

On two abyssal species of Scaphandridae G.O. Sars, 1878 (Gastropoda: Cephalaspidea) from the eastern Pacific

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ABSTRACT

Scaphander interruptus Dall, 1890 is a widespread, deep-water eastern Pacific species whose range is extended to California. The anatomical features of this species are similar to those of other members of *Scaphander* de Monfort, 1810, including the presence of a single lateral tooth on each half-row of the radula and the morphology of the penial complex. Another eastern Pacific species, *S. cylindrellus* Dall, 1908 is reassigned to the genus *Cylichnium* Dall, 1908 because of the presence of a multidenticulate radula, a female copulatory organ and its shell morphology.

Additional Keywords: *Scaphander*, *Cylichnium*, Panamic, deep sea, redescrptions.

INTRODUCTION

The family Scaphandridae, recently resurrected by Malaquias et al. (2009), is poorly known in the eastern Pacific, particularly in the deep sea. Two species are problematic and in need of revision. A review of the literature and material collected from several localities has raised doubts about the taxonomic placement of *Scaphader cylindrellus* Dall, 1908. Newly collected material of *Scaphander interruptus* Dall, 1890 showed a previously unrecorded variability in shell morphology and has allowed for anatomical studies. The present paper deals with these two species and attempts to place them taxonomically in light of recent studies on the systematics of Scaphandridae (Valdés 2008; Malaquias et al. 2009; Eilertsen and Malaquias, 2013a). Additionally, new information on their morphological variability, range, and internal anatomy is provided.

MATERIALS AND METHODS

The material examined is deposited at the Natural History Museum of Los Angeles County (LACM), the Department of Invertebrate Zoology and Geology at the California

Academy of Sciences, San Francisco (CASIZ), the Benthic Invertebrate Collection of the Scripps Institution of Oceanography (SIO), and the National Museum of Natural History (USNM). The material is noted here as “shell” for empty shells and “specimen” for complete specimens including shell and soft parts. The material was unsuitable for molecular work.

The specimens were dissected for examination of the reproductive and digestive system anatomy. The reproductive anatomy was examined under a Nikon SMZ-100 dissecting microscope and drawn with the aid of a *camera lucida*. The gizzard plates and radulae were isolated from surrounding tissue by submerging them in NaOH 10%, then rinsed in water, dried and examined under a Cambridge 360 Scanning Electron Microscope at the University of Southern California Center for Electron Microscopy and Microanalysis.

SYSTEMATICS

Genus *Scaphander* de Monfort, 1810

Type Species: *Bulla lignaria* Linnaeus, 1758 (Mediterranean and northeastern Atlantic), by original designation.

Scaphander de Montfort, 1808–10 [1810]: 334.

Diagnosis: Shell external, oblong, tapered posteriorly, with the spire concealed by callus and covered with a thin periostracum. Microsculpture consisting of spiral lines or series of pits. Aperture as long as the shell, narrow above, much wider below. Radula with single, hamate lateral teeth. Rachidian teeth generally absent, a vestigial rachidian tooth present in several species. Reproductive system monaulic. Penis unarmed, connected to the prostate by a long duct. Gizzard with two large, paired kidney-shape to sub-triangular plates and an unpaired thin, elongate plate.

Remarks: *Scaphander* is a genus of predominantly deep-sea cephalaspidean sea slugs, with species distributed

worldwide from the Arctic to the Antarctic (Eilertsen and Malaquias, 2013a). The shell morphology and anatomy of *S. lignarius* (Linnaeus, 1758), the type species, have been summarized and illustrated by Thompson (1976) and by Eilertsen and Malaquias (2013a). Eilertsen and Malaquias (2013a) provided the first molecular phylogeny for this group including Atlantic and Western Pacific species, and Eilertsen and Malaquias (2013b) examined the digestive system morphology and diet of this group.

***Scaphander interruptus* Dall, 1890 (Figures 1–10)**

Scaphander interruptus Dall, 1890: 297, pl. 12, fig. 12.
Dall, 1908: 239.

Shell Morphology: Shell up to 22 mm in length and 11 mm in width (LACM 73-109), involute, oval (Figure 1). Aperture as long as the shell, wider anteriorly and constricted posteriorly. Lip rising slightly above the apex (Figures 1, 6, 7). The sculpture consists of spiral lines of oval pits, with alternating rows of wider and narrower pits (Figure 2).

Digestive System: The buccal mass is small and connects dorsally with the esophagus and the salivary glands (Figure 10). At its posterior end two strong retractor muscles attach. The esophagus opens into a large muscular gizzard, which contains three gizzard plates. Two of the gizzard plates are large and oval (Figure 3), whereas the third one is elongate (Figure 4). The radular formula is $12 \times 1.0.1$ ($n = 1$). Lateral teeth are hamate, with a number of small denticles (Figure 5).

Reproductive System: The reproductive system is monaulic, but the female parts of the reproductive system were not seen. The penial complex consists of a bulbous, muscular penis and an oval prostate connected to the penis by an elongate duct (Figure 9).

Material Examined: CALIFORNIA (all specimens collected by K. L. Smith, R/V NEW HORIZON), approximately 226 km west of Point Arguello, Santa Barbara County (34°44' N, 123°07' W), 4100 m depth, 1 fragment of shell, 22 July 1991 (LACM 91-130.2); (34°43' N, 123°07' W), 4100 m depth, 1 broken shell, 1 August 1991 (LACM 91-131.3); (34°45' N, 123°04' W), 4100 m depth, 1 specimen, dissected, 21 October 1991 (LACM 91-133.3); (34°44' N, 123°12' W), 4100 m depth, 1 fragment of shell, 4 November 1993 (LACM 93-74.1); (34°42' N, 123°08' W), 4100 m depth, 1 fragment of shell, 7 November 1993 (LACM 93-75.2); (34°43' N, 123°14' W), 4100 m depth, 1 shell, 12 October 1996 (LACM 1996-85.3). COSTA RICA, 14 miles from Punta Guiones (9°45'18" N, 85°52'24" W), 12 May 1973, 1866 m depth, 1 shell, leg. R/V VELERO IV (stn. 18932) (LACM 73-109). PERU, West of Isla Lobos de Tierra (6°26' S, 81°05' W), 1025 m depth, 1 shell, leg. McLean and Del Solar, 23 January 1974 (LACM 74-18). CHILE:

R/V USS ALBATROSS Expedition, station 2788, west coast of Chile (45°35' S, 75°55' W), 1050 fathoms (1920.24 m), 3 shells, 11 February 1888 (SYNTYPES, USNM 97075).

Geographic Range: This species was originally described from Chile. It is otherwise known from southern California, Baja California, Costa Rica, and Peru (present paper).

Remarks: *Scaphander interruptus* Dall, 1890 is the only species of the genus known from the eastern Pacific. Examination of the type series (Figure 6) confirms the identity of the material here studied as *S. interruptus*; the anatomical examinations conducted confirm the placement of this species in *Scaphander*. The radula, with a single lateral tooth, the presence of three gizzard plates, two of them larger, and the morphology of the penial complex (with a simple unarmed penis and a single unmodified prostate), are characteristics of this genus (Gosliner, 1994; Eilertsen and Malaquias, 2013a).

Keen (1971, fig. 2256) assigned a shell collected off Bahía Magdalena, Baja California, Mexico to *S. interruptus*. Examination of this specimen (Figure 8; CASIZ 156489) revealed some differences in shell morphology and sculpture with the other specimens of *S. interruptus* here studied. In typical specimens of *S. interruptus* the lip rises over the spire and the sculpture is composed of clearly visible oval pits, whereas the specimen from Bahía Magdalena has a shorter lip and the sculpture is not well marked. The specimen from Bahía Magdalena is here regarded as indeterminate.

Genus *Cylichnium* Dall, 1908

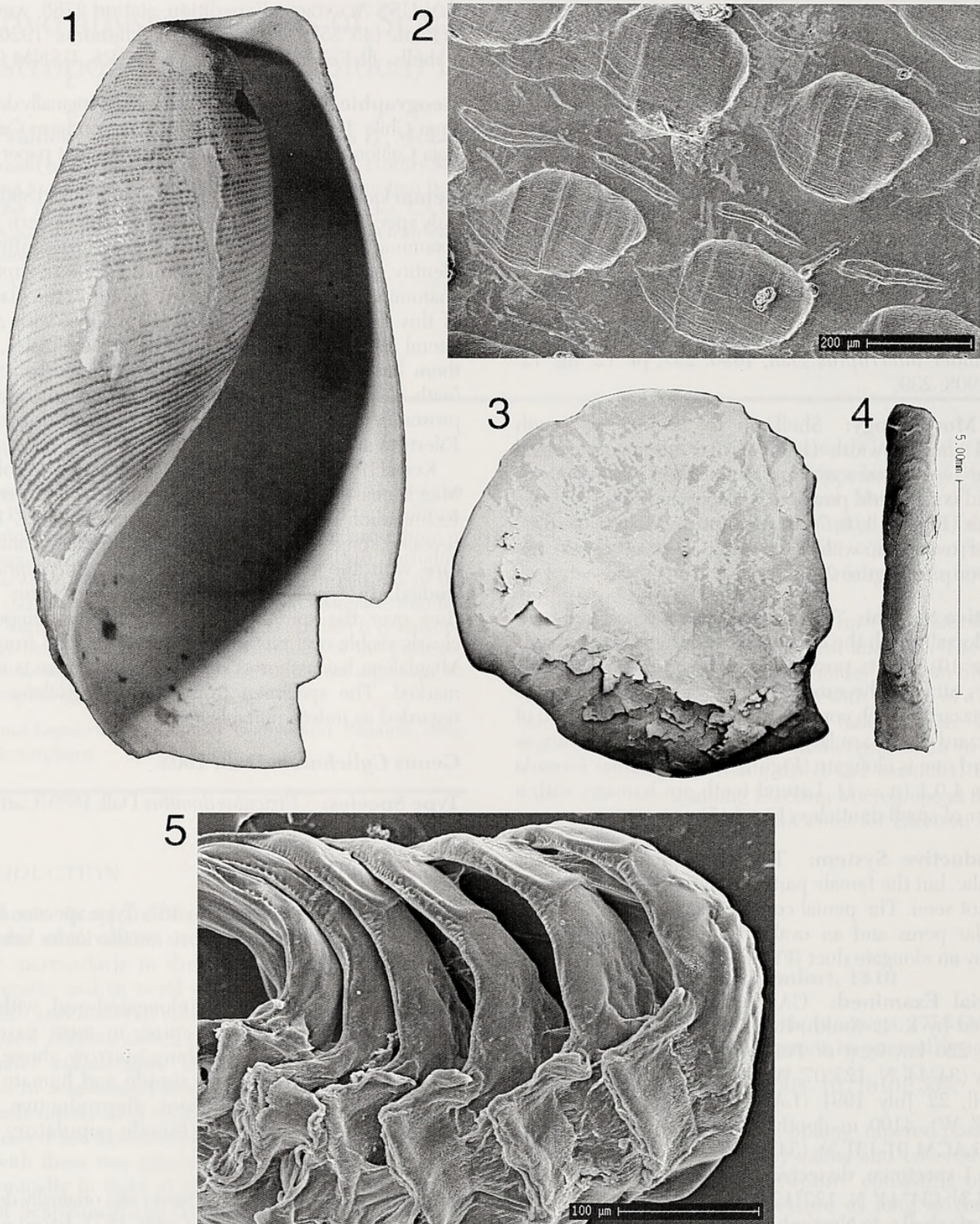
Type Species: *Utriculo domitus* Dall, 1889 (Caribbean), by original designation.

Cylichnium Dall, 1908: 242.

Volvulopsis Schepman, 1913: 463. Type species, by original designation: *Volvulopsis ancillarioides* Schepman, 1913 (Indonesia).

Diagnosis: Shell external, elongated-oval, with somewhat elevated or covered spire, in most cases with fine spiral lines. Aperture long, narrow above, wider below. Radula with several simple and hamate lateral teeth. Rachidian teeth absent. Reproductive system monaulic, with a complex female copulatory organ. Penis unarmed.

Remarks: The genus *Cylichnium* was originally described as a subgenus of *Cylichnella* Gabb, 1873, based on three species, *Utriculo domitus* Dall, 1889 (the type species by original designation), from Guadeloupe, *Cylichnella pizarro* Dall, 1908 from Panama, and *Cylichnella atahualpa* Dall, 1908 also from Panama (Dall, 1908). Subsequently, several other species were assigned to this genus: *C. matsumotoi* Habe, 1955 (from Japan), *C. waldae* Bouchet, 1975 (from the Atlantic), and *C. oliviformis* (Watson, 1883). Bouchet (1975) transferred *Aceras africana* Fischer in Locard, 1897 and its synonym *Aceras*



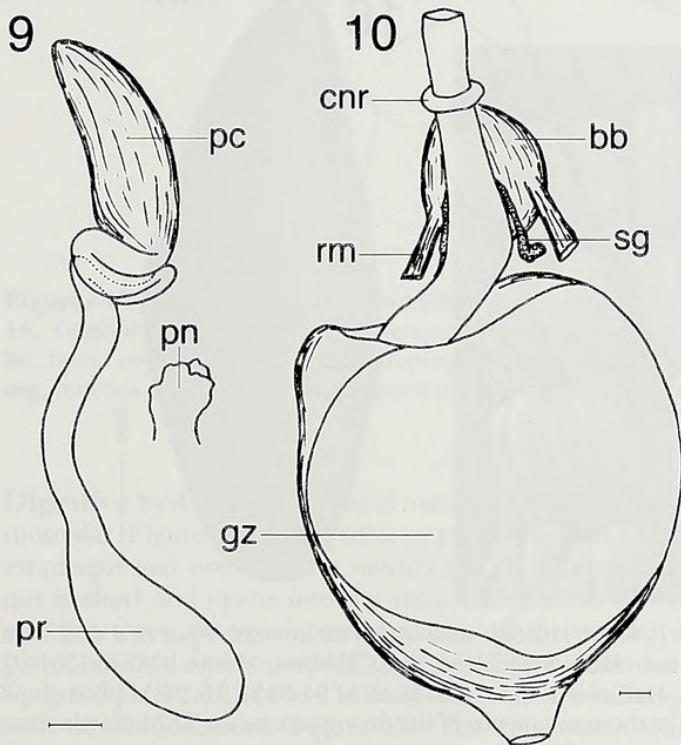
Figures 1–5. *Scaphander interruptus* Dall, 1890. **1.** Costa Rica (LACM 73-109), shell length 24 mm. **2.** SEM photograph of the shell microsculpture (LACM 91-133.3). **3, 4.** SEM photographs of a gizzard plates (LACM 91-133.3). **5.** Radular teeth (LACM 91-133.3).

fischeri Locard, 1897 to *Cylichnium*, based on anatomical examination of newly collected specimens. A review of the original description of *Cylichnium* shows that the type species (*U. domitus*) has a short, conical shell, with an aperture about 4/5 of the shell length and a pointed apex,

so it appears to be a juvenile specimen. On the other hand, the two Panamanian species *C. pizarro* and *C. atahualpa* are much smaller than other *Cylichnium* and are most likely members of the genus *Cylichna* Lovén, 1846, as already suggested by Keen (1971). Valdés



Figures 6–8. *Scaphander interruptus* Dall, 1890. **6.** Syntype (USNM 97075). **7.** Specimen from Isla Lobos de Tiera, Peru (LACM 74-18), shell length 15 mm. **8.** Indeterminable specimen assigned to *S. interruptus* by Keen (1971), collected off Bahía Magdalena, Baja California, Mexico (CASIZ 156489), shell length 12 mm.



Figures 9–10. *Scaphander interruptus* Dall, 1890, anatomy (LACM 91-133.3). **9.** Penial complex; scale bar = 1 mm. **10.** Anterior portion of the digestive system; scale bar = 1 mm. Abbreviations: **bb**, buccal bulb; **cnr**, circumesophageal nerve ring; **gz**, gizzard; **pc**, penal capsule; **pn**, penis; **pr**, prostate; **rm**, retractor muscle; **sg**, salivary gland.

(2008) described two additional species of *Cylichnium*, *C. mucronatum* Valdés, 2008 and *C. nanum* Valdés, 2008 from deep waters in the tropical Indo-Pacific, and synonymized *C. matsumotoi* Habe, 1955 and *C. sumatrense* Thiele, 1925 with *C. ancillarioides*.

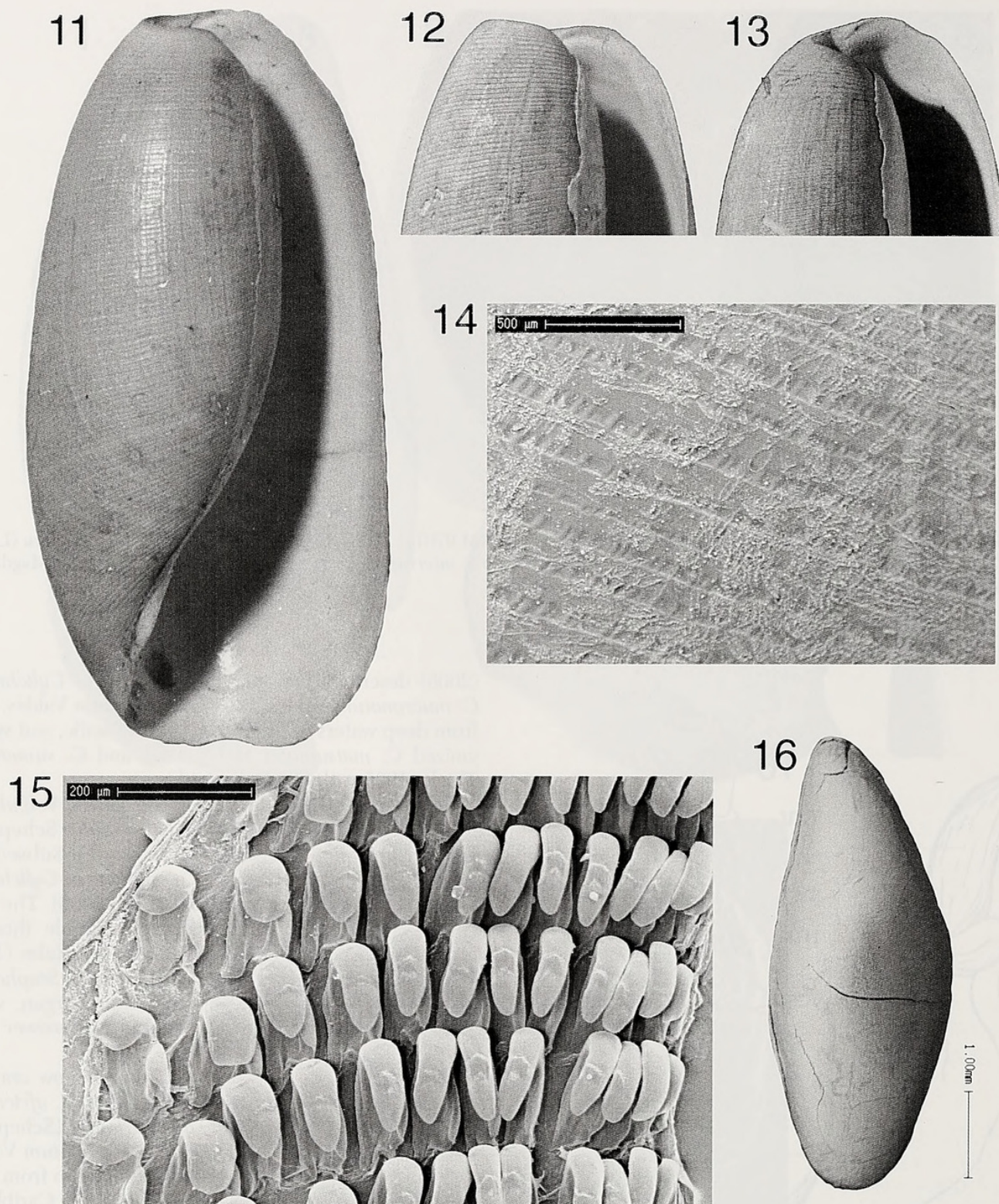
Schepman (1913) described the genus *Volvulopsis* based on the single species *V. ancillarioides* Schepman, 1913, from Indonesia (959-1301 m depth). Subsequent authors regarded *Volvulopsis* as a synonym of *Cylichnium* Dall, 1908 (see Bouchet, 1975; Valdés, 2008). The shell characteristics of *V. ancillarioides* resemble those of adult species assigned to *Cylichnium* by Habe (1955) and Bouchet (1975). *Cylichnium* differs from *Scaphander* in the presence of a female copulatory organ, wider radula with several lateral teeth and a narrower shell (Valdés, 2008).

Following these revisions, *Cylichnium* now contains six valid species [*C. domitus* (Dall, 1889), *C. africanum* (Fischer in Locard, 1897), *C. ancillarioides* (Schepman, 1913), *C. waldae* Bouchet, 1975, *C. mucronatum* Valdés, 2008 and *C. nanum* Valdés, 2008], all of them from deep waters in the tropical Indo-Pacific, Japan, the Caribbean, and the eastern Atlantic.

***Cylichnium cylindrellum* (Dall, 1908) (Figures 11–18)**

Scaphander cylindrellus Dall, 1908: 239, pl. 8. fig. 1; Keen, 1971: 800, fig. 2255.

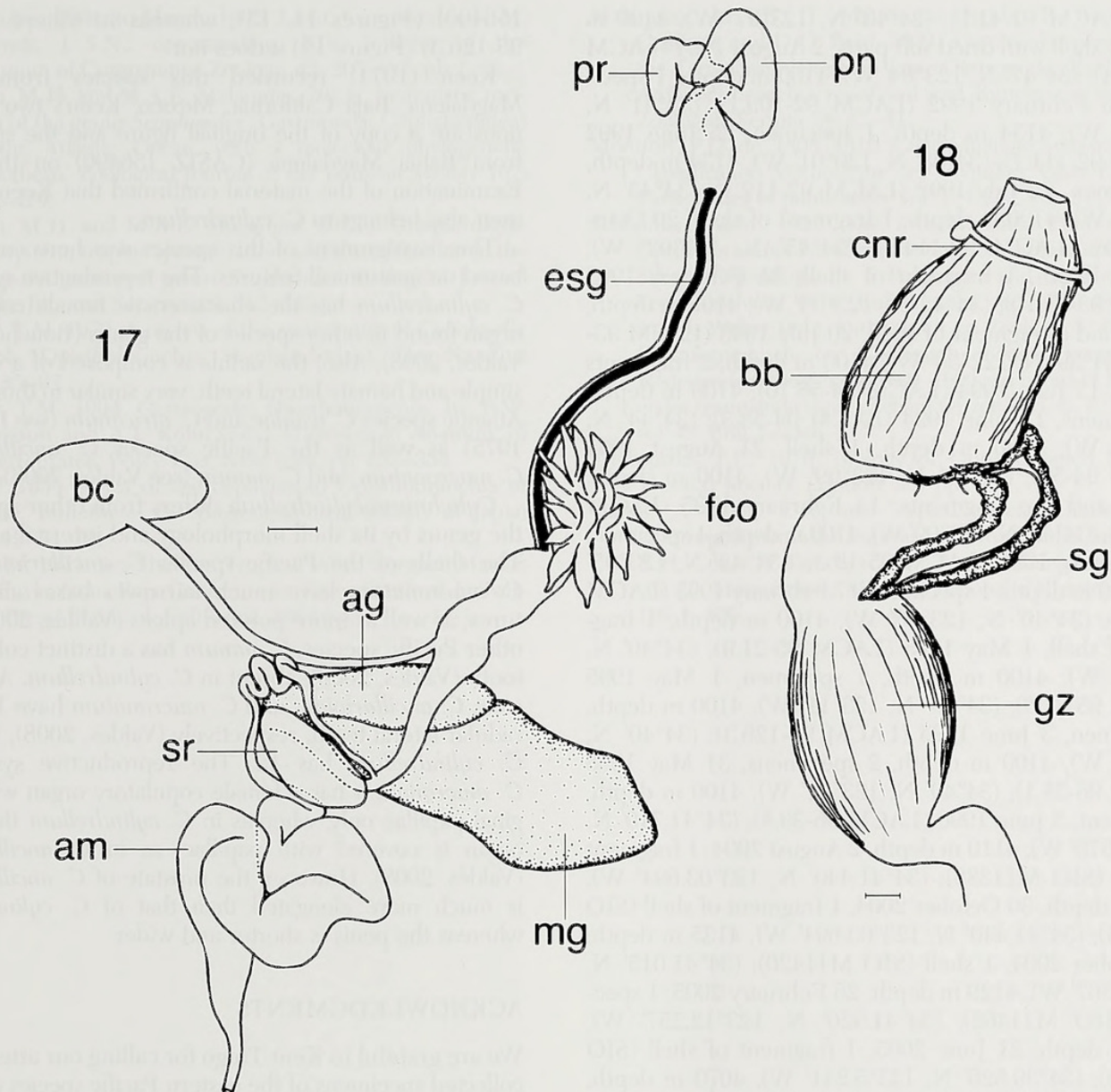
Shell Morphology: Shell 33 mm in length and 16 mm in diameter (holotype), somewhat cylindrical, with nearly parallel sides (Figure 11). Aperture as long as the shell,



Figures 11–16. *Cylichnium cylindrellum* (Dall, 1908). **11.** Holotype (USNM 110563), shell length 29 mm. **12.** Apex of a shell from Santa Barbara County, California (LACM 95-126.3). **13.** Apex of a shell from Bahía Magdalena, Baja California, Mexico (CASIZ 156490). **14.** SEM photograph of the shell microsculpture (LACM 94-58.3). **15.** Half-row of the radula (LACM 94-58.3). **16.** SEM photograph of a gizzard plate (LACM 94-58.3), showing several fractures produced as the consequence of the drying process for SEM examination.

wider anteriorly and constricted posteriorly. Apex sunken, convex. Lip raising above the apex in some specimens (Figures 11, 13), whereas in others the lip is lower than the apex (Figure 12). Sculpture with fine spiral grooves

crossed by microscopic axial lines only present in the spiral grooves (Figure 14). All specimens were preserved, so information on the external coloration and shape of the body is unavailable.



Figures 17–18. *Cylichnium cylindrellum* (Dall, 1908), anatomy (LACM 94-58.3). **17.** Reproductive system; scale bar = 1 mm. **18.** Anterior portion of the digestive system; scale bar = 1 mm. Abbreviations: am, ampulla; ag, albumen gland; bb, buccal bulb; bc, bursa copulatrix; cnr, circumesophageal nerve ring; esg, external seminal groove; fco, female copulatory organ; gz, gizzard; mg, mucous gland; pn, penis; pr, prostate; sg, salivary gland; sr, seminal receptacle.

Digestive System: The buccal mass is large and heavily muscular (Figure 18). At its posterior end it connects to the esophagus and two elongate salivary glands. The esophagus is short and opens into the muscular gizzard, which contains three subequal gizzard plates. All three gizzard plates are oval and smooth (Figure 16). The radular formula is $20 \times 12.0.12$ ($n = 1$). All lateral teeth are hamate, with no denticulations (Figure 15). The innermost tooth of each row is wider than the outer lateral teeth and has a lateral prolongation on its outer edge.

Reproductive System: The reproductive system is monaulic (Figure 17). The ampulla is large and convoluted. It connects to the narrow and elongate post-ampullary

duct. The seminal receptacle enters the post-ampullary duct that continues distally to the common general atrium. Also entering the common atrium are the female glands and the bursa copulatrix (or gametolytic gland). From the gonophore an open seminal groove runs anteriorly to the protusible cephalic penis and the prostate. At the vaginal opening there is a complex female copulatory organ.

Material Examined: CALIFORNIA (all specimens collected by K. L. Smith, R/V NEW HORIZON), approximately 226 km west of Point Arguello, Santa Barbara County ($34^{\circ}44' N$, $123^{\circ}11' W$), 4100 m depth, 1 specimen, 18 February 1990 (LACM 90-162.1); ($34^{\circ}45' N$, $123^{\circ}07' W$), 4100 m depth, 1 specimen, dissected, 24 June

1991 (LACM 91-41.1); (34°43' N, 123°07' W), 4100 m depth, 1 shell with dried soft parts, 2 August 1991 (LACM 91-132.4); (34°47' N, 123°04' W), 4100 m depth, 1 specimen, 26 February 1992 (LACM 92-109.1); (34°41' N, 123°03' W), 4134 m depth, 1 specimen, 25 June 1992 (LACM 92-111.1); (34°38' N, 120°01' W), 4134 m depth, 1 specimen, 22 July 1992 (LACM 92-112.1); (34°43' N, 123°04' W), 4100 m depth, 1 fragment of shell, 20 October 1992 (LACM 92-114.2); (34°45' N, 123°02' W), 4100 m depth, 1 fragment of shell, 24 February 1993 (LACM 93-21.10); (34°42' N, 123°08' W), 4100 m depth, 1 shell and a fragment of shell, 20 July 1993 (LACM 93-43.7); (34°39' N, 122°58' W), 4100 m depth, 2 fragments of shell, 17 June 1994 (LACM 94-58.10); 4100 m depth, 2 specimens, 17 June 1994 (LACM 94-58.3); (34°44' N, 123°13' W), 4100 m depth, 1 shell, 21 August 1994 (LACM 94-59); (34°42' N, 123°09' W), 4100 m depth, 1 shell and two fragments, 14 February 1995 (LACM 95-19.2); (34°42' N, 123°09' W), 4100 m depth, 1 specimen, 14 February 1995 (LACM 95-19.3); (34°42' N, 123°05' W), 4100 m depth, 1 specimen, 17 February 1995 (LACM 95-20.3); (34°40' N, 123°03' W), 4100 m depth, 1 fragment of shell, 1 May 1995 (LACM 95-21.9); (34°40' N, 123°03' W), 4100 m depth, 1 specimen, 1 May 1995 (LACM 95-21.8); (34°40' N, 123°11' W), 4100 m depth, 1 specimen, 3 June 1995 (LACM 95-126.3); (34°40' N, 123°11' W), 4100 m depth, 2 specimens, 31 May 1996 (LACM 96-38.1); (34°40' N, 123°11' W), 4100 m depth, 1 fragment, 5 June 1996 (LACM 96-39.8); (34°41.710' N, 123°12.570' W), 4110 m depth, 2 August 2004, 1 fragment of shell (SIO M11388); (34°41.440' N, 123°03.694' W), 4135 m depth, 30 October 2004, 1 fragment of shell (SIO M11435); (34°41.440' N, 123°03.694' W), 4135 m depth, 30 October 2004, 1 shell (SIO M11420); (34°41.015' N, 123°09.367' W), 4129 m depth, 26 February 2005, 1 specimen (SIO M11462); (34°41.920' N, 123°12.257' W), 4079 m depth, 21 June 2005, 1 fragment of shell (SIO M11488); (34°39.826' N, 123°5.241' W), 4070 m depth, 23 June 2005, 1 shell (SIO M11496). MEXICO, Off Bahía Magdalena, Baja California (24°23' N, 113°18.9' W), 3390–3580 m depth, 1 shell, leg. Lowenstam (CASIZ 156490). PERU, R/V USS ALBATROSS Expedition, station 4672, 88 mi (163 km) southwest of Palominos Light, 2845 fathoms (5200 m), shell with no body parts (HOLOTYPE, USNM 110563).

Geographic Range: This species, originally described from Peru, has also been found in Baja California, Mexico (Keen, 1971) and southern California (present paper).

Remarks: Our material of *Cylichnium cylindrellum* from southern California clearly matches the original description and holotype of this species. The mid-whorl microsculpture shows the paired spiral grooves and the general outline of the shell is very similar to that of the holotype. Some variability has been observed in the southern California material, in some specimens the lip raises slightly above the apex (LACM 95-19.2, CASIZ

156490) (Figures 11, 13), whereas in others (LACM 95-126.3) (Figure 12) it does not.

Keen (1971) recorded this species from Bahía Magdalena, Baja California, Mexico. Keen's two illustrations are a copy of the original figure and the specimen from Bahía Magdalena (CASIZ 156490) on the right. Examination of the material confirmed that Keen's specimen also belongs to *C. cylindrellum*.

The reassignment of this species was here conducted based on anatomical features. The reproductive system of *C. cylindrellum* has the characteristic female copulatory organ found in other species of the genus (Bouchet, 1975; Valdés, 2008). Also, the radula is composed of a series of simple and hamate lateral teeth, very similar to those of the Atlantic species *C. waldae* and *C. africanum* (see Bouchet, 1975) as well as the Pacific species *C. ancillarioides*, *C. mucronatum*, and *C. nanum* (see Valdés, 2008).

Cylichnium cylindrellum differs from other species of the genus by its shell morphology and internal anatomy. The shells of the Pacific species *C. ancillarioides* and *C. mucronatum* have much narrower bases and apertures, as well as more pointed apices (Valdés, 2008). The other Pacific species, *C. nanum* has a distinct columellar tooth (Valdés, 2008), absent in *C. cylindrellum*. Anatomically, *C. ancillarioides* and *C. mucronatum* have 10 and 6 radular lateral teeth, respectively (Valdés, 2008), whereas *C. cylindrellum* has 12. The reproductive system of *C. mucronatum* has a female copulatory organ with marginal papillae only, whereas in *C. cylindrellum* the entire organ is covered with papillae, as in *C. ancillarioides* (Valdés, 2008). However, the prostate of *C. ancillarioides* is much more elongated than that of *C. cylindrellum*, whereas the penis is shorter and wider.

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LITERATURE CITED

- Bouchet, P. 1975. Opisthobranches de profondeur de l'Océan Atlantique. I.- Cephalaspidea. Cahiers de Biologie Marine 16: 317–365.
- Dall, W.H. 1890. Scientific results of explorations by the U.S. Fish Commission steamer Albatross. No. VII. Preliminary report on the collection of Mollusca and Brachiopoda obtained in 1887–88. Proceedings of the United States National Museum 12: 219–362, pls 5–14.
- Dall, W.H. 1908. Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried on by the U.S. Fish Commission steamer "Albatross," during 1891, Lieut. Commander Z.L. Tanner, U.S.N., commanding, XXXVII and Reports of the scientific results of the expedition to the eastern tropical Pacific, in charge of Alexander Agassiz, by the U.S. Fish Commission Steamer "Albatross," from

- October, 1904, to March, 1905, Lieut. Commander L. M. Garrett, U.S.N., commanding, XIV. Bulletin of the Museum of Comparative Zoology, **43**: 205–487, pls 1–22.
- Eilertsen, M.H. and M.A.E. Malaquias. 2013a. Systematic revision of the genus *Scaphander* (Gastropoda, Cephalaspidea) in the Atlantic Ocean, with a molecular phylogenetic hypothesis. Zoological Journal of the Linnean Society **167**: 389–429.
- Eilertsen, M.H. and M.A.E. Malaquias. 2013b. Unique digestive system, trophic specialization, and diversification in the deep-sea gastropod genus *Scaphander*. Biological Journal of the Linnean Society **109**: 512–525.
- Gosliner, T.M. 1979. A review of the systematics of *Cylichnella* Gabb (Opisthobranchia: Scaphandridae). The Nautilus **93**: 85–92.
- Gosliner, T.M. 1994. Gastropoda: Opisthobranchia. In: F.W. Harrison and A.J. Kohn (eds) Microscopic Anatomy of Invertebrates. Wiley-Liss, New York, pp. 253–355.
- Habe, T. 1955. A list of the cephalaspid Opisthobranchia of Japan. Bulletin of the Biogeographical Society of Japan **16–19**: 54–79.
- Keen, A.M. 1971. Sea Shells of Tropical West America. Marine Mollusks from Baja California to Peru. Stanford University Press, Stanford, California, 1064 pp.
- Malaquias, M.A.E., J. Mackenzie-Dodds, P. Bouchet, T. Gosliner, and D.G. Reid. 2009. A molecular phylogeny of the Cephalaspidea *sensu lato* (Gastropoda: Euthyneura): Architectibranchia redefined and Runcinacea reinstated. Zoologica Scripta **38**: 23–41.
- Montfort, P.D. de, 1808–1810. Conchyliologie Systématique, et Classification Méthodique des Coquilles. Chez F. Schoell, Paris. Dates of publication: vol. 1 [1808], vol. 2 [1810].
- Schepman, M.M. 1913. The Prosobranchia, Pulmonata and Opisthobranchia Tectibranchiata (tribe Bullomorpha) of the Siboga Expedition, Pt. 6 Pulmonata and Opisthobranchia Tectibranchiata, tribe Bullomorpha, pp. 453–494, 2 pls. In: M. Weber (ed.), Uitkomsten op Zoologisch, Botanisch, Oceanographisch en Geologisch gebied verzameld in Nederlandsch Oost-Indië 1899–1900 aan boord H.M. Siboga onder commando van Luitenant ter zee 1^e kl. G. F. Tydeman, vol. 49. Brill, Leiden.
- Thompson, T.E. 1976. Biology of Opisthobranch Molluscs. The Ray Society, London, 207 pp.
- Valdés, A. 2008. Deep-sea “cephalaspidean” heterobranchs (Gastropoda) from the tropical southwest Pacific. In: V. Héros, R.H. Cowie, P. Bouchet (eds.) Tropical Deep-Sea Benthos, vol. 25. Mémoires du Muséum national d'Histoire naturelle **196**: 1–806.



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