Pholadomya gigantea* in the Early Cretaceous of Argentina: taxonomy, taphonomy and paleogeographic implications. *Acta Palaeontologica Polonica* 52 (2): 375-390.
- Legarreta, L.; Uliana, M.A. 1999. El Jurásico y Cretácico de la Cordillera Principal y la Cuenca Neuquina. I, Facies sedimentarias. In *Geología Argentina* (Caminos, R.; editor). Segemar: 399-416. Buenos Aires.
- Martínez, S. 2008. Shallow water Asteroidea and Ophiuroidea of Uruguay: composition and biogeography. *Revista de Biología Tropical* 56: 205-214.
- Maury, C.J. 1930. O Cretaceo da Parahyba do Norte. *Serviço Geologico E Mineralogico do Brasil Monographia* 8: 1-305.
- Medina, F.A.; Del Valle, R.A. 1983. Un nuevo asteroideo cretácico de la Isla Vicecomodoro Marambio. *Contribuciones del Instituto Antártico Argentino* 286: 1-7.
- Melo, J.H.G. 1988. The Malvinokaffric realm in the Devonian of Brazil. In *Devonian of the World* (McMillan, N.J.; Embry, A.F.; Glass, D.J.; editors). Canadian Society of Petroleum Geologists 1: 669-70.
- Meyer, C.A. 1984. Palökologie und Sedimentologie der Echinodermenlagerstätte Schofgraben (mittleres Oxfordian, Weissenstein, Kt. Solothurn). *Eclogae Geologicae Helvetiae* 77 (3): 649-673.
- Meyer, C.A. 1988. Ein neuer Seestern aus den Solothurner Schildkrötenkalken (Oberes Kimmeridgien, Kt. Solothurn). *Eclogae geologicae Helvetiae* 81 (3): 843-856.
- Mortensen, T. 1925. On some echinoderms from South Africa. *Annals and Magazine of Natural History*, series 9, 16 (91): 146-154.
- Néraudeau, D.; Breton, G. 1993. Astérides du Cénomaniens de Charente-Maritime (SW France). *Geobios* 26: 105-120.
- Neumann, C.; Hess, H. 2001. *Coulonia parva* sp. nov., a new species of Astropectinidae (Asteroidea; Echinodermata) from the Santonian (Upper Cretaceous) of Sierra de Montsech (Southern Pyrenees, Spain). *Paläontologische Zeitschrift* 75: 7-11.
- Neumann, C.; Jagt, J.W.M. 2011. *Pentasteria? splendida*, a new Early Cretaceous astropectinid starfish from northern Germany. *Swiss Journal of Paleontology* 130: 123-127.
- Ortega, I.; Martín, A.; Díaz, Y. 2011. Distribución, parámetros poblacionales y dieta de *Astropecten marginatus* (Asteroidea: Astropectinidae) en el Atlántico venezolano. *Revista de Biología Tropical* 59: 53-69.
- Oyen, C.W.; Portell, R.W. 2001. Diversity patterns and biostratigraphy of Cenozoic echinoderms from Florida. *Palaeogeography, Palaeoclimatology, Palaeoecology* 166: 193-218.
- Penchaszadeh, P.E.; Molinet, R. 1983. Diet of the sea-star *Tethyaster vestitus* Say (Astropectinidae) in the Golfo Triste (Venezuela). *Bulletin of Marine Science* 33: 187-191.
- Perrier, E. 1884. Mémoire sur le étoiles de mer recueillies dans la Mer des Antilles et le Golfe de Mexique. *Nouvelles Archives du Muséum d'Histoire Naturelle*, Paris 2 (6): 127-276.
- Philippi, A. 1837. Über die mit *Asterias auranciaca* verwanten und verwechselten Asterien der sicilanschen Kuste. *Archiv für Naturgeschichte* 3: 193-194.
- Rodríguez, D.L.; Pazos, P.J.; Aguirre-Urreta, M.B. 2007. Cretaceous ophiuroid trace fossils from the Neuquén Basin. In *Ichnology at the crossroads: A multidimensional approach to the science of organism-substrate interactions* (Bromley, R.G.; Buatois, L.A.; Mángano, M.G.; Genise, J.F.; Melchor, R.N.; editors). Society of

- Economic Paleontologists and Mineralogists (SEPM) Special Publication 88: 97-105.
- Say, T. 1825. On the species of the Linnaean genus *Asterias* inhabiting the coast of the United States. *Journal of the Academy of Natural Sciences of Philadelphia* 5: 141-154.
- Schwarz, E. 2002. Estratigrafía, bioestratigrafía y secuencias de la Formación Mulichinco, Cuenca Neuquina, Argentina. ¿Nuevos enfoques? *In Congreso Geológico Argentino*, No. 15, Actas I: 806-811. El Calafate.
- Schwarz, E.; Spalletti, L.A.; Howell, J.A. 2006. Sedimentary response to a tectonically induced sea-level fall in a shallow back-arc basin: the Mulichinco Formation (Lower Cretaceous), Neuquén Basin, Argentina. *Sedimentology* 53: 55-81.
- Sladen, W.P. 1885. Report on the scientific results of the voyage of H.M.S. Challenger. *Narrative* 1 (2): 607-617.
- Sladen, W.P. 1889. Report on the Asteroidea. The Voyage of H.M.S. 'Challenger' 1873-1876. *Zoology* 30 (51): 893 p.
- Smith, A.B.; Paul, C.R.C.; Gale, A.S.; Donovan, S.K. 1988. Cenomanian and Lower Turonian echinoderms from Wilmington, south-east Devon, England. *Bulletin of the British Museum (Natural History), Geological Series* 42: 1-245.
- Smith, A.G.; Smith, D.G.; Funnell, B.M. 1994. *Atlas of Mesozoic and Cenozoic Coastlines*. Cambridge University Press: 109 p. Cambridge.
- Spencer, W.K.; Wright, C.W. 1966. Asterozoans. *In Treatise of Invertebrate Paleontology, Part U, Echinodermata* 3 (Moore, R.C.; editor). Geological Society of America, Boulder, and University of Kansas Press: U4-U107. Lawrence.
- Srivastava, D.K.; Pandey, D.K.; Alberti, A.; Fürsich, F.T. 2010. Record of *Advenaster* Hess, 1955 (Asteroidea) from the Bathonian Patcham Formation of Kala Jhar in Habo Dome, Kachchh Basin, India. *Journal of the Palaeontological Society of India* 55: 65-69.
- Taylor, P.D.; Lazo, D.G.; Aguirre-Urreta, M.B. 2009. Lower Cretaceous bryozoans from Argentina: a 'by catch' fauna from the Agrio Formation (Neuquén Basin). *Cretaceous Research* 30 (1): 193-203.
- Twenhofel, W.H.; Shrock, R.R. 1935. *Invertebrate paleontology*. McGraw-Hill Book Company: 511 p. New York and London.
- Valette, A. 1929. Note sur quelques stellerides jurassiques du Laboratoire de Géologie de la Faculté des Sciences de Lyon. *Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon* 16: 5-39.
- Vergani, G.D.; Tankard, A.J.; Belotti, J.; Welsink, H.J. 1995. Tectonic evolution and paleogeography of the Neuquén Basin, Argentina. *In Petroleum basins of South America* (Tankard, A.J.; Suárez, R.; Welsink, H.J.; editors). American Association of Petroleum Geologists, Memoir 62: 383-402.
- Verrill, A.E. 1899. Revision of certain genera and species of starfishes with descriptions of new forms. *Transactions of the Connecticut Academy* 10: 145-234.
- Villier, L. 2008. Sea star ossicles from the Callovian black clays of the Łuków area, eastern Poland. *Neues Jahrbuch für Geologie und Paläontologie* 247 (2): 147-160.
- Villier, L.; Kutscher, M. 1999. How dissociated ossicles can further our understanding of the origins of the Neoasteroidea. An example from the Toarcian of Western Europe. *In Echinoderm Research 1998* (Candia Carnevali, D.; Bonasoro, F.; editors). Balkema: 417-422. Rotterdam.
- Villier, L.; Kutscher, M.; Mah, C.L. 2004. Systematics and palaeoecology of middle Toarcian Asteroidea (Echinodermata) from the 'Seuil du Poitou', Western France. *Geobios* 37: 807-825.
- Villier, L.; Breton, G.; Atrops, F. 2007. Une nouvelle étoile de mer (*Prothrissacanthias africanus* gen. nov. sp. nov.) du Berriasien d'Algérie. *Revue de Paléobiologie, Genève* 26 (2): 413-424.
- Vullo, R.; Néraudeau, D.; Videt, B. 2003. Un faciès de type falun dans le Cénomanien basal de Charente-Maritime (France). *Annales de Paléontologie* 89 (3): 171-189.
- Weaver, C.E. 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. *Memoir of the University of Washington* 1: 1-469.
- Wood-Mason, J.; Alcock, A. 1891. Natural history notes from H.M. Indian marine survey steamer 'Investigator', Commander R.F. Hoskyn, R.N., commanding. Series II, No. 1. On the results of deep-sea dredging during the season 1890-1891. *In Annals and Magazine of Natural History*, No 8, Series 6 (48): 427-452, plate 7.
- Wright, C.W. 1967. Evolution and classification of Asterozoa. *In Echinoderm Biology* (Millott, N.; editor). Academic Press: 159-162. London.