

Research Article

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A new species of *Paraberrapex* Jensen, 2001 (Cestoda: Lecaniccephalidea) from *Squatina guggenheim* Marini (Squatiniformes: Squatinidae) off Argentina

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Abstract: *Paraberrapex atlanticus* sp. n. (Cestoda: Lecaniccephalidea) is described from the spiral intestine of the angel shark *Squatina guggenheim* Marini from coastal waters off Buenos Aires Province, Argentina. *Paraberrapex atlanticus* sp. n. can be distinguished from the only species described in the genus, *P. manifestus* Jensen, 2001 in having cocoons 5–6 times longer with more eggs per cocoon, the extension of the uterine duct, the distribution of vitelline follicles, and the size and density of microtriches on the bothridial surfaces. The presence of *P. atlanticus* sp. n. in *S. guggenheim* confirms the specificity of *Paraberrapex* Jensen, 2001 for squatiniform sharks.

Keywords: tapeworms, *Paraberrapex atlanticus* sp. n., southwestern Atlantic Ocean, angel sharks

Paraberrapex Jensen, 2001 was erected for *Paraberrapex manifestus* Jensen, 2001 from the angel shark, *Squatina californica* Ayres. *Paraberrapex* along with *Aberrapex* Jensen, 2001 are unique lecanicephalideans in their scolex configuration; they lack an apical organ and apical modification of the scolex proper (Jensen 2001, 2005). Despite their similarity in the scolex configuration, *Paraberrapex* can be distinguished from *Aberrapex* on the basis of a vagina that is medial in position rather than lateral throughout its length in the proglottid, an ovary that is bilobed rather than tetralobed in cross section, and acetabular surfaces covered with slender gladiate and coniform spinitriches rather than hastate spinitriches (Jensen 2001, 2005, Koch et al. 2012).

Recent molecular phylogenetic analyses suggest that lecanicephalideans lacking apical organs are the earliest diverging lecanicephalideans (Caira et al. 2014). Though *Paraberrapex* was the only non-apical organ-bearing genus included in these analyses, it is placed as the sister taxon to all lecanicephalideans with apical organs represented by 18 species in 11 genera (Caira et al. 2014). *Paraberrapex* has remained monotypic since its inception and its geographical distribution is restricted to the Gulf of California (Jensen 2001, 2005).

During a parasitological survey of tapeworms from elasmobranchs along the coast of Argentina, specimens of a new species of *Paraberrapex* were collected from the angular angel shark, *Squatina guggenheim* Marini. Previous records of lecanicephalideans from the southwestern Atlantic Ocean are restricted to a single species, *Aberrapex arrhynchum* (Brooks, Mayes et Thorson, 1981), from the southern eagle ray, *Myliobatis goodei* Garman, off Uruguay (Brooks et al. 1981, Jensen 2001, 2005). The new species of *Paraberrapex* is described herein, representing the first record of this genus from the Atlantic Ocean.

MATERIALS AND METHODS

Cestodes examined in this study were recovered from the spiral intestines of 13 specimens of *Squatina guggenheim* caught in September and November 2008 off Puerto Quequén, Buenos Aires Province, Argentina (38°53'00"S; 58°27'00"W) (host field numbers VIPQ-11/04, AMPQ-93, AMPQ-94, AMPQ-95, AMPQ-98, AMPQ-103, AMPQ-105, AMPQ-110 and AMPQ-144), and along the continental shelf off Argentina in March 2011 (PD3-211 at 41°03'13"S; 64°06'14"W), August 2012 (PD5-10 at 37°17'45"S; 56°27'00"W and PD5-168 at 36°21'00"S; 54°32'24"W), and March 2013 (PD7-515 at 40°58'14"S; 62°00'21"W). The specimens from Puerto Quequén were caught by commercial trawlers;

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all other specimens were caught with bottom trawls on board the Oceanographic Vessel 'Puerto Deseado' (CONICET).

All tapeworms were removed from the spiral intestine of their respective host, relaxed in seawater, fixed in 4% formalin and transferred to 70% ethanol for storage. The specimens prepared for light microscopy were hydrated in a graded ethanol series, stained with Harris' haematoxylin, dehydrated in a graded ethanol series, cleared in methyl salicylate and mounted in Canada balsam. Worms prepared for scanning electron microscopy (SEM) were hydrated in a graded ethanol series, post-fixed in 1% osmium tetroxide overnight at room temperature, dehydrated in a graded ethanol series and dried using hexamethyldisilazane. Specimens were mounted on stubs with carbon tape, coated with *ca* 40 nm of gold/palladium in a Thermo VG Scientific Polaron SC 7630 and examined in a Philips XL 30 scanning electron microscope. Shape terminology follows Clopton (2004). Terminology for the shape of microtriches follows Chervy (2009). Detached mature proglottids were embedded in paraffin and serial cross sections were cut at a thickness of 10 μ m. Sections were stained with Harris' haematoxylin, counterstained with eosin and mounted in Canada balsam.

Gravid proglottids were opened with insect pins to free the cocoons, which were then temporarily mounted using distilled water. Whole and temporary mounts and sections were observed and measured using an Olympus BX51 compound microscope. Drawings were made with the aid of a camera lucida. Measurements are given as the range, followed in parentheses by the mean, standard deviation, number of worms examined and the total number of observations if more than one measurement per worm was taken. All measurements are in micrometres unless otherwise stated. Photographs were taken using a Nikon Coolpix 950 digital camera attached to a Zeiss Axioskop.

Museum abbreviations used are as follows: IPCAS – Institute of Parasitology, Biology Centre of the Czech Academy of Sciences, České Budějovice, Czech Republic; MACN-Pa – Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina.

RESULTS

Paraberrapex atlanticus sp. n.

Figs. 1–3

ZooBank number for species:

urn:lsid:zoobank.org:act:A9510779-90A8-4C93-B08B-D8186D2A0BFB

Description (based on 14 worms: whole mounts of 9 complete worms, 5 strobilae without scolices, 8 mature detached proglottids and 2 gravid detached proglottids, histological sections of 2 mature proglottids and 1 gravid proglottid, 5 specimens observed with SEM and temporary mounts of 16 of cocoons). Worms 2.17–3.03 mm (2.59 ± 0.28 mm; 9) long, maximum width at level of scolex, 15–19 (17 ± 1 ; 9) proglottids, euapolytic (Fig. 1A). Scolex 140–200 (163 ± 24 ; 8) long, 210–300 (234 ± 27 ; 8) wide, consisting of 4 finely deltoid acetabula (Figs. 1C, 2A). Acetabula 105–150 (127 ± 14 ; 9) long, 103–140 (115 ± 12 ; 9) wide. Apical modification of scolex proper and apical organ absent. Apex of scolex (Fig. 2B) and

scolex proper (right half of Fig. 2F) covered with papilliform to acicular filitriches. Distal acetabular surface covered with coniform spinitriches and capilliform filitriches (Fig. 2E), proximal acetabular surface covered with slender gladiate spinitriches and acicular to capilliform filitriches (Fig. 2D, left half of Fig. 2F); spinitriches denser on proximal than distal acetabular surface. Strobila covered with acicular to capilliform filitriches transitioning into small scolopate spinitriches at posterior margins (Fig. 2C). Cephalic peduncle absent.

Proglottids craspedote, non-lancinate. Immature proglottids 15–18 (15 ± 1 ; 9) in number, initially wider than long, becoming longer than wide with maturity. Only 1 mature proglottid per strobila, longer than wide (Fig. 1A), 705–1370 (1068 ± 236 ; 14) long, 140–220 (180 ± 22 ; 14) wide. Mature detached proglottids 2.30–3.80 mm (3.11 ± 0.61 mm; 7) long, 250–395 (307 ± 54 ; 7) wide. Gravid detached proglottids 4.40–4.85 mm (4.63 ± 0.23 mm; 3) long, 451–610 (535 ± 80 ; 3) wide. Testes 23–40 (30 ± 4 ; 11; 4) in number, 28–63 (42 ± 10 ; 11; 4) long, 25–67 (43 ± 10 ; 11; 4) wide, distributed in 2–3 columns in dorsoventral view, extending in field from anterior margin of proglottid to cirrus-sac on poral side and to slightly posterior to genital pore on aporal side (Fig. 1A,B), 1 row deep in cross section (Fig. 1D). Vas deferens extending anteriorly along midline of proglottid from posterior to ovary, entering cirrus sac at anterodistal margin (Fig. 1B,H). External and internal seminal vesicle absent. Cirrus sac pyriform, curved anteriorly, 30–70 (44 ± 13 ; 9) long, 33–110 (59 ± 22 ; 9) wide in attached mature proglottids (Fig. 1B,G), 97–260 (122 ± 53 ; 7) long, 95–165 (115 ± 22 ; 7) wide in detached mature proglottids, containing coiled cirrus. Cirrus unarmed, 10–27 (15 ± 7 ; 6) wide at base in detached proglottids, up to 940 long when everted.

Ovary H-shaped in dorsoventral view (Fig. 1B,H), bilobed in cross section (Fig. 1E), 90–188 (153 ± 13 ; 5) long, 40–90 (61 ± 19 ; 5) wide in attached mature proglottids, 245–630 (439 ± 129 ; 7) long, 85–260 (145 ± 58 ; 7) wide in mature detached proglottids. Mehlis' gland posterior to ovary, 48–65 (54 ± 7 ; 5) in diameter in mature detached proglottids. Vagina slender, merging with oviduct between posterior lobes of ovary, extending from ootype along median line of proglottid, opening posterior to cirrus sac into genital atrium (Fig. 1B,G,H). Genital pores lateral, irregularly alternating, 39–57% (49 ± 5 ; 18) of proglottid length from posterior margin in attached and detached mature proglottids.

Uterus saccate, extending along midline of proglottid from slightly anterior to ovarian bridge to level of genital pore; uterine duct connecting to uterus at its anterior end (Fig. 1B,G). Vitelline follicles in 1–2 lateral bands on each lateral margin of proglottid (Fig. 1B,D–E), extending throughout entire proglottid, interrupted by cirrus sac dorsally, becoming sparse at level of ovary (Fig. 1B,H); vitelline follicles 4–5 (5 ± 0.5 ; 5; 3) long, 5–7 (6 ± 1 ; 5; 3) wide in attached mature proglottids, 25–125 (50 ± 18 ; 7; 4) long, 15–95 (44 ± 22 ; 7; 4) wide in detached mature proglottids. Eggs round, packaged in elongate co-

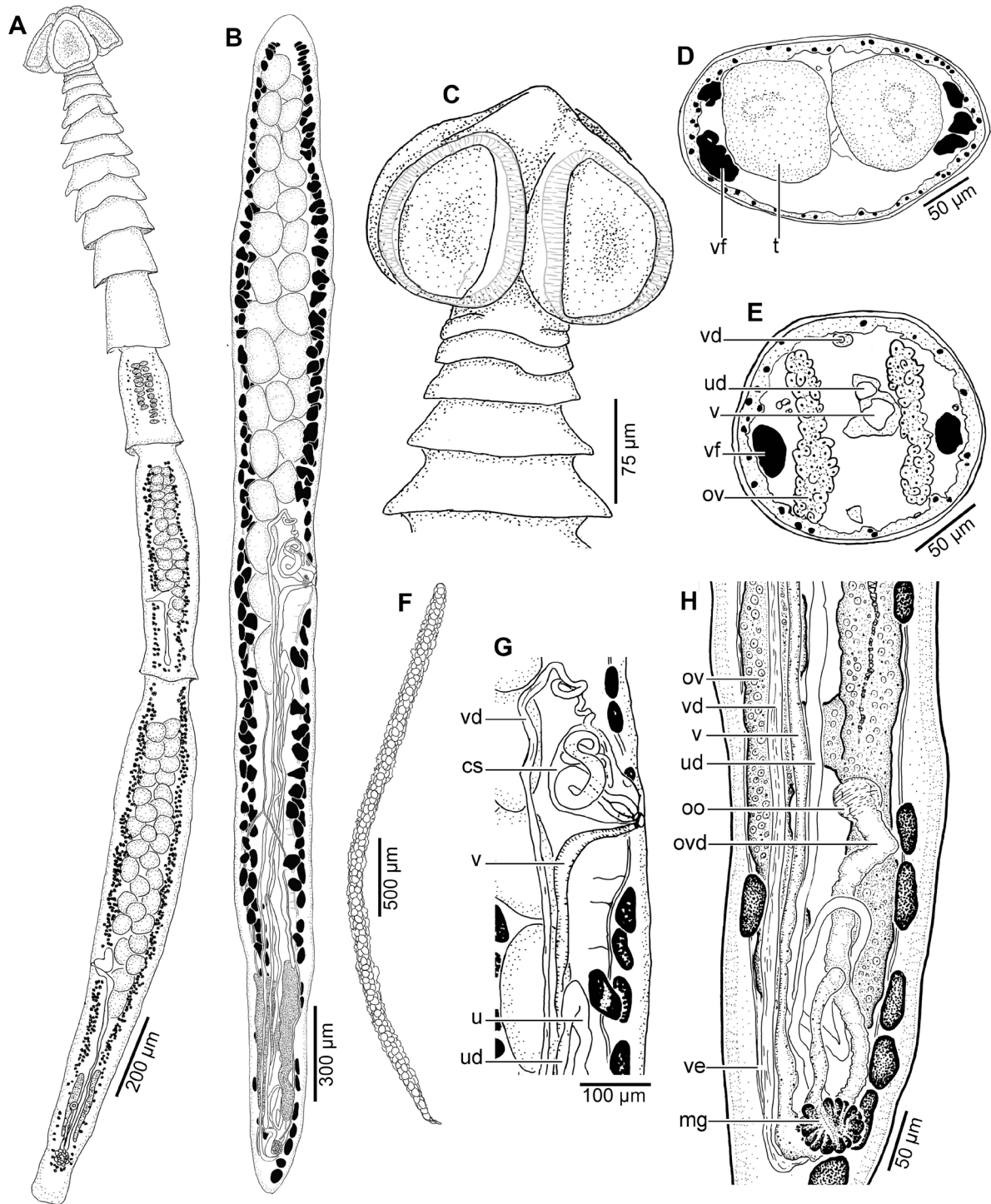


Fig. 1. *Paraberrapex atlanticus* sp. n. from *Squatina guggenheim* Marini. **A** – entire worm (holotype MACN-Pa No. 578/1); **B** – detached mature proglottid (paratype MACN-Pa No. 578/3); **C** – scolex (paratype MACN-Pa No. 578/2); **D**, **E** – cross section of a detached mature proglottid at level anterior to the cirrus sac (**D**) and at level of the ovary (**E**); **F** – cocoon with eggs; **G** – detail of terminal genitalia; **H** – detail of ootype region of a detached proglottid. *Abbreviations:* cs – cirrus sac; mg – Mehlis' gland; oo – oocapt; ov – ovary; ovd – oviduct; t – testis; u – uterus; ud – uterine duct; v – vagina; vd – vas deferens; ve – vas efferens; vf – vitelline follicle.

coons of 129–229 (169 ± 30 ; 16) oncospheres arranged in 2–3 columns (Figs. 1F, 3A–C). Cocoons 2.64–4.19 mm (3.45 ± 0.50 mm; 16) long, 60–75 (65 ± 5 ; 16) wide.

Type host: *Squatina guggenheim* Marini (Squatiniiformes: Squatinidae).

Type locality: Off Puerto Quequén, Buenos Aires Province, Argentina ($38^{\circ}53'00''\text{S}$; $58^{\circ}27'00''\text{W}$).

Additional localities: Near Río de la Plata estuary ($36^{\circ}21'00''\text{S}$; $54^{\circ}32'24''\text{W}$), off Villa Gesell ($37^{\circ}17'45''\text{S}$; $56^{\circ}27'00''\text{W}$), off Carmen de Patagones ($40^{\circ}58'14''\text{S}$; $62^{\circ}00'21''\text{W}$), San Matías Gulf ($41^{\circ}03'13''\text{S}$; $64^{\circ}06'14''\text{W}$).

Site of infection: Spiral intestine.

Specimens deposited: Holotype MACN-Pa No. 578/1, 6 paratypes MACN-Pa No. 578/2–7 (entire worms, cross sections of detached mature proglottids and cocoons), 4 paratypes

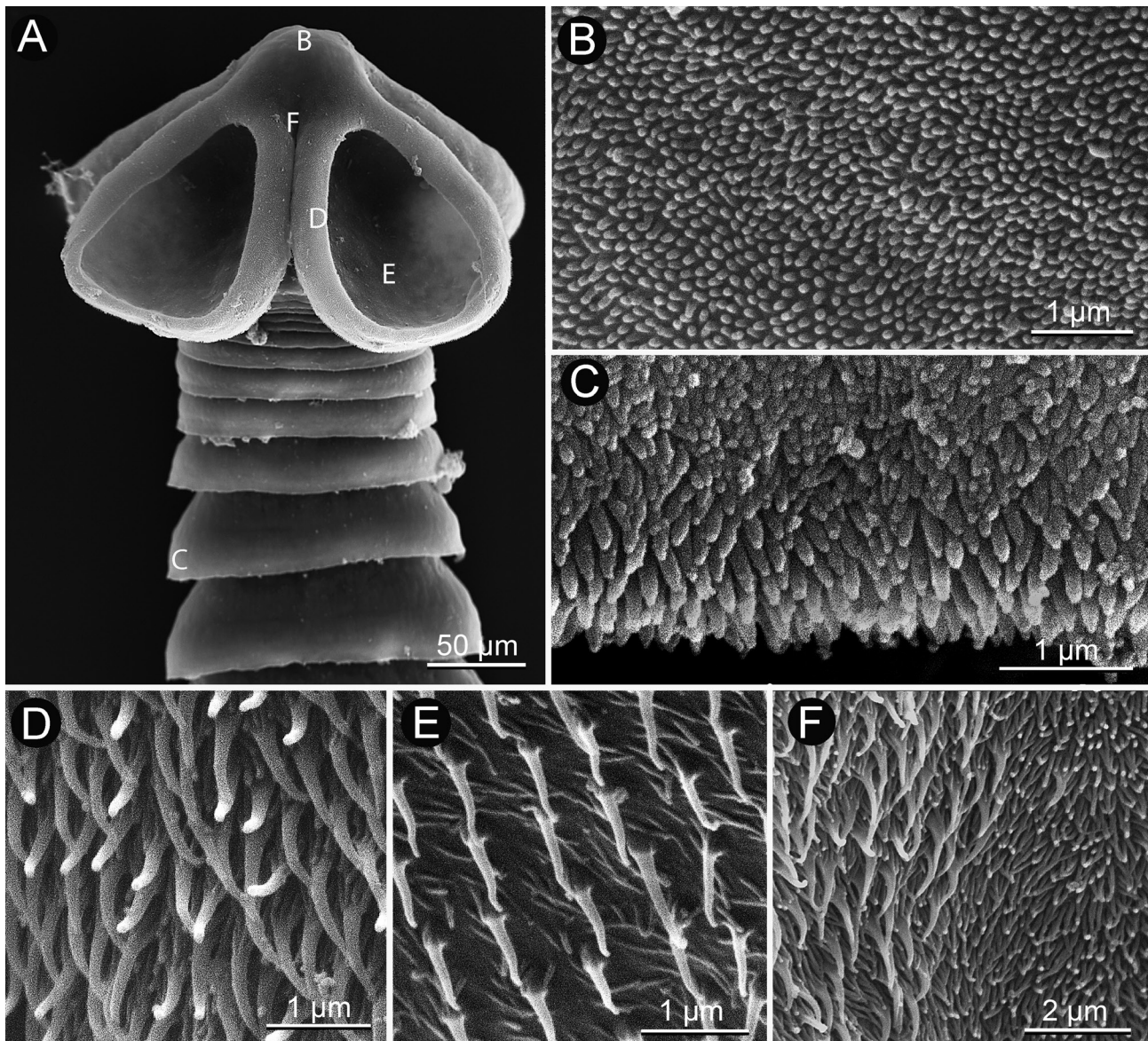


Fig. 2. *Paraberrapex atlanticus* sp. n. from *Squatina guggenheim* Marini, scanning electron micrographs. **A** – scolex and most anterior immature proglottids; small letters indicate locations of details shown in Fig. 2B–F; **B** – apex of scolex; **C** – posterior margin of immature proglottid; **D** – proximal acetabular surface; **E** – distal acetabular surface; **F** – scolex proper (right) and proximal acetabular surface (left).

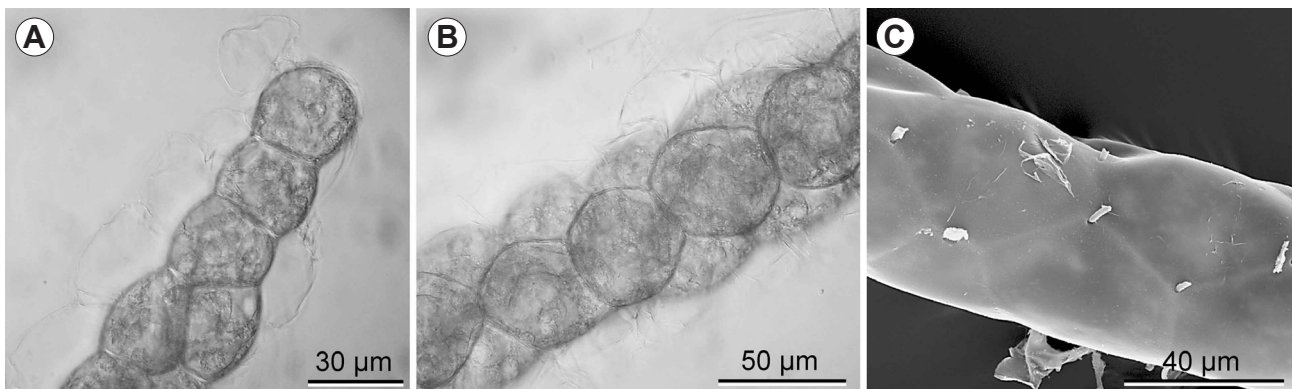


Fig. 3. Cocoons of *Paraberrapex atlanticus* sp. n. from *Squatina guggenheim* Marini. **A**, **B** – light micrographs of terminal end (A) and middle region (B); **C** – scanning electron micrograph showing detail of cocoon surface.

(entire worms, cross sections of detached mature proglottids and cocoons) IPCAS C-702. Additional specimens (whole mounts, histological sections and specimens prepared for SEM) retained in the personal collection of Verónica Ivanov.

Prevalence: 92% (12 of 13 individuals examined infected).

Etymology: The name of this species refers to its distribution, being this the first record of the genus in the Atlantic Ocean.

Remarks. *Paraberrapex atlanticus* sp. n. is consistent with the generic diagnosis of *Paraberrapex* by having a scolex without apical modification of the scolex proper or an apical organ, proglottids without postvaginal testes, a bilobed ovary in cross section, and a vagina that runs along the midline of the proglottid. *Paraberrapex atlanticus* can be distinguished from *P. manifestus* in having cocoons that are 5–6 times longer (2.6–4.2 mm vs 0.5–0.7 mm), with a greater number of eggs per cocoon (129–229 vs 69–112). In addition, in *P. atlanticus* the uterine duct joins the uterus at its anterior end rather than at about half of the length of the uterus (38–78% of uterus length from the posterior end). The vitelline follicles are interrupted dorsally at the level of cirrus sac in *P. atlanticus*, whereas they are uninterrupted in *P. manifestus*. Whereas the microtrich pattern in both species is similar overall, the filitriches on the distal and proximal bothridial surfaces are conspicuously longer and the spinitriches are less dense in *P. manifestus*.

DISCUSSION

The vast majority of lecanicephalidean diversity is in the Indo-Pacific region (Jensen 2005, 2006, Koch et al. 2012, Mojica et al. 2013, 2014, Cielocha et al. 2014). Generic and species diversity is greatest in tropical waters, diminishing in temperate zones (Jensen 2005), and no records of lecanicephalideans exist in cold waters. With the description of *Paraberrapex atlanticus* the distribution of *Paraberrapex* is expanded from the eastern Pacific Ocean to also include the southwestern Atlantic Ocean. Previous to this study, there was a single record of a lecanicephalidean from off the coast of Uruguay, *Aberrapex arrhynchum*.

The limited reports of lecanicephalideans in this area could be related to a gap in lecanicephalidean distribution, lack of studies, lack of suitable hosts or a combination of them all. Lecanicephalideans are mainly parasites of batoids, although a few species have been reported from sharks (Caira et al. 1997, Jensen 2005). They have been found in all batoid orders, except in Rajiformes, with great generic diversity in Dasyatidae and Myliobatidae (Caira and Jensen 2014). Most batoids along the coast off Argentina are rajiform skates (69%) (Cousseau et al. 2010), unsuitable hosts for lecanicephalideans. However, there are at least 19 species of elasmobranchs in 4 orders (i.e. Myliobatiformes, Rhinopristiformes, Squatiniformes and Torpediniformes) that might be good candidates to host lecanicephalideans.

On the basis of recent collections of elasmobranchs in the Argentine Sea, lecanicephalideans have not been found from several specimens of *Discopyge tschudii* Heckel (Torpediniformes) and *Zapteryx brevirostris* (Müller et

Henle) (Rhinopristiformes), although putative novel species of *Aberrapex* have been collected from *M. goodei* and *M. ridens* Ruocco, Lucifora, Díaz de Astarloa, Mabrugaña et Delpiani. Intensive collections in this area are providing evidence that the diversity of lecanicephalideans has been underestimated.

The genera reported from the southwestern Atlantic, *Aberrapex* and *Paraberrapex*, share a unique scolex morphology for a lecanicephalidean, lacking an apical organ and apical modification of the scolex proper. Whereas species of *Aberrapex* are parasites of Myliobatiformes in the genera *Myliobatis* Cuvier, *Taeniura* Müller et Henle and *Aetomylaeus* Garman (see Jensen 2001, 2006, Koch et al. 2012), *Paraberrapex* is restricted to Squatiniformes (Jensen 2001, 2006): *Paraberrapex manifestus* is a parasite of *Squatina californica* in the Gulf of California, and *P. atlanticus* was found in *S. guggenheim* off Argentina. Among the 22 valid species of *Squatina* Duméril (see Vaz and De Carvalho 2013, Froese and Pauly 2015), only five species have been reported as parasite hosts. These are, in addition to *S. californica* and *S. guggenheim*, *S. japonica* Bleeker, *S. squatina* (Linnaeus) and *S. australis* Regan (see Yamaguti 1934, Williams 1968, Beveridge and Campbell 2001, Palm 2004). However, no species of *Paraberrapex* have been reported from these latter three species.

The presence of species of *Paraberrapex* in both *S. californica* and *S. guggenheim* is quite interesting. Stelbrink et al. (2010) carried out a comprehensive phylogenetic reconstruction of 17 of the 22 species of *Squatina* based on molecular sequence data. The phylogenetic hypotheses resulting from the analyses showed *Squatina* monophyletic. Moreover, Stelbrink et al. (2010) recognised four geographic clades: (1) European, North African and Asian species, (2) South African species, (3) Australian species, and (4) North and South American species. Their American clade (Clade 4) included five species: *S. armata* (Philippi) (southeastern Pacific), *S. californica* (northeastern Pacific), *S. dumeril* Lesueur (northwestern Atlantic), *S. guggenheim* and *S. occulta* Vooren et da Silva (southwestern Atlantic) (Stelbrink et al. 2010). Considering that most species of *Squatina* occur in small areas and transoceanic migrations are thought to be extremely unlikely (see Stelbrink et al. 2010), and that, to date, *Paraberrapex* has been only reported from species of *Squatina* in the western hemisphere, it is possible that *Paraberrapex* is restricted to the waters surrounding North and South America. Curiously, the trypanorhynch species *Grillotia* (*C.*) *carvajalregorum* Menoret et Ivanov, 2009 has also been reported from *S. californica* and *S. guggenheim* in the northeastern Pacific and the southwestern Atlantic, respectively (see Menoret and Ivanov 2009, 2012, Beveridge and Campbell 2010). Actually, *G. (C.) carvajalregorum* co-occurs with *P. atlanticus*, being collected from the same host individuals. It would be interesting to generate molecular sequenced data for specimens of *G. (C.) carvajalregorum* from different hosts and areas of distribution to corroborate its identity as a single species or to reveal the presence of cryptic species.

If *Paraberrapex* is in fact restricted to western species of *Squatina* in the hemisphere, it would be expected to find at least seven more species in this genus, one in each of the seven remaining species of *Squatina* occurring off North and South America.

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