

New *Scutellastra* (Gastropoda: Patellidae) species from the lower Miocene Navidad Formation of central Chile and the lower-middle Miocene Cantaure Formation of Venezuela

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ABSTRACT

New species of the patellid gastropod genus *Scutellastra* are described from the lower Miocene Navidad Formation of central Chile and the lower-middle Miocene Cantaure Formation of Venezuela. *Scutellastra arayae* new species is the first fossil record of a patellid from Chile and *S. venezuelana* new species is the first from tropical America. This genus is today restricted to southern Africa and the western Pacific, with the exception of *S. mexicana* from Central America. Together with contemporaneous fossil occurrences in New Zealand, these new records show that *Scutellastra* had a much wider distribution when water temperatures were higher during the mid-Cenozoic.

Additional Keywords: Paleontology, marine, Patellogastropoda

INTRODUCTION

The systematic position of the genus *Scutellastra* H. and A. Adams, 1854 was considered problematic in the Southern Synthesis (Lindberg, 1998), whereas it is clearly included in Patellidae in the phylogenetic analysis of Ridgway et al. (1998). Further investigations by Koufopanou et al. (1999), Lindberg (2007), and Nakano and Ozawa (2007) suggested that the genus *Scutellastra* may be polyphyletic with respect to the genera *Helcion* Montfort, 1810 and *Cymbula* H. and A. Adams, 1854. Lindberg (2007) also mentioned a “scutellastrid clade” being the “sister taxon of [...] the Patellidae” but did not formally name it. It would contain the genera *Scutellastra*, *Helcion*, and *Cymbula*. We here follow the traditional view that recognizes the sole family Patellidae within Patelloidea (Bouchet and Rocroi, 2005).

Extant species of *Scutellastra* are present almost exclusively in the Atlantic, in southern Africa, and in the Indian Ocean, in southern Australia (Ridgway et al., 1998), with few species extending throughout the western Pacific, and only *S. mexicana* (Broderip and Sowerby, 1829) is present in the eastern Pacific, in the Americas, ranging from western Mexico to Peru. Species of *Scutellastra* are usually intertidal, but some live just subtidally (Lindberg, 1998). They are generally found in tropical to subtropical regions, with the species of southern Australia being the temperate end-members. The fossil record of *Scutellastra* goes back to the upper Cretaceous of Japan (Kase and Shigeta, 1996).

Patellogastropod limpets are a dominant group today in intertidal environments of Pacific southern South America, represented by the nacellid genus *Nacella* (Valdovinos and R  th, 2005; Gonz  lez-Wevar et al., 2011) and the lottiid genus *Scurria* (Espoz et al., 2004). The Chilean fossil record of limpets in beds older than Pleistocene is scarce. Only a single specimen of *Nacella* (*Patinigera*) *intiforma* DeVries, 2008 from the Huenteguapi Sandstone (Le Roux et al., 2008) on Arauco Peninsula and the holotype of *Nacella* (*Patinigera*) *nielseni* DeVries, 2008 from Chilo   Island (Watters and Fleming, 1972) are known from the Neogene of Chile. The only other large patellogastropod limpet is the smooth-shelled nacellid *Cellana fuenzalidai* (Herm, 1969) from the Pliocene of northern Chile (Herm, 1969; Lindberg and Hickman, 1986). All these belong in the family Nacellidae.

The tropical American Neogene patellogastropod limpet record is even poorer, with no fossil species at all described from any of the rich Caribbean or Panamic Pacific assemblages, except for the shell illustrated by Lindberg (2007, text-figure 8B) as *Scutellastra* sp. from

the Pliocene of Venezuela. Lindberg (2007) did not provide the locality for this specimen, but, according to its locality record, it was collected at approximately 300 m south of Casa Cantaura (D.R. Lindberg personal communication), which is the only place where we have found representatives of *Scutellastra* in Venezuela. It is undoubtedly conspecific with the new Venezuelan species described herein and dates therefore from the Miocene, not Pliocene.

GEOLOGY OF FOSSIL-BEARING LOCALITIES

Chile: The Chilean *Scutellastra* comes from reddish sandstones of the Navidad Formation (Encinas et al., 2006) at Punta Perro, central Chile (Figure 1). These deposits were dated as upper Miocene by Finger et al. (2007, locality PPN) based on misidentified foraminifera (Finger, 2013). The mollusk assemblage was interpreted as being reworked from lower Miocene beds based on comparison with southern Peru (DeVries and Frassinetti, 2003; Finger et al., 2007), an interpretation confirmed with strontium isotope dating by Nielsen and Glodny (2009). Recently revised identification of stratigraphic index foraminifera (Finger, 2013), however, now agrees with a lower Miocene age for the Navidad Formation

and also explains earlier assignments to younger ages (e.g., Ibaraki, 1992). These new data provide a consensus for the lower Miocene age of the Navidad Formation. The displacement scenario of Finger et al. (2007) is still valid, although it has now been demonstrated that contemporaneous shallow-water deposits were transported into bathyal depths, as indicated by the strontium isotope data of Nielsen and Glodny (2009). Many shallow-water taxa occur in sediments intercalated with deep-water deposits containing a completely different fauna (see Finger et al., 2007).

The assemblage from the same concretionary block that contained the *Scutellastra* specimen includes *Pinna semicostata*, *Glycymeris* sp., *Astele chilensis*, *Echinophoria monilifer*, *Distorsio ringens*, *Glossaulax pachystoma*, *Magnatica subsolida*, *Sinum subglobosum*, *Lamprodomina dimidiata*, *Testallium cepa*, *Austrotoma echinulata*, *Inquisitor lingulacanthinus*, *Dentalium* sp. and represents the typical shallow-water Navidad assemblage (see Finger et al., 2007; Griffin and Nielsen, 2008; Kiel and Nielsen, 2010).

Venezuela: The Venezuelan *Scutellastra* material herein described and discussed comes from the San José de Cocodite region in the Paraguaná Peninsula of northern Venezuela (Falcon State). The collection site where

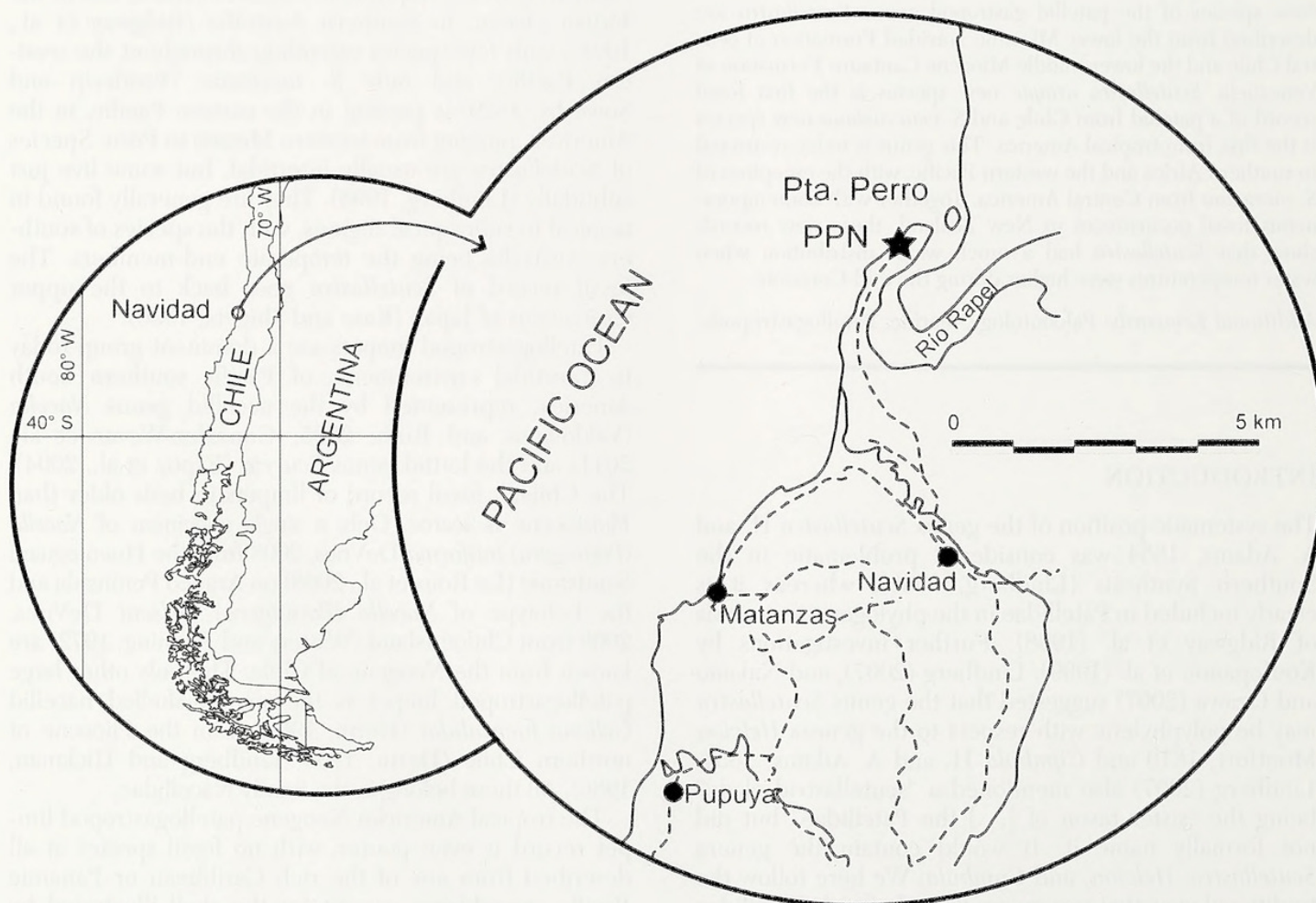


Figure 1. Geographic location of the study site in the Punta Perro region, in Chile.

it originates from is located in the Cantaure area, 3.4 km West of the church of the village of San José de Cocodite (as the crow flies), at an altitude of approximately 140 m above sea-level on a acacia and cactus covered area approximately 400 m south of Casa Cantaure with the approximate geographic coordinates: 11°56'24.1" N, 70° 01' 04.5" W (Figure 2; location of Casa Cantaure after Griffiths et al., 2013: 11°56'35.9" N, 70°01'10.8" W).

The specimens were collected from a thick, friable, yellow, fine sandstone bed containing an abundant and diversified molluscan assemblage (mostly gastropods and bivalves with rare nautiloid cephalopods), as well as other elements such as barnacles and corals. This bed is part of the Cantaure Formation (Jung, 1965; Hunter and Bartok, 1974), which, as a whole, according to Díaz de Gamero (1974), is correlated with the planktonic foraminiferal biozones *Globigerinatella insueta* and *Praeorbulina glomerosa* of Bolli (1966), biozones N7 and N8 of Blow (1969), which in turn, according to the latest geologic time scale of Gradstein et al. (2012), correspond to the Lower to Middle Miocene transition, upper Burdigalian to lower Langhian. Rey (1996) corroborates this biostratigraphic correlation stating that the Cantaure calcareous nannofossil assemblage contains the *Helicosphaera ampliaperita* and *Sphenolithus heteromorphus* markers corresponding

to the biozones NN4 and NN5 of Martini (1971), which broadly correlate with the above mentioned foraminiferal zones.

In several recent papers, however, the Cantaure Formation continues to be assigned to the Lower Miocene, Burdigalian, after the traditional correlation of Díaz de Gamero (1974) and Rey (1996). Aguilera and Rodríguez de Aguilera (1999), based on planktonic foraminifera data from a personal communication by Collins, place the Cantaure Formation in the Lower Miocene, Burdigalian. Griffiths et al. (2013), based on $^{87}\text{Sr}/^{86}\text{Sr}$ isotope data obtained from corals, assign an age of between 16.3 and 16.6 Ma to the fossils of Cantaure, placing them in the Burdigalian. These authors further comment that the isotopic results obtained are in good agreement with the traditional biostratigraphic age estimates for the Cantaure Formation based on the identification of the N7–N8 planktonic foraminiferal zones by Díaz de Gamero (1974) and the nannofossil biozones NN4–NN5 by Rey (1996). Anderson and Roopnarine (2005), on the other hand, in their Table 2, place the Cantaure Formation in the Burdigalian–Langhian, straddling the Lower–Middle Miocene boundary.

The Cantaure Formation consists of a sedimentary sequence approximately 75 m in thickness and mainly

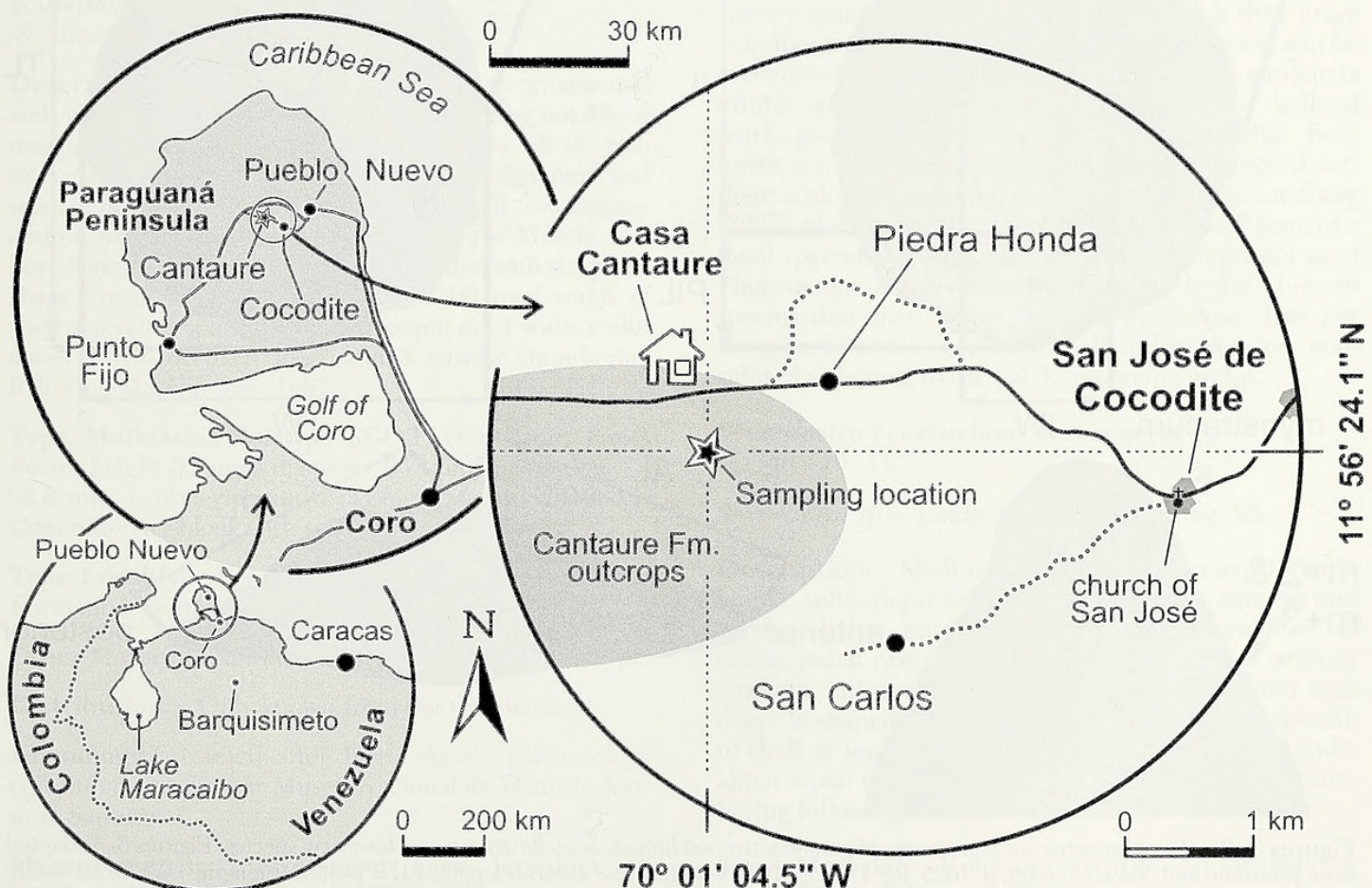


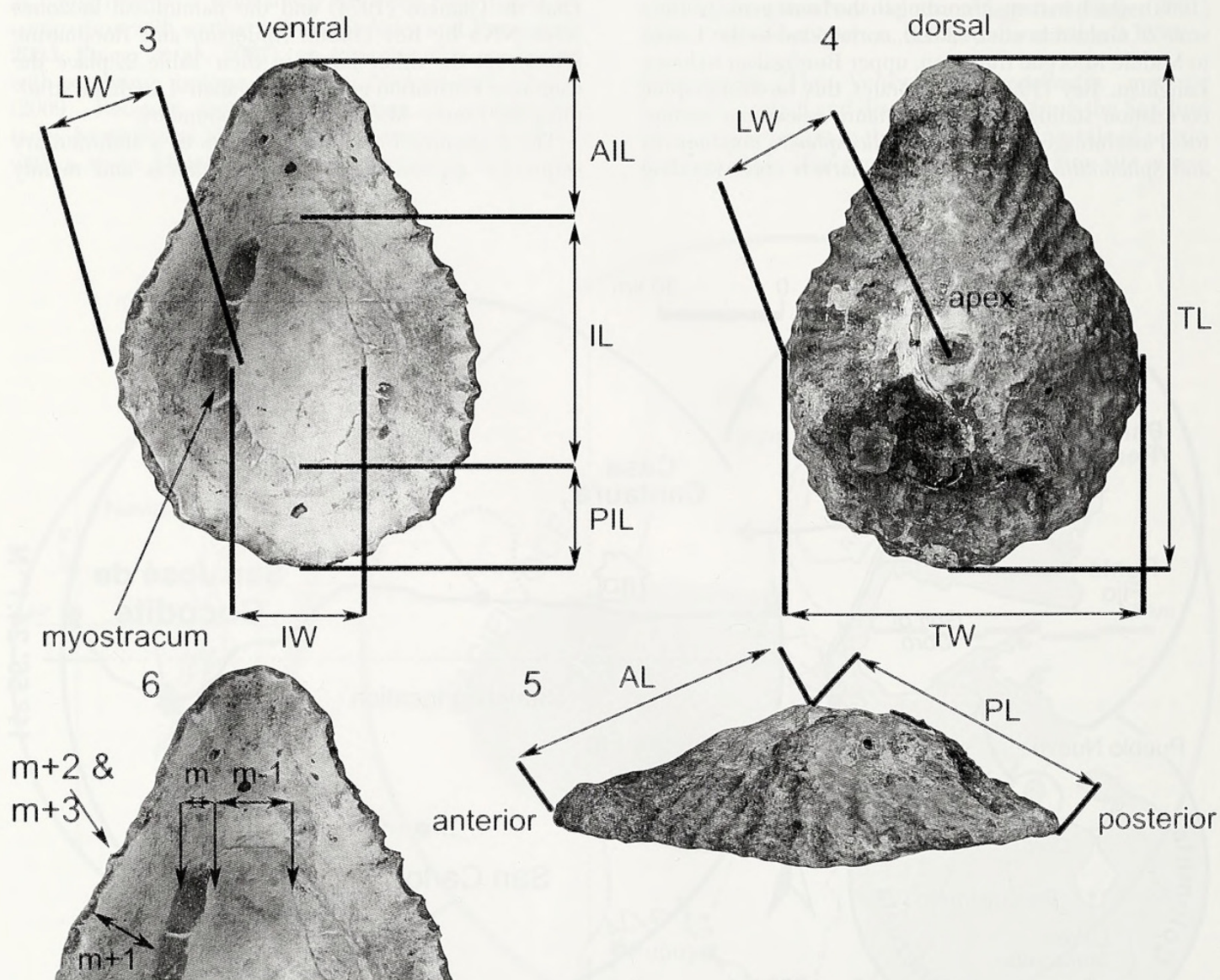
Figure 2. Geographic location of the study site in the Cantaure region, Paraguaná Peninsula, in Venezuela.

composed of fossiliferous silts, silty sandstones, and fine to medium sandstones interbedded with thin algal limestones (Hunter and Bartok 1974; L xico Estratigr fico de Venezuela, 1997; Aguilera et al., 2013). A diverse fossil assemblage, particularly rich in mollusks, but also featuring corals, decapods and cirripedian crustaceans, and fish remains, has been identified in the sediments of the Cantaure section, especially in its lower part (e.g. Jung 1965; Nolf and Aguilera 1998; Aguilera and Rodrigues de Aguilera, 1999; Griffiths et al., 2013). Locally, decimetric boulders of limestone with *in situ*-attached valves of the shallow marine bivalve *Spondylus* sp. may be observed within the friable fine sandstone beds. This fossil assemblage is indicative of a shallow to coastal tropical marine environment, with clear water and marine euhaline salinity (Jung, 1965; D az de Gamero, 1974; Nolf and Aguilera, 1998; Aguilera et al., 2013; Griffiths et al., 2013).

MATERIALS AND METHODS

The Chilean material described herein comes from the Covacevich and Frassinetti collection, housed in the Museo Nacional de Historia Natural, Santiago, Chile. The Venezuelan material described here is from the Gibson-Smith collection, housed in the Naturhistorisches Museum Basel (NMB), Switzerland, and the Bernard Landau collection, housed in the Naturhistorisches Museum Wien, Austria.

In the systematic descriptions of the new species, we have followed the morphometric model suggested by Jerardino and Navarro (2008) and MacClintock (1967) (Figures 3–6). Following the convention established by MacClintock (1967), the layers are numbered by reference to the myostracum (m); starting at the outside of the shell, they are designated m+3, m+2, m+1, m and



Figures 3–6. Morphometric measurements of patellogastropod limpet; *Scutellastra venezuelana* new species. Figures 3–5 adapted from Jerardino and Navarro (2008, p. 1025, fig. 1) TL = Total length; AL = anterior length; PL = posterior length; TW = total width; LW = lateral width; AIL = anterior inner length; IL = inner length; PIL = posterior inner length; IW = inner width; LIW = lateral inner width. Figure 6 adapted from MacClintock (1967) m = myostracum.

m-1. Although MacClintock (1967) distinguished m+2 and m+3 layers in the shells of patellids, Ridgeway et al. (1998) found that these were not clearly separable. In both new species the width of the m+1 layer is greater than half of the width of the combined outer (m+1, m+2, m+3) layers (see Figures 3, 5, 7, 10, 12). This character is seen in the genera *Scutellastra*, *Lottia*, and *Acmaea* (Ridgeway et al., 1998). The relatively large and solid shells with strong radial dorsal sculpture suggest placement in the genus *Scutellastra*.

Abbreviations: SGO.PI., Museo Nacional de Historia Natural, Santiago, Chile; NHMW, Naturhistorisches Museum Wien, Austria; NMB, Naturhistorisches Museum Basel, Switzerland.

SYSTEMATIC PALEONTOLOGY

Superfamily Patelloidea Rafinesque, 1815
Family Patellidae Rafinesque, 1815

Genus *Scutellastra* H. and A. Adams, 1854

Type Species: *Patella plicata* Born, 1778 (= *P. barbara* Linnaeus, 1758) by subsequent designation of Wenz (1938, see Ridgeway et al., 1998); Recent, South Africa.

Scutellastra arayae new species (Figures 7–9)

Description: Shell large, thick, oval, heavily ornamented with very coarse irregular radial ribs projecting notably at margin. Seven primary ribs, one secondary rib in each interspace, one tertiary rib between primaries and secondaries, additional lesser ribs in all interspaces and on major ribs. Apex situated anteriorly. Muscle scar horseshoe-shaped, open anteriorly. Venter with deep, U-shaped myostracum (m); m-1 about 1/3 total width of shell at level of opening of myostracum; m+1 wide, width about 4/5 in of m-1, m+2 and 3 narrow (numbering following MacClintock, 1967).

Type Material: Holotype SGO.PI.6650 from Punta Perro, height 55 mm, diameter 93 mm (incomplete) × 92.6 mm, Covacevich and Frassinetti locality 241080.1. Concretionary block with small *Pinna semicostata*.

Type Locality: Punta Perro, lower Miocene Navidad Formation, central Chile.

Other Material Examined: Known only from holotype.

Distribution: Only known from the type locality.

Etymology: Named after Ivette Araya, paleontology collections manager at Museo Nacional de Historia Natural, Santiago.

Measurements: Measurements follow Jerardino and Navarro (2008). Total length (TL) > 93 mm; anterior length (AL) ~ 51.3 mm; posterior length (PL) unknown;

total width (TW) 92.6 mm; lateral width (LW) 50 mm; anterior inner length (AIL) 19 mm; inner length (IL) 60 mm; posterior inner length (PIL) unknown; inner width (IW) 36.2 mm; lateral inner width (LIW) > 26.2 mm.

Discussion: *Scutellastra arayae* new species has few coarse projecting ribs and can be easily distinguished from species with a smooth or crenulate margin, including *S. mexicana*. The apex of *S. arayae* lies anteriorly while that of *S. flexuosa* (Quoy and Gaimard, 1834) from Australia is nearly central. *Scutellastra chapmani* (Tenison-Woods, 1876) from Australia and *S. longicosta* (Lamarck, 1819) from South Africa have better defined and more projecting ribs. *Scutellastra barbara* (Linnaeus, 1758) and *S. exusta* (Reeve, 1854), both from South Africa have more and finer ribs.

According to Beu and Maxwell (1990) two fossil species of *Scutellastra* are known from New Zealand, the upper Oligocene–early Miocene *S. aurorae* Fleming, 1973 and the early Miocene *S. cooperi* (Powell, 1938), which would both be roughly contemporaneous with the Chilean species. Judging from the original figures, *S. aurorae* has a rather smooth margin and more and weaker ribs while *S. cooperi* has stronger projecting ribs than *S. arayae*.

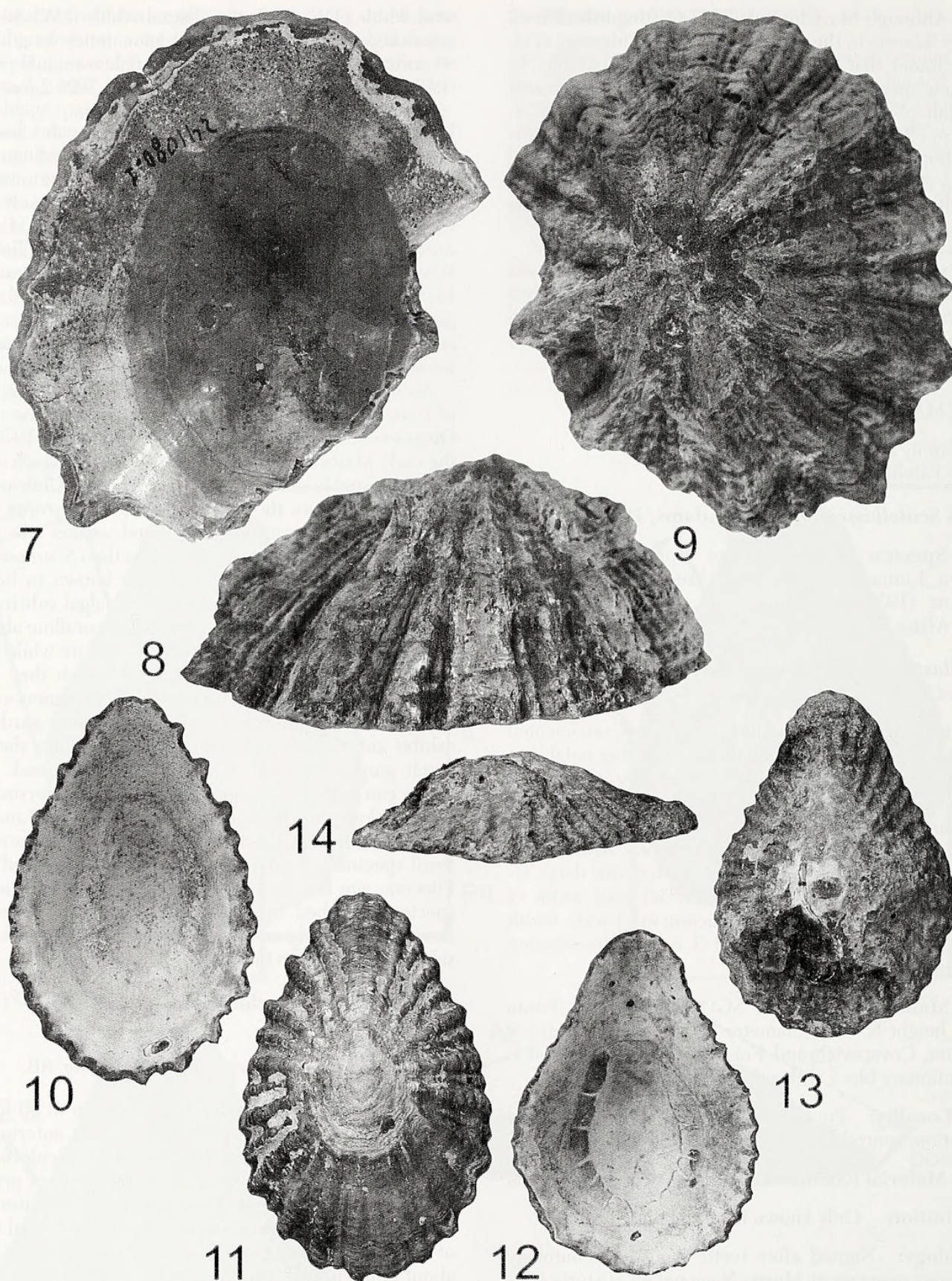
Several species of *Scutellastra* are known to be gardeners. Some species garden coralline algal substrate in their periphery, feeding either on those coralline algae or on other red algae growing on this substrate while other species maintain patches of algae on which they graze (Lindberg, 2007). Patch and periphery gardeners can be recognized morphologically since periphery gardeners exhibit an anteriorly extended shell while the shells of patch gardeners have a rounded anterior end. Both forms can thus be recognized in the fossil record and their ecology may be inferred as was done by Lindberg (2007) who figured the typically extended shell form of a fossil specimen from Venezuela that was reported as of Pliocene age but, as mentioned earlier, is the Miocene species described below. *Scutellastra arayae* does not show an anteriorly extended shell and is therefore considered to belong to the patch-gardening group.

Scutellastra venezuelana new species (Figures 10–14)

Scutellastra sp.—Lindberg, 2007, p. 230, fig. 8B.

Description: Shell moderately large, up to 90 mm in length, solid, depressed, pear-shaped, with anterior end produced, but not constricted at neck. Sculpture of coarse radial ribs on dorsum, most of which of primary strength and deeply corrugate the margin. Venter with deep, U-shaped myostracum (m); m-1 about total width of shell at level of opening of myostracum; m+1 wide, about equal in width to m-1, m+2 and 3 narrow (numbering following MacClintock, 1967).

Type Material: Holotype NHMW 2013/0566/0002, height 9.7 mm, diameter 34.0 mm × 22.5 mm; paratype 1, NHMW 2013/0566/0001, height 16.9 mm, diameter



Figures 7–14. *Scutellastra* species. **7–9.** *Scutellastra arayae* new species. Holotype SGO.PI.6650, height 55 mm, diameter $>93 \times 92.6$ mm. Punta Perro, lower Miocene Navidad Formation, central Chile. **10–14.** *Scutellastra venezuelana* new species. From 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela, Cantaure Formation, upper Burdigalian-lower Langhian, lower-middle Miocene boundary. **10–11.** Holotype NHMW 2013/0566/0002, height 9.7 mm, diameter $34.0 \text{ mm} \times 22.5 \text{ mm}$. **12–14.** Paratype 1 NHMW 2013/0566/0001. Height 16.9 mm, diameter $60.5 \text{ mm} \times 43.0 \text{ mm}$.

60.5 mm × 43.0 mm; paratype 2, NHMW 2013/0566/0003, height 10.6 mm, diameter 38.5 mm × 27.8 mm; paratype 3, NHMW 2013/0566/0004, height 10.5 mm, diameter 40.3 mm × 27.6 mm; paratype 4, NMB H20223, height 15.9 mm, diameter 62.0 mm × 42.2 mm, NMB locality 17516; paratype 5, NMB H20224, height 14.7 mm, diameter 59.0 mm × 43.2 mm, NMB locality 17516.

Type Locality: 1 km southwest of Casa Cantaure, about 10 km west of Pueblo Nuevo, Falcón, Venezuela, Cantaure Formation, upper Burdigalian-lower Langhian, lower-middle Miocene boundary.

Other Material Examined: Maximum dimensions: diameter 89.1 mm × 58.7 mm. NHMW 2013/0566/0005 (8); NMB locality 17516 NMB (31 unnumbered specimens), same locality as type material.

Distribution: Only known from the type locality.

Etymology: Named after the country of origin, Venezuela. The gender of *Scutellastra* is feminine.

Measurements: Measurements follow Jerardino and Navarro (2008) of paratype 1. Total length (TL) 60.5 mm; anterior length (AL) 36.5 mm; posterior length (PL) 29.3 mm; total width (TW) 43.0 mm; lateral width (LW) 26.9 mm; anterior inner length (AIL) 20.3 mm; inner length (IL) 29.2 mm; posterior inner length (PIL) 12.7 mm; inner width (IW) 16.1 mm; lateral inner width (LIW) 16.8 mm.

Discussion: The rostration developed in *Scutellastra venezuelana* new species makes it superficially similar to the extant *Scutellastra cochlear* (Born, 1778) from the coasts of South Africa, but this species differs in having an even more pronounced rostration, which is somewhat pinched at the neck. Although this tendency to rostration is most strongly developed in *S. cochlear* and *S. venezuelana*, this character is probably convergent as it is developed to some degree in several other *Scutellastra* species; i.e. the eastern Pacific species *S. mexicana* (Broderip and Sowerby, 1829) and the Indo-Pacific species *S. optima* (Pilsbry, 1927). More importantly, *S. venezuelana* differs from both *S. cochlear* and *S. mexicana* in having coarser dorsal ribs, almost all of which are of primary strength, whereas both *S. cochlear* and *S. mexicana* have finer ribbing, with several orders of major and minor ribs.

Despite the superficial similarity between the shells of *S. cochlear* and *S. venezuelana*, there are no common factors between the Venezuelan and South African molluscan faunas, and the new Venezuelan species is much more likely to be related to the eastern Pacific *S. mexicana*. The similarity between these species is likely to be due to common ecological factors. According to Lindberg (2007), the tendency to rostration and an angular rather than rounded profile when viewed from the dorsal aspect are associated with gardening limpets that maintain the garden around the periphery of the shell. Lindberg (2007) suggested that the rostration might allow these limpets to

graze their gardens without leaving the vicinity of their home depressions.

Scutellastra venezuelana new species is quite unlike the Chilean *S. araya* new species, which is less flattened, the primary ribs are much broader and the shell does not develop the pronounced rostration so typical of *S. venezuelana*, *S. cochlear* and *S. mexicana*.

CONCLUSIONS

In the Recent American shallow marine faunas, *Scutellastra* is known only from the extant species *S. mexicana* occurring from West Mexico to Peru. This paper introduces two new species from the American fossil record. *Scutellastra araya* new species is the oldest and the southernmost record from the Americas. It is also the first patellid recognized from Cenozoic deposits of Chile. *Scutellastra venezuelana* new species is only slightly younger, straddling the early-middle Miocene boundary, it is the first record for the genus in the tropical American Neogene and the Caribbean/western Atlantic identified to species-level. This new record adds the genus *Scutellastra* to the list of Paciphile genera, i.e., genera which, following the closure of the Central American Seaway, disappeared from the Caribbean and became restricted to the Pacific side of their original wider distribution. For full list of Paciphile genera see Landau et al. (2009).

The biogeographic pattern of dispersal of patellid gastropods has been fairly controversial. This is not helped by the very poor fossil record for the group. "*Patella*" *soyaensis* Kase and Shigeta, 1996 from the upper Cretaceous of northern Japan, assigned to *Scutellastra* by Ridgway et al. (1998) is the oldest record for the genus, although the generic placement was questioned by Koufopanou et al. (1999). Together with the records from New Zealand, these new lower and lower-middle Miocene American records are among the oldest undisputed records for the genus. Koufopanou et al. (1999) suggested that *S. mexicana* was a relict from a formerly widespread Tethyan distribution of early *Scutellastra* species (Powell, 1973; Ridgway et al., 1998). They predicted that further *Scutellastra* should be discovered in the Atlantic and Mediterranean regions. These findings support their hypothesis.

Through comparison with the current biogeographic distribution of *Scutellastra* spp., as far as the Chilean record is concerned, it becomes evident that this fossil species is yet another piece of evidence that (1) shallow-water or, as in this case, even intertidal taxa were displaced into bathyal depth of the Navidad Formation (see Finger, 2013), (2) sea surface temperatures along the Chilean coast were significantly higher during the early Miocene than they are today (Nielsen and Glodny, 2009), and (3) discovery of this new species confirms the results of Kiel and Nielsen (2010) that, although the Navidad assemblage is relatively well described, there remain many more species to be discovered. The Venezuelan

record (1) illustrates again the importance of the Cantaure assemblage, as one of the very few tropical Neogene assemblages representing rocky bottom habitats (Vermeij, 2001; Landau et al., 2009; Landau and Vermeij, 2010), and (2) adds to the number of species known to have been distributed throughout the Neogene Gatunian province, but today restricted to the Panamic Pacific.

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