

New species of *Rockacestus* (Cestoda, Phyllobothriidea) from skates of the genus *Bathyraja* (Rajiformes, Arhynchobatidae) in the Southwestern Atlantic Ocean with comments on the distribution of the genus

Guillermina García Facal^{1,2}, Verónica A. Ivanov^{1,2†}, Adriana Menoret^{1,2}

1 Universidad de Buenos Aires, Facultad de Ciencias Exactas y Naturales, Departamento de Biodiversidad y Biología Experimental, Laboratorio de Sistemática y Biología de Parásitos de Organismos Acuáticos (SIBIPOA), Buenos Aires, Argentina

2 CONICET-Universidad de Buenos Aires, Instituto de Biodiversidad y Biología Experimental (IBBEA), Buenos Aires, Argentina

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Corresponding author: Guillermina García Facal (guillefacal@gmail.com); Adriana Menoret (menoret.a@gmail.com)

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Abstract

Three new species of *Rockacestus* Caira, Bueno & Jensen, 2021 were recovered from arhynchobatid skates taken between 37°S–55°S in the Magellanic Province, Southwestern Atlantic Ocean. *Rockacestus blasi* **sp. nov.** was found in *Bathyraja macloviana* (Norman, 1937), whereas *Rockacestus magellanicus* **sp. nov.**, and *Rockacestus ottaviano* **sp. nov.** were found in *Bathyraja magellanica* (Philippi, 1902). These species differ from their congeners in having a particular combination of anatomical features, including a moderate to highly folded bothridia, presence of a uteroduct, and a seminal receptacle. Cross-sections of mature proglottids were made for the first time in members of the genus. In addition, the microthrix pattern was described in detail, focusing on the distal bothridial surface, including the apical sucker and marginal loculi resulting in a common microthrix configuration with filitriches and small lanceolate, lingulate, and a particular kind of coniform spinitriches. The diagnosis of *Rockacestus* is revised to include several features exhibited by the new species. The distribution data of the species currently assigned to *Rockacestus* are compiled and updated. The finding of *R. blasi* **sp. nov.**, *R. magellanicus* **sp. nov.**, and *R. ottaviano* **sp. nov.** not only increases the number of members of *Rockacestus* in the Magellanic Province in the Southwestern Atlantic from one to four but also expands our knowledge of phyllobothriideans and their association with the softnose skates of the genus *Bathyraja* Ishiyama, 1958 in the Southern Hemisphere.

Key Words

Bathyraja, genus distribution, MPA Namuncurá/Burdwood Bank, *Rockacestus blasi* sp. nov., *Rockacestus magellanicus* sp. nov., *Rockacestus ottaviano* sp. nov., Southern Hemisphere

Introduction

The genus *Rockacestus* Caira, Bueno & Jensen, 2021 was recently erected to house phyllobothriidean species bearing folded bothridia, with apical sucker and marginal loculi, which parasitize rajiform skates (Caira et al. 2021).

The genus currently comprises ten species formally described from Arhynchobatidae and Rajidae skates, mostly inhabiting temperate and cold waters in the Northern and Southern Hemispheres (Kay 1942; Williams 1968a,

1968b; Schmidt 1986; Wojciechowska 1991; Caira et al. 2021). *Rockacestus brittanicus* (Williams, 1968) described from *Raja montagui* Fowler, 1910, *Rockacestus williamsi* (Schmidt, 1986) recovered from *Leucoraja fullonica* (Linnaeus, 1758), and *Rockacestus piriei* (Williams, 1968) found in *Leucoraja naevus* (Müller & Henle, 1841) were reported from the Northern European Seas Province sensu Spalding et al. (2007) (see Williams 1968a, 1968b). Caira et al. (2021) described *Rockacestus carvajali* Caira, Bueno & Jensen, 2021 from *Dipturus chilensis* (Guichenot, 1848) off Chilóe

† This paper was mostly discussed prior to the death of Verónica A. Ivanov in January 2020.

between the limits of the Magellanic and the Warm Temperate Southeastern Pacific Provinces, while *Rockacestus radioductus* (Kay, 1942) was found in *Beringraja binoculata* (Girard, 1855) in the Cold Temperate Northeast Pacific (Kay 1942; Caira et al. 2021). *Rockacestus conchai* Caira, Bueno & Jensen, 2021 was recovered from *Bathyraja albomaculata* (Norman, 1937) off Malvinas Islands in the Magellanic Province (Caira et al. 2021). The remaining four species of *Rockacestus* registered from the southernmost latitudes to date (i.e., *Rockacestus arctowskii* [Wojciechowska, 1991], *Rockacestus georgiensis* [Wojciechowska, 1991], *Rockacestus rakusai* [Wojciechowska, 1991], and *Rockacestus siedleckii* [Wojciechowska, 1991]) mostly parasitize skate species of the genus *Bathyraja* Ishiyama, 1958 with records in the Scotia Sea, and the Continental high Antarctic Province (Wojciechowska 1991).

During fieldworks conducted between 2011–2016 off Argentina in the Southwestern Atlantic Ocean (SWA), skates of the genus *Bathyraja* were found to be parasitized with cestodes of three new species of *Rockacestus*. The descriptions of the new species include detailed morphological features; cross-sections of mature proglottids are presented for the first time for the genus. Likewise, more information on microtriches of the genus is presented.

Materials and methods

Sampling

Tapeworms examined in this study were collected from a total of ten skates belonging to two species of the genus *Bathyraja*: five specimens of *Bathyraja macloviana* (Norman, 1937) and five specimens of *Bathyraja magellanica* (Philippi, 1902) (Rajiformes, Arhynchobatidae). The skates were caught from different localities along the SWA. Three specimens of *B. macloviana* were caught off Río Grande, Tierra del Fuego Province at 54°29.50'S, 65°3.16'W (assigned unique host number PD3-026), off Necochea, Buenos Aires Province at 39°53.99'S, 57°0.64'W (PD3-255) and 39°52.64'S, 56°38.72'W (PD3-257) all in March 2011. Two specimens of *B. macloviana* were caught off Villa Gesell, Buenos Aires Province at 37°33.10'S, 55°19.20'W (PD5-205) in August 2012 and off the Marine Protected Area Namuncurá/Burdwood Bank at 53°55.92'S, 61°31.93'W (PD12-430) in April 2016. Additionally, one specimen caught off Buenos Aires Province at 39°34.28'S, 56°16.16'W was examined in March 2011 and showed no signs of infection with phyllobothriideans. The specimens of *B. magellanica* were caught off Río Grande, Tierra del Fuego Province at 53°26.35'S, 64°58.56'W (assigned unique host number PD4-059) and 54°1.68'S, 67°6.81'W (PD4-097) in April 2012, 53°51.36'S, 67°03.84'W (PD10-039) in March 2014, 54°19.91'S, 64°14.26'W (PD12-479) in April 2016, and off the Marine Protected Area Namuncurá/Burdwood Bank at 54°32.60'S, 60°1.28'W (PD12-045) in March 2016. Also, five uninfected specimens were caught off Tierra del Fuego Province at 55°03.34'S, 66°07.82'W in March 2014. All hosts were obtained with

bottom trawls on board the RV *Puerto Deseado* (CONICET). All tapeworms were removed from the spiral intestine of their respective host, relaxed in seawater, fixed in 10% formalin, and transferred to 70% ethanol for storage.

Preparation of specimens for light microscopy and scanning electron microscopy

Methods for preparing specimens as whole mounts for descriptive work using light microscopy and scanning electron microscopy (SEM) followed Menoret and Ivanov (2021). The terminal proglottid of one specimen of *Rockacestus* from *B. macloviana*, one tapeworm of *Rockacestus* from *B. magellanica*, and one detached mature proglottid of a specimen of *Rockacestus* from *B. magellanica* were embedded in paraffin, and serial cross-sections were cut at a thickness of 8 µm. Sections were stained with Harris' haematoxylin, counterstained with eosin, and mounted in Canada balsam. Whole mounts and histological sections were examined and measured using Olympus BX 51 and Zeiss Axioscope compound microscopes. Micrographs of whole mounts and histological sections were taken using Olympus LC30 camera; drawings were made with the aid of a drawing tube, both attached to the Olympus BX 51 compound microscope. Measurements are expressed as the range, followed in parentheses by the mean, standard deviation (when $n \geq 3$), and the number of worms from which the measurements were taken. Measurements of genitalia and reproductive structures were taken from mature proglottids of mature and gravid worms. All measurements are in micrometres unless otherwise stated.

Mapping and geographic sites

Geographic coordinates in degrees and minutes of type locality and additional localities of the species of the species of *Rockacestus* were extracted from the original descriptions. Estimated coordinates were assigned to those records that lacked such information in the original publication. The geographic distribution of the *Rockacestus* species was charted using the PANMAP software v.0.9.6 (Diepenbroek et al. 2002).

Terminology

Terminology of microtriches follows Chervy (2009). Valid species of *Rockacestus* follow Caira et al. (2021). Valid host names follow Froese and Pauly (2023). Marine bioregions follow Spalding et al. (2007) for a global scale and Sabadin et al. (2020) for regionalization in the SWA.

Material examined and museum abbreviations

The museum material examined includes light micrographs of one paratype of *R. carvajali* (USNM No.

1638652), and two paratypes of *R. conchali* (USNM Nos. 1638654 and 1638655), provided by Anna Phillips from the Smithsonian National Museum of Natural History–Invertebrate Zoology Collection, Washington, D.C., USA. Museum abbreviations are as follows: MACN-Pa, Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina; MLP-He, Museo La Plata, Colección Helminológica, Buenos Aires, Argentina.

Results

Order Phyllobothriidea Caira, Jensen, Waeschenbach, Olson & Littlewood, 2014

Genus *Rockacestus* Caira, Bueno & Jensen, 2021

Rockacestus blasi sp. nov.

<https://zoobank.org/E014EFBD-32EB-489A-9449-B1E5B4D45A9D>

Figs 1A, 2, 3, 7A–C, 8

Type material. *Holotype* whole mature worm, off Villa Gesell, Buenos Aires Province, Argentina (37°33.10'S, 55°19.20'W), 98.7 m, 06 Aug. 2012, A. Menoret leg., MACN-Pa No. 783.

Paratypes 1 whole mature worm, 1 whole gravid worm, 1 detached gravid proglottid, same data as holotype, MACN-Pa Nos. 784/1–3. One detached gravid proglottid, same data as for preceding, MLP-He No. 8097. One whole mature worm, 1 detached gravid proglottid, off Río Grande, Tierra del Fuego Province, Argentina (54°29.50'S, 65°3.16'W), 133 m, 16 Mar. 2011, V. A. Ivanov & A. Menoret leg., MACN-Pa Nos. 786/1–2. Nine whole gravid worms, cross-section of 2 attached mature proglottid, off Necochea, Buenos Aires Province, Argentina (39°52.64'S, 56°38.72'W), 91.3 m, 27 Mar. 2011, V. A. Ivanov & A. Menoret leg., MACN-Pa Nos. 785/1–9, 785/11–24. Three whole gravid worms, same data as for preceding, MLP-He No. 8096. One whole gravid worm, off Necochea, Buenos Aires Province, Argentina (39°53.99'S, 57°0.64'W), 94 m, same data as for preceding, MACN-Pa No. 785/10. One whole immature worm, off the Marine Protected Area Namuncurá/Burdwood Bank, Argentina (53°55.92'S, 61°31.93'W), 184 m, 19 Apr. 2016, A. Menoret leg., MACN-Pa No. 787.

Description. Based on 18 specimens (14 whole gravid worms, 3 whole mature worms, 1 immature worm), 3 detached gravid proglottids, cross-sections of 1 mature proglottid, and 3 scoleces examined with SEM. Worms apolytic, proglottids craspedote. Specimens possessing mature proglottids, 26.8–45.2 (35.7 ± 9.2 , $n = 3$) mm long, 140–204 (163 ± 36 , $n = 3$) proglottids per worm. Specimens possessing gravid proglottids, 22.3–50.9 (36.1 ± 7.6 , $n = 14$) mm long, 106–162 (128 ± 18 , $n = 14$) proglottids per worm (Fig. 1A). Maximum width at level of scolex or immature proglottid. Scolex composed of 4 bothridia, 400–830 (621 ± 127 , $n = 17$) long, 580–1,220 (891 ± 193 , $n = 17$) wide. Bothridia folded, 375–685 (506 ± 100 , $n = 8$) long, 425–750 (571 ± 113 , $n = 8$) wide when folded, sessile anteriorly, free posteriorly; with apical sucker and



Figure 1. Light micrographs of whole worms of *Rockacestus* from the Southwestern Atlantic Ocean. **A.** *Rockacestus blasi* sp. nov. (holotype MACN-Pa No. 783) from *Bathyrāja macloviana*; **B.** *Rockacestus magellanicus* sp. nov. (holotype MACN-Pa No. 789) from *Bathyrāja magellanicus*; **C.** *Rockacestus ottaviano* sp. nov. (holotype MACN-Pa No. 793) from *Bathyrāja magellanicus*.

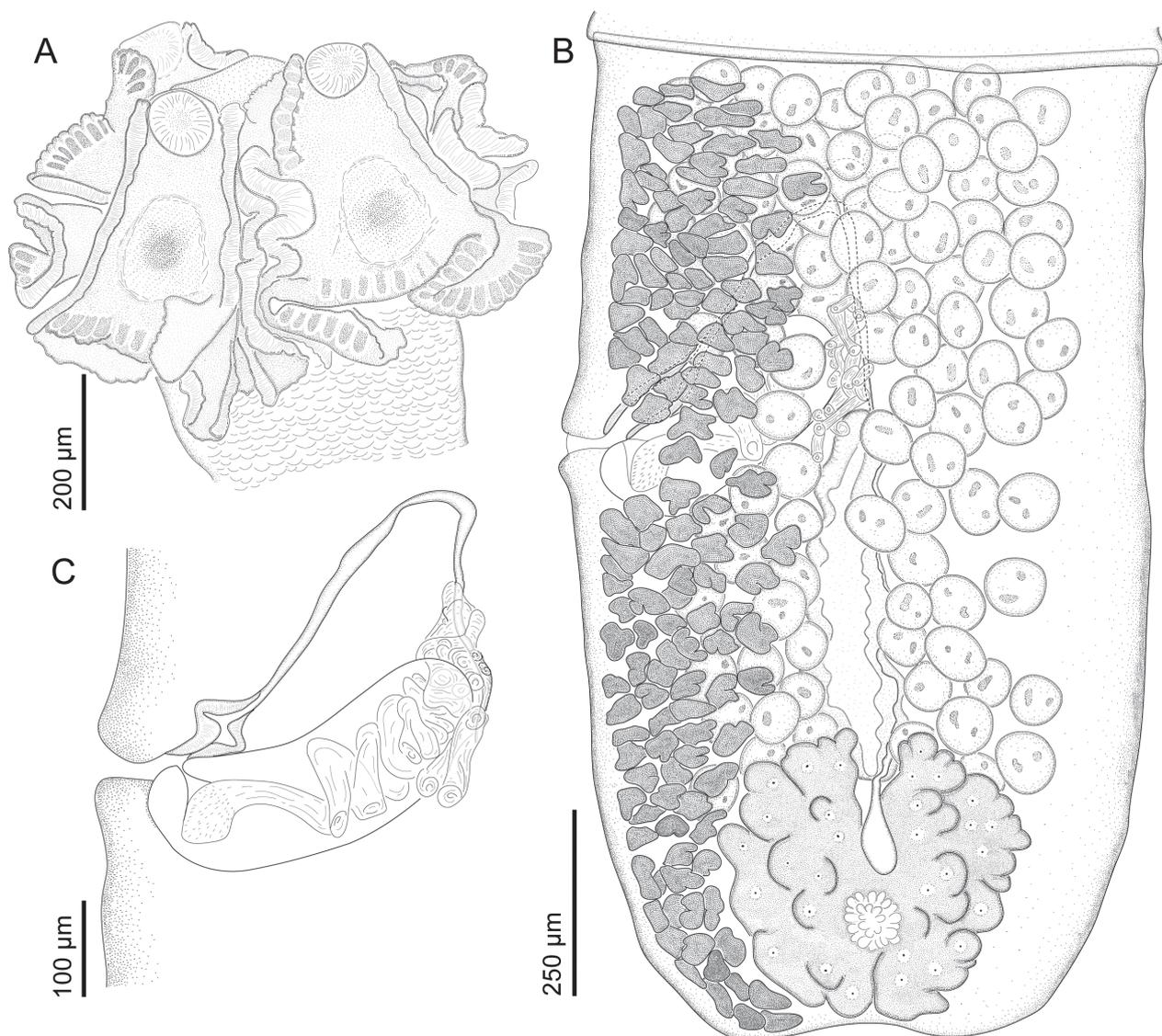


Figure 2. Line drawings of *Rockacestus blasi* sp. nov. from *Bathyraja macloviana*. **A.** Scolex (holotype MACN-Pa No. 783); **B.** Terminal mature proglottid (holotype MACN-Pa No. 783); **C.** Detail of terminal genitalia, terminal mature proglottid (holotype MACN-Pa No. 783).

marginal loculi (Figs 2A, 3A, 8B). Posterior part of each bothridium with weak depression surrounded by circular band of muscle (Fig. 2A). Apical sucker, 80–123 (107 ± 14 , $n = 13$) long, 85–135 (113 ± 13 , $n = 13$) wide (Figs 2A, 3A, B). Cephalic peduncle, absent. Neck 8.8–18.5 (14.0 ± 3.0 , $n = 17$) mm long.

Apex of scolex proper covered with acicular filitriches. Proximal bothridial surface covered with acicular filitriches (Fig. 3I). Distal bothridial surface covered with acicular filitriches interspersed with lingulate spinitriches, lingulate spinitriches increasing in density posteriorly (Fig. 3F, J). Distal surface of apical sucker covered with acicular filitriches interspersed with lingulate spinitriches; posterior half of external rim of apical sucker with small lanceolate spinitriches (Fig. 3B–E). Distal surface of marginal loculi covered with papilliform to acicular filitriches interspersed with short coniform spinitriches (Fig. 3G, H). Capilliform filitriches

on neck and strobila arranged in scutes (Fig. 3K). Cilia not observed.

Specimens possessing mature proglottids with 133–202 (158 ± 38 , $n = 3$) immature proglottids and 2–7 (5 ± 3 , $n = 3$) mature proglottid per worm. Mature proglottids becoming longer than wide posteriorly (Fig. 1A). Terminal mature proglottid, 940–1,360 ($1,180 \pm 216$, $n = 3$) long, 600–800 (727 ± 110 , $n = 3$) wide, length-to-width ratio, 1.6–1.7 (1.6 ± 0.1): 1. Specimens possessing gravid proglottids with 99–146 (120 ± 17 , $n = 14$) immature proglottids, 4–8 (7 ± 1.5 , $n = 14$) mature proglottids, and 1–2 (1 ± 0.4 , $n = 14$) gravid proglottids per worm. Gravid proglottids longer than wide. Terminal gravid proglottid, 1,180–1,820 ($1,591 \pm 203$, $n = 14$) long, 620–970 (783 ± 97 , $n = 14$) wide, length-to-width ratio, 1.4–2.9 (2.1 ± 0.4): 1 (Fig. 2B).

Testes spherical to slightly oblong, 75–96 (86 ± 9 , $n = 4$) in total number, 55–88 (78 ± 10 , $n = 17$) long, 54–

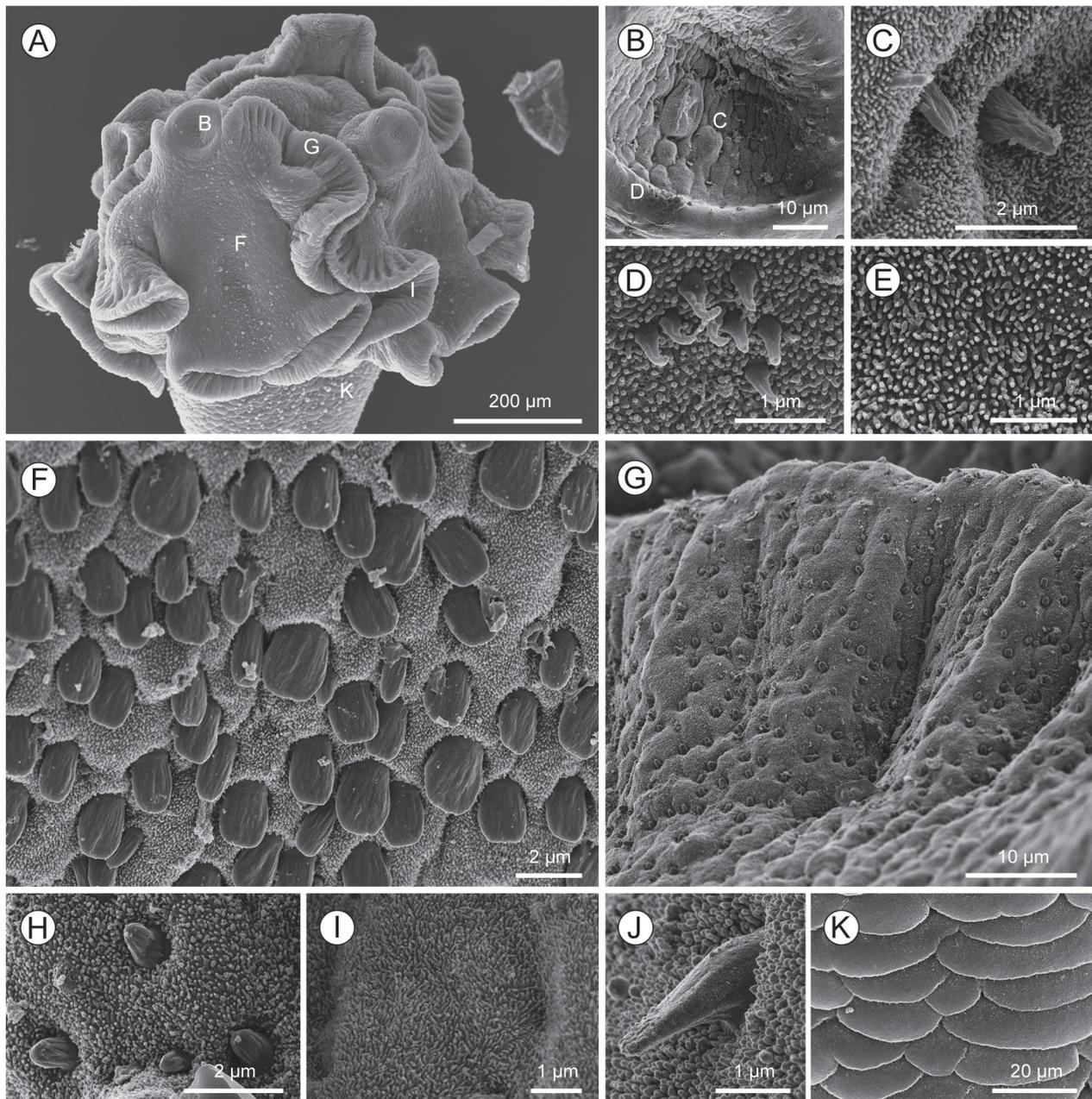


Figure 3. *Rockacestus blasi* sp. nov. from *Bathyraja macloviana*, scanning electron micrographs. **A.** Scolex, small letters indicate the location of details shown in Fig. 3B, 3F–G, 3I, 3K; **B.** Apical sucker, small letters indicate location of detail shown in Fig. 3C–D; **C.** Distal surface of apical sucker, acicular filitriches and lingulate spinitriches; **D.** Surface of the external apical sucker rim, lanceolate spinitriches; **E.** Detail of distal surface of the apical sucker, acicular filitriches; **F.** Distal bothridial surface, lingulate spinitriches; **G.** Distal surface of marginal loculi, acicular filitriches and short coniform spinitriches; **H.** Detail of distal surface of marginal loculi; **I.** Proximal bothridial surface, acicular filitriches; **J.** Distal bothridial surface, detail of lingulate spinitriches; **K.** Scutes on surface of neck.

93 (77 ± 10 , $n = 17$) wide, extending from anterior margin of proglottid to anterior quarter of the ovary; arranged in 6–8 columns anteroposteriorly and 3–4 layers deep in cross-section observed in anterior portion of proglottid (Figs 2B, 7A). Postvaginal testes present. Cirrus sac oval, curved anteriorly, 276–450 (379 ± 42 , $n = 16$) long, 115–175 (148 ± 19 , $n = 16$) wide. Cirrus coiled, armed with minute spinitriches. Vas deferens highly coiled, anterior and adjacent to medial margin of cirrus sac, entering cirrus sac through anterior margin (Figs 2B, C, 7B).

Ovary lobulated, H-shaped in frontal view, X-shaped in cross-section at level of isthmus, 230–580 (350 ± 79 , $n = 17$) long, 250–610 (456 ± 83 , $n = 17$) wide (Figs 2B, 7C). Vagina thick-walled, extending anteriorly from ootype region forming a seminal receptacle, then running laterally along vas deferens bulk to anterior quarter of proglottid, recurving posteriorly to enter genital atrium anterior to cirrus sac (Figs 2B, C, 7C). Vagina and cirrus open into a small common genital atrium, 40–85 (66 ± 14 , $n = 16$) deep. Genital pores al-

ternate irregularly, 54–73% (61 ± 5 , $n = 17$) of proglottid length from posterior margin of proglottid. Vitellarium follicular, follicles irregular in shape, 31–52 (41 ± 9 , $n = 17$) long, 50–80 (70 ± 10 , $n = 17$) wide, arranged in 2 lateral bands almost reaching midline in anterior third of proglottid, each band consisting of multiple columns (5 columns of follicles anterior to cirrus sac), extending throughout the length of proglottid, uninterrupted by ovary, partially interrupted by genital atrium (Figs 2B, 7A–C). Uterus saccate, restricted to region between ovary and cirrus sac, running anteriorly up to genital pore level; uterine duct not observed (Fig. 2B). Mehlis' gland, 80–115 (101 ± 8 , $n = 15$) long, 60–110 (94 ± 13 , $n = 15$) wide, posterior to the ovarian isthmus (Fig. 2B).

Detached gravid proglottids, 2,300–2,525 ($2,392 \pm 118$, $n = 3$) long, 725–775 (758 ± 29 , $n = 3$) wide, length-to-width ratio, 3.0–3.3 (3.2 ± 0.1): 1.

Host. *Bathyraja macloviana* (Norman, 1937), Patagonian skate (Rajiformes, Arhynchobatidae) (type host). Prevalence of infection, 83% in *B. macloviana* (5 hosts infected out of 6 examined).

Etymology. This species is named in memory of the first author's father, Blas García Mallarín for his invaluable love, support, and encouragement over the years.

Distribution. This species is widespread along the continental shelf of Argentina occurring from waters off Buenos Aires Province to southeast Patagonia including the Marine Protected Area Namuncurá/Burdwood Bank, Argentina (Fig. 9).

Remarks. Specimens of *R. blasi* sp. nov. can easily be distinguished from five valid species in the genus by the total length. *Rockacestus blasi* sp. nov. is longer than *R. carvajali* and *R. conchai* (22.3–50.9 mm vs. 13.1–14.5 mm and 9.9–16.9 mm, respectively), and is shorter than *R. brittanicus*, *R. georgiensis* and *R. williamsi* (22.3–50.9 mm vs. 170–250 mm, 60–170 mm, and 90 mm, respectively). *Rockacestus blasi* sp. nov. differs from *R. piriei*, *R. radioductus*, and *R. rakusai* in possessing fewer testes (75–96 vs. 137–165, ≥ 100 , and 120–165, respectively). *Rockacestus blasi* sp. nov. can also be distinguished from *R. radioductus* in the distribution of testes (arranged in 6–8 columns in anteroposterior view vs. more than 15), the distribution of the vitelline follicles in the anterior third of the proglottid (reaching almost the midline of the proglottid vs. restricted to lateral bands), and in the position of the genital pore (54–73% from the posterior margin of the proglottid vs. equidistant from the anterior and posterior margin of the proglottid). *Rockacestus blasi* sp. nov. can be distinguished from *R. arctowski* by the number of proglottids (140–204 vs. 24–98, respectively). *Rockacestus blasi* sp. nov. is different than *R. siedleckii* in the length of the scolex (400–830 vs. 840–960, respectively) and in the size of the apical sucker (80–135 vs. 185–220, respectively). Finally, *R. blasi* sp. nov. can be distinguished from 9 members in the genus by being apolytic instead of euapolytic.

Rockacestus magellanicus sp. nov.

<https://zoobank.org/E935F2CC-AFED-490F-98B7-C426CC919F07>
Figs 1B, 4A–C, 5, 7D–F

Type material. *Holotype* whole mature worm; off Río Grande, Tierra del Fuego Province, Argentina ($53^{\circ}51.36'S$, $67^{\circ}03.84'W$), 58 m, 31 Mar. 2014, A. Menoret leg., MACN-Pa No. 789.

Paratypes 1 whole mature worm, 1 mature strobila, 2 detached mature proglottid, cross-section of 1 detached mature proglottid, off Río Grande, Tierra del Fuego Province, Argentina ($54^{\circ}19.91'S$, $64^{\circ}14.26'W$), 122 m, 22 Apr. 2016, A. Menoret leg., MACN-Pa Nos. 790/1–14. One strobila, 1 detached mature proglottid, same data as preceding, MLP-He No. 8098. One whole mature worm, off Río Grande, Tierra del Fuego Province, Argentina ($53^{\circ}26.35'S$, $64^{\circ}58.56'W$), 130 m, 1 Apr. 2012, A. Menoret leg., MACN-Pa No. 792. One whole mature worm, off the Marine Protected Area Namuncurá/Burdwood Bank ($54^{\circ}32.60'S$, $60^{\circ}1.28'W$), 98 m, 30 Mar. 2016, A. Menoret leg., MACN-Pa No. 791. One whole mature worm, same data as preceding, MLP-He No. 8099.

Description. Based on 7 specimens (5 whole mature worms and 2 strobilae without scoleces), 5 detached mature proglottids, 3 detached gravid proglottids, cross-sections of 1 detached mature proglottid, and 3 scoleces examined with SEM. Worms euapolytic, 9.9–19.5 (14.4 ± 4.0 , $n = 5$) mm long, 61–115 (90.3 ± 23 , $n = 7$) craspedote proglottids per worm (Fig. 1B). Maximum width at level of scolex or immature proglottids. Scolex composed of 4 bothridia, 520–810 (631 ± 113 , $n = 5$) long, 779–1,050 (944 ± 116 , $n = 5$) wide (Figs 4A, 5A). Bothridia folded, 450–471 ($n = 2$) long, 411–550 ($n = 2$) wide when folded, sessile anteriorly, free posteriorly, with apical sucker and marginal loculi. Posterior part of each bothridium with weak depression surrounded by circular band of muscle (Figs 4A, 5A). Apical sucker, 70–105 (84 ± 17 , $n = 4$) long, 70–100 (85 ± 17 , $n = 4$) wide (Figs 4A, 5A, B). Cephalic peduncle, absent. Neck, 3.6–8.3 (5.4 ± 2.0 , $n = 5$) mm long.

Apex of scolex proper covered with acicular filitriches (Fig. 5H). Proximal bothridial surface covered with acicular filitriches (Fig. 5G). Distal bothridial surface covered with acicular filitriches interspersed with lingulate spinitriches, lingulate spinitriches increasing in density posteriorly (Fig. 5E, F). Distal surface of apical sucker covered with acicular filitriches interspersed with lingulate spinitriches; posterior half of external rim of apical sucker with lanceolate spinitriches (Fig. 5B–D). Distal marginal loculi surface covered with papilliform to acicular filitriches interspersed with short coniform spinitriches (Fig. 5I, L). Capilliform filitriches on neck and strobila arranged in scutes (Fig. 5J, K). Cilia observed in proximal and distal bothridial surfaces, including apical sucker and marginal loculi (Fig. 5G, L).

Immature proglottids wider than long, 59–109 (84 ± 23 , $n = 7$) in number. Mature proglottids wider than long, becoming longer than wide with maturity, 2–7 (4 ± 2 , $n = 7$)

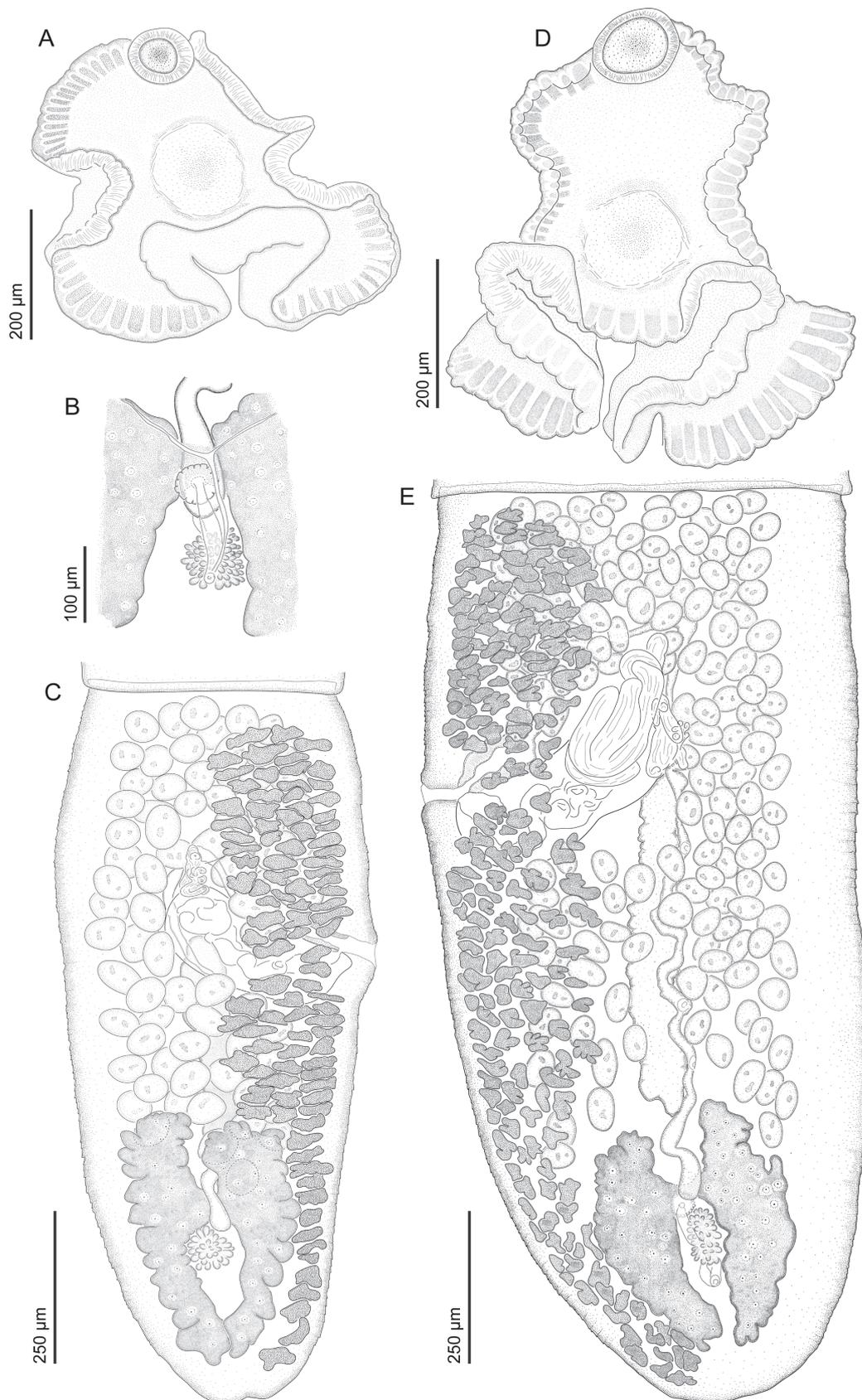


Figure 4. Line drawings of species of *Rockacestus* from the Southwestern Atlantic. **A–C.** *Rockacestus magellanicus* sp. nov. from *Bathyrāja magellanica*; **A.** Bothridium (paratype MLP-He No. 8099); **B.** Detail of ootype region, mature proglottid (paratype MACN-Pa No. 790/4); **C.** Terminal mature proglottid (paratype MLP-He No. 8098); **D–E.** *Rockacestus ottavianoii* sp. nov. from *Bathyrāja magellanica*; **D.** Bothridium (paratype MACN-Pa No. 794/1); **E.** Terminal mature proglottid (holotype MACN-Pa No. 793).

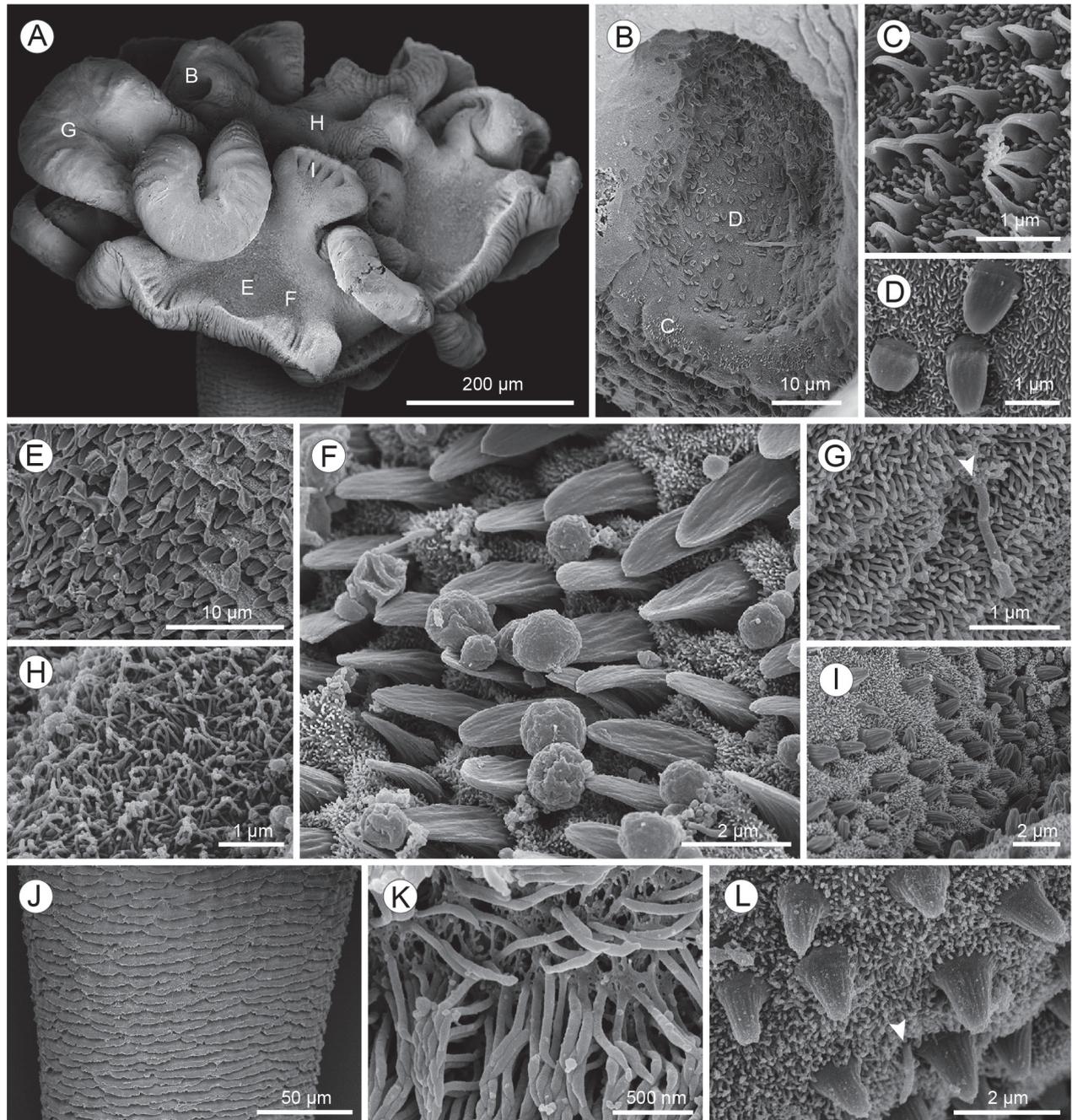


Figure 5. *Rockacestus magellanicus* sp. nov. from *Bathyraja magellanica*, scanning electron micrographs. **A.** Scolex, small letters indicate the location of details shown in Fig. 5B, 5E–I; **B.** Apical sucker, small letters indicate the location of details shown in Fig. 5C–D; **C.** Surface of the external apical sucker rim, acicular filitriches and lanceolate spinitriches; **D.** Distal apical sucker surface, acicular filitriches and lingulate spinitriches; **E–F.** Distal bothridial surface, acicular filitriches and lingulate spinitriches; **G.** Proximal bothridial surface, acicular filitriches, and cilium (white arrow); **H.** Apex of scolex, acicular filitriches; **I.** Distal surface of marginal loculi, acicular filitriches and coniform spinitriches; **J.** Scutes on surface of neck; **K.** Detail of scutes, capilliform filitriches; **L.** Detail of microtriches in marginal loculi and cilium (white arrow).

in number (Fig. 1B). Terminal mature proglottid longer than wide, 925–1,430 ($1,115 \pm 201$) long, 376–680 (502 ± 111) wide, length-to-width ratio, 1.4–2.7 (2.3 ± 0.4 , $n = 6$): 1 (Fig. 4C).

Testes oblong, 67–89 (76 ± 8 , $n = 6$) in total number, 51–67 (62 ± 6 , $n = 6$) long, 44–57 (49 ± 5 , $n = 6$) wide, extending from anterior margin of proglottid to anterior quarter of ovary; arranged in 5–6 columns anteroposteriorly and 2 layers deep in cross-section observed in anterior por-

tion of proglottid (Figs 4C, 7D). Cirrus sac oval, curved anteriorly, 200–340 (269 ± 58 , $n = 6$) long, 95–140 (118 ± 18 , $n = 6$) wide. Cirrus coiled, armed with minute spinitriches. Vas deferens highly coiled, extending anteriorly to vagina bend, overlapping medial margin of cirrus sac, entering cirrus sac through ventral margin (Figs 4C, 7E).

Ovary lobulated, H-shaped in frontal view, X-shaped in cross-section at level of isthmus, 255–615 (418 ± 135 , $n = 6$) long, 163–375 (246 ± 75 , $n = 6$) wide (Figs 4B, C,

7F). Vagina thick-walled, extending anteriorly from ootype region forming a seminal receptacle to bulk of vas deferens, then descending laterally along anterior margin of cirrus sac to enter genital atrium anterior to cirrus (Figs 4C, 7F). Vagina and cirrus sac join into genital atrium, 40–60 (53 ± 12 , $n = 3$) deep. Genital pores alternate irregularly, 62–75% (68 ± 5 , $n = 6$) of proglottid length from posterior margin of proglottid.

Vitellarium follicular, follicles irregular in shape, 15–34 (26 ± 7 , $n = 6$) long, 38–55 (47 ± 6 , $n = 6$) wide, arranged in 2 lateral bands almost reaching midline in anterior third of proglottid, each band consisting of multiple columns (4 columns of follicles anterior to cirrus sac), extending throughout proglottid length, uninterrupted by ovary, partially interrupted by genital atrium (Figs 4C, 7D–F). Uterus saccate, restricted to region between ovary and cirrus sac, running anteriorly up to genital pore level; uterine duct observed (Figs 4C, 7F). Mehlis' gland, 55–110 (77 ± 20 , $n = 5$) long, 55–75 (71 ± 9 , $n = 5$) wide, posterior to ovarian isthmus (Fig. 4B, C).

Detached mature proglottids, 1,650–2,075 ($1,875 \pm 207$, $n = 5$) long, 550–770 (654 ± 99 , $n = 5$) wide, length-to-width ratio, 2.7–3.2 (2.9 ± 0.2 , $n = 5$): 1. Detached gravid proglottids, 2,300–2,525 ($2,392 \pm 118$, $n = 3$) long, 725–775 (758 ± 29 , $n = 3$) wide, length-to-width ratio, 3.0–3.3 (3.2 ± 0.1): 1.

Host. *Bathyraja magellanica* (Philippi, 1902), Magellan skate (Rajiformes, Arhynchobatidae) (type host). Prevalence of infection, 40% in *B. magellanica* (4 hosts infected out of 10 examined).

Etymology. The specific name refers to the species distribution along the Magellanic Province in the Argentine Sea, SWA.

Distribution. This species is known from southern waters off Tierra del Fuego Province, Argentina including the Marine Protected Area Namuncurá/Burdwood Bank, Argentina (Fig. 9).

Remarks. *Rockacestus magellanicus* sp. nov. is shorter than *R. blasi* sp. nov., *R. brittanicus*, *R. georgiensis*, *R. piriei*, *R. radioductus*, *R. rakusai*, *R. siedleckii*, and *R. williamsi* (9.9–19.5 vs. 22.3–250 mm in total length, respectively). Specimens of *R. magellanicus* sp. nov. have fewer testes than those of *R. carvajali* (67–89 vs. 46–55, respectively). Moreover, *R. magellanicus* sp. nov. has lingulate spinitriches and acicular filitriches on the distal surface of the bothridia whereas *R. carvajali* has only papilliform filitriches. *Rockacestus magellanicus* sp. nov. differs from *R. conchai* in the scolex width (779–1,050 vs. 1,122–1,775, respectively), size of bothridia (450–471 long by 411–550 wide vs. 478–624 long by 600–830 wide, respectively). Additionally, *R. magellanicus* sp. nov. has acicular filitriches and small lingulate spinitriches on the distal surface of apical sucker whereas *R. conchai* only has acicular filitriches. *Rockacestus magellanicus* sp. nov. is different from *R. arctowskii* in the size of the cirrus sac (200–340 long by 95–140 wide vs. 370–480 long by 154–215 wide, respectively) and in the size of the apical sucker (70–105 long by 70–100 wide vs. 212–250 in diameter, respectively).

Rockacestus ottaviano sp. nov.

<https://zoobank.org/75E09CF2-DC8D-470D-97EA-1ACEA43C6644>

Figs 1C, 4D, E, 6, 7G–I

Type material. *Holotype* whole mature worm, off Río Grande, Tierra del Fuego Province, Argentina ($54^{\circ}1.68'S$, $67^{\circ}6.81'W$), 193 m, 2 Apr. 2012, A. Menoret leg., MACN-Pa No. 793.

Paratypes 1 whole mature worm, 1 whole mature strobila (SEM voucher), cross-section of 1 attached mature proglottid, same data as holotype, MACN-Pa Nos. 794/1–13. One whole mature worm, same data as for preceding, MLP-He No. 8100.

Description. Based on 4 specimens (3 whole mature worms, and 1 strobila without scolex), cross-sections of 1 mature proglottid, and 2 scoleces examined with SEM. Worms euapolytic, 23.1–53.1 (39.1 ± 13.8 , $n = 4$) mm long, 124–195 (156 ± 36 , $n = 3$) craspedote proglottids per worm (Fig. 1C). Maximum width at level of scolex. Scolex composed of 4 bothridia, 590–750 (648 ± 70 , $n = 4$) long, 978–1,250 ($1,133 \pm 36$, $n = 4$) wide (Figs 4D, 6A). Bothridia folded, 530–600 (570 ± 36 , $n = 3$) long, 520–720 (613 ± 101 , $n = 3$) wide when folded, sessile anteriorly, free posteriorly, consisting of apical sucker and marginal loculi. Posterior part of each bothridium with weak depression surrounded by circular band of muscle (Figs 4D, 6A). Apical sucker 100–130 (113 ± 15 , $n = 3$) long, 110–140 (125 ± 13 , $n = 3$) wide (Figs 4D, 6A, B). Cephalic peduncle, absent. Neck 11.6–25.3 (19.4 ± 6.0 , $n = 4$) mm long.

Apex of scolex proper covered with acicular to capilliform filitriches (Fig. 6E). Proximal bothridial surface covered with acicular filitriches (Fig. 6H). Distal bothridial surface covered with acicular filitriches interspersed with lingulate spinitriches, lingulate spinitriches increasing in density posteriorly (Fig. 6F, G). Distal surface of apical sucker covered with acicular filitriches interspersed with small lingulate spinitriches; posterior half of external rim of apical sucker with lanceolate spinitriches (Fig. 6B–D); cilia found throughout distal surface of apical sucker. Distal surface of marginal loculi covered with acicular filitriches interspersed with short coniform spinitriches (Fig. 6I, L). Capilliform filitriches on neck and strobila arranged in scutes (Fig. 6J, K).

Immature proglottids wider than long, 123–179 (150 ± 28 , $n = 3$) in number (Fig. 1C). Mature proglottids wider than long, becoming longer than wide with maturity, 2–16 (6 ± 7 , $n = 4$) in number (Fig. 1C). Terminal mature proglottid longer than wide, 970–1,460 ($1,220 \pm 207$) long, 570–760 (663 ± 81) wide, length-to-width ratio, 1.4–2.3 (1.9 ± 0.4 , $n = 4$): 1 (Fig. 4E).

Testes oblong, 92–152 (108 ± 39 , $n = 3$) in total number, 55–68 (60 ± 5 , $n = 4$) long, 43–52 (46 ± 4 , $n = 4$) wide, extending from anterior margin of proglottid to anterior quarter of ovary; arranged in 6–7 columns antero-posteriorly and 2 layers deep in cross-section observed in anterior portion of proglottid (Figs 4E, 7G). Cirrus sac oval, curved anteriorly, 350–395 (365 ± 26 , $n = 3$) long, 125–165 (138 ± 23 , $n = 3$) wide. Cirrus coiled, armed with

minute spinitriches. Vas deferens highly coiled, extending anteriorly to vagina bend, overlapping medial portion of cirrus sac, anterior to cirrus sac (Fig. 4E).

Ovary lobulated, H-shaped in frontal view, X-shaped in cross-section at level of isthmus, 345–500 (408 ± 81 , $n = 3$) long, 235–355 (292 ± 60) wide (Figs 4E, 7I). Vagina thick-walled, extending anteriorly from the ootype region forming a seminal receptacle, to bulk of vas deferens de-

scending laterally along anterior margin of cirrus sac to enter genital atrium anterior to cirrus (Figs 4E, 7I). Vagina and cirrus sac join into genital atrium, 50–60 (55 ± 7 , $n = 2$) deep. Genital pores alternate irregularly, 68–74% (71 ± 2 , $n = 4$) of proglottid length from posterior margin of proglottid. Vitellarium follicular, follicles irregular in shape, 28–55 (39 ± 12 , $n = 4$) long, 43–50 (46 ± 3 , $n = 4$) wide, arranged in 2 lateral bands almost reaching the mid-

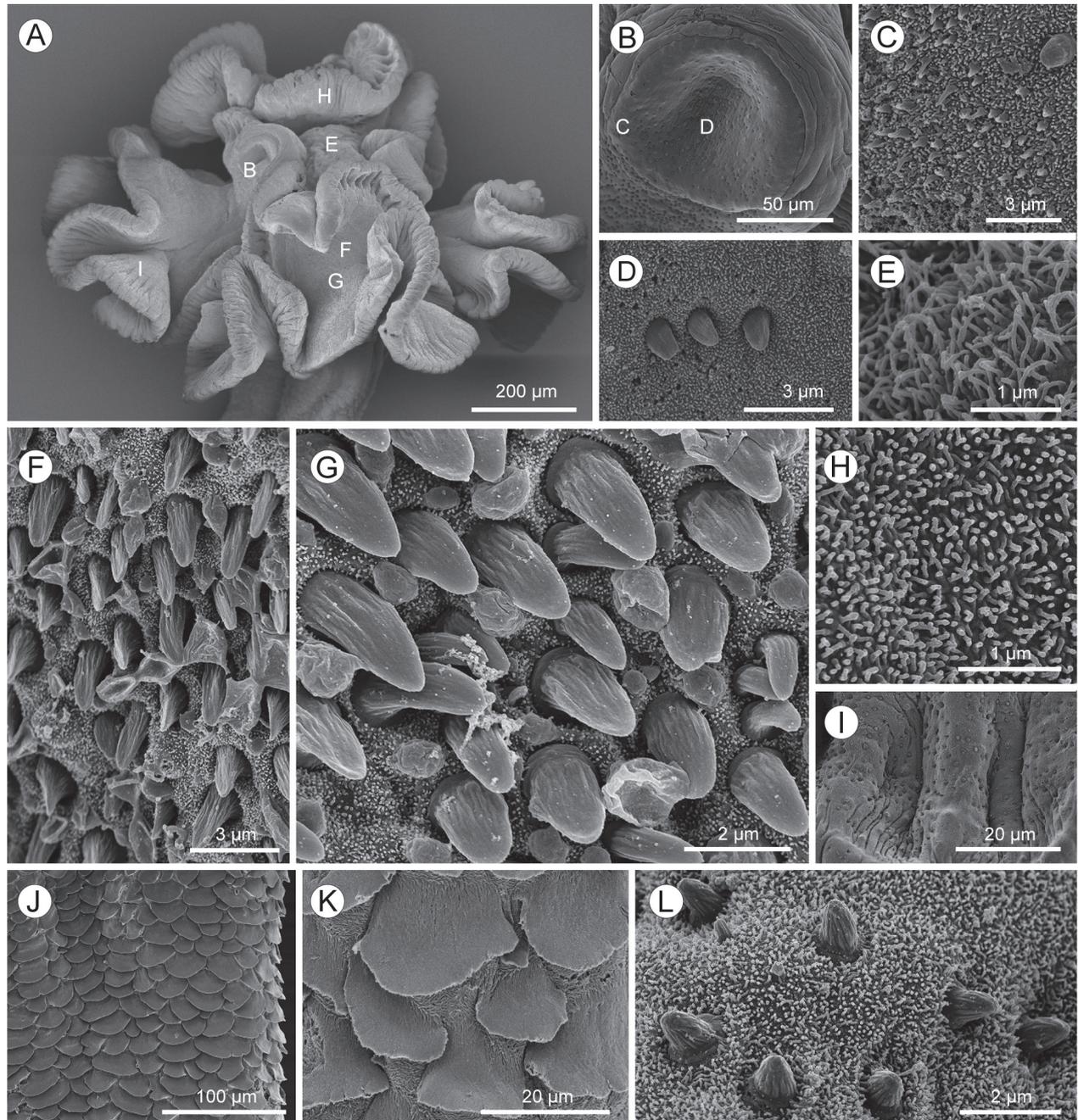


Figure 6. *Rockacestus ottaviano* sp. nov. from *Bathyraja magellanica*, scanning electron micrographs. **A.** Scolex, small letters indicate the location of details shown in; **B.** Apical sucker, small letters indicate the location of details shown in Fig. 6C, D; **C.** Surface of the external apical sucker rim, acicular filitriches and small lingulate spinitriches; **D.** Detail of distal apical sucker surface, lingulate spinitriches; **E.** Apex of scolex, acicular to capilliform filitriches; **F, G.** Distal bothridial surface, acicular filitriches and lingulate spinitriches; **H.** Proximal bothridial surface, acicular filitriches; **I.** Distal surface of marginal loculi, acicular filitriches and short coniform spinitriches; **J, K.** Scutes on surface of neck; **L.** Detail of microtrichies on marginal loculi.

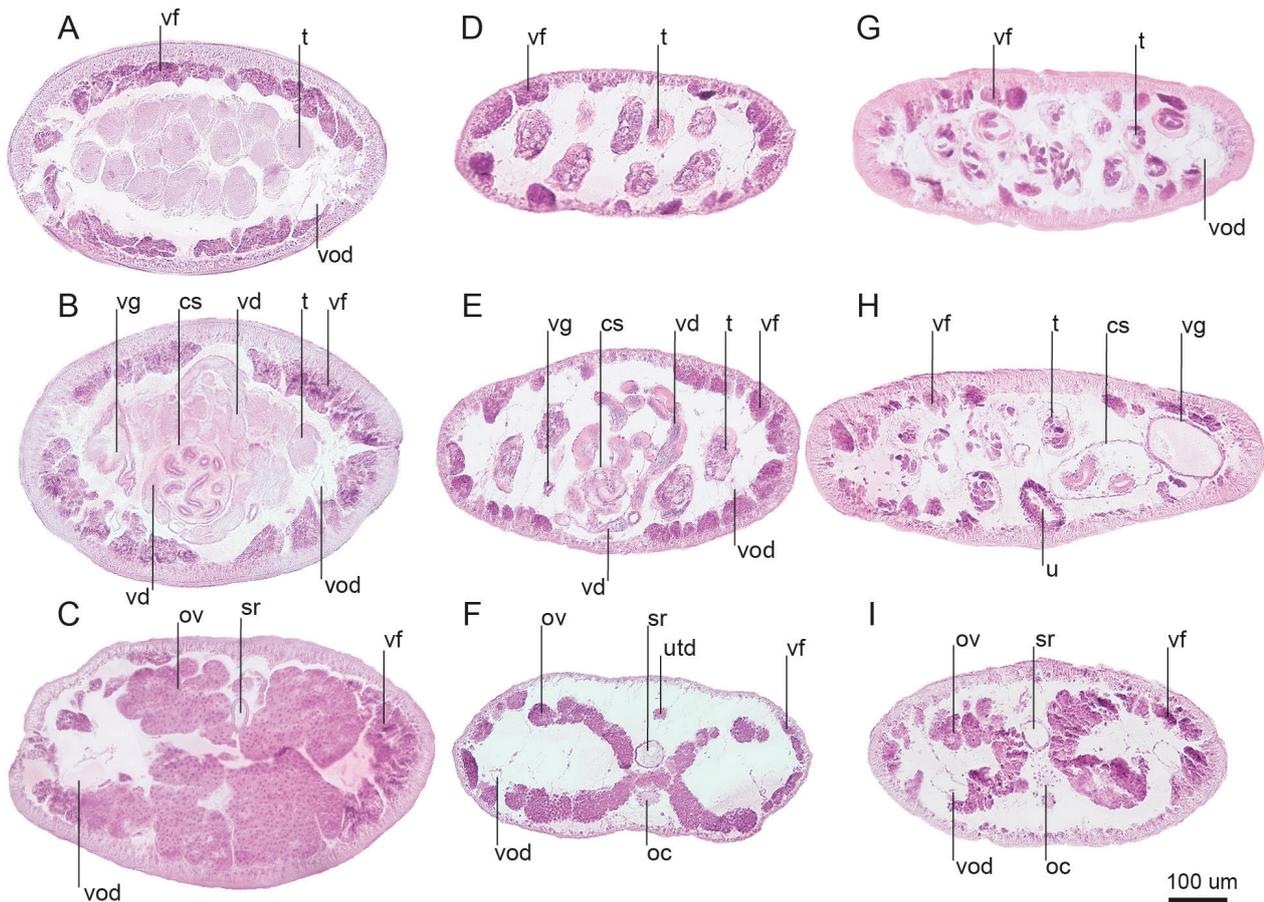


Figure 7. Light micrographs of cross-sections of mature proglottids of species of *Rockacestus* off Argentina. **A–C.** *Rockacestus blasi* sp. nov.; **A.** At the level of the testes, anterior to the cirrus sac; **B.** At the level of the cirrus sac; **C.** At the level of ovarian isthmus; **D–F.** *Rockacestus magellanicus* sp. nov.; **D.** At the level of the testes, anterior to the cirrus sac; **E.** At the level of the cirrus sac; **F.** At the level of ovarian isthmus; **G–I.** *Rockacestus ottaviano* sp. nov.; **G.** At the level of the testes, anterior to the cirrus sac; **H.** At the level of the cirrus sac; **I.** At the level of ovarian isthmus; **cs** — cirrus sac; **oc** — ovicapt; **ov** — ovary; **sr** — seminal receptacle; **t** — testes; **u** — uterus; **ut** — uteroduct; **vd** — vas deferens; **vf** — vitelline follicle; **vg** — vagina; **vod** — ventral osmoregulatory duct.

line in anterior third of proglottid, each band consisting of multiple columns (5–6 columns anterior to cirrus sac) of follicles, extending throughout the length of proglottid, uninterrupted by ovary, interrupted partially by genital atrium (Figs 4E, 7G–I). Uterus saccate, restricted to region between ovary and cirrus sac running anteriorly up to genital pore level, uterine duct observed (Figs 4E, 7H). Mehlis’ gland, 90–110 (99 ± 9, n = 4) long, 63–100 (76 ± 17, n = 4) wide, posterior to ovarian isthmus (Fig. 4E).

Host. *Bathyraja magellanica* (Philippi, 1902), Magellan skate (Rajiformes, Arhynchobatidae) (type host). Prevalence of infection, 10% in *B. magellanica* (1 host infected out of 10 examined).

Etymology. This species is named in honor of Juan Manuel Ottaviano for his genuine and loyal friendship over the years.

Distribution. This species is known from its type locality, off Río Grande, Tierra del Fuego Province, Argentina (54°1.68’S, 67°6.81’W).

Remarks. *Rockacestus ottaviano* sp. nov. can be distinguished from *R. arctowskii*, *R. carvajali*, *R. conchai*,

and *R. magellanicus* sp. nov. by having more testes (92–152 vs. 60–80, 46–55, 51–73, and 67–89, respectively) and a greater number of proglottids (124–195 vs. 24–98, 75–81, 64–105, and 61–115, respectively). *Rockacestus ottaviano* sp. nov. is easily distinguished from three of its congeners by the worm length by being shorter than *R. brittanicus*, *R. georgiensis*, and *R. williamsi* (23.1–53.1 vs. 170–250, 60–170, and 90 mm, respectively). *Rockacestus ottaviano* sp. nov. can be distinguished from three species in the genus by having different size of apical sucker. In *R. rakusai* and *R. siedleckii*, it is bigger than in *R. ottaviano* sp. nov. (250–310 and 185–220 in diameter vs. 100–130 long by 110–140 wide, respectively), whereas in *R. piriei* it is smaller (90 in diameter vs. 100–130 long by 110–140 wide, respectively). *Rockacestus ottaviano* sp. nov. has a narrower scolex (978–1,250 in scolex width) and bigger testes (43–52 long by 55–68 wide) than *R. radioductus* (1,800–2,000 in scolex width; 40 in testes diameter). Finally, *R. ottaviano* sp. nov. is euapolytic and has testes distributed in 2 layers deep in cross-section, whereas *R. blasi* sp. nov.

is apolytic and has testes arranged in 3–4 layers deep in cross-section.

Update of generic diagnosis and distribution of valid species of *Rockacestus*

The diagnosis of *Rockacestus* sensu Caira et al. (2021) is revised to include the three species described below from the skates of the genus *Bathyraja* from continental shelf waters off Argentina. The generic diagnosis is updated as follows: worms euapolytic or apolytic; scolex spinitriches lingulate, lanceolate, coniform, filitriches papilliform or acicular; genital pores lateral, in midhalf or anterior half of proglottid, irregularly alternating; testes arranged in 2–4 rows in cross-section; vagina with

seminal receptacle present or absent; uteroduct present or absent.

The valid species now include, *Rockacestus arctowskii* (Wojciechowska, 1991), *Rockacestus blasi* sp. nov., *Rockacestus brittanicus* (Williams, 1968), *Rockacestus carvajali* Caira, Bueno & Jensen, 2021, *Rockacestus conchali* Caira, Bueno & Jensen, 2021, *Rockacestus georgiensis* (Wojciechowska, 1991), *Rockacestus magellanicus* sp. nov., *Rockacestus ottavianoii* sp. nov., *Rockacestus piriei* (Williams, 1968), *Rockacestus radioductus* (Kay, 1942), *Rockacestus rakusai* (Wojciechowska, 1991), *Rockacestus siedleckii* (Wojciechowska, 1991), and *Rockacestus williamsi* (Schmidt, 1986).

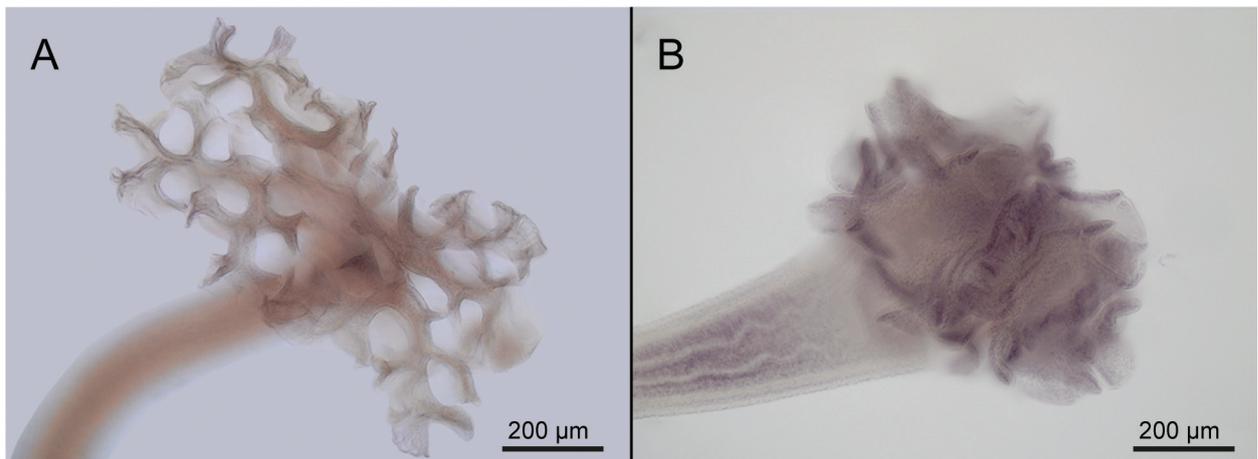


Figure 8. Light micrographs of scoleces of *Rockacestus blasi* sp. nov. **A.** Bothridia fixed while still attached to the host tissue (paratype MACN-Pa No. 787); **B.** Bothridia properly relaxed and fixed (paratype MACN-Pa No. 784/2).

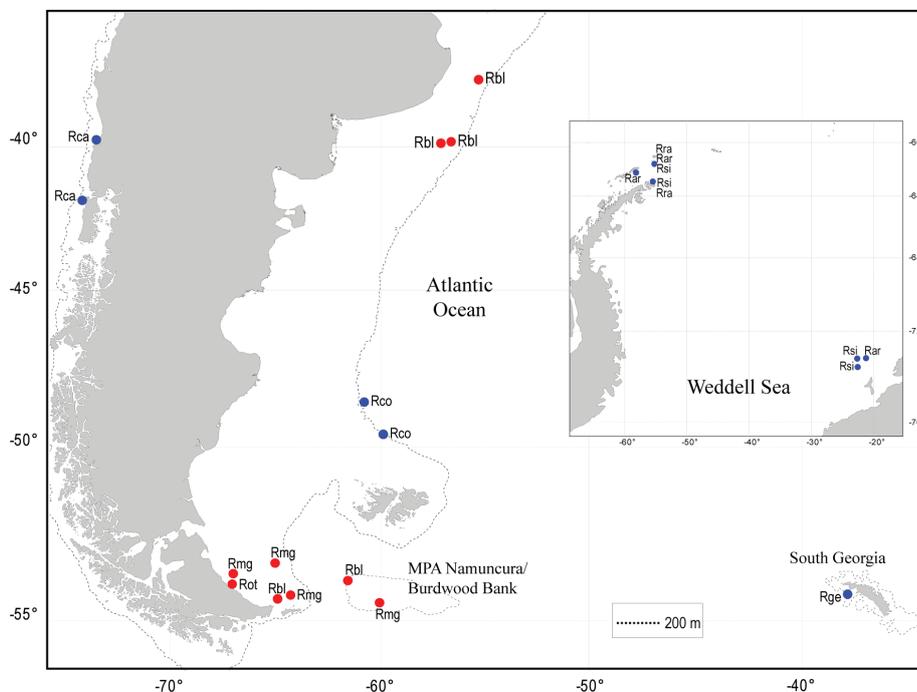


Figure 9. Geographic distribution of the valid species of *Rockacestus* from the Southern Hemisphere. Symbols: red dot: new records; blue dot: previous records; **Rar** – *Rockacestus arctowskii*; **Rbl** – *Rockacestus blasi* sp. nov.; **Rca** – *Rockacestus carvajali*; **Rco** – *Rockacestus conchali*; **Rge** – *Rockacestus georgiensis*; **Rma** – *Rockacestus magellanicus* sp. nov.; **Rot** – *Rockacestus ottavianoii* sp. nov.; **Rra** – *Rockacestus rakusai*; **Rsi** – *Rockacestus siedleckii*.

The genus is widespread among temperate waters of the East Pacific and Atlantic Oceans, with *R. brittanicus*, *R. piriei*, and *R. williamsi* inhabiting the Northeast Atlantic Ocean; *R. radioductus* in the Northeast Pacific Ocean, *R. carvajali* from off Chiloé Island in the Southeast Pacific Ocean, and *R. conchai* off Malvinas Islands in the SWA. A subset of *Rockacestus* species also inhabits sub-Antarctic and Antarctic waters, with *R. georgiensis* from off South Georgia Island, *R. rakusai* registered off the Antarctic Peninsula, and records of *R. arctowskii* and *R. siedleckii* off the Antarctic Peninsula and the Weddel Sea. *Rockacestus blasi* sp. nov., *R. magellanicus* sp. nov. and *R. ottaviano* sp. nov. are restricted to the Magellanic Province *sensu* Sabadin et al. (2020) in the SWA. The finding of the new species increases the species richness from two to five in marine waters around South America. Thus, the known latitudinal range of the genus in the Northern Hemisphere covers from 48°N to 58°N whereas in the Southern Hemisphere *Rockacestus* now ranges between 37 to 74°S (Fig. 9).

Discussion

Scolex

A well-relaxed tapeworm scolex represents a challenge, as it often results in a contracted material, making difficult a proper characterization of the actual shape of the bothridia. For example, among members of the Phyllobothriidea, specimens of *Guidus* show a marked bothridial projection, and those of *R. piriei* exhibits highly folded bothridia when attached to the gut mucosa of their hosts (figs 13, 14 in Williams [1968b], fig. 4E in Menoret and Ivanov [2021]).

Among the scoleces herein described, *R. magellanicus* sp. nov. and *R. ottaviano* sp. nov. exhibit bothridia with a higher degree of folding than *R. blasi* sp. nov. A few specimens of *R. blasi* sp. nov. were fixed while still attached to the host, appearing to have significantly folded bothridia (Fig. 8A). However, the typical scolex of these specimens is obtained once removed from the host and properly relaxed (Fig. 8B).

Rockacestus conchai was originally described as having a scolex with highly folded bothridia, however, it resembles the contracted scoleces of *R. piriei* and *R. blasi* sp. nov. (see Fig. 8A). Therefore, the degree of the bothridial folding would be a useful character to distinguish between species, as long as it is verified that this variability is not given by an artifact of the fixation technique.

Ultrastructure of the scolex (SEM)

The surface of the scolex has been analyzed with SEM in five of the now 13 valid species of *Rockacestus*. Among the five species, *R. carvajali* and *R. conchai* were partially studied, with *R. carvajali* mostly characterized by

papilliform filitriches (see fig. 8B, D, E in Caira et al. [2021]). The new species of *Rockacestus* from off Argentina, in addition to *R. conchai*, exhibit a common microtrich pattern, with acicular filitriches distributed along the bothridial surfaces, capilliform filitriches arranged in scutes on the neck, and lingulate spinitriches in most of the distal bothridial surface. Both the apical sucker and the marginal loculi are novel results of the present study and characterize *R. blasi* sp. nov., *R. magellanicus* sp. nov., and *R. ottaviano* sp. nov. by the presence of small lingulate and lanceolate spinitriches on the distal surface of the apical sucker and coniform spinitriches with rounded tips covering the distal surface of the marginal loculi (Figs 3C, D, G, 5B, D, I, L, 6B, D, I, L).

Given that most of these species studied with SEM exhibit a variety of spinitriches, it is likely that the scolex of *R. carvajali* has been based on micrographs with a low resolution or magnification. It would be important to complete the study all along the distal bothridial surface in *R. carvajali* and *R. conchai*, such as the apical sucker and the marginal loculi, to verify if they are similar in the type and distribution of microtriches and cilia to those observed in the new species of *Rockacestus* off Argentina. The majority of spinitriches found in *Rockacestus* belong to morphotypes rarely observed among the phyllobothriideans. For example, lingulate-like spinitriches were reported in the phyllobothriid *Crossobothrium laciniatum* Linton, 1889 (see Ruhnke 2011) but they actually are trullate spinitriches *sensu* Chervy (2009). In contrast, the lanceolate spinitriches exhibited by the new species and described in this study have not yet been reported among members of the order. Additionally, the particular kind of short coniform spinitriches with rounded tips observed in the marginal loculi of these three new species (Figs 3G, 5I, L, 6I, L) is reported for the first time among cestodes, showing an increasing variety of microtriches as new cestode taxa are discovered. Therefore, the diversity of spinitriches in the genus should be extended to include coniform and lanceolate morphotypes rather than only lingulate (not gladiate) as mentioned in the original diagnosis of *Rockacestus*.

Proglottid and terminal genitalia characters

Among the diagnostic features of the genus, Caira et al. (2021) characterized *Rockacestus* by being euapolytic and lacking a seminal receptacle.

Specimens of *R. brittanicus* were originally described by Williams (1968a) as euapolytic, however, this author showed a uterus filled with eggs in the terminal proglottids (see fig. 13 in Williams [1968a]). This discrepancy, also noticed by Ruhnke (2011), could be resolved once the type material of *R. brittanicus* is examined. To date, *R. blasi* sp. nov. remains the only apolytic species in the genus. Kay (1942) described *R. radioductus* having a seminal receptacle and provided ink drawings of its morphology (fig. 5 in Kay [1942]), being the first report of this structure in the

genus. Furthermore, Wojciechowska (1991) mentioned an enlarged vagina in the proximal portion between the ovary lobes in *R. arctowskii*, *R. georgiensis*, *R. rakusai*, and *R. siedleckii* (see fig. 1B in Wojciechowska [1991]). In addition, a vagina enlarged in a seminal receptacle near the ovary isthmus is observed in whole mounts and confirmed in cross-sections of mature proglottids of *R. blasi* sp. nov., *R. magellanicus* sp. nov. and *R. ottaviano* sp. nov. (Fig. 7C, F, I). Therefore, the genus now consists of apolytic and euapolytic specimens and a seminal receptacle is present in some species. In addition, some information such as the size of the Mehlis' gland, the presence or absence of an uteroduct, and the entrance site of the vas deferens in the cirrus sac were described for the first time for the Argentinian species of *Rockacestus*.

Host associations and host-specificity

Previous records of *Rockacestus* include a total of nine oioxenous species found in marine skates belonging to the families Rajidae (i.e., *R. brittanicus*, *R. carvajali*, *R. georgiensis*, *R. piriei*, *R. radioductus*, and *R. williamsi*), and Arhynchobatidae (i.e., *R. arctowskii*, *R. conchai*, and *R. rakusai*) (Kay 1942; Williams 1968a, 1968b; Schmidt 1986; Wojciechowska 1991; Caira et al. 2021). The exception is *R. siedleckii*, which parasitizes two different species of *Bathyraja* (see Wojciechowska 1991; Rocka and Zditowiecki 1998). The finding of the three species described in this study, not only increases the number of oioxenous species of the genus, but also brings the total number of species of *Rockacestus* as parasites of arhynchobatid skates to seven. This study comprises the first report of *Rockacestus* species in *B. macloviana* and *B. magellanica*. Furthermore, it is the second record of a single softnose skate species harboring several species of *Rockacestus* (Wojciechowska 1991; Rocka and Zditowiecki 1998; this paper).

To date, a total of seven species of *Bathyraja* skates were registered as hosts of phyllobothriideans (Franzese et al. 2023; this work). Among them, *Rockacestus* most resembles *Guidus* Ivanov, 2006 since both exhibit a tight association with *Bathyraja* skates from the SWA and off Antarctica (Menoret and Ivanov 2021). Although *B. maccaini* and *B. magellanica* host several phyllobothriideans, more surprising is that a single individual of *B. magellanica* became a suitable host for a complex of phyllobothriidean species. Particularly, our individual PD4-097 was found to host simultaneously *R. ottaviano* sp. nov., *Guidus francoi* Menoret & Ivanov, 2021, and *Guidus magellanicus* Menoret & Ivanov, 2021.

Beer et al. (2019), relying only on sequencing, identified several species of a new genus of phyllobothriids recovered from seven species of *Bathyraja* from the Malvinas Islands Shelf. Their specimens not deposited into any museum were later considered by Caira et al. (2021) as members of *Rockacestus*. It would be interesting to identify these specimens at specific level in order to estimate more precisely the richness of the genus in the SWA.

Geographic distribution

Species of *Rockacestus* are closely associated with temperate, sub-Antarctic, and Antarctic waters. The Northern Hemisphere is represented only by a few species, including *R. brittanicus*, *R. piriei*, *R. radioductus*, and *R. williamsi*, as parasites of rajid skates (Kay 1942; Williams 1968a, 1968b; Schmidt 1986). In contrast, the remaining nine species occur in the Southern Hemisphere, mostly parasitizing arhynchobatid skates of the genus *Bathyraja* (Wojciechowska 1991; Caira et al. 2021; this paper). Ten species (i.e., *R. brittanicus*, *R. carvajali*, *R. conchai*, *R. georgiensis*, *R. magellanicus* sp. nov., *R. ottaviano* sp. nov., *R. piriei*, *R. radioductus*, *R. rakusai*, and *R. williamsi*) are restricted to their type locality and surrounding areas. In contrast, *R. arctowskii*, *R. blasi* sp. nov., and *R. siedleckii* do not show this pattern. *Rockacestus arctowskii* and *R. siedleckii* were recorded off the Antarctic Peninsula and in the eastern part of the Weddell Sea, whereas *R. blasi* sp. nov. is, to date, the species with the broadest latitudinal range (37°S–54°S) occurring from waters off Buenos Aires Province to southeast Patagonia (Fig. 9). The southern distribution of *R. magellanicus* sp. nov. and *R. ottaviano* sp. nov. resembles members of *G. francoi* and *G. magellanicus* as they remain locally restricted to the Magellanic Province in the SWA despite the wider distribution of their host. Although reports in the SWA have increased in the recent years due to focused sampling efforts in the area (Menoret and Ivanov 2009, 2012a, 2012b, 2014, 2015, 2021, 2023; Mutti and Ivanov 2016; Menoret et al. 2017; Franzese and Ivanov 2018, 2020a, 2020b, 2021; Franzese et al. 2022, 2023), it would be interesting to see if the composition of the *Rockacestus* fauna which is currently restricted to the type locality changes as the sampling area of host continues to expand.

Recently, Sabadin et al. (2020) proposed a bioregionalization scheme of the SWA, based on chondrichthyan assemblages, and showed that eight species of *Bathyraja*, including *B. magellanica*, are dominant species of batoids in the Magellanic Province. Regarding the tight association of the genera *Rockacestus* and *Guidus* with the genus *Bathyraja* in the SWA and considering that the nine new geographic records of *Rockacestus* herein reported are in the Magellanic Province, we, therefore, expect that as the sampling spectrum increases among *Bathyraja* species in the region, the discovery of new species of *Rockacestus* and *Guidus* will also increase. Finally, *R. blasi* sp. nov. and *R. magellanicus* sp. nov. are new reports of phyllobothriideans after *Guidus argentinense* Ivanov, 2006, off a marine protected area (see Menoret and Ivanov 2021). The discovery of new species of *Rockacestus* from skates of the genus *Bathyraja* from off Argentina increases the number of species from one to four in the SWA and the number of valid species in the genus from ten to 13, expanding its geographical range and bringing the percentage of phyllobothriideans inhabiting the Southern Hemisphere to 39%.

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