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On the occurrence of the deep-sea barnacle *Tetrachaelasma southwardi* Newman & Ross, 1971 (Cirripedia, Balanomorpha, Bathylasmatidae) in the Mar del Plata Submarine Canyon, Argentina: supplementary description and taxonomic remarks on the genus

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Abstract

Tetrachaelasma southwardi Newman & Ross, 1971, a bathylasmatine balanomorph, has been recorded from the Mar del Plata Submarine Canyon (ca. 38°S, off the coast of Argentina), at two stations located at significantly different depths (1950 m and 2934 m). A total of 29 specimens, complete or damaged but with soft parts intact, were collected. This unusually large number of well-preserved specimens allows us to add supplementary descriptions and document intraspecific morphological variations. The differences between *T. southwardi* and *T. tasmanicum* Buckeridge, 1999, the second species of this genus, are re-evaluated. A map and an updated list including all the records of the genus *Tetrachaelasma* Newman & Ross, 1971 are provided. The distribution of the genus *Tetrachaelasma* in the Southern Ocean is discussed. Furthermore, a single specimen of another bathylasmatine balanomorph, which was assigned to the genus *Bathylasma* Newman & Ross, 1971, was also obtained at the 1950 m station herein studied. This is the first record of the genus *Bathylasma* from the South-West Atlantic. This specimen has one *T. southwardi* attached to it, marking the first time that members of these two genera have been found living together.

Key Words

Bathylasma sp., distribution, South-West Atlantic, *Tetrachaelasma southwardi*, *T. tasmanicum*

Introduction

On the genera *Tetrachaelasma* and *Bathylasma*

The genus *Tetrachaelasma* contains only two species, which inhabit much greater depths than any other Balanomorpha, up to 3600 m (Newman and Ross 1971, 1976; Buckeridge 2010; Table 1). Newman and Ross (1971) erected this genus for the reception of *T. southwardi*, a new species that these authors described based on seven complete specimens taken by the RV "Eltanin" at a single station in the Central South Pacific (2304–2328 m depth). Newman and Ross (op. cit.) also listed among the material studied loose plates taken by the RV "Eltanin" at three other localities, i.e., off southern Chile (1190–1263 m depth), off Malvinas/Falkland Is. (1720–1739 m depth), and at the Sars Bank in the Drake Passage (1207–1591 m depth). Furthermore, Newman and Ross (1976) reported extensive accumulations of loose plates of *Tetrachaelasma* sp. on the flanks of a seamount off Madagascar at comparable depths (~1800 m). In addition, the RV "Atlantis II" obtained about 70 disarticulated plates of *T.* cf. *southwardi* at the Mid-Atlantic Ridge (ca. 41°S) in 1980 (see the SIO-BIC website in the References section). More recently, Buckeridge (1999) described the second species of the genus, *T. tasmanicum*, based on a single incomplete specimen (comprising the carina, left carinolateral, scuta, and terga, plus body parts) and numerous loose plates collected at the South Tasman Rise (2030–3600 m depth) by the RV "Rig Seismic". All these records, and a few others retrieved from the website, are listed in Table 1 and charted in Fig. 9.

An unusually high number of *T. southwardi* specimens, complete or damaged but all with soft parts intact, were recently collected at two stations from considerably different depths (1950 m and 2934 m). This material was taken from the Mar del Plata Submarine Canyon (ca. 38°S, off the coast of Argentina) during the Talud Continental I and III expeditions performed by the RV "Puerto Deseado". Based on this material, supplementary descriptions of *T. southwardi* are presented, and intraspecific morphological variations are documented. In addition, the differences between *T. southwardi* and *T. tasmanicum* are discussed. Furthermore, a second bathylasmatine balanomorph was collected at the 1950 m depth station, which was assigned to the genus *Bathylasma* Newman & Ross, 1971. This genus encompassed four extant and four fossil species (see Araya and Newman 2018). This is the first time that the genus *Bathylasma* has been recorded from the South-West Atlantic.

A brief review of the family Bathylasmatidae Newman & Ross, 1971

Newman and Ross (1971) erected the deep-sea family Bathylasmatidae to include the new genera *Bathylasma*, *Tetrachaelasma*, and *Aaptolasma* (currently a synonym of *Hexelasma*), as well as the previously known genera *Hexelasma* Hoek, 1913 and *Tessarelasma* Withers, 1936. Later, Newman and Ross (1976) grouped Bathylasmatidae, Tetraclitidae Gruvel, 1903, and Coronulidae Leach, 1817, under the superfamily Balanomorphoidea (new status, Coronuloidea Leach, 1817; see Newman and Ross (1977)), and divided the bathylasmatids into the subfamilies Bathylasmatinae and Hexelasmatinae. In addition, Newman and Ross (1976) suggested that Bathylasmatidae gave rise to Tetraclitidae (see fig. 5).

Foster (1978) stated that "the relationship between *Pachylasma* and *Hexelasma* is obvious; they are weakly constructed, deep-sea forms with wide parietal alae and no radial interlocking of the plates." Accordingly, Foster (1978) placed the bathylasmatids in the family Pachylasmatidae Utinomi, 1968, contradicting the proposal by Newman and Ross (1976). Foster's nomenclatural decision was subsequently followed by Jones (2000, 2012), who included the subfamilies Bathylasmatinae and Hexelasmatinae in Pachylasmatidae, under the superfamily Pachylasmatoidea Utinomi, 1968.

Buckeridge and Newman (2010) revised the classification of Balanomorpha and grouped Bathylasmatidae and Tetraclitidae under the superfamily Tetraclitoidea Gruvel, 1903. More recently, Chan et al. (2017), in a molecular phylogenetic study for Balanomorpha, proposed that Bathylasmatidae is more closely associated with Tetraclitoidea than with Pachylasmatoidea. This result is consistent with the proposal by Newman and Ross (1976), Buckeridge and Newman (2010), as well as with a molecular phylogenetic study of Tetraclitoidea presented by Tsang et al. (2015). Finally, Chan et al. (2021), in a thorough revision of the barnacle classification, placed Bathylasmatidae in the superfamily Coronuloidea, together with Tetraclitidae, Austrobalanidae Newman & Ross, 1976, Coronulidae, and Chelonibiidae Pilsbry, 1916.

Bathylasmatidae currently encompasses the subfamilies Hexelasmatinae (genus *Hexelasma*) and Bathylasmatinae (genera *Bathylasma*, *Tetrachaelasma*, *Tessarelasma*, and *Mesolasma* Foster, 1981). The former subfamily has a wall of six plates with longitudinal chitinous laminae and/or strips, whereas the latter subfamily has four or six plates and lacks chitinous material. *Tessarelasma* is only known from a fossil record from India. *Tetrachaelasma* is the only living genus with four wall plates. A key for the identification of extant genera is presented by Araya and Newman (2018). For diagnoses of the subfamilies and genera, see Jones (2000).

Description of the study area

The Mar del Plata Submarine Canyon is located in the southwestern Atlantic Ocean at around 38°S (Fig. 1). This canyon is not connected to the Argentine continental shelf and has a typical "V" shape (Violante et al. 2010; Bozzano et al. 2017). It begins on the upper continental slope at a depth of ~500–1000 m and extends for about 110 km downslope to reach a depth of ~3900 m (Voigt et al. 2013). Oceanographically, this canyon is located in one of the most dynamic and highly variable areas of the world ocean, the Brazil/Malvinas Confluence, which is generated by the encounter of the Brazil and Malvinas/Falklands currents (Piola and Matano 2001; Matano et al. 2010; Preu et al. 2013).

Material and methods

Field work

Twenty-nine specimens (complete or damaged) and a few loose plates of *Tetrachaelasma southwardi* were collected from the Mar del Plata Submarine Canyon during the Talud Continental I and III expeditions, carried out by the RV "Puerto Deseado" in 2012 and 2013, respectively. The specimens were obtained at two stations, one at 1950 m depth using an epibenthic sledge, similar to the one designed by Hessler and Sanders (1967), and the other at 2934 m depth using a bottom otter trawl (Fig. 1). In addition, one specimen identified as *Bathylasma* sp. was also collected at the 1950 m depth station (see Material Examined section).

Table 1. Records of *Tetrachaelasma* species reported in this study and by previous authors. Abbreviations: CSIRO-MIIC — Commonwealth Scientific and Industrial Research Organization – Marine Invertebrate Image Collection; GBIF — Global Biodiversity Information Facility; NMNH — National Museum of Natural History, Smithsonian Institution; SIO-BIC — Scripps Institution of Oceanography – Benthic Invertebrate Collection. Links to these institutions/organizations in the References section. Note: The catalog numbers for *T. southwardi* are those published on the NMNH website, not those mentioned in Newman and Ross (1971) and Jones (2000).

Species	Ships and/ or Cruises (Institutions)	Stations	Geographic coordinates	Depths (m)	Dates	Locations	Catalog numbers	References and/ or websites
T. southwardi	RV "Eltanin" (SOSC)	Sta. 6	52°10'S, 142°10'W	2304–2328	Mar 21, 1965	South Pacific Ocean	USNM 125305 (Holotype) USNM 125306 USNM 125307	Newman and Ross (1971), NMNH
T. southwardi	RV "Eltanin" (USARP)	Sta. 216	52°53'S, 75°36'W	1190–1263	Sep 16, 1962	Off southern Chile	USNM 125309	Newman and Ross (1971), NMNH
T. southwardi	RV "Eltanin" (USARP)	Sta. 376	54°03'S, 56°03'W	1720–1739	Dec 20–21, 1962	Off Malvinas/ Falkland Is.	USNM 125308	Newman and Ross (1971), NMNH
T. southwardi	RV "Eltanin" /Cruise 05	†	59°45'S, 68°50'W to 59°46'S, 68°50'W	1207–1591	Oct 10, 1962	Sars Bank in Drake Passage	-	Weisbord (1965, 1967)
T. southwardi	RV "Puerto Deseado" / Talud Continental I	Sta. 25	37°51.688'S, 54°10.550'W	1950	Aug 15, 2012	Mar del Plata Submarine Canyon	MACN-In 44478	Current study
T. southwardi	RV "Puerto Deseado" / Talud Continental III	Sta. 45	38°1.913'S, 53°39.268'W	2934	Sep 05, 2013	Mar del Plata Submarine Canyon	MACN-In 44479	Current study
T. cf. *southwardi*	RV "Atlantis II" (WHOI)	Dredge 06	41°14.9'S, 16°36.2'W	2175–2600	Jun 20, 1980	Mid-Atlantic Ridge, South Atlantic Ocean	BIC C8156	SIO-BIC
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D12	45°09.0'S to 45°10.2'S, 145°25.1'E to 145°23.8'E	2100–3000	Feb 05, 1995	South Tasmania	-	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D25	49°04.3'S to 49°04.0'S, 146°16.0'E to 146°17.4'E	2420–3300	Feb 12, 1995	South Tasmania	CPC 34698-34702	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D41	44°14'S, 149°26'E	2850	Feb 18, 1995	South Tasmania	-	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D43	43°54.0'S, 151°19.2'E to 43°54.0'S, 151°17.8'E	2030–3600	Feb 19, 1995	South Tasmania	-	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D44	44°36.3'S to 44°36.0'S, 147°14.7'E to 147°14.8'E	2250–2400	Feb 22, 1995	South Tasmania	-	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D45	44°39.2'S to 44°39.5'S, 147°26.4'E to 147°26.5'E	2600–2800	Feb 22, 1995	South Tasmania	-	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D53	45°21.8'S to 45°21.1'S, 146°43.2'E to 146°43.7'E	2770–3000	Feb 25, 1995	South Tasmania	–	Buckeridge (1999)
T. tasmanicum	RV "Rig Seismic" / Cruise 147	Sta. D57	44°31.7'S to 44°32.8'S, 146°00.4'E to 146°00.6'E	2300–2850	Feb 26, 1995	South Tasmania	CPC 34697 (Holotype)	Buckeridge (1999)
T. tasmanicum	RV "Thomas G. Thompson" / Cruise TT200801	Sta. J2-390-008-002	43°48'25.2"S, 150°20'24.0"E	2082	Jan 05, 2009	South Tasmania	MIIC 02727	CSIRO-MIIC
T. tasmanicum	RV "Thomas G. Thompson" / Cruise TT200801	Sta. J2-392-012-001	45°18'01.4"S, 146°07'15.6"E	2213	Jan 11, 2009	South Tasmania	MIIC 02729	CSIRO-MIIC
T. tasmanicum	RV "Thomas G. Thompson" / Cruise TT200801	Sta. J2-390-015	43°49'42.2"S, 150°30'00.0"E	1061	Jan 08, 2009	South Tasmania	NMV J68079	GBIF
T. tasmanicum	RV "Thomas G. Thompson" / Cruise TT200801	Sta. J2-391-011	45°22'27.2"S, 144°35'34.8"E	3271	Jan 08, 2009	South Tasmania	NMV J68084	GBIF
Tetrachaelasma sp.	RV "Argo" / CIRCE Expedition	Sta. DR124	26°29'S, 46°07'E	1783–1838	Sep 29, 1968	South Madagascar	BIC C8158	Newman and Ross (1976), SIO-BIC

† Weisbord (1965, 1967) did not report the station number. Newman and Ross (1971) ambiguously mentioned "Sta. 225" and "Sta. 255", for the material taken in the Sars Bank.

All the specimens were fixed on board in 10% seawater formalin (buffered with sodium borate) and later transferred to 96% ethanol in the laboratory.

Laboratory work

The shell and opercular plates were disassembled from most of the specimens. When necessary, terga and scuta were cleaned by soaking in dilute bleach (sodium hypochlorite). Parietes, opercular plates, and rostral-carina diameters were measured to the nearest 0.01 mm using a digital calliper.

Some specimens were dissected under a stereomicroscope (Leica MZ8), and appendages were temporarily mounted on slides in glycerin medium. Drawings of the appendages were prepared using a Carl Zeiss (Axioskop) compound microscope equipped with a camera lucida. Line drawings were rendered in digital format using a Wacom tablet and the Adobe Illustrator program after Coleman (2003). All dissected appendages were finally dismounted from the temporary slides and stored in 96%

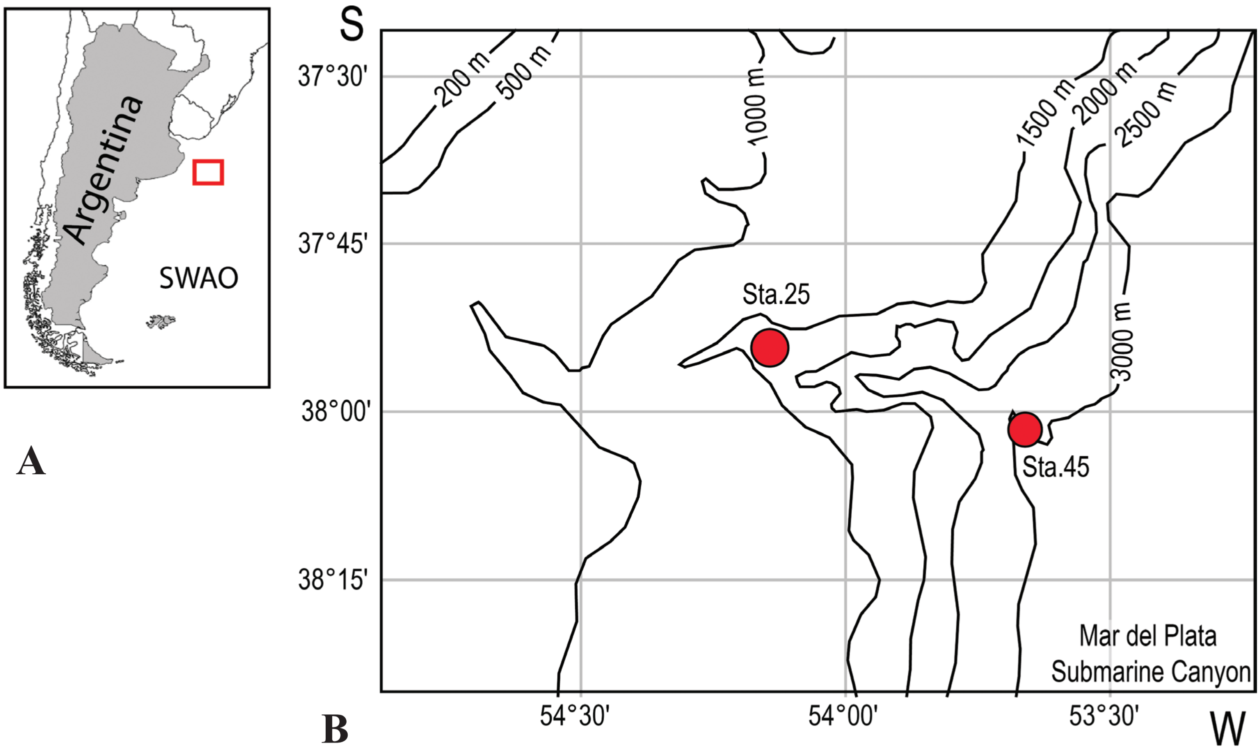

Figure 1. A. Study area location (inset); **B.** Map including the two stations sampled at the Mar del Plata Submarine Canyon. The seabed topography of the study area is represented by roughly calculated isobaths. Abbreviation: **SWAO** — South-West Atlantic Ocean.

ethanol, along with other soft body remains, the wall, and opercular plates.

Light photographs were taken with a Nikon D7500 digital camera equipped with a Sigma 105 mm f2.8 EX macro lens and the Zerene stacking software v.1.04 (Zerene Systems LLC 2023).

For SEM images, the labrum of two specimens was cleaned with 0.5% Triton X-100 nonionic detergent and ultrasonicated. Afterwards, the specimens were dehydrated through a graded ethanol series and later transferred to increasing concentrations of hexamethyldisilazane (HMDS). Specimens in HMDS 100% were allowed to air dry and then mounted on aluminum stubs and coated with gold-palladium. Finally, the material was examined using a Zeiss Gemini SEM 360 microscope.

High-resolution images of the parietes, terga, and scuta of the holotype of *Tetrachaelasma southwardi* Newman & Ross, 1971, deposited in the National Museum of Natural History (USNM 125305), were used for comparison purposes.

Table 1 includes records from regular scientific publications as well as records taken from web databases where the name of a trained taxonomist in Cirripedia is responsible for the identification.

The two stations at the Mar del Plata Submarine Canyon (Fig. 1) and all the records of the *Tetrachaelasma* species around the world (Fig. 9) were charted using the PanMap software v.0.9.6 (Diepenbroek et al. 2002).

All specimens studied were deposited in the Invertebrate Collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN-In).

Abbreviations and terminology

The following abbreviations are used in the text: R for rostrum, C for carina, CL for carinolateral, S for scutum, and T for tergum.

Antenniform cirral articles are defined as those articles with only one whorl of distal setae; however, if the antenniform cirral article also has lateral filter setae, then the latter are equal to or shorter than the whorl of distal setae.

The following terminology is used to describe the scuto-tergal articulation:

- Scutal articular ridge (***sar***): prominent outgrowth extending along a-a' that fits into the tergal articular furrow (Fig. 2A, B).
- Upper articular furrow (***uaf***): scutal distal groove that receives the tergal articular ridge (Fig. 2C).
- Lower articular furrow (***laf***): scutal proximal groove that receives the vertical articular ridge of the tergum (Fig. 2C).
- Tergal articular ridge (***tar***): prominent distal outgrowth that fits into the upper articular furrow of the scutum (Fig. 2E).
- Vertical articular ridge (***var***): slanted outgrowth of the tergum extending along b-b'. Its wider basal part fits into the lower articular furrow of the scutum (Fig. 2D, E).
- Tergal articular furrow (***taf***): broad and deep groove extending along c-c' that receives the scutum articular ridge (Fig. 2D, E, F).

Results

Superfamily Coronuloidea Leach, 1817
Family Bathylasmatidae Newman & Ross, 1971
Subfamily Bathylasmatinae Newman & Ross, 1976

Genus *Tetrachaelasma* Newman & Ross, 1971

Diagnosis. Shell conical or columnar, with 4 thick, solid, calcareous wall plates, including compound rostral plate, paired CL, and C (R-CL-C). Parietes covered with numerous fine bristles along horizontal growth lines; chitinous laminae absent. External alar growth lines diverge from the inferior alar margin; superior alar margin with narrow, coarse welting. Carina supports large alae that internally contribute to nearly half the total sheath circumference. Radii absent. Basis membranous. Scutum articular ridge distinctly projected beyond the articular margin. Tergum slightly thinner than scutum; articular margin sinusoidal in internal view but smoothly concave in external view; with few depressor muscle crests, weak to well developed, extending at the most ⅓ along basal margin. Rami of cirri II and III antenniform; intermediate articles of cirrus VI bearing 3 or 4 pairs of major setae. Mandible quadridentoid. Caudal appendages absent. Deep-sea species, Southern Ocean.

Type species. *Tetrachaelasma southwardi* Newman & Ross, 1971.

Current species composition. *T. southwardi* Newman & Ross, 1971 and *T. tasmanicum* Buckeridge, 1999.

Remarks. Newman and Ross (1971) established the genus *Tetrachaelasma* (a name that refers to the wall of four plates) to include *T. southwardi*. In addition, they discussed the affinities with *Bathylasma* and presented a key to separate the five genera of the family Bathylasmatidae. Newman and Ross (1976) placed this genus in the subfamily Bathylasmatinae. Buckeridge (1999) gave a brief diagnosis of this genus and described its second species, *T. tasmanicum*. Jones (2000) re-examined the holotype of *T. southwardi* and provided a more complete diagnosis of the genus. However, this author failed to include *T. tasmanicum*, a species that had been published the previous year. More recently, Araya and Newman (2018) presented an updated key to separate the extant genera currently in the family.

Tetrachaelasma southwardi Newman & Ross, 1971

Figs 2–9, 11

Hexelasma antarcticum Borradaile, 1916. —Weisbord 1965: 1015–1016 (Sars Bank material); 1967: 51–56, pl. I, figs 7–8, pl. II, figs 7–8 (Sars Bank material).

Tetrachaelasma southwardi Newman & Ross, 1971: 152–155, fig. 74, pls. XXVI–XXXI (description). —Buckeridge 1999: 521, 522, 526 (comparison with *T. tasmanicum*). —Jones 2000: 150, 237–239 (remarks on the holotype, tables 24, 25, fig. 50 (distribution map)).

Material examined. ***Talud Continental I*** expedition, RV "Puerto Deseado", Mar del Plata Submarine Canyon, Sta. 25, 37°51.688'S, 54°10.550'W, 1950 m depth, 15 Aug 2012, epibenthic sledge, coll. I. Chiesa; 21 complete or damaged specimens (all with soft body parts intact) and 1 batch of disarticulated plates, namely: 1 damaged specimen (R missing) [wall and opercular plates disarticulated, mouthparts dissected, T and S photos] (MACN-In 44478a); 1 complete specimen [wall and opercular plates disarticulated, mouthparts dissected, T and S photos, labrum SEM] (MACN-In 44478b); 1 complete specimen [not dissected] (MACN-In 44478c); 1 complete specimen [not dissected] (MACN-In 44478d); 1 complete specimen [not dissected, photos of the habitus] (MACN-In 44478e); 1 complete specimen [wall and opercular plates disarticulated; mouthparts dissected; R, C, T, and S photos; cirral counts] (MACN-In 44478f); 1 complete specimen [not dissected, photos of the habitus] (MACN-In 44478g); 4 complete specimens, attached one over the other [not dissected, photos of the habitus] (MACN-In 44478h-k); 1 complete specimen [wall and opercular plates disarticulated; mouthparts and cirri drawn; R, C, T, and S photos; cirral counts] (MACN-In 44478l); 1 damaged specimen (R and both CL missing) [wall and opercular plates disarticulated, mouthparts dissected] (MACN-In 44478m); 1 complete specimen [not dissected] (MACN-In 44478n); 1 damaged specimen, with a large number of developing eggs in the mantle cavity (R and left CL missing) [wall and opercular plates disarticulated, mouthparts dissected] (MACN-In 44478o); 1 complete specimen [wall and opercular plates disarticulated, mouthparts dissected, photo serpulid epibiont] (MACN-In 44478p); 1 complete specimen [not dissected] (MACN-In 44478q); 1 damaged specimen (R missing) [wall plates disarticulated] (MACN-In 44478r); 1 damaged specimen (R missing) [not dissected] (MACN-In 44478s); 1 complete specimen [not dissected] (MACN-In 44478t); 1 complete specimen [not dissected, photo soft octocoral *Alcyonium* sp. epibiont] (MACN-In 44478u); batch of plates: 4 R, 3 C, 3 CL (MACN-In 44478v).

Talud Continental III expedition, RV "Puerto Deseado", Mar del Plata Submarine Canyon, Sta. 45, 38°1.913'S, 53°39.268'W, 2934 m depth, 05 Sep 2013, bottom otter trawl, colls. I. Chiesa and A. Martinez; 8 complete or damaged specimens (all with soft body parts intact) and 1 batch of disarticulated plates, namely: 1 complete specimen [wall plates articulated, opercular plates disarticulated; mouthparts dissected; habitus, T and S photos] (MACN-In 44479a); 1 complete specimen [wall and opercular plates disarticulated] (MACN-In 44479b); 1 complete specimen [not dissected, photos of the habitus] (MACN-In 44479c); 1 damaged specimen (R and left CL missing) [wall and opercular plates disarticulated, mouthparts dissected, T and S photos, cirral counts] (MACN-In 44479d); 1 damaged specimen (R and right CL missing) [wall and opercular plates disarticulated] (MACN-In 44479e); 1 damaged specimen (R and both CL missing) [wall and opercular plates disarticulated, mouthparts dissected] (MACN-In 44479f); 1 damaged specimen (R and 1 CL missing) [wall and opercular plates disarticulated, mouthparts dissected] (MACN-In 44479g); 1 damaged specimen (R and both CL missing) [wall and opercular plates disarticulated, mouthparts dissected, T and S photos, labrum SEM, cirral counts] (MACN-In 44479h); batch of plates: 3 R (one of them with a *Regioscalpellum* epibiont, photo), 3 C, 4 CL (MACN-In 44479i).

Supplementary description. Newman and Ross (1971) gave a detailed description of *T. southwardi*. Jones (2000) re-examined the holotype and summarized the main features of the species in tables 24–25. All the information presented in these tables had already been mentioned by Newman and Ross (1971). Therefore, we only consider the original description of Newman and Ross (1971) for comparison purposes.

Size (rostro-carinal diameter): 13.0–47.1 mm (n = 13).

Shell conical in young specimens and conical or columnar in older (larger) specimens (Fig. 3).

Shell wall covered with yellow cuticle and numerous fine bristles. Growth lines all along the plates are equidistant from each other (Fig. 3A–E). However, basally growth lines are narrowly spaced in a columnar specimen (Fig. 3G) as well as in some isolated plates (Fig. 11E), all of them collected at 2934 m depth. Bristles are as long as, or longer than, the distance between growth lines.

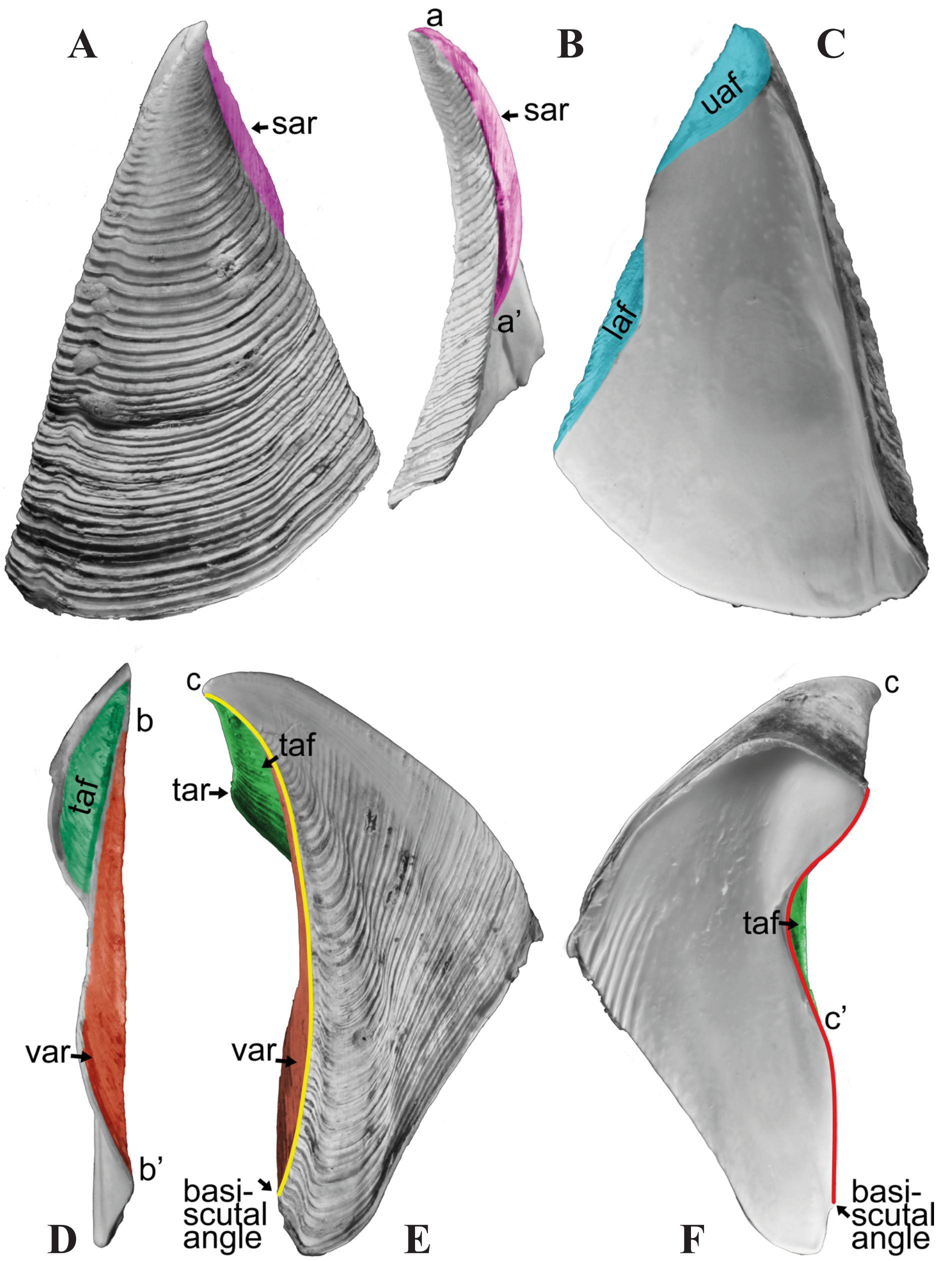

Figure 2. *Tetrachaelasma southwardi* Newman & Ross, 1971. Nomenclature used for the scuto-tergal articulation (the specimen shown in Fig. 4J–L is taken as a model). Scutum: **A.** Exterior view; **B.** Lateral view; **C.** Interior view. Tergum: **D.** Lateral view; **E.** Exterior view, smoothly concave articular margin painted in yellow; **F.** Internal view, sinusoidal articular margin painted in red. Abbreviations: **a-a'** – distal and basal ends of the scutum articular ridge; **b-b'** – distal and basal ends of the vertical articular ridge; **c-c'** – distal and basal ends of the tergal articular furrow; ***laf*** – lower articular furrow; ***sar*** – scutum articular ridge; ***taf*** – tergal articular furrow; ***tar*** – tergal articular ridge; ***uaf*** – upper articular furrow; ***var*** – vertical articular ridge.

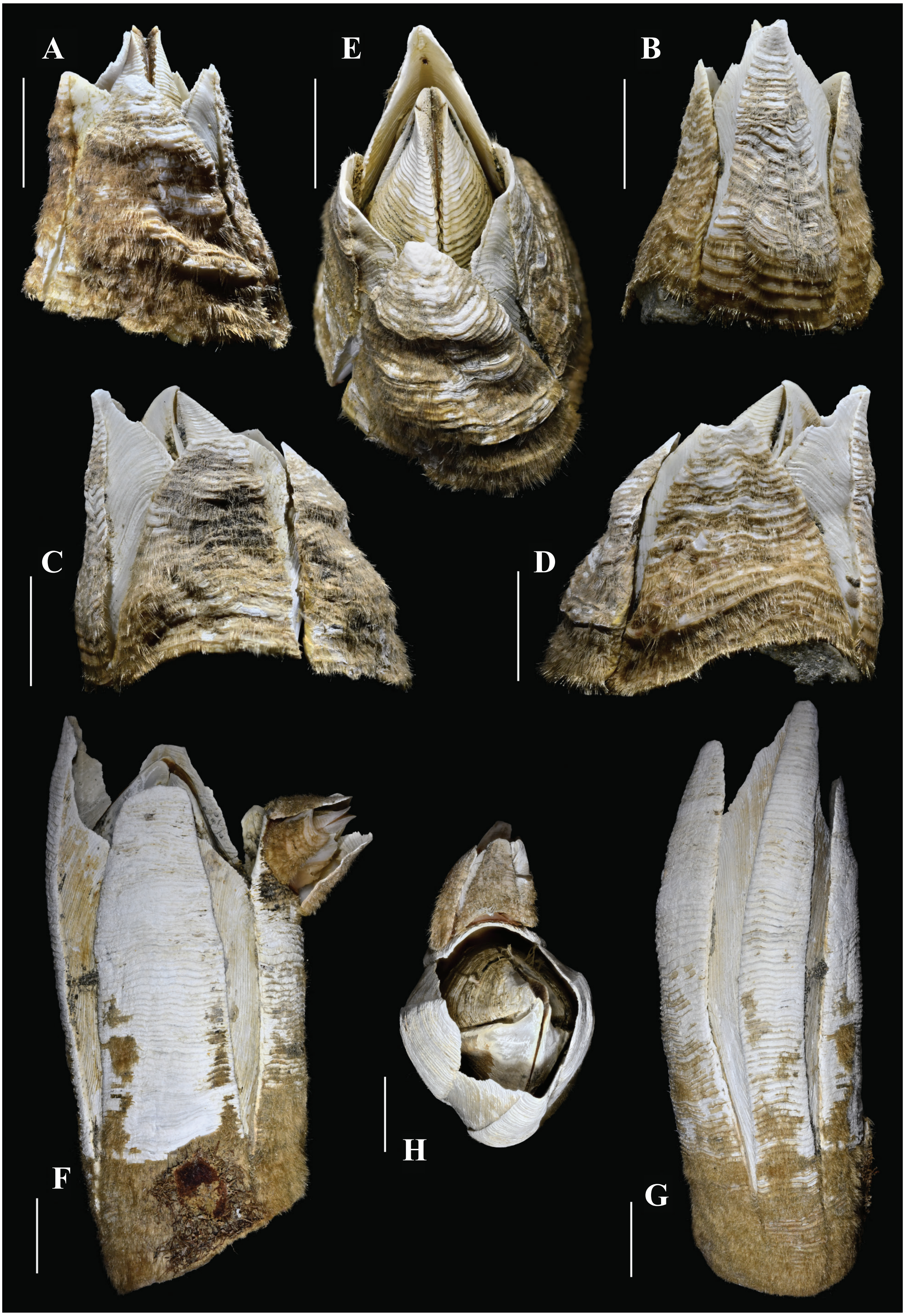

Figure 3. *Tetrachaelasma southwardi* Newman & Ross, 1971. Specimen (MACN-In 44478g): **A.** Rostral view; **B.** Carinal view; **C, D.** Left and right carinolateral views, respectively; **E.** Top view. Specimen (MACN-In 44479a, columnar) with a small specimen (MACN-In 44479b) attached to its rostrum: **F.** Left carinolateral view; **G.** Carinal view; **H.** Top view. Scale bars: 10 mm.

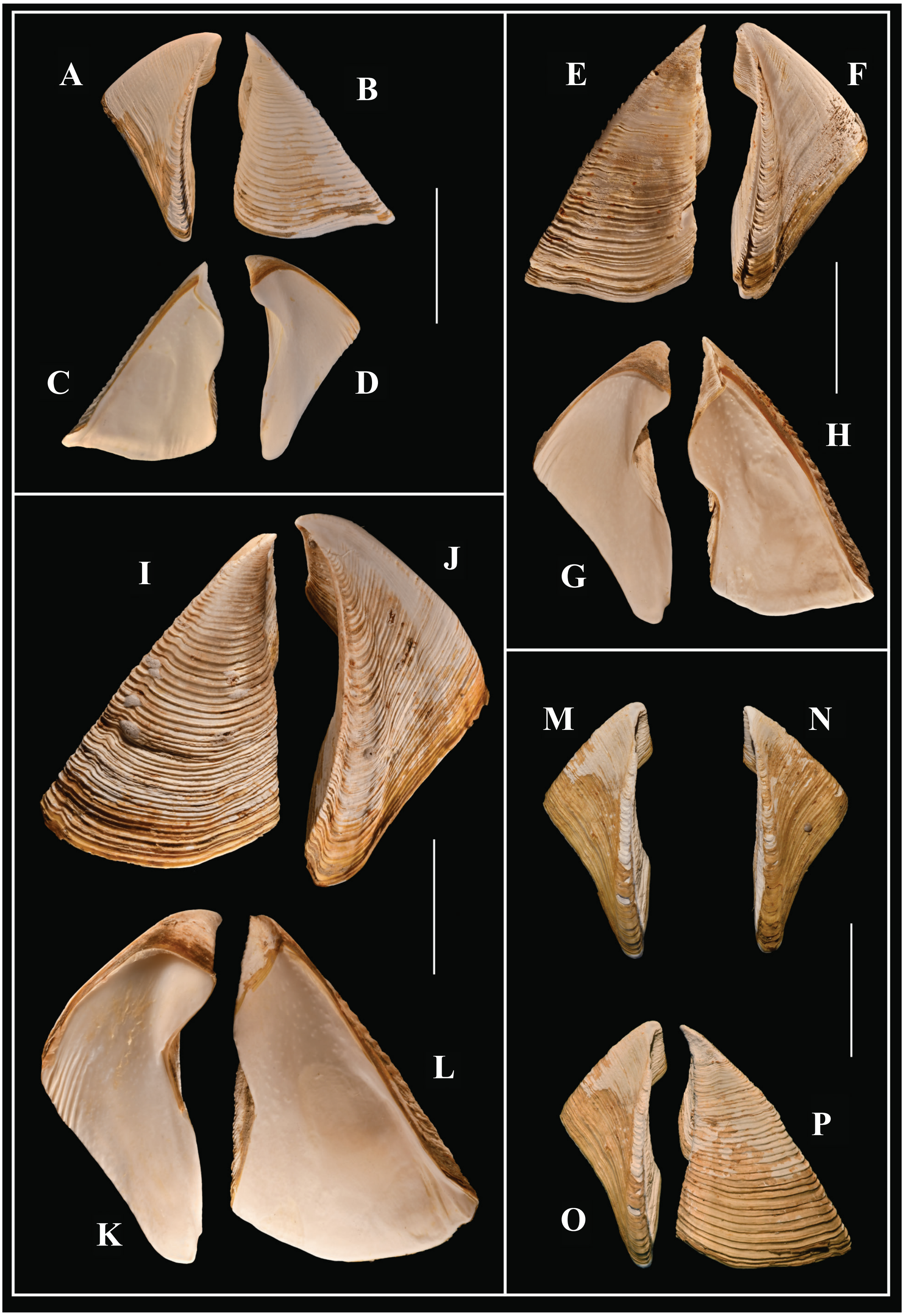

Figure 4. *Tetrachaelasma southwardi* Newman & Ross, 1971. Intraspecific variation of opercular plates among the material collected at 1950 m depth. Specimen (MACN-In 44478f): **A, D.** Left tergum in external and internal views, respectively; **B, C.** Left scutum in external and internal views, respectively. Specimen (MACN-In 44478a): **E, H.** Right scutum in external and internal views, respectively; **F, G.** Right tergum in external and internal views, respectively. Specimen (MACN-In 44478b): **I, L.** Right scutum in external and internal views, respectively; **J, K.** Right tergum in external and internal views, respectively. Specimen (MACN-In 44478l): **M, N.** Left and right terga in external view; **O, P.** Left tergum and scutum in external view. Scale bars: 10 mm.

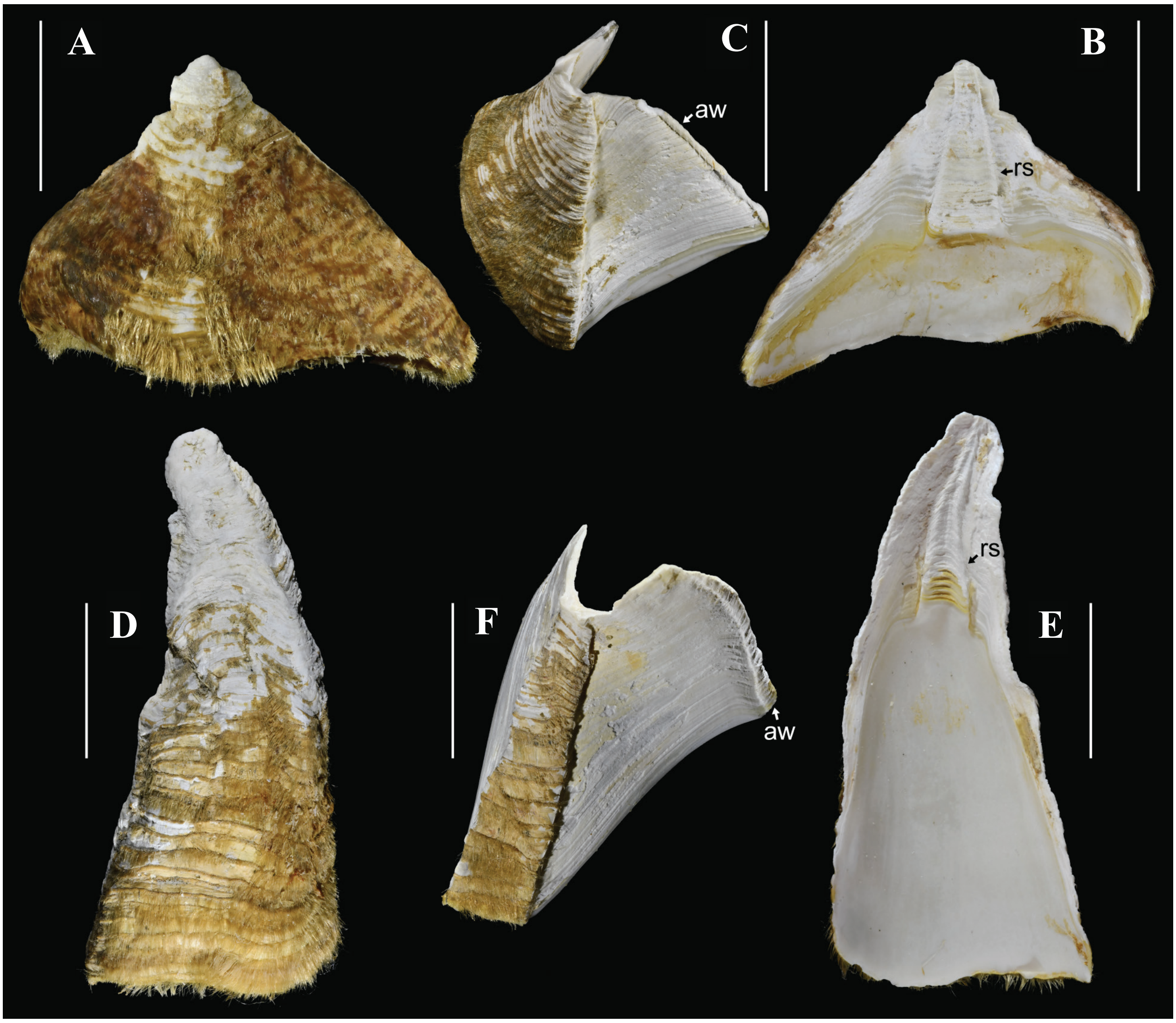

Figure 5. *Tetrachaelasma southwardi* Newman & Ross, 1971. Specimen (MACN-In 44478f): **A, B.** Rostrum in external and internal views, respectively; **C.** Carina in lateral view. Specimen (MACN-In 44478l): **D, E.** Rostrum in external and internal views, respectively; **F.** Carina in lateral view. Abbreviations: **aw** – alar welting; **rs** – rostral sheath. Scale bars: 10 mm.

Rostrum (Figs 3, 5A, B, D, E), 1.4–2.7 times (n = 13) wider than carina, only slightly bowed transversely, shape variable. In eight of the 13 specimens measured, the rostrum is the widest plate. In contrast, in five specimens, one of the CL plates (exceptionally both) is slightly wider than the rostrum. The sheath is flanked by very broad articular areas receiving alae of CL plates and occupies 1/2 to 1/3 of the height of the rostrum in nine out of the 11 specimens dissected (Fig. 5E); in the remaining two specimens, it occupies almost 2/3 of the height of the plate (Fig. 5B).

Carinolaterals (Fig. 3C, E, F), as mentioned by Newman and Ross (1971).

Carina (Figs 3, 5C, F) is the highest and narrowest of the wall plates. Shape variable. As mentioned by Newman and Ross (1971), it supports large alae that internally contribute to nearly half the total circumference of the sheath. Externally, alar growth lines similar to those of CL plates.

Scutum (Figs 4, 6), as mentioned by Newman and Ross (1971), except for the articular ridge (***sar***), which varies from prominent to moderately projected beyond the articular margin (compare Fig. 4B, C, E, H, with Fig. 4I, L). Note: The exposure of the ***sar*** depends on the shape (straight or twisted) of the scutum and on the angle of inclination at which the scutum is positioned. Adductor muscle pit shallow; boundaries weakly defined, i.e., not limited above and laterally by a distinct line (Figs 4C, H, L, 6D, I, M). External surface worn smooth at the apex in large specimens (Figs 4E, 6H, L). Some external growth lines may be slightly inflected close to the occludent margin, occasionally forming a weak apico-basal ridge (see Fig. 6E). Note: This apico-basal ridge is also present in *T. tasmanicum* (see Buckeridge 1999).

Tergum (Figs 4, 6) fully agrees with Newman and Ross's 1971 description, except for: the separation of the tergal spur from the articular margin, measured at base, varies from almost imperceptible to as much as 0.48 of

Figure 6. *Tetrachaelasma southwardi* Newman & Ross, 1971. Intraspecific variation of opercular plates among the material collected at 2934 m depth. Specimen (MACN-In 44479h): **A, D.** Right scutum in external and internal views, respectively; **B, C.** Right tergum in external and internal views, respectively; **E.** Left scutum in external view, slightly slanted to make the apico-basal ridge more visible; **F.** Joined right tergum and scutum in internal view. Specimen (MACN-In 44479d): **G, J.** Left tergum in external and internal views, respectively; **H, I.** Left scutum in external and internal views, respectively. Specimen (MACN-In 44479a): **K, N.** Left tergum in external and internal views, respectively; **L, M.** Left scutum in external and internal views, respectively. Abbreviations: **abr** – apico-basal ridge; **in** – indentation (worn) on articular margin. Scale bars: 10 mm.

spur width (n = 12; compare Fig. 4A, F, J with Fig. 6G, K). Internal surface with 2–7 depressor muscle crests, weak to well developed, extending at the most ⅓ along the basal margin (n = 13; compare Fig. 4G with Fig. 4K).

The following information not reported by Newman and Ross (1971) is added: in six of the specimens obtained at 1950 m depth, the basal margin of the tergum is 1.2 times the length of the occludent margin (Fig. 4A, D, F, G) [exception: basal and occludent margins are equal in length in the largest specimen dissected, Fig. 4J, K]. In contrast, in six of the specimens obtained at 2934 m depth, the basal margin is equal to or slightly shorter than the occludent margin (Fig. 6B, C, F, G, J, K, N) [exception: basal margin longer than the occludent margin in two very small specimens]. The apex of the tergum is worn smooth only in the largest specimens (Figs 4F, J, 6G, K). In a few specimens, the articular margin of both terga is eroded near distal end, resulting in two rounded indentations (Fig. 6K).

In addition, Newman and Ross (1971) stated, "Terga… with articular margin thrown into sinusoidal curve;" This character is herein described in more detail: Sinusoidal articular margin only fully visible in the internal view of tergum (Fig. 2F, red line); the amplitude of the sinusoidal curve increases as the basal part of the ***var*** develops (compare Fig. 4A, D with Fig. 4F, G). On the other hand, the articular margin is smoothly concave in the external view of tergum, running parallel to the outer edge of the external furrow (Fig. 2E, yellow line; see also Figs 4A, F, J, 6G). In some specimens, the basal part of the ***var*** is more developed in one tergum than in the opposite one (see Fig. 4M, N).

The crest of the labrum (Fig. 7) is slightly concave, with many small serrate setae and a few small teeth just below it; in contrast, Newman and Ross (1971) reported that the crest is smooth. Interior surface of the labrum with a dense bundle of downwardly pointed setae on either side. Palps as described by Newman and Ross (1971).

Mandibles (Fig. 8A, B) agree with the description presented by Newman and Ross (1971) and the photograph of the holotype USNM 125305 (left mandible?) available on the website of the National Museum of Natural History, Smithsonian Institution (link to the NMNH website in the References section).

First maxillae slightly differ from Newman and Ross's (1971) description, i.e., lower lobe rounded (Fig. 8D) or somewhat straighter (Fig. 8C). Lower cutting margin with about 18–22 strong setae and 5–17 short—some of them pectinate—setae, just above the inferior angle (n = 3).

Second maxillae (Fig. 8E) slightly bilobed (not bilobed after Newman and Ross (1971)).

Cirri (Fig. 8F–I), as mentioned by Newman and Ross (1971). The cirral formula is provided in Table 2. Cirrus II: rami subequal in length, anterior ramus with the largest numbers (up to 8) of antenniform articles. Cirrus III: posterior ramus slightly longer than anterior one, carrying the largest number (up to 30) of antenniform articles.

Penis (Fig. 8J), as mentioned by Newman and Ross (1971). A more detailed description is provided: 3 or 4 times longer than the pedicel of cirrus VI, finely annulated along all its length (annuli more evident on proximal two thirds); distal third with small setae lateral and distally. Basidorsal point absent.

Caudal appendages absent.

Settlement and epibionts. Of the 21 specimens of *Tetrachaelasma southwardi* collected at Sta. 25 (1950 m depth), 16 were complete. Most of these specimens were detached from the substrate (Fig. 11C) or attached to single rocks (Fig. 11A). One complete specimen was attached to an isolated CL plate, which has its external surface covered with yellow cuticle and numerous fine bristles and, therefore, most likely belongs to a living specimen of *T. southwardi* that was disarticulated during dredging. In addition, four complete specimens had settled one over the other (Fig. 11D).

Table 2. *Tetrachaelasma southwardi* Newman & Ross, 1971. Cirral formula of four specimens (two collected at 1950 m depth, two at 2934 m depth) from the Mar del Plata Submarine Canyon. Articles not fully separated (partially fused) were counted as single ones. The numbers of antenniform articles of the cirri II and III are given in parentheses. The cirri I-IV of the specimen (MACN-In 44781) are illustrated in Fig. 8.

Specimen (Depth)	Cirral ramus	I	II	III	IV	V	VI
MACN-In 44478l (1950 m)	Left anterior	17	22 (4)	25 (4)	30	32	38
	Left posterior	16	24 (4)	42 (30)	33	36	40
	Right anterior	15	22 (4)	22 (3)	33	36	38
	Right posterior	15	25 (4)	36 (25)	31	36	36
MACN-In 44478f (1950 m)	Left anterior	15	20 (5)	25 (3)	27	30	32
	Left posterior	14	22 (2)	30 (9)	29	30	25
	Right anterior	16	23 (8)	24 (3)	27	29	31
	Right posterior	14	22 (4)	28 (11)	27	32	25
MACN-In 44479d (2934 m)	Left anterior	16	24 (5)	30 (7)	33	34	41
	Left posterior	14	24 (3)	40 (3)	33	39	42
	Right anterior	13	23 (7)	32 (5)	33	39	33
	Right posterior	15	25 (6)	39 (26)	35	38	37
MACN-In 44479h (2934 m)	Left anterior	12	20 (2)	31 (9)	29	33	34
	Left posterior	12	19 (2)	46 (39)	30	32	34
	Right anterior	13	23 (3)	28 (8)	29	34	34
	Right posterior	13	24 (3)	24†	30	33	34

† Broken (terminal articles missing).

Of the eight *T. southwardi* obtained at Sta. 45 (2934 m depth), three were complete. Of these, one small specimen is attached to the R plate of a second one (Fig. 3F, H). The third specimen has a rounded mark on its R and right CL plates, evidence that another specimen had been living on them (Fig. 11F).

Several associations were observed among the materials studied. Two specimens of *T. southwardi* from Sta. 25 (1950 m depth) carried epibionts: one has a soft octocoral *Alcyonium* sp. on its R and left CL plates (Fig. 11C), and the other has tubes of serpulid polychaete worms on its scuta (Fig. 11B). Station 45 (2934 m depth) includes a pilose scalpellid barnacle attached to an isolated R plate (Fig. 11E). As this plate was covered with cuticles and numerous fine bristles, it likely belongs to a living specimen (of *T. southwardi*?) that was disarticulated during dredging. This scalpellid fits well with the diagnosis of the genus *Regioscalpellum* proposed by Gale (2016); however, this author pointed out that the classification of the Scalpellidae is clearly provisional. In addition, one specimen of *T. southwardi*, also from Sta. 25, is attached to a specimen of the genus *Bathylasma* (additional information in the *Bathylasma* sp. section).

Distribution. *Tetrachaelasma southwardi* was previously recorded in the Southern Ocean—from both the

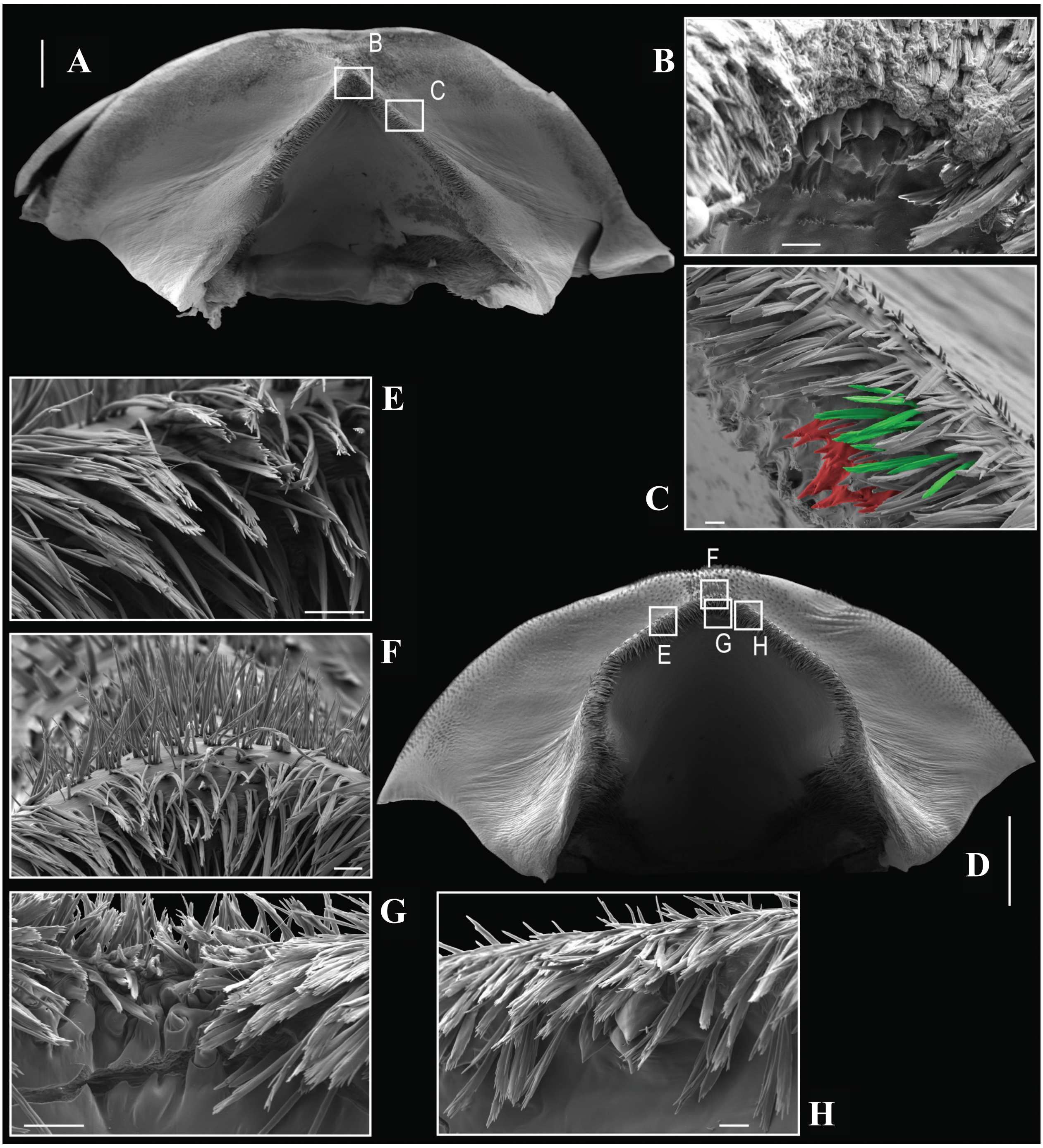

Figure 7. *Tetrachaelasma southwardi* Newman & Ross, 1971. Labrum SEM photographs (palps removed). Specimen (MACN-In 44478b): **A.** General aspect from above; **B, C.** Details of the crest; serrate setae in green, teeth in red. Specimen (MACN-In 44479h): **D.** General aspect from above; **E–H.** Details of the crest. Scale bars: 300 µm (**A, D**); 10 µm (**B, C, E–H**).

Pacific and the Atlantic—and is now reported from the Mar del Plata Submarine Canyon. Depths range: 1190–2934 m. All the records are listed in Table 1 and mapped in Fig. 9.

Remarks. The supplementary description presented above is based on 29 specimens and a few loose plates collected in the Mar del Plata Submarine Canyon at two localities with significantly different depths (1950 m and 2934 m, Fig. 1). All these specimens have been assigned to *Tetrachaelasma southwardi* Newman & Ross, 1971. However, it should be noted that these specimens differ from the original description of *T. southwardi* as follows (characters mentioned in the original description are included in parentheses): (1) the adductor muscle pit of the scutum, which is weakly developed (pit deep, bounded above and lateral by a distinct line); (2) the crest of the labrum with abundant setae (without setae); and (3) the second maxilla, which is slightly bilobed (not bilobed).

(1) In regard to the adductor muscle pit, we had the opportunity to examine images of the scutum of the

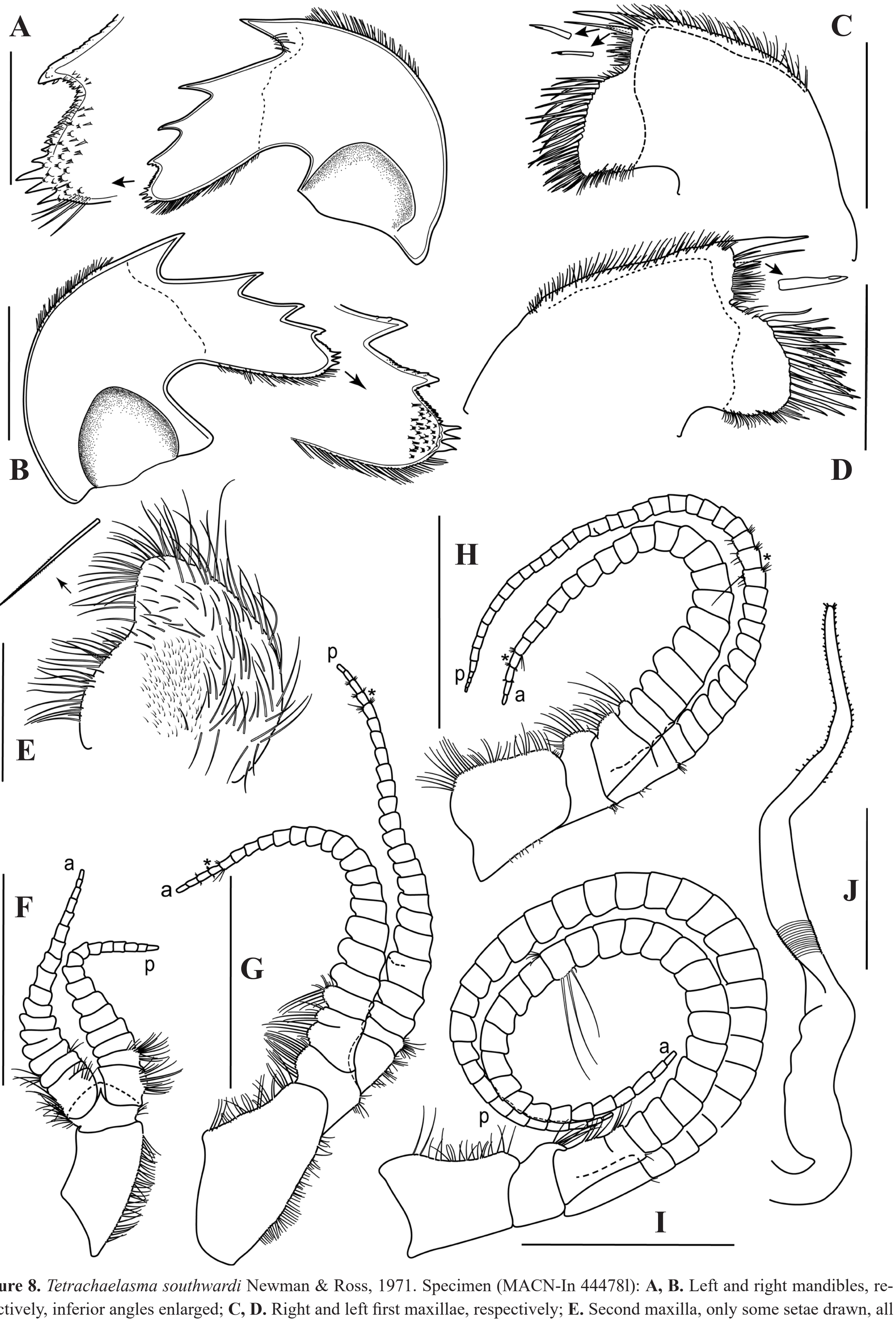

Figure 8. *Tetrachaelasma southwardi* Newman & Ross, 1971. Specimen (MACN-In 44478l): **A, B.** Left and right mandibles, respectively, inferior angles enlarged; **C, D.** Right and left first maxillae, respectively; **E.** Second maxilla, only some setae drawn, all of them serrulate (see detail); **F–I.** Left cirri I-IV, respectively; the first antenniform article is indicated with an asterisk; **J.** penis, only a short section of annuli is drawn. Abbreviations: **a** – anterior ramus; **p** – posterior ramus. Scale bars: 1 mm (**A–E**); 0.5 mm (**F–J**).

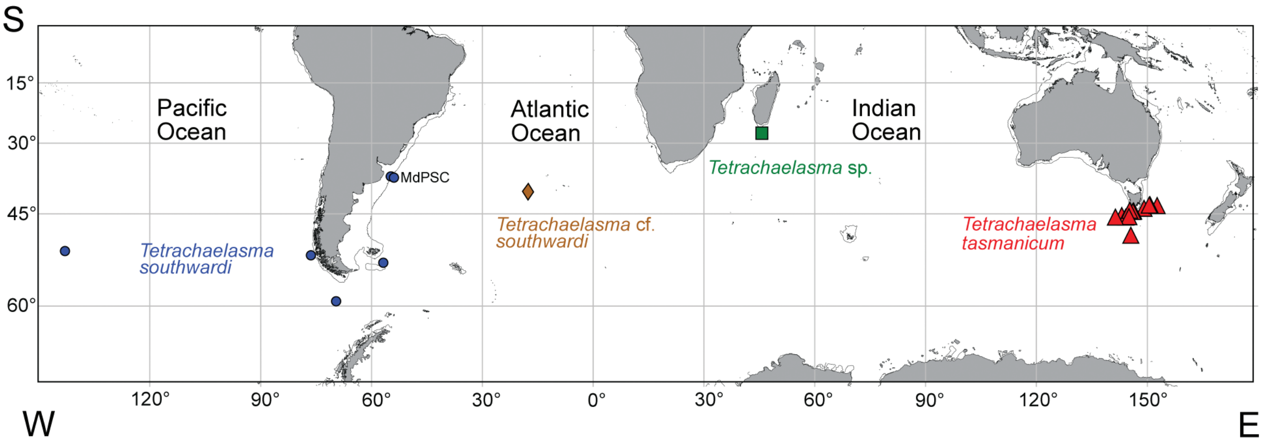

Figure 9. Distribution of the genus *Tetrachaelasma* Newman & Ross, 1971. *T. southwardi* Newman & Ross, 1971 (circles); *T.* cf. *southwardi* (diamond); *T. tasmanicum* Buckeridge, 1999 (triangles); *Tetrachaelasma* sp. (square). See Table 1 for additional information. Abbreviation: **MdPSC** – Mar del Plata Submarine Canyon.

holotype (see Material and Methods). In these images, the adductor muscle pit does not appear to be sharply delimited. However, this character is difficult to quantify and depends on the assessment of the individual taxonomist to some extent.

(2) The crest of the labrum of the material studied herein is covered with many short serrate setae but lacks teeth projecting beyond it. In contrast, Newman and Ross (1971) stated that the crest of the labrum of *T. southwardi* is smooth; however, these authors show in fig. 74G small setae on each side of the crest (see also the Discussion section).

(3) The second maxilla of the material studied herein is slightly bilobed. However, Newman and Ross (1971) wrote, "Second maxillae not bilobed, but setae divided in 2 groups by a median nearly naked area." As the concavity between the two lobes is very shallow in our material (Fig. 8E), this difference with the holotype is subtle.

In addition, the specimens from the Mar del Plata Submarine Canyon show some degree of intraspecific variation in the development of the scutum articular ridge (***sar***) and the tergum vertical articular ridge (***var***), the separation of the tergal spur from the basi-scutal angle, and the tergal basal/occludent proportions. Furthermore, the parietes also show great intraspecific variation, i.e., most of the specimens are roughly conical, but two are columnar (cylindrical). Only one of all these characters, the tergal basal/occludent proportion, seems to be associated with the station, i.e., the terga are usually more elongated in the specimens from 1950 m depth than in those from 2934 m depth. Intraspecific morphological variation has also been reported for other deep-sea barnacles (Chan et al. 2016; Lin et al. 2020). Molecular studies are needed to confirm whether the observed differences in the tergal basal/occludent proportions are phenotypic variations induced by environmental conditions or reflect genetic distance between the specimens from the two sampled stations. However, these studies will only be possible when additional specimens suitable for molecular techniques are available.

Genus *Bathylasma* Newman & Ross, 1971

Bathylasma Newman & Ross, 1971: 142, 143 (diagnosis, list of species, key). —Jones 2000: 231–233 (diagnosis, tables 20, 21, fig. 49 (distribution map)). —Araya and Newman 2018: 4, 5, 10, 11 (diagnosis, table 2, key).

Type species. *Balanus coralliformis* Hoek, 1883.

Bathylasma sp.

Figs 10, 11G

Material examined. ***Talud Continental I*** expedition, RV "Puerto Deseado", Mar del Plata Submarine Canyon, Sta. 25, 37°51.688'S, 54°10.550'W, 1950 m depth, 15 Aug 2012, epibenthic sledge, coll. I. Chiesa. 1 complete specimen assigned to the genus *Bathylasma* (MACN-In 44480), having a specimen of *T. southwardi* (MACN-In 44478l) attached to it.

Remarks. This specimen is assigned to the genus *Bathylasma* Newman & Ross, 1971, by having: six solid wall plates with prominent horizontal growth lines covered with fine bristles; articular margin of tergum straight (not sinusoidal as in *Tetrachaelasma*); and basis membranous. It has the wall plates severely eroded, but the hirsute cuticle remains partially visible on the left CL2.

This genus encompassed four extant and four fossil species (see Araya and Newman 2018). This new finding represents the first record of the genus *Bathylasma* from the South-West Atlantic. In addition, our specimen was collected at 1950 m, a depth comparable to the deepest record for the genus, i.e., 1800–2000 m reported for *Bathylasma chilense* Araya & Newman, 2018 in the South-East Pacific (Araya and Newman 2018).

The *Bathylasma* sp. reported herein has a specimen of *T. southwardi* settled on the C and left CL2 plates. In addition, there is a rounded mark on its R and right CL1 plates, evidence that a second specimen (*T. southwardi*?) had also been affixed to it (Fig. 11G). This is the first time

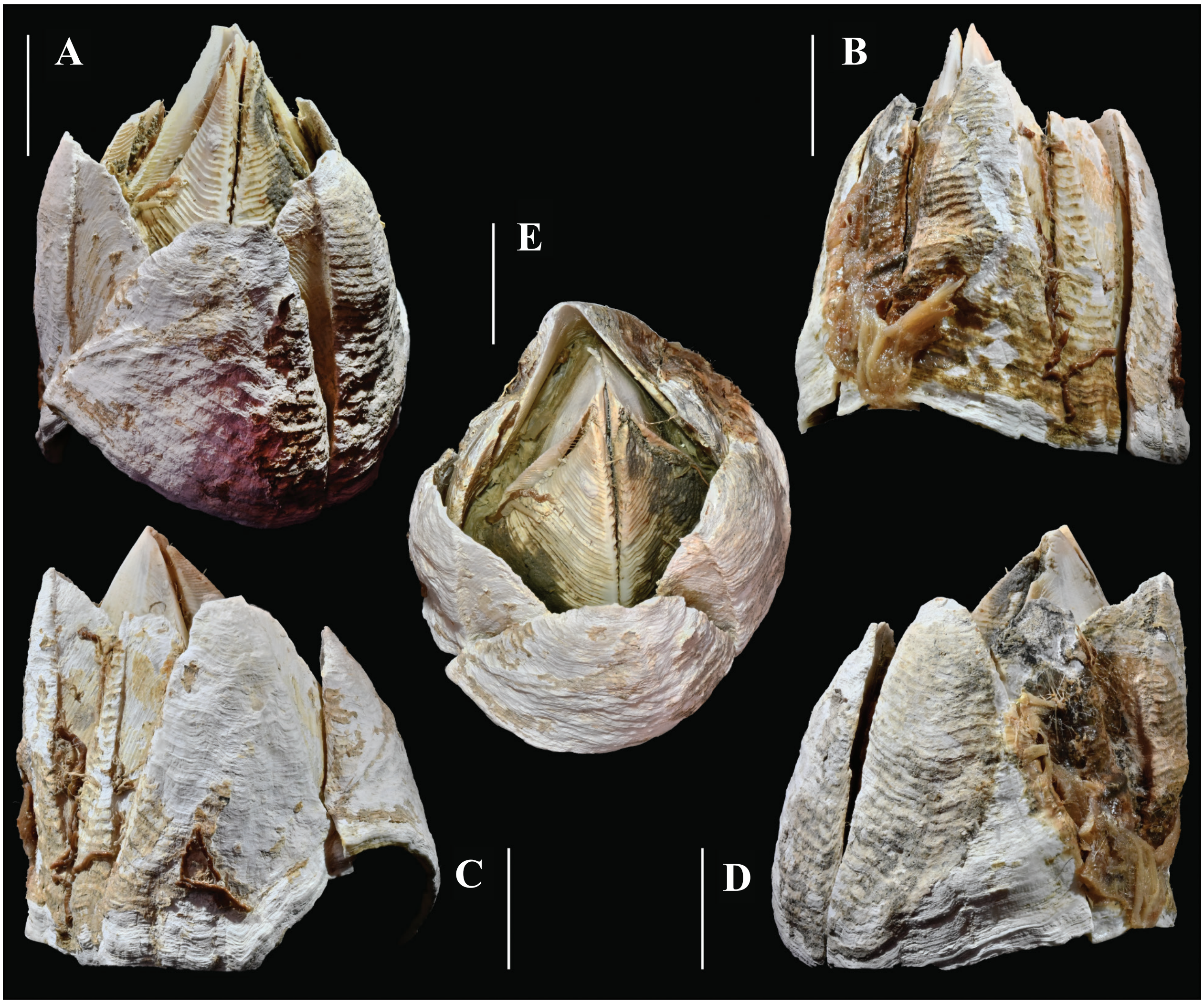

Figure 10. *Bathylasma* Newman & Ross, 1971. Specimen (MACN-In 44480): **A.** Rostral view; **B.** Carinal view; **C, D.** Left and right carinolateral views, respectively; **E.** Top view. Scale bars: 10 mm.

that members of these two genera have been reported living together.

The poor condition of this specimen of *Bathylasma* prevents its identification as a known species or a new species. In order to preserve the only specimen available, it is advisable not to dissect the soft parts of this specimen until additional material is obtained.

Discussion

Taxonomic status of *T. southwardi* and *T. tasmanicum*

Tetrachaelasma encompasses only two species: *T. southwardi* Newman & Ross, 1971, recorded from just a few, widely apart, stations in the Southern Ocean, and *T. tasmanicum* Buckeridge, 1999, restricted to South Tasmania (Table 1, Fig. 9).

Buckeridge (1999) stated that *T. southwardi* and *T. tasmanicum* are two closely related species, distinguished mainly by (1) the tergal articulation (sinusoidal vs. smoothly concave), (2) the ornamentation of the crest of the labrum (smooth vs. with teeth), and (3) the tergal spur (almost contiguous with articular margin vs. removed from articular margin as much as ⅓ its width).

(1) Newman and Ross (1971) stated that the articular margin of the tergum of *T. southwardi* is more or less sinusoidal, a character also used to define the genus. Conversely, Buckeridge (1999) stated that the tergum of *T. tasmanicum* has a smoothly concave articular margin (as opposed to sinusoidal).

The term "sinusoidal" was coined by Newman and Ross (1971) to describe the S-shaped aspect of the tergal articular margin. In our specimens, the sinusoidal margin is only fully visible in the internal view and results from the combination of the concave tergal articular ridge (***tar***) and the convex vertical articular ridge (***var***) (see Fig. 2F, red line). By contrast, in external view, the articular margin is smoothly concave and runs parallel to the outer edge of the external furrow (Fig. 2E, yellow line). Thus, the tergal articular margin is sinusoidal or smoothly concave, depending on the view (internal or external).

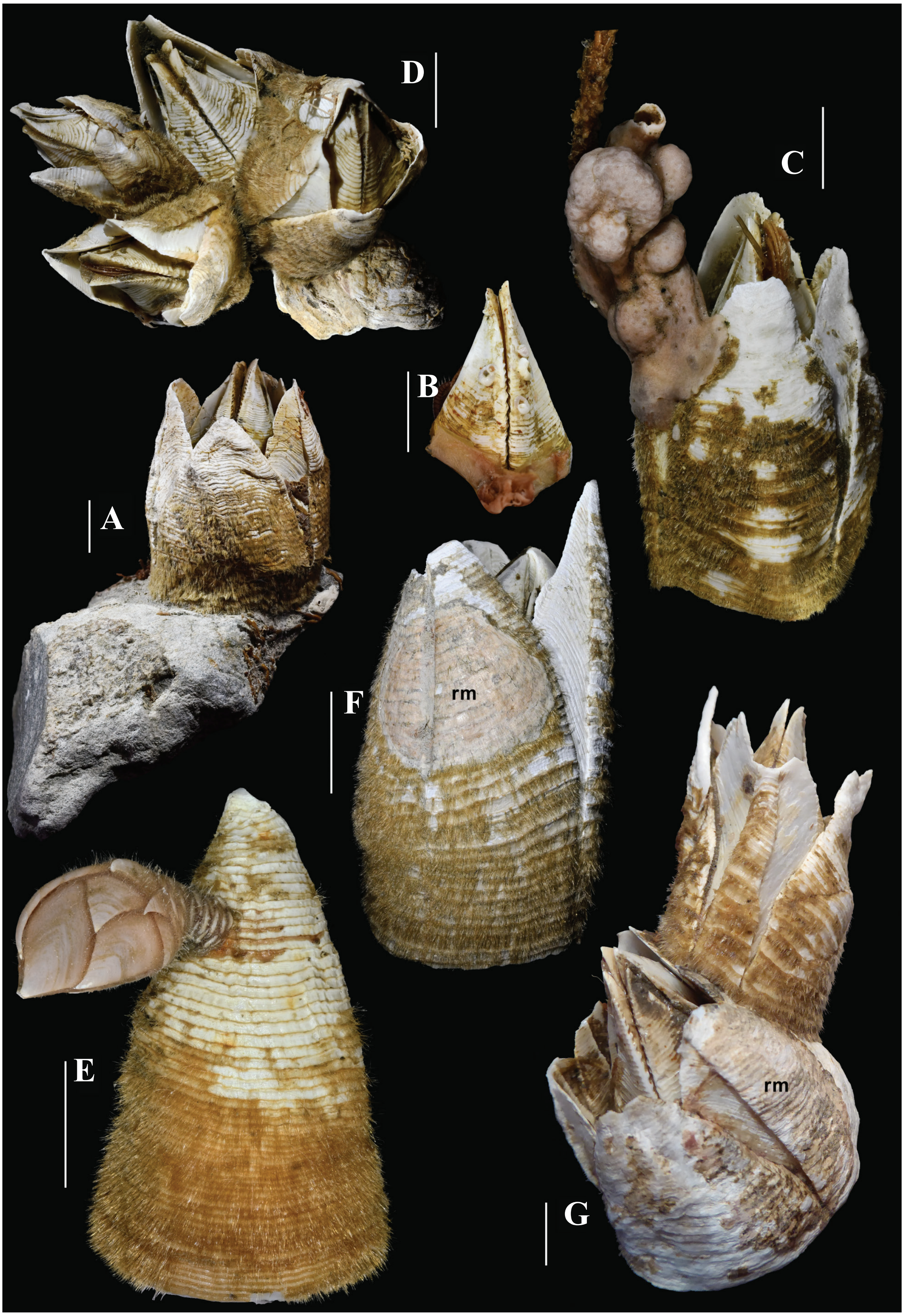

Figure 11. *Tetrachaelasma southwardi* Newman & Ross, 1971. **A.** Specimen (MACN-In 44478e) attached to a rock; **B.** Scuta of specimen (MACN-In 44478p) with serpulid tubes (Polychaeta); **C.** Specimen (MACN-In 44478u) with *Alcyonium* sp. (Octocorallia) epibiont; **D.** Group of four specimens (MACN-In 44478h–k); **E.** Isolated rostral plate (MACN-In 44479i) with a *Regioscalpellum* sp. (Scalpellidae) on it; **F.** Specimen (MACN-In 44479c) with a rounded mark left by another specimen attached to it. *Bathylasma* Newman & Ross, 1971. **G.** Specimen (MACN-In 44480) with a *T. southwardi* specimen attached to it and a rounded mark left by a second balanomorph barnacle. Abbreviation: **rm** – rounded mark.

Newman and Ross (1971: pl. XXVI) presented images of the tergum of the holotype of *T. southwardi*. In these images, the articular margin of the tergum looks sinusoidal in both external (fig. E) and internal (fig. G) views. However, in the holotype, the articular margin is eroded in the middle part, and the external furrow is eroded distally. This condition was confirmed after examining high-resolution images of the holotype, which is deposited in the NMNH, Smithsonian Institution (see Material and Methods). In conclusion, the S-shaped aspect of the articular margin of the tergum of the holotype, in external view, is due to it being worn in the middle part.

Based on this new information, it appears that the tergal articular margin of both *T. southwardi* (including the type material and our specimens) and *T. tasmanicum* do not differ from each other, i.e., the articular margin is sinusoidal in the internal view and smoothly concave in the external view for both species. Thus, the S-shaped tergal articular margin is an important character to define the genus, but it seems not to be a reliable character to separate its two current species.

(2) The labrum of the specimens herein examined has short serrate setae on the crest and small teeth contiguous to them on its inner surface, i.e., teeth are neither on the top of the crest nor projecting beyond the crest. Newman and Ross (1971) stated that the crest of the labrum of *T. southwardi* is smooth. Although neither setae nor teeth are shown in the central part of the crest by these authors in fig. 74H, setae are shown on the lateral part of the crest in fig. 74G. It remains to be confirmed whether the central setae are actually absent in the holotype of *T. southwardi*. One possibility is that the holotype´s setae were worn, detached, or covered with biofilm (see embedded top setae in Fig. 7B), thus preventing their observation under a light microscope. In contrast, Buckeridge (1999) stated that *T. tasmanicum* has small teeth on the crest of the labrum. However, fig. 4D presented by this author is not detailed enough, and there is a possibility that the teeth are actually setae. It is worth noting that high magnification is necessary to distinguish small teeth from short serrate setae. Thus, the type material of these two species should be re-examined, preferably under SEM, to clarify this matter.

(3) The distance that separates the tergal spur from the articular margin is quite variable in our material. Thus, this character does not appear to be useful to separate *T. southwardi* from *T. tasmanicum*.

One character not mentioned in previous descriptions is the shape of the basal margin of the scutum. This appears to be gently convex in the holotype of *T. southwardi* (see figs F and H in pl. XXVI, in Newman and Ross (1971)), and also in our material (Figs 4, 6). In contrast, in *T. tasmanicum*, the basal margin of the scutum is strongly flexed, with an obtuse angle of about 120 degrees (see figs 1C, 2C, D in Buckeridge (1999)).

In addition, neither Newman and Ross (1971) nor Buckeridge (1999) reported the ratio between the basal and occludent margins of the tergum. The basal/occludent ratio of the holotype of *T. southwardi* was calculated from high-resolution images provided by the curator of the NMNH (see Material and Methods). These images correspond to figs E and G (pl. XXVI) presented by Newman and Ross (1971). In addition, the basal/occludent ratio of *T. tasmanicum* was calculated based on figs 2C and D (Buckeridge 1999). These measurements result in a basal margin longer than the occludent margin for the holotype of *T. southwardi* and similar basal and occludent lengths for the holotype of *T. tasmanicum*. However, this comparison is based on indirect evidence obtained from the holotypes. The examination of additional specimens from both type localities (Central South Pacific and South Tasmania) is required to confirm whether or not these two species differ in their basal/occludent ratio of the tergum.

The cuticular growth lines are related to the molting cycle, but how these lines depend on parameters such as food availability, temperature, and other environmental factors is unknown for deep-sea barnacles (Yusa et al. 2018). In a large columnar specimen (MACN-In 44479a) collected at 2934 m depth and in a few isolated plates (MACN-In 44479i) from the same station, most basal horizontal growth lines are narrowly spaced (Figs 3F, G, 11E). Newman and Ross (1971) did not have columnar specimens, but the holotype, a medium-sized (carina: ca. 2.9 mm) conical individual, shows a few narrowly spaced horizontal growth lines basally (see figs A–C in pl. XXVI, in Newman and Ross (1971)). It is worth noting that the holotype of *T. tasmanicum*, a large columnar specimen, has narrowly spaced horizontal growth lines. However, these closely spaced lines are not confined to the basal part of the parietes but extend along their entire surface (figs 1A, B, in Buckeridge (1999)). This narrowly spaced pattern was also observed in additional columnar specimens of *T. tasmanicum* collected recently (see the CSIRO-MIIC website in the References section CSIRO-MIIC 2024).

In conclusion, *Tetrachaelasma southwardi* and *T. tasmanicum* are suspected to be cryptic species that require additional morphological and molecular studies to be distinguished from each other.

Distribution and biology of the genus *Tetrachaelasma*

Tetrachaelasma southwardi was not common among the material collected during the Talud Continental I, II, and III expeditions. This species was found in only two out of the 46 stations taken between 1000 m and 3447 m depth during these three surveys. No images were captured or quantitative data recorded at any of the 46 stations sampled, preventing an assessment of the abundance of *T. southwardi*. However, finding 29 specimens in these two samples suggests that this deep-sea barnacle could be relatively abundant in some benthic assemblages in the Mar del Plata Submarine Canyon. In support of this, a deep-sea barnacle tentatively identified as *T. tasmanicum* was reported at high density (32.1 ind/m^2) off southern Tasmania at 2171 m depth (Thresher et al. 2014).

Regarding the presence of *T. southwardi* in southern South America, only loose plates have been reported until now. These plates were collected by the RV "Eltanin" in 1962 and 1965, off the Malvinas/Falkland Is. (1720–1739 m depth), at the Sars Bank in the Drake Passage (1207–1591 m depth), and off southern Chile (1190–1263 m depth) (see Newman and Ross (1971); Table 1, Fig. 9). The current record of *T. southwardi* at ca. 37°50'S is the most septentrional latitude reported for this species in the South-West Atlantic. This finding, however, is not entirely unexpected, as many other benthic invertebrate species that are distributed in Antarctic and/or sub-Antarctic waters have also been recorded from the Mar del Plata Submarine Canyon (Farias et al. 2015; Olguín et al. 2015; Pastorino 2016, 2019; Pastorino and Sánchez 2016; Roccatagliata and Alberico 2016; Lauretta and Penchaszadeh 2017; Rivadeneira et al. 2017; Maggioni et al. 2018; Bernal et al. 2019, 2021; Lauretta and Martinez 2019; Teso et al. 2019; Pereira et al. 2020; Roccatagliata 2020; Flores et al. 2021; Pertossi et al. 2021; Rumbold et al. 2021; Schejter et al. 2021; Pacheco et al. 2022; Pereira 2022; Sánchez et al. 2023). This distribution pattern can be explained by the presence of the Malvinas/Falklands Current, a branch of the Antarctic Circumpolar Current (ACC) that flows northward along the continental slope of Argentina up to around 38°S (Piola and Gordon 1989; Matano et al. 2010).

Tetrachaelasma species inhabit great depths around the Southern Ocean (Fig. 9). Most of its distribution area is under the influence of the Antarctic Circumpolar Current. The ACC is a large and strong ocean current that encircles Antarctica and connects the major ocean basins—the Pacific, Atlantic, and Indian Oceans (Rintoul et al. 2001). This current flows eastward between 40° and 60°S, and its influence extends to the seafloor down to 4000 m depth (Orsi et al. 1995; Barker and Thomas 2004; Barker et al. 2007; Dueñas et al. 2016).

Circumpolar Subantarctic/Antarctic distributions have been documented for *Bathylasma corolliforme* (Hoek, l883) as well as for other living and fossil barnacles (Newman and Ross 1971; Buckeridge 2015). This circumpolar distribution has also been reported for many other invertebrates, including stylasterid corals, molluscs, echinoids, sea stars, isopods, and decapods (Leese et al. 2010; Díaz et al. 2011; Pérez-Barros et al. 2014; Farias et al. 2015; Moles et al. 2015; Dambach et al. 2016; Pastorino 2016; Lauretta and Martinez 2019; Güller et al. 2020; Bernal et al. 2021; Pacheco et al. 2022).

Knowledge about the life cycle of deep-sea balanomophs is very limited, and no information is available on the *Tetrachaelasma* species. A closely related Antarctic deep-sea species, *Bathylasma corolliforme*, has nauplius larvae that are well adapted to planktonic life (Dayton et al. 1982; Foster 1989). Thus, it can be inferred that the members of *Tetrachaelasma* have free nauplii as well.

Seamounts are numerous but poorly sampled in the Southern Ocean and may act as stepping stones for species dispersal (Auscavitch and Waller 2017). Due to the patchy distribution of hard substrata in the deep sea, barnacle larvae must travel long distances on inhospitable soft bottoms to reach a suitable habitat for settlement. Therefore, it is expected that the nauplius larvae of *T. southwardi* have an extended life and are passively transported over long distances by the ACC (and off Argentina by one of its branches, the Malvinas/Falklands Current). A comparable hypothesis was proposed by Buhl-Mortensen and Høeg (2006) for the dispersal of the widespread deep-sea *Arcoscalpellum michelottianum* (Seguenza, 1876).

Bathylasma hirsutum (Hoek, 1883) and *B. corolliforme* feed passively, with the cirri simply extending into the current (Southward and Southward 1958; Dayton et al. 1982). Since *Bathylasma* is a genus closely related to *Tetrachaelasma*, we can assume that its members are also passive feeders. The presence of medium to strong bottom currents around the Mar del Plata Submarine Canyon (see Steinmann et al. 2020; Bozzano et al. 2021) supports this hypothesis.

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