

New species of *Thyasira*, *Mendicula*, and *Axinulus* (Bivalvia, Thyasiroidea) from Sub-Antarctic and Antarctic waters

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Abstract Three new thyasirid species from the Sub-Antarctic and Antarctic waters are described: *Thyasira patagonica*, *Mendicula sudamericana*, and *Axinulus antarcticus*. *T. patagonica* is characterized by its strong com-marginal sculpture, shell as height as length or higher than long, posterior auricle delimited by a deep submarginal sulcus, and a long and sloping straight anterior half of dorsal margin. *M. sudamericana* distinguished by its longer than high shell outline, elongated tooth-like enlargement anterior to beak, gills with only one demibranch at each side, and foot with a marked heel. *A. antarcticus* has a minute, subquadrate shell, hinge with a small swelling anterior to beak, gills with a single demibranch, and the lateral body pouch elongated and almost smooth. The present study provides the first reliable record of thyasirids, with a single demibranch from the Southern Ocean. Moreover, characters for a better definition of *Mendicula* are provided.

Keywords Thyasiridae · Thyasirinae · Axinopsinae · Southern Ocean

Introduction

In a recent revision of the Sub-Antarctic and Antarctic thyasirids, five species were recognized as valid (Zelaya 2009): *Conchoceleus fuegiensis* (Dall, 1890) and

Parathyasira magellanica (Dall, 1901) distributed from Chiloé, Chile to Tierra del Fuego; *Thyasira debilis* (Thiele, 1912), a circumantarctic species inhabiting northward up to Tierra del Fuego; *Parathyasira dearborni* (Nicol, 1965), distributed from the Ross Sea to the Weddell Sea, extending northward up to the southernmost islands of the Scotia Arc; and *Thyasira falklandica* (Smith, 1885) and *Thyasira scotiana* Zelaya, 2009 only known from Malvinas (Falkland) Islands and South Orkney, respectively. Two other species described for the area were regarded as *nomen dubia*: *Loripes pertenuis* Smith, 1881 and *Axinus bongraini* Lamy, 1911.

In the present study, the knowledge of the diversity of thyasirids from the Sub-Antarctic and Antarctic waters is increased by describing three new species in the genera *Thyasira*, *Mendicula*, and *Axinulus*.

Materials and methods

The material studied is housed at the Museo de La Plata, Argentina (MLP); Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”, Argentina (MACN); Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Germany (ZMH); Museum für Naturkunde, Germany (ZMB); the Natural History Museum, Great Britain (NHM); United States National Museum, Smithsonian Institution, USA (USNM); Muséum National d’Histoire Naturelle, France (MNHN); and National Institute of Water and Atmospheric Research, New Zealand (NIWA). The number of specimen/specimens (spm/spms) (i.e. intact animal with softparts) and valve/valves (v/vs) from each sampling station is indicated.

Shell morphology was described and figured using scanning electron microscopy (SEM). The measurements

This contribution is dedicated to the memory of Marta Angélica Szereszowiez (1945–2009).

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provided refer to: L the maximum anteroposterior distance; H the maximum dorsoventral distance perpendicular to L ; W the maximum distance across both valves. The mean values and SD for the W/H ratio and the number of measurements (n) are given. For the anatomical studies, specimens were decalcified by rinsing in 5% formalin with 2% acetic acid, and dissected under a stereoscopic microscope.

For comparative purposes, 35 parcels of *Mendicula ferruginosa* from the North Sea (MNHN without numbers), and the types of *T. falklandica* (two syntypes: NHM 1887.2.9.2791-2), *T. debilis* (holotype: ZMB 63112), *Thyasira scotiana* (holotype: MLP 5566-1), *P. magellanica* (holotype: USNM 122745), *P. dearborni* (holotype: USNM 653099), and *C. fuegiensis* (holotype, USNM 87589) were studied. Comparisons with other species of *Mendicula* and *Axinulus* were based on the previous literature (Payne and Allen 1991; Oliver and Killeen 2002).

Systematics

Thyasiridae Dall, 1901

Thyasira Lamarck, 1818 (ex Leach, MS)

Type Species: *Tellina flexuosa* Montagu, 1803 (by monotypy)

Thyasira patagonica new species

Figures 1, 2, 3a, b

Type locality: 54°51'36.5"S 68°13' 49.6"W, 40 m, Beagle Channel, Tierra del Fuego.

Type material: Holotype (MLP 13115) and five paratypes from the type locality (two paratypes MLP 13116; three paratypes MACN-In 37643).

Other material examined: Beagle Channel: 54°53'S 67°42'W, 66–68 m (24 spms & 16 vs, MLP 13117); 54°57'S 67°01'W, 30–40 m (5 spms & 1 v, MLP 13118); 54°48'S 68°16'W, 27 m (1 spm, MLP 13119); 54°51'58"S 68°10'44"W, 16 m (6 spms, MLP 13120; 5 spms, MACN-In 37644). Magellan Strait: 53°52'S 71°13'W, 25 m (1 spm & 11 vs, MLP 13121); 53°42'02"S 72°20'38"W, 35 m (1 spm, MLP 13122); 53°38'44"S 72°24'32"W, 35 m (1 spm & 3 vs, MLP 13123); 53°38'47"S 72°24'22"W, 50–60 m (5 spms & 1 v, MLP 13124); 53°39'46"S 72°30'18"W, 50 m (1 spm & 3 vs, MLP 13125); 53°39'41"S 72°20'28"W, 100 m (2 spms & 2 vs, MLP 13126); 53°41'15"S 72°20'32"W, 25 m (2 spms & 1 v, MLP 13127).

Known distribution: Magellan region at the Beagle Channel and Strait of Magellan, 16–100 m (Fig. 1).

Fig. 1 Known distribution of *Thyasira patagonica* new species: ⊗: type locality; ●: other material examined

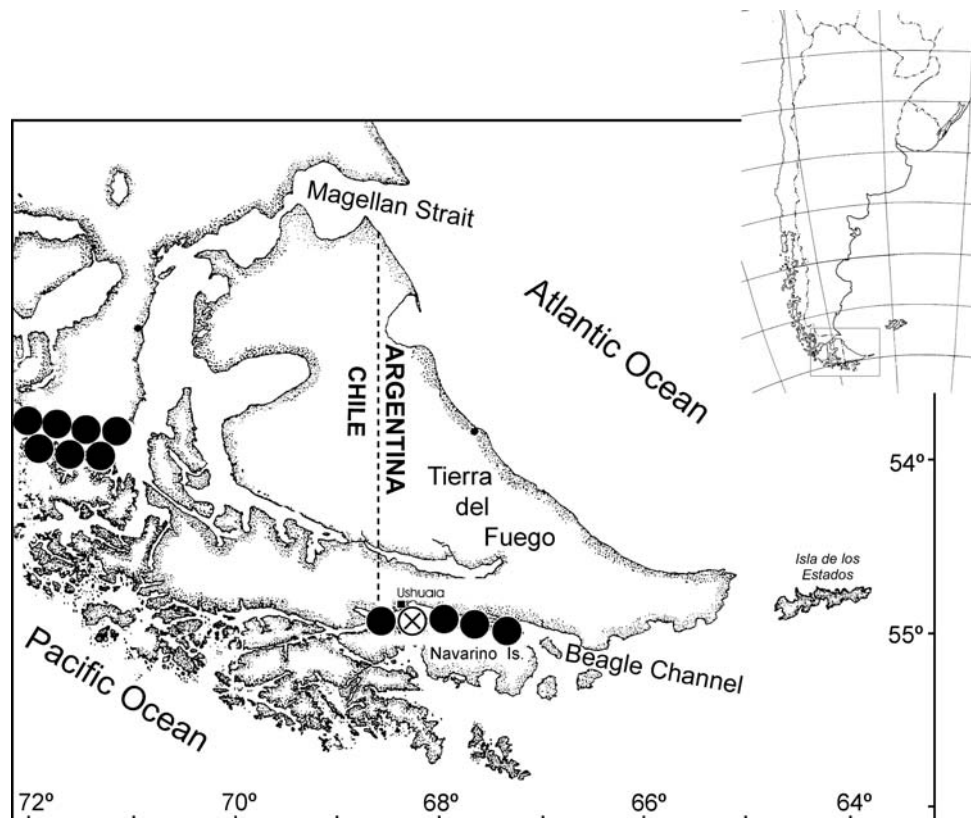
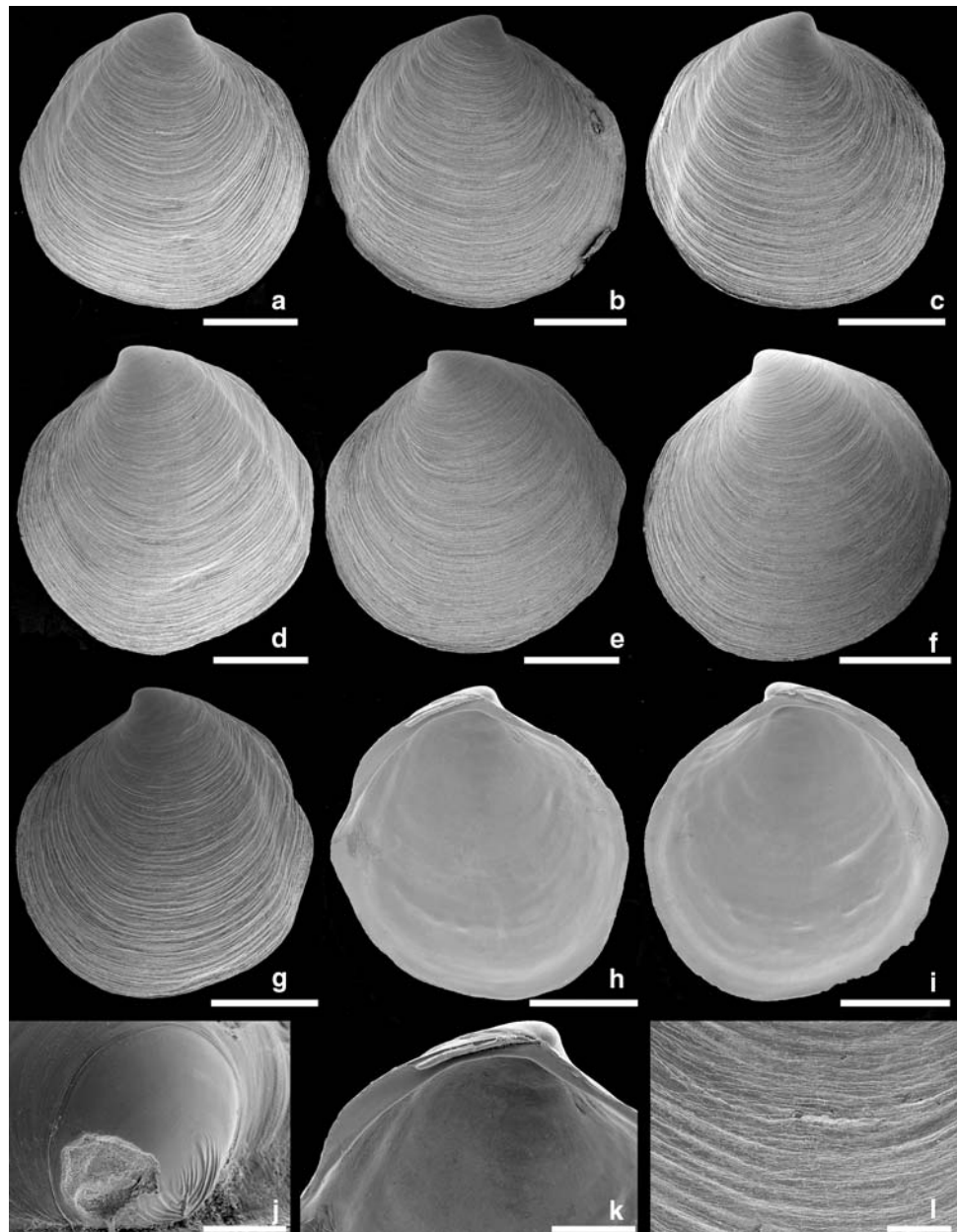


Fig. 2 *Thyasira patagonica* new species. **a, d** Holotype (MLP 13115). **b, e, g, j** Specimens from 54°53'S, 67°42'W, 66–68 m (MLP 13117). **c, f, h, i, k, l** Paratypes (MLP 13116). **a–c** Outer view right valve, **d–g** outer view left valve, **h** inner view left valve, **i** inner view right valve, **j** prodissoconch, **k** hinge plate, **l** detail of shell sculpture. Scale bars **a–i** 1 mm, **j** 50 μ m, **k** 500 μ m, **l** 200 μ m



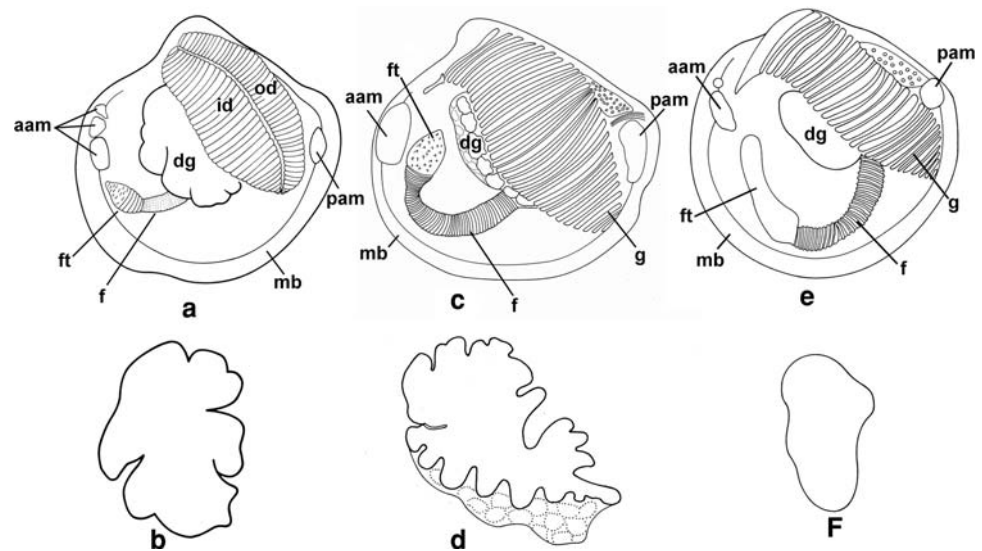
Etymology: The species name refers to Patagonia, the geographical area from where the specimens were collected.

Diagnosis: A higher than long or as height as length *Thyasira*, with long, straight, sloping anterodorsal margin, deep posterior and submarginal sulci, well-differentiated posterior auricle, and strong commarginal ribs.

Description: Shell of medium size (maximum observed $H = 5.5$ mm), somewhat inflated ($W/H = 0.56 \pm 0.02$, $n = 11$), nearly equilateral, white, usually translucent, sometimes chalky. Shell higher than long or as height as length (Fig. 2a–i). Anterior end slightly expanded. Anterodorsal margin long, straight, and sloping, imperceptibly connected with the anterior margin. Anterior margin

widely rounded, sometimes slightly angled. Ventral margin evenly curved or somewhat expanded at the anteroventral angle, particularly in the left valve (Fig. 2d–g). Posterior sulcus well demarcated; posterior margin straight or slightly sinuated (Fig. 2a–i). First posterior fold wide and strong; second posterior fold well developed, but narrower. Submarginal sulcus well marked, producing a narrow marginal sinus (Fig. 2h, i, k). Auricle well differentiated, extending along almost the entire length of submarginal sulcus. Lunule wide, poorly defined. Beaks pointed, subcentrally located, anteriorly directed. Prodissoconch outline ovate, about 135- μ m diameter; initial part sculptured with 15–17 lamellated folds, sometimes bifurcated at the base, symmetrically distributed with respect to the

Fig. 3 Gross anatomy (**a, c, d**) and detail of the digestive gland (**b, d, e**) of *T. patagonica* new species (**a, b**), *M. sudamericana* new species (**c, d**), and *Axinulus antarcticus* new species (**e, f**). *aam* anterior adductor muscle, *dg* digestive gland *f* foot, *ft* foot tip, *id* inner demibranch, *g* gill, *mb* mantle border, *od* outer demibranch, *pam* posterior adductor muscle



central (Fig. 2j). Shell surface with strong and irregular commarginal ribs (Fig. 2l). Anterior and posterior ends frequently covered by sediment. Periostracum translucent forming commarginal folds. Hinge plate narrow, edentulous, with a narrow posterior ligamental groove (Fig. 2h, i, k). Ligament internal, externally visible, representing one-third of the length of submarginal sulcus.

Anatomy: Mantle margin free for about three-fourth of its length, enlarged at the anterior part by development of glandular tissue (Fig. 3a). A single posterior siphonal aperture, the anal, present. Transverse section of anterior adductor muscle elongated showing three well-defined areas in larger specimens; transverse section of posterior adductor muscle ovate, smaller than the anterior one (Fig. 3a). Gills: both inner and outer demibranchs, comprising 35–40 filaments in larger specimens, present (Fig. 3a); outer demibranch about half the height of the inner one. Ascending and descending lamellae of inner demibranch similar in size; descending lamella of outer demibranch one-half length of ascending lamella. Labial palps with three to four prominent sorting ridges. Digestive gland with four main lobes: a large anterior auricular lobe, a ventral lobe posteriorly projected, and two smaller posterior lobes; anterior lobe with a central shallow depression; ventral and posterior lobes partially divided in four rounded portions with rounded subdivisions (Fig. 3b). Foot vermiform, corrugated at the stem and base of the bulbous tip; anterior part of bulbous tip with granules (Fig. 3a); heel not demarcated.

Remarks: *Thyasira patagonica* is similar to *Thyasira scotiana* Zelaya 2009 from the South Orkney, from which it differs by having a deep submarginal sulcus and a

well-defined auricle. That species also has a larger prodissoconch (210 vs. 135 μm diameter), shows a flatter shell outline, and reaches a larger size.

Thyasira falklandica differs from *T. patagonica* by a stronger shell, with more elongate shell outline, the anterior end markedly pointed, the anterior part of dorsal margin flattened distally, and the submarginal sulcus and sinus not differentiated.

Thyasira debilis, another Sub-Antarctic and Antarctic species, strikingly differs from *T. patagonica* by having a longer than high shell outline, with the anterior part of dorsal margin horizontally projected, the beaks displaced posteriorly, posterior area of shell poorly discernible from the central area, and the hinge plate with a tubercle anterior to the beak. Furthermore, *T. debilis* has a smaller and less lobed digestive gland than *T. patagonica*, and a shorter descending lamella of outer demibranch.

Parathyasira magellanica and *P. dearborni* clearly differs from *T. patagonica* by the presence of a deeply incised, with almost vertical margins, submarginal sulcus (lacking auricle); and *Conchocele fuegiensis* by having a larger and rectangular shell outline, with the anterior part of dorsal margin sloping steeply.

Mendicula Iredale 1924

Type species by OD: *Lucina induta* Hedley, 1907 (non von Martens, 1887)

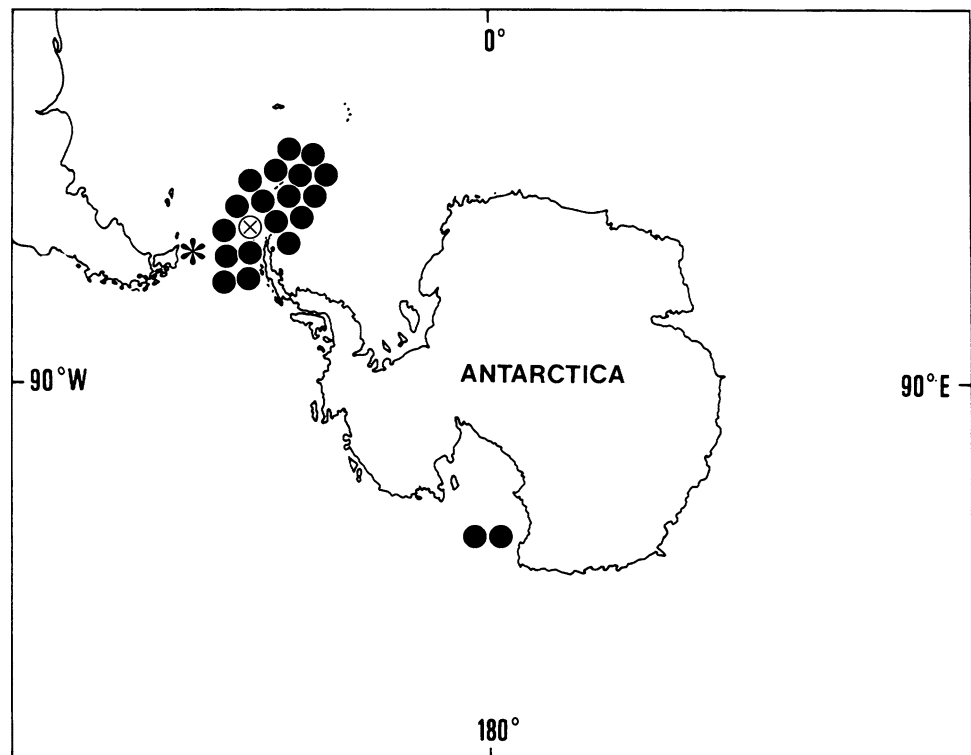
(=*Mendicula memorata* Iredale, 1924, replacement name)

Mendicula sudamericana new species

Figures 3c, d, 4, 5

Type locality: 55°28'48"S 66°03'24"W, Drake Passage, 1,279 m.

Fig. 4 Known distribution of *Axinulus antarcticus* new species (⊗: type locality; ●: other material examined) and *Mendicula sudamericana* new species (*)



Type material: Holotype (ZMB 103644-a) and 25 paratypes from the type locality (3 paratypes MLP 13128; 3 paratypes MACN-In 37645; 19 paratypes ZMB 103644-b).

Known distribution: Only known from the type locality (Fig. 4).

Etymology: The species name derives from South America.

Diagnosis: Shell outline ovate, longer than high, expanded anteriorly. Beaks central to slightly posterior. Hinge plate with elongated tooth-like enlargement anterior to beak, narrow posteriorly. Gills with only one demibranch. Digestive gland multilobed. Heel well marked.

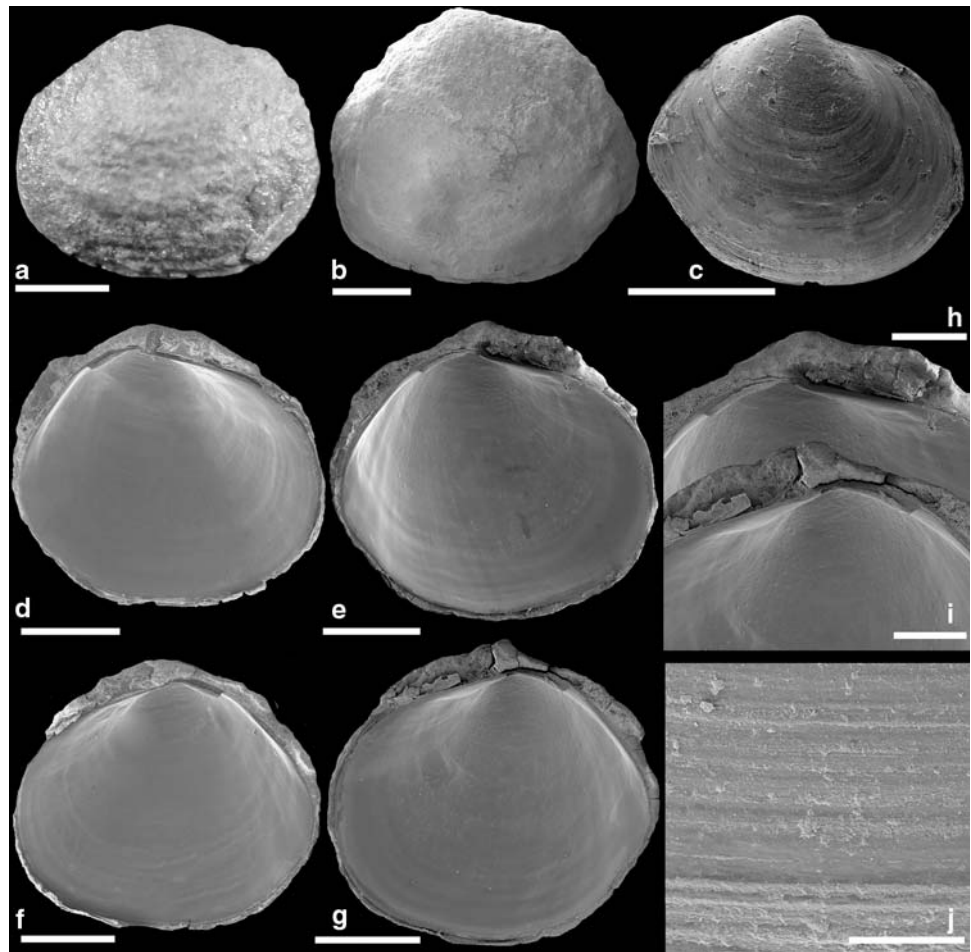
Description: Shell small (maximum observed $H = 3.7$ mm), ovate, longer than high, somewhat inflated ($W/H = 0.60 \pm 0.02$, $n = 10$), delicate, slightly inequilateral. Anterior end expanded, particularly in smaller specimens (Fig. 5a–g). Anterodorsal margin long, straight, sloping gently. Anterior margin rounded, imperceptibly connected with dorsal and ventral margins (Fig. 5d–g). Ventral margin broadly rounded. Posterodorsal margin long, sloping faster than the anterior part, almost straight. Primary sulcus only defined by a long and oblique flattening of the posterior margin; first and second posterior folds not differentiated (Fig. 5a–c). Auricle absent. Lunule short and broad. Beaks low, globose, subcentrally located, anteriorly directed (Fig. 5c). Shell surface whitish, shiny, sculptured with strong, widely separated commarginal

cords (Fig. 5c, j); shell surface usually completely covered by a thick, adherent sediment coat, masking external shell outline (Fig. 5a, b). Inner surface of valves beige, shiny, mimicking outer shell sculpture. Adductor muscle scars white, not raised. Hinge plate narrow, with an elongated tooth-like enlargement anterior to beak (Fig. 5d–i). Ligament long, representing one-fourth the dorsal margin length, strong, completely internal, not visible from the exterior (Fig. 5d–i).

Anatomy: Mantle margin free for about three-fourth of its length, without glandular widening. A small posterior (anal) aperture, present. At this point, the gill axis joins the mantle margin. Section of anterior and posterior adductor muscles rounded, the posterior one smaller (Fig. 3c). Only one demibranch, the inner, present, comprising about 40 filaments in larger specimens (Fig. 3c). Ascending lamellae three-fourth the length of descending one. Labial palp small, smooth. Digestive gland elongated, narrowing posteriorly, markedly lobed at the margins (Fig. 3d). Foot long, slender, and vermiform, corrugated at the stem and base of the tip; distal tip bulbous, with granulated surface (Fig. 3c). Base with a groove. Heel well marked.

Remarks: *M. sudamericana* closely resembles *M. ferruginosa* (Forbes, 1844) (properly figured by Oliver and Killeen 2002: pl. 22, A–C), which differs by having a markedly shorter anterodorsal margin, resulting in a less expanded anterior end, and a more rounded shell outline. In addition, the hinge plate in *M. ferruginosa* is edentulous or

Fig. 5 *Mendicula sudamericana* new species. **a–d, f** Paratypes (ZMB 103644-b). **e, g–i** Holotype (ZMB 103644-a). **a–c** Outer view. **a** Stereoscopic microscope photographs. **b, c** SEM micrographs. **b** Specimen with the outer shell surface crusted. **c** Specimen from which the crusting layer was removed. **d–g** Inner views: **d, e** left valve; **f–g** right valve. **h, i** Hinge plate: **h** left valve; **i** right valve. **j** Detail of shell sculpture. Scale bars **a–g**: 1 mm; **h, i**: 500 μ m; **j**: 100 μ m



has a short and stout anterior tubercle, while in *M. sudamericana* there is a relatively large and elongated tooth-like element. Another difference between these two species seems to be originated in the number of filaments of the gill: Payne and Allen (1991) reported up to 33 filaments in *M. ferruginosa* (maximum size for the species: 4.3 mm *H*), while *M. sudamericana* has 42–44 filaments, even in smaller specimens (2.6–3.0 mm *H*; this study).

Mendicula memorata, another species similar to *M. sudamericana*, differs in having the posterodorsal margin longer and arcuated, and more prominent and anteriorly displaced beaks.

The ovate shell outline, with shallow posterior sinus and straight posterior margin of *M. sudamericana* resembles the Sub-Antarctic and Antarctic *T. debilis*. However, in *M. sudamericana* the anterior part of dorsal margin slopes while in *T. debilis* it is almost horizontal. *T. debilis* has a well-differentiated auricle, which is absent in *M. sudamericana*. Furthermore, these species differs anatomically: *M. sudamericana* has only one (the inner) demibranch, the digestive gland large and multilobed, the foot with heel, and the posterior adductor muscle large and

ovate; instead, *T. debilis* has both (inner and outer) demibranchs, the digestive gland small and only poorly lobed, the food without heel, and the posterior adductor muscle small and rounded.

Axinulus Verrill & Bush, 1898

Type species: *Axinulus brevis* Verrill & Bush, 1898

Axinulus antarcticus new species

Figures 3e, f, 4, 6

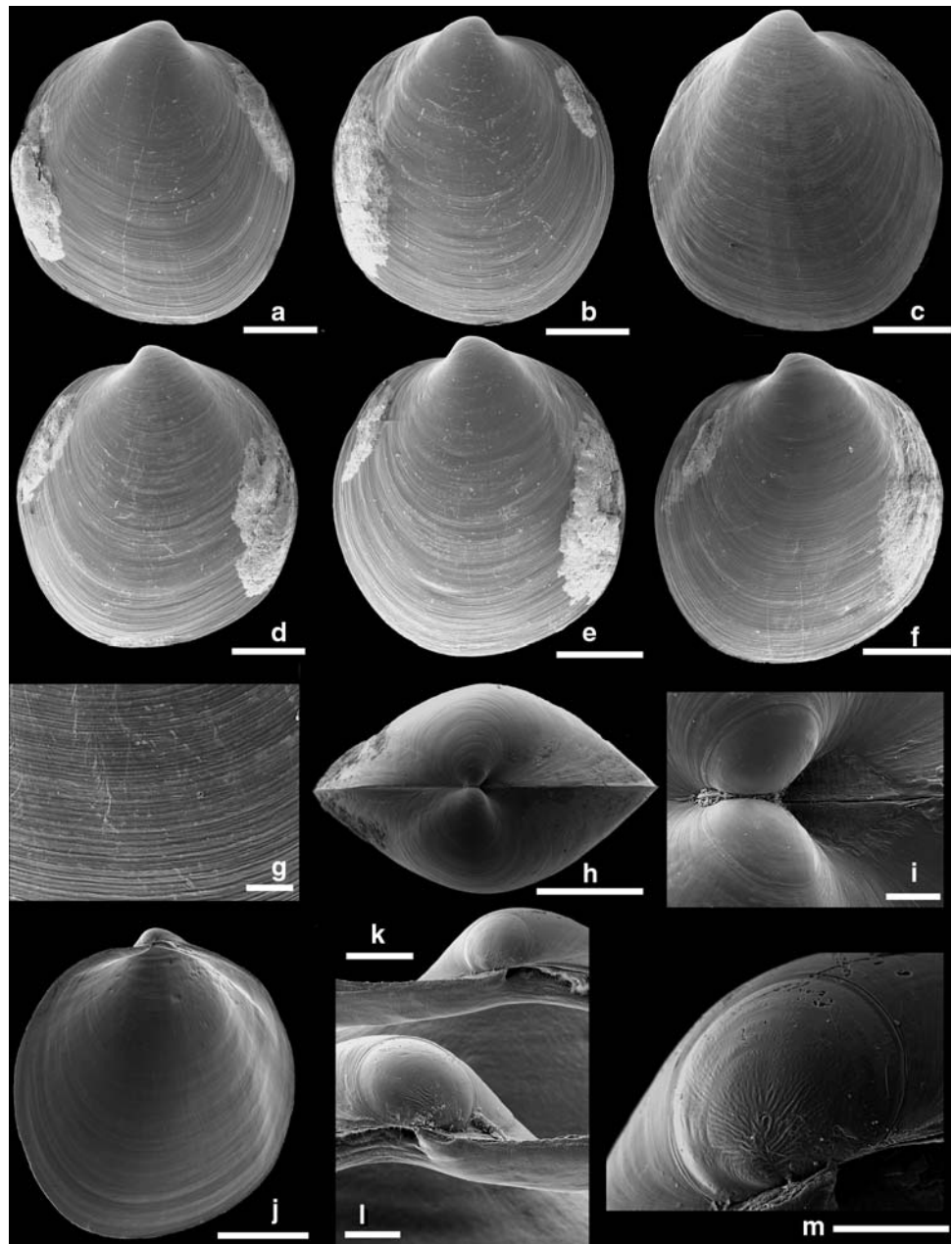
Thyasira bongraini: Mühlenhard-Siegel 1989: 162 (in part) (*non* Lamy, 1910)

Type locality: 61°23'27"S 55°26'49"W, South Shetland Islands 285 m.

Type material: Holotype (MLP 13129) and 16 paratypes from the type locality (MLP 13130, MACN-In 37646, ZMH 51847).

Other material examined: South Orkney Islands: 60°59'11"S 43°27'25"W, 402 m (1 spm, MLP 13131); 61°10'49"S 45°42'43"W, 322 m (42 spms, MLP 13132); 60°47'12"S 45°44'24"W, 237 m (5 spms, ZMH 32997);

Fig. 6 *Axinulus antarcticus* new species. **a, d** Holotype (MLP 13129). **b, c, e–m** Paratypes (MLP 13130). **a–c** Outer view right valve. **d–f** Outer view left valve. **g** Detail of shell sculpture. **h** Dorsal view. **i** Lunule. **j** Inner view right valve. **k–l** Hinge plate. **k** Right valve. **l** Left valve. **m** Prodissoconch. Scale bars **a–f, h**: 500 μ m; **g, k**: 100 μ m; **i, m**: 50 μ m



61°03'12"S 45°24'06"W, 248 m (9 spms, ZMH 32998); 61°07'30"S 46°31'30"W, 289 m (88 spms, ZMH 32999); 60°55'00"S 46°47'48"W, 320 m (38 spms, ZMH 33000); 60°25'06"S 45°39'30"W, 285 m (8 spms, ZMH 33001); 60°23'06"S 46°44'00"W, 280 m (25 spms, ZMH 33003); 60°34'54"S 44°17'00"W, 240 m (2 spms, ZMH 32995); 60°51'18"S 44°12'00"W, 178 m (2 spms, ZMH 32996); 60°23'06"S 46°20'24"W, 265 m (5 spms, ZMH 33002). South Shetland Islands: 61°13'48"S 54°39'12"W, 280 m (35 spms, ZMH 33007; 32 spms, ZMH 33006); 61°18'30"S 54°40'18"W, 370 m (21 spms, ZMH 33008; 11 spms, ZMH 33009); 61°21'48"S 56°00'36"W, 368 m (14 spms, ZMH 33011; 28 spms, ZMH 33010); 61°12'42"S

55°56'24"W, 134 m (2 spms, ZMH 33014; 1 spm, ZMH 33015); 61°09'42"S 56°10'18"W, 290 m (26 spms, ZMH 33012; 1 spm, ZMH 33013); 61°09'00"S 56°07'12"W, 208 m (30 spms, ZMH 33017; 7 spms, ZMH 33016); 61°03'54"S 55°58'48"W, 262 m (25 spms, ZMH 33019); 61°00'18"S 55°13'36"W, 195 m (7 spms, ZMH 33023); 60°50'54"S 55°37'24"W, 242 m (144 spms, ZMH 33021); 61°00'18"S 55°13'36"W, 195 m (1 spm, ZMH 33022); 60°53'36"S 55°46'06"W, 260 m (10 spms, ZMH 33024); 62°49'18"S 60°13'30"W, 850 m (3 spms, ZMH 33025); 62°46'36"S 60°54'48"W, 140 m (16 spms, ZMH 33028); 63°16'48"S 63°44'30"W, 340 m (3 spms, ZMH 33030; 23 spms, ZMH 33029); 62°09'36"S 58°21'00"W, 485 m

(1 spm, ZMH 32992); 62°05'18"S 57°39'00"W, 265 m (1 spm, ZMH 32990; 11 spms, ZMH 32989); 61°01'42"S 55°02'24"W, 185 m (8 spms, ZMH 33036); 60°56'24"S 55°40'00"W, 112 m (1 spm, ZMH 33037); 63°18'00"S 63°42'48"W, 300 m (10 spms, ZMH 33042; 9 spms, ZMH 33043); 60°55'00"S 55°23'48"W, 227 m (1 spm, ZMH 33045); 62°49'30"S 60°57'30"W, 184 m (9 spms, ZMH 33038; 5 spms, ZMH 33038; 24 spms, ZMH 33038; 11 spms, ZMH 33038); 62°49'30"S 60°57'30"W, 184 m (49 spms, ZMH 33046). Gerlache Strait: 63°43'00"S 61°13'36"W, 180 m (4 spms, ZMH 33026); 63°43'00"S 61°13'36"W, 180 m (3 spms, ZMH 33027). Antarctic Peninsula: 65°23'36"S 66°10'06"W, 420 m (6 spms, ZMH 33031); 65°54'54"S 66°52'18"W, 175 m (36 spms, ZMH 33032; 17 spms, ZMH 33033); 66°32'06"S 68°30'06"W, 500 m (4 spms, ZMH 33034); 62°51'00"S 56°00'00"W, 133 m (18 spms, ZMH 32988; 1 spm, ZMH 32955; 5 spms, ZMH 278; 24 spms, ZMH 33004); 62°59'00"S 57°05'00"W, 68 m (four spms, ZMH 32991); 63°11'30"S 58°47'00"W, 93 m (3 spms, ZMH 32993; 3 spms, ZMH 33005); 66°39'18"S 69°23'36"W, 344 m (3 spms, ZMH 33044). Ross Sea: 74° 30'S 179° 40'E, 238–301 m (1 spm and 1 v, NIWA 48769); 74°49'S 164°18'W, 364 m (1 spm, MLP 13133).

Known distribution: Antarctic waters, from the Ross Sea to South Orkneys, 68–850 m (Fig. 4).

Etymology: The species name refers to the geographic range inhabited for the species.

Diagnosis: Shell minute, subquadrate, anterodorsal margin short. Lunule short and broad. Hinge with a small swelling anterior to beak. Gill with single demibranch. Lateral body pouch elongated, almost smooth.

Description: Shell minute (maximum observed $H = 2.9$ mm), nearly equilateral, subquadrate, somewhat inflated ($W/H = 0.58 \pm 0.02$, $n = 10$), delicate, translucent (Fig. 6a–f, h, j). Anterior end slightly expanded, higher than the posterior one (Fig. 6a–f). Anterior part of dorsal margin very short, horizontal, and straight. Posterodorsal margin moderately long, moderately sloping, straight. Anterior margin widely curved, almost vertical, sometimes forming a weak angle in the middle, imperceptibly connected with dorsal and ventral margins. Ventral margin slightly arcuate, projected at the anteroventral angle, particularly in the left valve (Fig. 6a–f). Posterior sulcus weak, originating straight posterior margin (Fig. 6a–f, j). First and second posterior folds low and rounded. Auricle narrow, but well differentiated. Lunule short and wide (Fig. 6i). Beaks low, globose, anteriorly projected. Prodissoconch ovate, of about 115 μ m diameter, sculptured with numerous, sometimes bifurcated folds, radiating from a central axis (Fig. 6m). Shell surface whitish, glossy,

sculptured with densely packed commarginal striae; inter-spaces narrow (Fig. 6g). Periostracum thin, translucent. Anterior and posterior ends frequently covered by sediments. Hinge plate narrow, edentulous, with a small swelling, below beaks (Fig. 6l, m). Ligament occupying one-third the length of posterior auricle, internal, but exteriorly visible (Fig. 6j).

Anatomy: Mantle margin free for about three-fourth of its length, fused posteriorly forming a small (anal) aperture. At this point, the gill axes join the mantle margin. Section of anterior adductor muscle elongated, formed by two differentiated areas; section of posterior adductor muscle rounded, one-third the size of anterior one (Fig. 3d). Only one demibranch, the inner, present, comprising 22–25 filaments in larger specimens (Fig. 3d). Ascending and descending lamellae of similar size. Descending lamellae of left and right demibranchs fused posteriorly. Labial palps minute, smooth. Digestive gland small, inflated, ovate in outline, with the anterior margin slightly undulated but not lobulated (Fig. 3e). Foot long, slender, and vermiform at the stem, with elongated tip (Fig. 3d). Heel not present.

Remarks: *A. antarcticus* closely resembles *Axinulus croulinensis* (Jeffreys, 1847), particularly in general shell outline and sculpture; however, the posterior part of dorsal margin is straighter in *A. antarcticus*. The digestive gland has no lobes in *A. antarcticus* being present in *A. croulinensis*.

When compared with *A. brevis*, *A. antarcticus* has a horizontal anterodorsal margin, while in *A. brevis* slopes. In *A. brevis*, the primary sulcus generates a small indentation in the posterior margin, while in *A. antarcticus* the posterior margin is straight. *A. brevis* does not have well-defined lunule and shell surface is smooth (Payne and Allen 1991), while *A. antarcticus* has well-differentiated lunule and commarginal sculpture.

Axinulus allenii Carozza, 1981 clearly differs from *A. antarcticus* by having a more projected anterior end, a longer anterior part of dorsal margin, and the posterior area more flattened.

Axinulus antarcticus resembles the sympatric *T. debilis*. However, *A. antarcticus* has subquadrate shell outline, subcentrally located beaks, a single demibranch at each side, and not lobed digestive glands, *T. debilis* has a subovate shell outline, posteriorly located beaks, anterior end projected, two demibranchs, and lobed digestive glands.

The re-examination of the material previously studied by Mühlenhard-Siegel (1989) housed at the ZMH reveals that some of the specimens she reported under *T. bongraini* actually belong to *A. antarcticus*.

Discussion

On the generic and suprageneric assignment of the species described

The generic assignment of thyasirid species is frequently problematic, resulting in a history of confused nomenclature (Mikkelsen et al. 2007). This fact originates in the absence of clear diagnostic characters. Furthermore, the anatomy of some type species is still unknown. Thus, several species were described or placed under tentative genera (e.g. Payne and Allen 1991; Oliver and Sellanes 2005; Oliver and Levin 2006). Several studies contributed to define the diagnostic characters for *Thyasira* (e.g. Payne and Allen 1991; Oliver and Killeen 2002). Although the current definition probably does not encompass the total range of variability (i.e. some species still remain as *Thyasira* s.l.), *T. patagonica* shows all the characters recognized as diagnostic for *Thyasira* s.s., namely, an ovate shell outline with bisulcate posterior area, both inner and outer demibranchs, and the foot having the distal end divided in two parts and heel absent.

Mendicula and *Axinulus* are poorly defined. *Mendicula* is characterized by having a higher than long or as high as long shell outline; the hinge plate with cardinal tubercles present and lateral teeth absent; the escutcheon with simple margin; the lunule margin rounded; the adductor scars “normal” (not raised); the digestive gland slightly lobed; and the foot with heel (Oliver and Levin 2006). In addition, in this genus the outer shell surface appears covered by a thick adherent sediment coat. *M. sudamericana* shows the above-mentioned set of characters, except the shell outline which is longer than high. This condition was only found in *Leptaxinus* Verrill and Bush, 1898 (Oliver and Levin 2006) a genus that strikingly differs from *Mendicula* by having lateral teeth, and smaller and simple digestive gland. The distinctive shell outline of *M. sudamerica* is here regarded as part of the intrageneric variability for *Mendicula*.

Axinulus was diagnosed as having: a higher than long shell outline, with simple escutcheon margin, rounded lunule margin, adductor scars “normal” (not raised), lateral teeth absent, digestive gland simple, and foot without heel (Oliver and Levin 2006). Although cardinal tubercles are absent in the type species (Oliver and Levin 2006) in other species of the genus, small swellings or tubercles may be present below beaks (Scott 1986; Payne and Allen 1991). *A. antarcticus* share all the above-mentioned characters.

Both *Mendicula* and *Axinulus* were regarded as either subgenera of *Thyasira* (Payne and Allen 1991) or full genera (Oliver and Killeen 2002; Dufour 2005). Bernard (1983) proposed a new subfamily, Axinopsidinae, to include *Axinulus*, *Axinopsida* Keen and Chavan in Chavan, 1951, and *Adontorhina* Berry, 1947. According to the

author, the diagnostic characters of the subfamily are the presence of tubercles or pseudo dentition in hinge, a well-developed lunule, the absence of hypertrophied tip at the foot and the lacking of shell folds or sulci. Bernard’s proposal was adopted by Coan et al. (2000), who also included *Mendicula* and *Leptaxinus* in the subfamily. The distinction of axinopsidids and thyasiridids was “supported” (although weakly), in a molecular phylogeny based on the 18S rRNA and 28S rRNA (Taylor et al. 2007), but not in a phylogeny based on cytochrome *c* oxidase I (Mikkelsen et al. 2007). Unfortunately, none of the above-mentioned studies included members of *Axinopsida*, the type genus, which strikingly differs from *Axinulus*, *Mendicula*, and *Adontorhina* both in number of demibranchs (2 vs. 1, respectively) and gill morphology (gills types 1 vs. 2, respectively) (Dufour 2005). From the previous, it is clear that the status of *Axinulus* and *Mendicula*, and their sub-familiar assignment is still uncertain.

Relevancy of the new findings

In the present study, three new thyasirid species from the Sub-Antarctic and Antarctic waters are described. These new findings increase the current knowledge on the diversity of the genus *Thyasira* (thus far represented in the area by three species: *T. falklandica*, *T. debilis*, and *T. scotiana* from South Orkney); provide the first reliable record of *Mendicula* for the Sub-Antarctic waters; and the first record of *Axinulus* for the Southern Ocean. The new species of *Mendicula* and *Axinulus* are the first record of thyasirids with a single demibranch at the Sub-Antarctic and Antarctic waters.

To date, only two species have been regarded indubitably as members of *Mendicula*: *M. induta*, a species from the Australian waters, and *M. ferruginosa*, a species regarded as widespread: described from the Mediterranean, and reported in the Northern hemisphere as occurring at both the Pacific (Aleutian Islands and Bering Sea) and Atlantic Oceans (along American, European, and African coasts), with some additional records for the South Atlantic Ocean (Angola, Cape, and Argentine Basis) (Payne and Allen 1991). However, some records of “*M. ferruginosa*” from the North Pacific Ocean (e.g. Coan et al. (2000); Kamenev and Nadochy (2000)) are based on the specimens having a strong posterior enlargement in the hinge plate (a “lateral tooth”). This hinge plate morphology does not correspond with that present in *M. ferruginosa* (properly described and figured by Oliver and Killeen 2002) nor was reported for the genus *Mendicula*. Instead, this condition appears in *Odontogena* Cowan, 1964, which consequently may be revalidated as a distinct valid taxon (it was previously regarded as a synonym of *Mendicula* by Coan et al. (2000)). Clarke (1961) also assigned to

M. ferruginosa (as *Thyasira*) specimens from 55°29'S 37°57'W, Scotia Sea, 3,759 m. However, these specimens were not found at the Museum of Comparative Zoology where they should be housed (Baldinger A., pers. comm., May 2008). The uncertain identity of these specimens was also pointed out by Payne and Allen (1991: pp. 535).

Only three species are currently regarded as certainly belonging to *Axinulus*: *A. alleni*, from the Mediterranean Sea and the Angola and Cape Basins; and *A. brevis* and *A. croulinensis*, from the north Atlantic Ocean (at the American, European, and African coasts), and the south Atlantic Ocean (at Angola, Cape, and Argentine Basins, with the southernmost record at ~37°S) (Payne and Allen 1991). Consequently, the new species described here represents the southernmost record for the genus.

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