

## Eutetrarhynchid trypanorhynchs (Cestoda) from elasmobranchs off Argentina, including the description of *Dollfusiella taminii* sp. n. and *Parachristianella damiani* sp. n., and amended description of *Dollfusiella vooremi* (São Clemente et Gomes, 1989)

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**Abstract:** During a parasitological survey of teleosts and elasmobranchs in the Argentine Sea, 3 species of eutetrarhynchids were collected from the batoids *Myliobatis goodei* Garman and *Psammobatis bergi* Marini, and the shark *Mustelus schmitti* Springer. The specimens collected from *Mu. schmitti* were identified as *Dollfusiella vooremi* (São Clemente et Gomes, 1989), whereas the specimens from *My. goodei* and *Ps. bergi* resulted in new species of *Dollfusiella* Campbell et Beveridge, 1994 and *Parachristianella* Dollfus, 1946, respectively. *Dollfusiella taminii* sp. n. from *Ps. bergi* is characterised by a distinct basal armature with basal swelling and a heteroacanthous homeomorphous metabasal armature with 7–9 falcate hooks per principal row. *Parachristianella damiani* sp. n. from *My. goodei* lacks a distinct basal armature, having 2–3 initial rows of uncinete hooks, a heteroacanthous heteromorphous metabasal armature with the first principal row of small hooks, followed by rows with 10–14 large hooks. This is the first record of *Parachristianella* in the southwestern Atlantic. The amended description of *D. vooremi* includes the detailed description of the tentacular armature, including SEM micrographs of all tentacular surfaces. This species is characterised by a basal armature consisting of rows of uncinete and falcate hooks, a basal swelling and a metabasal armature with billhooks on the antiotherial surface and uncinete hooks on the bothrial surface. The scolex peduncle of *D. vooremi* is covered with enlarged spinitriches. This species is restricted to carcharhiniform sharks, since the report of *D. vooremi* in *Sympterygia bonapartii* Müller et Henle off Bahía Blanca (Argentina) is dubious.

**Keywords:** *Myliobatis goodei*, *Psammobatis bergi*, *Mustelus schmitti*, southwestern Atlantic, tapeworms

Eutetrarhynchid tapeworms currently comprise more than 90 marine species and 2 species reported from rivers in South America (Palm 2004, Campbell and Beveridge 2006, 2007, Schaeffner and Beveridge 2012, 2013a,b,c, Haseli 2013, Schaeffner 2014). Among the 17 genera considered valid in the family, *Dollfusiella* Campbell et Beveridge, 1994, *Prochristianella* Dollfus, 1946, and *Parachristianella* Dollfus, 1946 are the most species-rich with 27, 20 and 9 species, respectively. Although the eutetrarhynchids are well represented in a diverse array of hosts worldwide, only a few records exist from the southwestern Atlantic, all belonging to species of *Dollfusiella*. *Dollfusiella vooremi* (São Clemente et Gomes, 1989) was originally described from *Mustelus schmitti* Springer and *Mu. canis* (Mitchill) off the Brazilian coast and subsequently reported from *Mu. schmitti* collected off Mar del

Plata and from *Sympterygia bonapartii* Müller et Henle off Bahía Blanca in Argentina (São Clemente and Gomes 1989a, Tanzola et al. 1998, Alarcos et al. 2006). Also a pleurocerus of an unidentified species of *Dollfusiella* was reported from the teleost *Micropogonias furnieri* (Desmarest) in Brazil (Pereira and Boeger 2005).

During a parasitological survey of teleosts and elasmobranchs in the Argentine Sea, 3 species of eutetrarhynchids were collected from batoids (*Myliobatis goodei* Garman and *Psammobatis bergi* Marini) and sharks (*Mu. schmitti*). The specimens collected from *Mu. schmitti* were identified as *D. vooremi*, whereas the specimens from *My. goodei* and *Ps. bergi* resulted in new species of *Dollfusiella* and *Parachristianella*, respectively.

*Dollfusiella* was created to include species having a distinctive basal armature and basal swelling, heter-

oacanthous metabasal armature with hooks 1 and 1' not markedly separated, and hook files beginning on the antibothrial surface and terminating on the bothrial surface (Campbell and Beveridge 1994, Beveridge et al. 2004). Although species of this genus have been reported worldwide, most species of *Dollfusiella* have a relatively restricted geographical distribution, with the Australasian region being the most species-rich area (Schaeffner and Beveridge 2013c). Recently, Schaeffner and Beveridge (2013) presented a key for the identification of 26 valid species in the genus.

*Parachristianella* includes 9 valid species characterised by initial rows of uncinata hooks, a heteroacanthous, heteromorphous metabasal armature with hooks 1(1') separated, with hook files beginning on the internal surface and terminating on the external surface. Several species of *Parachristianella* have been reported from the Pacific and North Atlantic Oceans, but no previous record exists from the South Atlantic (Dollfus 1969, Beveridge 1990, Campbell and Beveridge 2007).

Recent molecular phylogenies of trypanorhynch suggest that *Dollfusiella* and *Parachristianella* are paraphyletic genera (Palm et al. 2009, Olson et al. 2010). However, only 6 species of *Dollfusiella* and 3 species of *Parachristianella* were included in both analyses, and the results are not conclusive. The new species of *Dollfusiella* and *Parachristianella* are described below, along with an amended description of *D. vooremi*.

## MATERIALS AND METHODS

Cestodes examined in this study were collected from three species of elasmobranchs, i.e. *Myliobatis goodei*, *Psammobatis bergi* and *Mustelus schmitti*. One specimen of *My. goodei* (host field number AMPQ-365) was collected during January 2011 off Playa Punta Negra, Necochea, Buenos Aires Province (38°61'S; 58°80'W). Three specimens of *Ps. bergi* (host field numbers VIPQ-054, VIPQ-055, VIPQ-060) were caught between 2008–2012 off Puerto Quequén, Buenos Aires Province (38°37'S; 58°53'W), and one specimen (host field number PD5-003) was collected off Necochea, Buenos Aires Province (38°46'S; 57°56'W). Two specimens of *Mu. schmitti* were caught off Mar del Plata, Buenos Aires Province (38°00'S; 57°33'W) and San Antonio Oeste, Rio Negro Province (40°50'S; 64°58'W), respectively. Most hosts were caught by commercial trawlers, with the exception of *My. goodei* that was collected using hooks and line, and *Ps. bergi* (PD5-003) caught with bottom trawls on board of the Oceanographic Vessel '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. 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, dehy-

drated in a graded ethanol series, and dried using hexamethyldisilazane. After dehydration, the specimens were mounted on stubs with carbon tape, coated with c. 40 nm of gold/palladium in a Thermo VG Scientific Polarons SC 7630 and examined in a Philips XL 30 scanning electron microscope. Terminology for the morphology of microtriches follows Chervy (2009).

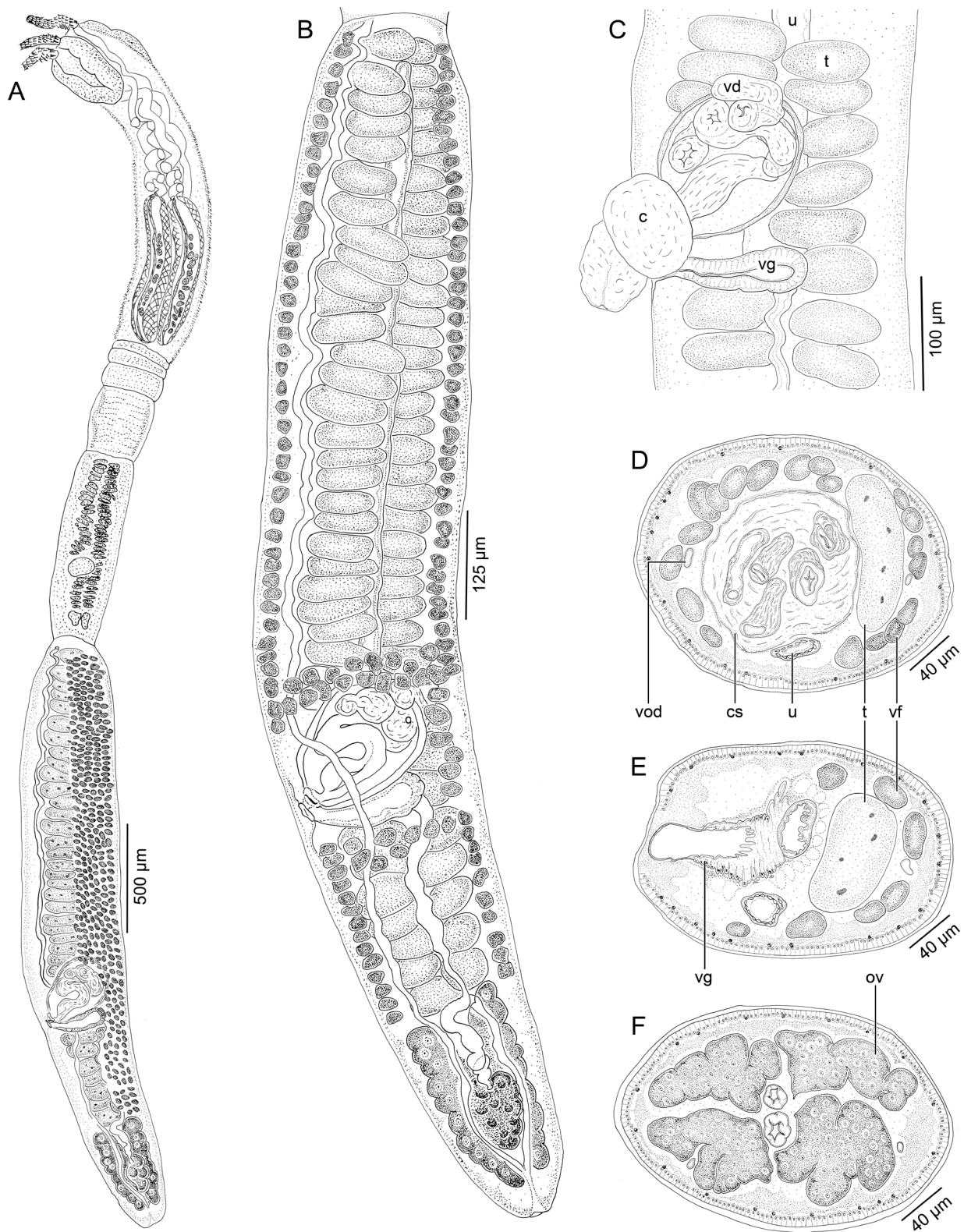
Gravid proglottids were embedded in paraffin and serial cross sections were cut at a thickness of 8 µm. Sections were stained with Harris' haematoxylin, counterstained with eosin and mounted in Canada balsam. One tentacle was removed from the scolex of some specimens and temporarily mounted in glycerine to study the tentacular armature in detail. Gravid proglottids were opened with insect pins to free the eggs, which were then temporarily mounted using distilled water. Terminology for the ontotaxy follows Campbell and Beveridge (1994). Whole and temporarily mounts and sections were observed and measured using an Olympus BX 51 compound microscope. Drawings were made with the aid of a drawing tube attached to the compound microscope. Measurements include the range, followed in parentheses by the mean, standard deviation (when  $n \geq 3$ ), number of worms examined ( $n$ ), and the total number of observations when more than one measurement per worm was taken ( $n$ ).

Features and measurements of the scolex were based on immature, mature, and/or gravid specimens, whereas worm length, maximum width and number of proglottids are referred only to mature and gravid worms. Host specificity categories follow Palm and Caira (2008). All measurements are in micrometres unless otherwise stated. Museum abbreviations used are as follows: IPCAS – Institute of Parasitology, Academy of Sciences of the Czech Republic, České Budějovice, Czech Republic; MACN-Pa – Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina; MNHN – Muséum National d'Histoire Naturelle, Paris, France.

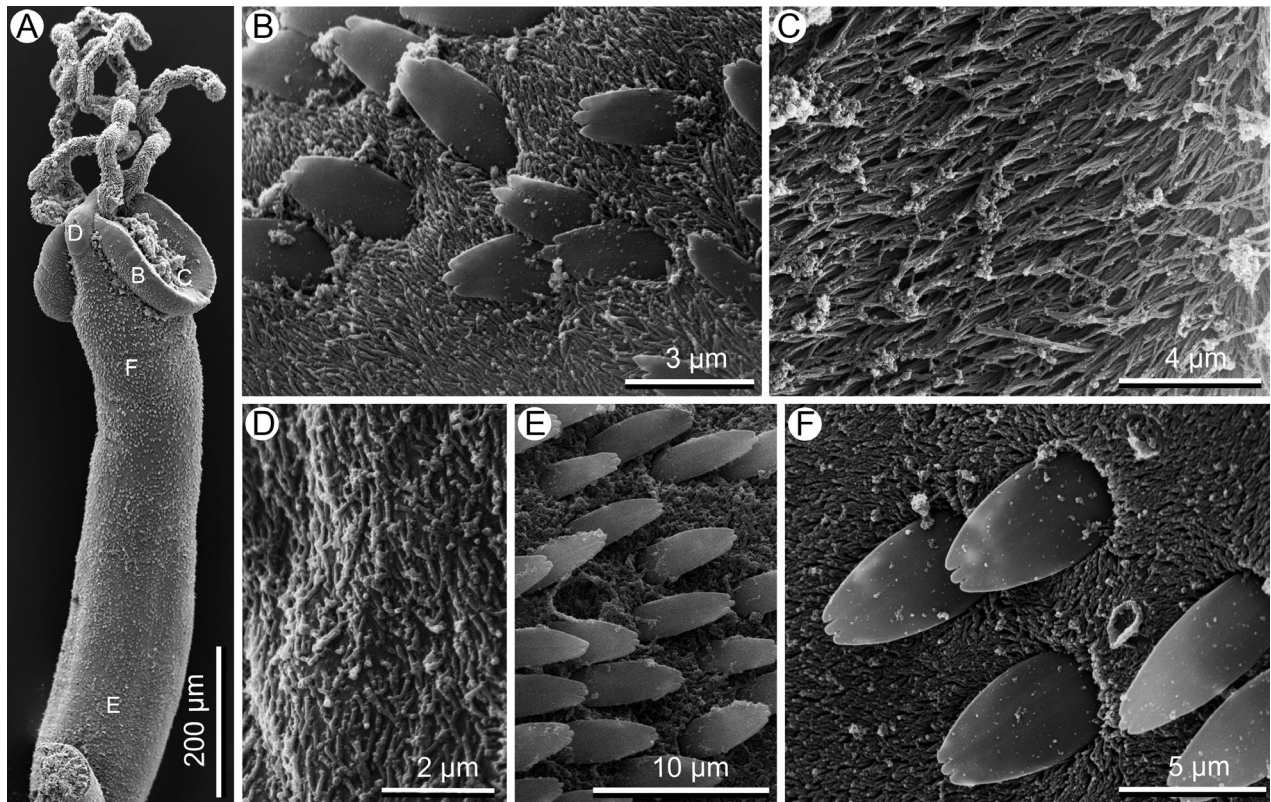
## RESULTS

*Dollfusiella taminii* sp. n. Figs. 1–4, Table 1

**Description** (based on 12 worms prepared as follows: 10 whole mounts of complete mature worms, histological sections of 2 mature proglottids, 2 immature specimens observed with SEM, and everted tentacles removed from 3 specimens). Worms apolytic, 2.7–4.5 mm ( $3.4 \pm 0.6$  mm,  $n = 10$ ) long, maximum width at level of pars bothrialis. Proglottids acraspedote, 5–8 ( $6 \pm 1$ ,  $n = 10$ ) per worm, 4–7 ( $5 \pm 1$ ,  $n = 10$ ) immature proglottids, 1 mature proglottid (Fig. 1A,B). Scolex 820–1070 ( $934 \pm 69$ ,  $n = 10$ ) long, maximum width at level of pars bothrialis, length to width ratio 2.6–4.4 ( $3.5 \pm 0.5$ ,  $n = 10$ ). Apex of scolex covered with acicular filitriches (Fig. 2D). Two subcircular bothria 200–270 ( $228 \pm 22$ ,  $n = 10$ ,  $n = 18$ ) long, 130–185 ( $151 \pm 21$ ,  $n = 5$ ,  $n = 6$ ) wide (Figs. 1A, 2A). Proximal bothrial surface covered with trifold spinitriches interspersed with acicular filitriches (Fig. 2B). Distal bothrial surface covered with capilliform filitriches (Fig. 2C). Pars bothrialis 210–270 ( $240 \pm 17$ ,  $n = 10$ ) long, 210–345 ( $290 \pm 40$ ,  $n = 10$ ) wide. Pars vaginalis 375–560 ( $466 \pm 53$ ,  $n = 10$ ) long, 160–220 ( $180 \pm 20$ ,  $n = 10$ ) wide; tentacle



**Fig. 1.** *Dollfusiella taminii* sp. n. from *Psammobatis bergi*. **A** – entire worm (holotype MACN-Pa No. 544/1); **B** – terminal proglottid, ventral view (holotype MACN-Pa No. 544/1); **C** – detail of terminal genitalia, dorsal view (paratype MACN-Pa No. 544/2). **D–F** – cross sections of a mature proglottid; **D** – at level of cirrus sac; **E** – at level of vagina near genital atrium; **F** – at level of ovary anterior to isthmus. Circummedullary vitelline follicles not drawn or partially drawn in figures A–C to allow the view of internal organs. *Abbreviations:* c – cirrus; cs – cirrus sac; ov – ovary; t – testis; u – uterus; vd – vas deferens; vf – vitelline follicle; vg – vagina; vod – ventral osmoregulatory duct.



**Fig. 2.** Scanning electron micrographs of *Dollfusiella taminii* sp. n. from *Psammobatis bergi*. **A** – scolex, small letters indicate locations of details shown in figures B–F; **B** – proximal bothrial surface (trifid spinitriches and acicular filitriches); **C** – distal bothrial surface (capilliform filitriches); **D** – apex of scolex (acicular filitriches); **E** – surface of pars bulbosa (bifid and trifid spinitriches interspersed with acicular filitriches); **F** – surface of pars vaginalis (trifid spinitriches and acicular filitriches).

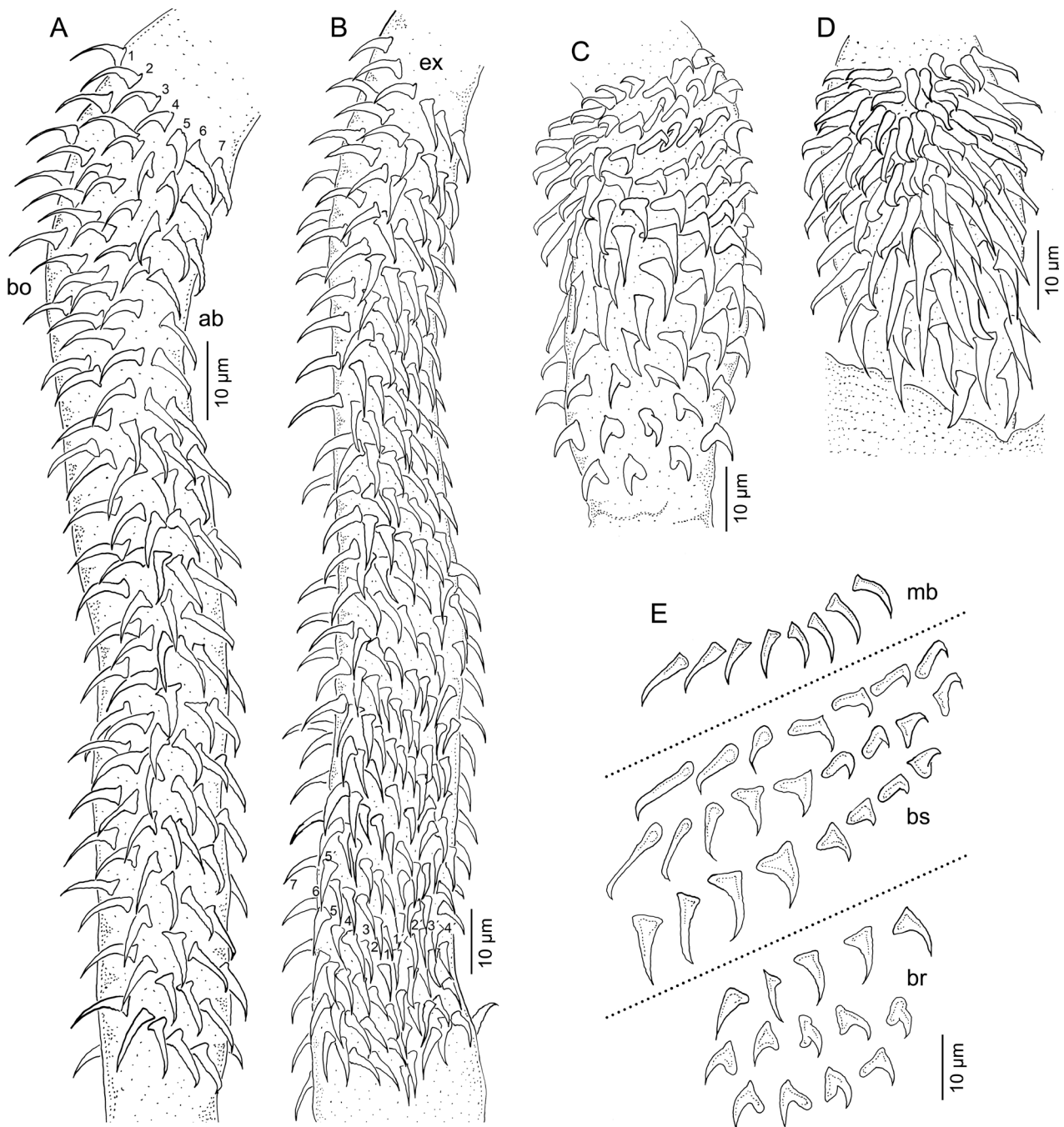
sheaths sinuous. Pars bulbosa 410–590 ( $473 \pm 51$ ,  $n = 10$ ) long, 173–210 ( $190 \pm 12$ ,  $n = 10$ ) wide. Scolex peduncle covered with trifid spinitriches interspersed with acicular filitriches from between bothria to posterior part of pars bulbosa (Fig. 2E,F). Bulbs elongate, 395–510 ( $460 \pm 35$ ,  $n = 10$ ,  $n = 20$ ) long, 60–92 ( $73 \pm 9$ ,  $n = 10$ ,  $n = 20$ ) wide, length to width ratio 4.5–8.2 ( $6.4 \pm 0.9$ ,  $n = 10$ ,  $n = 20$ ). Prebulbar organ present, 6–10 ( $8 \pm 1$ ,  $n = 8$ ,  $n = 8$ ) long, 10–15 ( $13 \pm 2$ ,  $n = 8$ ,  $n = 8$ ) wide. Retractor muscle originates at base of bulb, gland-cells surround retractor muscle up to anterior third of bulb (Fig. 1A). Scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa) 1 : 1.6–2.3 : 1.6–2.2.

Tentacles slender, up to 470 long, with prominent basal swelling. Diameter at base 17–22 ( $19 \pm 2$ ,  $n = 6$ ,  $n = 6$ ) without hooks, 25–30 ( $27 \pm 2$ ,  $n = 6$ ,  $n = 6$ ) with hooks. Diameter at basal swelling 25–27 ( $26 \pm 1$ ,  $n = 6$ ,  $n = 6$ ) without hooks, 35–38 ( $37 \pm 1$ ,  $n = 6$ ,  $n = 6$ ) with hooks. Distal diameter of tentacles 20–22 ( $21 \pm 1$ ,  $n = 3$ ,  $n = 3$ ) without hooks, 30–32 ( $31 \pm 1$ ,  $n = 3$ ,  $n = 3$ ) with hooks. Tentacular armature heteroacanthous typical, hooks hollow. Hooks arranged in ascending half spirals originating on antibothrial surface of tentacle, terminating on bothrial surface (Figs. 3, 4, Table 1). Distinctive basal armature present, initial 2–3 rows of uncinata hooks, with broad

base and recurved tip, followed by 1–2 rows of falcate hooks (Figs. 3C,D, 4A–C,G, Table 1). Basal swelling with 9–10 rows of hooks and 7–12 hooks per half spiral (Fig. 3C,D); rows on antibothrial surface V-shaped, with elongated billhooks projecting perpendicularly from surface of tentacle, densely packed, gradually changing in shape to uncinata hooks on bothrial surface (Figs. 3C–E, 4D,H).

Metabasal armature (from row 15–17 to distal tip of the tentacle) heteroacanthous, homeomorphous, with 7–9 hooks falcate per half spiral row (Figs. 3A,B,E, 4F,I, Table 1); hook files 1 and 1' not separated. Distal metabasal region with 10–12 hooks per half spiral row.

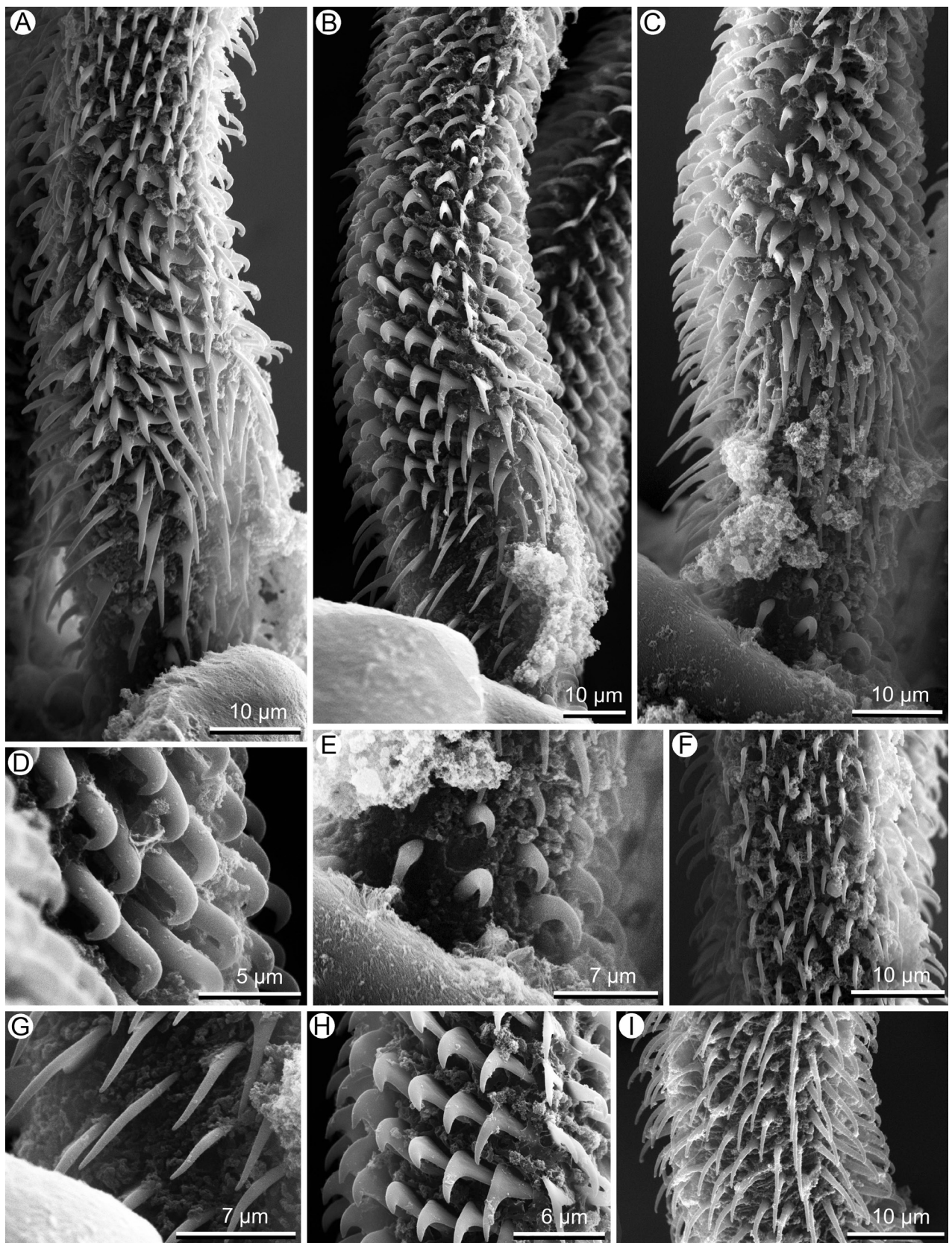
Immature proglottids wider than long to longer than wide with maturity. Mature proglottids longer than wide, 1 110–2225 ( $1530 \pm 365$ ,  $n = 10$ ,  $n = 10$ ) long, 200–280 ( $242 \pm 26$ ,  $n = 10$ ,  $n = 10$ ) wide, length to width ratio 4.7–8.6 ( $6.2 \pm 1.2$ ,  $n = 10$ ,  $n = 10$ ) (Fig. 1A,B). Genital pore 30–43% ( $38 \pm 0.02$ ,  $n = 10$ ,  $n = 10$ ) from posterior margin of proglottid. Testes oval, 33–53 ( $41 \pm 5$ ,  $n = 4$ ,  $n = 28$ ) long, 58–85 ( $70 \pm 10$ ,  $n = 4$ ,  $n = 28$ ) wide, 58–81 ( $69 \pm 8$ ,  $n = 5$ ,  $n = 5$ ) in number, arranged in 2 columns interrupted at level of cirrus sac on poral side, 22–29 ( $26 \pm 3$ ,  $n = 5$ ) prevaginal, 6–9 ( $7 \pm 1$ ,  $n = 5$ ) postvaginal, 30–43 ( $36 \pm 5$ ,  $n = 5$ ) antiporal (Fig. 1A–E). Cir-



**Fig. 3.** Tentacular armature of *Dollfusiella taminii* sp. n. from *Psammobatis bergi*. **A** – metabasal region, internal surface; **B** – metabasal armature, antibothrial surface, tentacle slightly rotated showing external surface; **C** – basal region, external surface; **D** – basal region, antibothrial surface, partially everted tentacle; **E** – profiles of hooks of basal and metabasal armature. *Abbreviations:* ab – antibothrial surface; bo – bothrial surface; br – basal rows; bs – basal swelling; ex – external surface; mb – metabasal hooks.

rus sac ovoid, thick-walled, 100–165 ( $138 \pm 29$ ,  $n = 6$ ) long, 80–150 ( $109 \pm 30$ ,  $n = 6$ ,  $n = 6$ ) wide, length to width ratio 1.1–1.37 ( $1.25 \pm 0.14$ ,  $n = 6$ ); cirrus unarmed, 450–590 (520,  $n = 2$ ) long, 105–110 (107,  $n = 2$ ) wide at base. Vas deferens coiled, extending to mid-proglottid (Fig. 1B,C). External and internal seminal vesicles not observed. Vagina opening posterior to cirrus sac, running to ootype region (Fig. 1B,E); seminal receptacle 17–27

( $22 \pm 4$ ,  $n = 4$ ) wide; vaginal wall thick, particularly in distal portion. Ovary lobulated, H-shaped in dorsoventral view, four-lobed in cross section at level of ovarian isthmus, 158–340 ( $258 \pm 63$ ,  $n = 6$ ) long, 110–165 ( $129 \pm 21$ ,  $n = 6$ ) wide (Fig. 1B,F). Vitelline follicles circummedullary, extending throughout entire proglottid, interrupted dorsally and ventrally at level of cirrus sac, reaching anterior margin of ovarian lobes; vitelline follicles 10–25



**Fig. 4.** Scanning electron micrographs of the tentacular armature of *Dollfusiella taminii* sp. n. from *Psammobatis bergi*. **A** – bothrial surface; **B** – external surface; **C** – internal surface; **D** – billhooks on antibothrial surface of basal swelling; **E** – unciniate hooks at base of the tentacle; **F** – metabasal region, bothrial surface; **G** – falcate hooks, basal region; **H** – unciniate hooks on bothrial surface of the basal swelling; **I** – metabasal region, internal surface.

**Table 1.** Oncotaxy and hooks measurements of *Dollfusiella taminii* sp. n.

Armature	Surface	Shape	Length	Width	Height	Guard	Toe
Basal							
Rows 1–3		uncinate	5–8 (7 ± 1)	4–6 (5 ± 1)	4–6 (5 ± 1)	1–2 (1.5 ± 0.5)	1–2 (1.5 ± 0.5)
Rows 4–5		falcate	8–12 (10 ± 1)	3–5 (4 ± 1)	-	-	-
Basal swelling	bothrial	uncinate	4–8 (6 ± 1)	3–5 (4 ± 1)	4–6 (5 ± 1)	2–4 (3 ± 1)	-
	antibothrial	billhook	6–9 (7 ± 1)	2–3 (2.5 ± 0.5)	-	-	-
Metabasal		falcate	6–9 (8 ± 1)	2–3 (2.5 ± 0.5)	-	-	-

(17 ± 4, n = 9, n = 17) long, 15–35 (27 ± 6, n = 9, n = 17) wide (Fig. 1A,B,D–F). Mehlis' gland posterior to ovarian isthmus, 73–105 (90 ± 13, n = 7, n = 7) long, 52–72 (60 ± 3, n = 7, n = 7) wide. Ventral osmoregulatory ducts lateral, poral duct deviates to mid proglottid at level of cirrus sac (Fig. 1A,B). Uterus median, tubular, extending to anterior extremity of proglottid; uterine pore absent (Fig. 1B–E).

**Type host:** Blotched sand skate *Psammodontus bergi* Marini (Rajiformes: Arhynchobatidae) (PD5-003, VIPQ-054, VIPQ-055, VIPQ-060).

**Type locality:** Puerto Quequén (38°37'S; 58°53'W), Buenos Aires Province, Argentina.

**Other locality:** Off Necochea (38°46'S; 57°56'W), Buenos Aires Province, Argentina.

**Site of infection:** Spiral intestine.

**Specimens deposited:** Holotype (mature worm) MACN-Pa No. 544/1, 3 paratypes (mature worms) MACN-Pa No. 544/2–4, 2 paratypes (mature worms) IPCAS No. C-661. Additional specimens (whole mounts, histological sections, and specimens prepared for SEM) retained in the personal collection of Verónica Ivanov.

**Prevalence and intensity of infection:** Prevalence 100% (4 hosts infected of 4 individuals examined); intensity 7–15 worms per host.

**Etymology:** This species is named after Leonardo L. Tamini, for his invaluable help during the field trips in Necochea.

**Remarks.** *Dollfusiella taminii* sp. n. can be distinguished from all the species of *Dollfusiella* described with heteromorphous hooks in the metabasal armature, i.e. *D. australis* (Prudhoe, 1969), *D. cortezensis* (Friggens et Duszynski, 2005), *D. elongata* Beveridge, Neifar et Euzet, 2004, *D. imparispinis* Schaeffner et Beveridge, 2013, *D. lineata* (Linton, 1909), *D. macrotrachela* (Heinz et Dailey, 1974), *D. ocallaghani* (Beveridge, 1990), *D. parva* Schaeffner et Beveridge, 2013, *D. spinulifera* (Beveridge et Jones, 2000), and *D. vooremi*.

Among the species with homeomorphous hooks in the metabasal armature, *D. taminii* differs from *D. carayoni* (Dollfus, 1942), *D. micracantha* (Carvajal, Campbell et Cornford, 1976), *D. geraschmidti* (Dollfus, 1974), *D. michiae* (Southwell, 1929), *D. musteli* (Carvajal, 1974), *D. schmidti* (Heinz et Dailey, 1974), *D. spinifer* (Dollfus, 1969), and *D. tenuispinis* (Linton, 1890) by possessing falcate hooks, instead of uncinat or spiniform hooks.

*Dollfusiella litocephala* (Heinz et Dailey, 1974) lacks the initial rows of uncinat hooks and the basal swelling with billhooks that are present in *D. taminii*. In *D. angustiformis* Schaeffner et Beveridge, 2013, the metabasal hooks increase gradually in size from the antibothrial to the bothrial surface, whereas they are of similar size in *D. taminii* sp. n. In addition, the new species lacks the enlarged billhooks on the antibothrial surface of the basal swelling described in *D. owensi* (Beveridge, 1990).

In some species of *Dollfusiella* (i.e. *D. aculeata* [Beveridge, Neifar et Euzet, 2004], *D. aetobati* [Beveridge, 1990], *D. hemispinosa* Schaeffner et Beveridge, 2013, *D. spinosa* Schaeffner et Beveridge, 2013, *D. martini* [Beveridge, 1990], and *D. bareldsi* [Beveridge, 1990]), there is a transitional zone between the basal swelling and the proximal metabasal armature, consisting of a few rows of hooks that differ in shape and/or size from those in the remaining metabasal armature. *Dollfusiella taminii* lacks those transitional hooks. It can further be distinguished from *D. aculeata* by a gradual change in hook shape from the antibothrial to the bothrial surface in the basal swelling (see fig. 18 in Beveridge et al. 2004, Fig. 3C,E in the present study). The examination of 2 paratypes of *D. aculeata* (MNHN 190HG) lead us to realise that the figure 18 in Beveridge et al. (2004) corresponds to the antibothrial surface instead of bothrial surface as indicated in the original caption.

The distribution of vitelline follicles seems to be an interesting feature in the distinction of species of *Dollfusiella*. The vitelline follicles are circummedullary interrupted at level of the cirrus sac and genital atrium in all the species described so far. However, the vitelline follicles reach the anterior margin of the ovary or overlap the ovary, and the postovarian follicles can be present or absent. Therefore, whereas *D. aculeata* has postovarian vitelline follicles observed in the paratypes (MNHN 190HG, MNHN 191HG), they reach the anterior margin of the ovary in the new species (Fig. 1A,B,D–E).

***Dollfusiella vooremi*** (São Clemente et Gomes, 1989)

Figs. 5–7, Table 2

Syn. *Eutetrarhynchus vooremi* São Clemente et Gomes, 1989

**Redescription** (based on 6 specimens prepared as follows: 5 whole mounts – 2 gravid worms and 3 immature worms, histological sections of 1 gravid proglottid, 5 de-

tached gravid proglottids, 1 immature worm observed with SEM, and everted tentacles removed from 2 specimens). Worms apolytic, 39.7–44.8 mm (42.2 mm,  $n = 2$ ) long, maximum width at level of gravid proglottids. Proglottids acraspedote, 40–51 (45,  $n = 2$ ) per worm, 30–38 (34,  $n = 2$ ) immature proglottids, 3–7 ( $5 \pm 2$ ,  $n = 2$ ) mature proglottids, 2–6 (4,  $n = 2$ ) gravid proglottids (Fig. 5A). Scolex 4.5–7.5 mm ( $5.7 \pm 0.1$  mm,  $n = 5$ ) long, maximum width at level of pars bothrialis or pars bulbosa, length to width ratio 14.2–17.3 ( $15.8 \pm 2.2$ ,  $n = 5$ ): 1. Two oval bothria, 220–360 ( $312 \pm 53$ ,  $n = 5$ ,  $n = 9$ ) long (Figs. 5A, 7A). Pars bothrialis 237–380 ( $312 \pm 65$ ,  $n = 5$ ) long, 350–530 ( $402 \pm 74$ ,  $n = 5$ ) wide. Pars vaginalis 1.1–2.2 mm ( $1.6 \pm 0.4$  mm,  $n = 5$ ) long, 210–280 ( $244 \pm 25$ ,  $n = 5$ ) wide, tentacle sheaths sinuous. Pars bulbosa 3.5–5.1 mm ( $4.3 \pm 0.7$  mm,  $n = 5$ ) long, 325–425 ( $375 \pm 48$ ,  $n = 5$ ) wide. Bulbs elongate, 3.4–4.9 mm ( $4.2 \pm 0.6$  mm,  $n = 5$ ,  $n = 9$ ) long, 115–160 ( $132 \pm 15$ ,  $n = 5$ ,  $n = 9$ ) wide, length to width ratio 24.1–41.3 ( $31.8 \pm 4.9$ ,  $n = 5$ ,  $n = 9$ ) (Fig. 5). Prebulbar organ present, 15–20 ( $17 \pm 2$ ,  $n = 5$ ,  $n = 6$ ) long, 25–30 ( $28 \pm 2$ ,  $n = 5$ ,  $n = 6$ ) wide. Retractor muscle originates at base of bulb, basal region of retractor muscle surrounded by gland cells. Pars postbulbosa, 35–65 ( $55 \pm 15$ ,  $n = 4$ ) long, 165–410 ( $282 \pm 88$ ,  $n = 4$ ) wide. Scolex ratio (pars bothrialis : pars vaginalis : pars bulbosa : pars postbulbosa) 1 : 4.7–6.1 : 12.7–13.4 : 0.2. Scolex peduncle covered with trifid spinitriches from between bothria to posterior part of pars bulbosa (Fig. 7G).

Tentacles elongate, up to 1900 long. Diameter at base 30–55 ( $41 \pm 9$ ,  $n = 5$ ,  $n = 9$ ) without hooks, 40–65 ( $51 \pm 8$ ,  $n = 5$ ,  $n = 9$ ) with hooks. Diameter at basal swelling 42–60 ( $47 \pm 6$ ,  $n = 5$ ,  $n = 9$ ) without hooks, 75–95 ( $82 \pm 7$ ,  $n = 5$ ,  $n = 9$ ) with hooks. Distal diameter of tentacles, 37–72 ( $50 \pm 13$ ,  $n = 5$ ,  $n = 7$ ) without hooks, 47–87 ( $67 \pm 12$ ,  $n = 5$ ,  $n = 7$ ) with hooks. Tentacular armature heteroacanthous, heteromorphous; hooks hollow. Hooks arranged in ascending half spirals originating on antibothrial surface, terminating on bothrial surface (Figs. 6, 7B–F, Table 2). Distinctive basal armature present, initial 3 rows of uncinuate hooks, with broad base and recurved tip; next 3 rows with falcate hooks, with broad base (Figs. 6A,B,D, 7B,E). Basal swelling (from row 7 to row 14) with 14–22 hooks per half spiral row (Figs. 6A,B,D, 7B,E, Table 2). Rows on antibothrial surface V-shaped, with densely packed billhooks projecting perpendicularly from surface of tentacle, hooks gradually changing shape to falcate and uncinuate hooks on bothrial surface (Figs. 6A,B,D, 7E).

Metabasal armature (from row 15 to distal tip of tentacle), 16–22 hooks per half spiral row, hooks 1 and 1' not separated (Figs. 6A–D, 7D,F). Billhooks on antibothrial surface, uncinuate hooks with broad base on bothrial surface (Figs. 6C,D, 7D,F). Hooks on internal and external surfaces gradually changing in shape and size from bothrial to antibothrial surface (Figs. 6A,C,D, 7D,F). Distal metabasal region with 15–18 hooks per half spiral (Fig. 6C).

Immature proglottids wider than long becoming longer than wide with maturity. Mature proglottids longer than wide, 1325–2775 ( $1953 \pm 484$ ,  $n = 2$ ,  $n = 10$ ) long, 530–800 ( $647 \pm 88$ ,  $n = 2$ ,  $n = 10$ ) wide, length to width ratio 1.7–4.2 ( $3.1 \pm 0.9$ ,  $n = 2$ ,  $n = 10$ ). Genital pores irregularly alternate irregularly, 31.4–41.7% ( $36.1 \pm 3.2$ ,  $n = 2$ ,  $n = 16$ ) from posterior margin of mature proglottid. Testes oval, 70–150 ( $97 \pm 18$ ,  $n = 2$ ,  $n = 18$ ) long, 105–180 ( $142 \pm 23$ ,  $n = 2$ ,  $n = 18$ ) wide, 50–75 ( $64 \pm 9$ ,  $n = 2$ ,  $n = 10$ ) in number, arranged in 2 longitudinal columns, 1 row deep in cross section, extending from anterior margin of proglottid to anterior margin of ovary, interrupted at level of cirrus sac in poral side, 18–32 ( $24 \pm 4$ ,  $n = 2$ ,  $n = 10$ ) prevaginal, 6–9 ( $7 \pm 1$ ,  $n = 2$ ,  $n = 7$ ) postvaginal, and 25–38 ( $32 \pm 4$ ,  $n = 2$ ,  $n = 10$ ) antiporal (Fig. 5A–E). Cirrus sac ovoid, 127–200 ( $170 \pm 21$ ,  $n = 2$ ,  $n = 10$ ) long, 100–175 ( $131 \pm 24$ ,  $n = 2$ ,  $n = 10$ ) wide, length to width ratio 1.1–1.6 ( $1.3 \pm 0.2$ ,  $n = 2$ ,  $n = 10$ ); cirrus unarmed, up to 295 long when everted (Fig. 5B,C,E). Vas deferens coiled, extending to mid-proglottid. External seminal vesicle present, internal seminal vesicle not observed (Fig. 5B,C,E).

Vagina thick-walled, opening into genital atrium posterior and ventral to cirrus sac, running posteriorly to ootype region (Fig. 5B,C,E). Ovary lobulated, bilobed in dorsoventral view, four-lobed in cross section at level of ovarian isthmus, 175–305 ( $226 \pm 44$ ,  $n = 2$ ,  $n = 9$ ) long, 410–680 ( $525 \pm 83$ ,  $n = 2$ ,  $n = 9$ ) wide (Fig. 5B). Vitelline follicles circummedullary, extending throughout entire proglottid, interrupted dorsally and ventrally at level of cirrus sac, reaching anterior margin of ovary (Fig. 5B,D,E); vitelline follicles 20–42 ( $32 \pm 7$ ,  $n = 2$ ,  $n = 15$ ) long, 15–45 ( $26 \pm 11$ ,  $n = 2$ ,  $n = 15$ ) wide. Mehlis' gland 105–180 ( $142 \pm 23$ ,  $n = 2$ ,  $n = 9$ ) in diameter, posterior to ovarian isthmus. Ventral osmoregulatory ducts lateral, poral duct deviates to mid proglottid at level of cirrus sac (Fig. 5B). Uterus saccate, 6–8 % ( $7 \pm 1$ ,  $n = 2$ ,  $n = 9$ ) from anterior margin of proglottid. Gravid proglottids 1875–2750 ( $2331 \pm 320$ ,  $n = 2$ ,  $n = 8$ ) long, 700–1125 ( $886 \pm 162$ ,  $n = 2$ ,  $n = 8$ ) wide, length to width ratio 2.1–3.6 ( $2.7 \pm 0.6$ ,  $n = 2$ ,  $n = 8$ ) (Fig. 5A). Detached gravid proglottids 1650–2775 ( $2205 \pm 427$ ,  $n = 5$ ) long, 820–1050 ( $929 \pm 95$ ,  $n = 5$ ) wide, length to width ratio 1.9–2.8 ( $2.4 \pm 0.4$ ,  $n = 5$ ). Intrauterine unembryonated eggs tear-shaped, 44–61 ( $52 \pm 5$ ,  $n = 8$ ) long, 23–26 ( $24 \pm 1$ ,  $n = 8$ ) wide, with 1 polar filament up to 87 long (Fig. 5F).

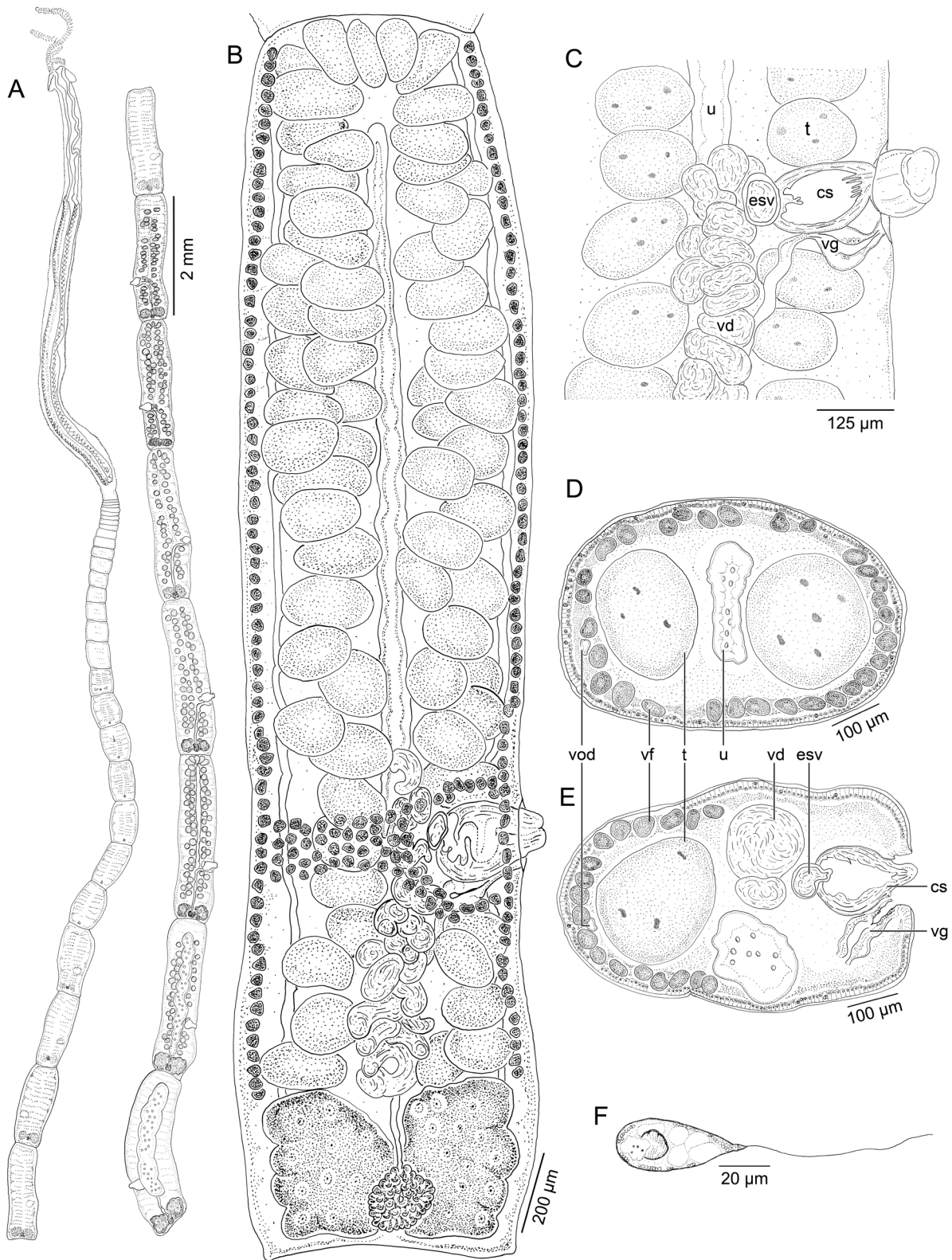
Type host: *Mustelus canis* (Mitchill), dusky smooth-hound (Carcharhiniformes: Triakidae).

Additional host: *Mustelus schmitti* Springer, narrownose smooth-hound (Carcharhiniformes: Triakidae).

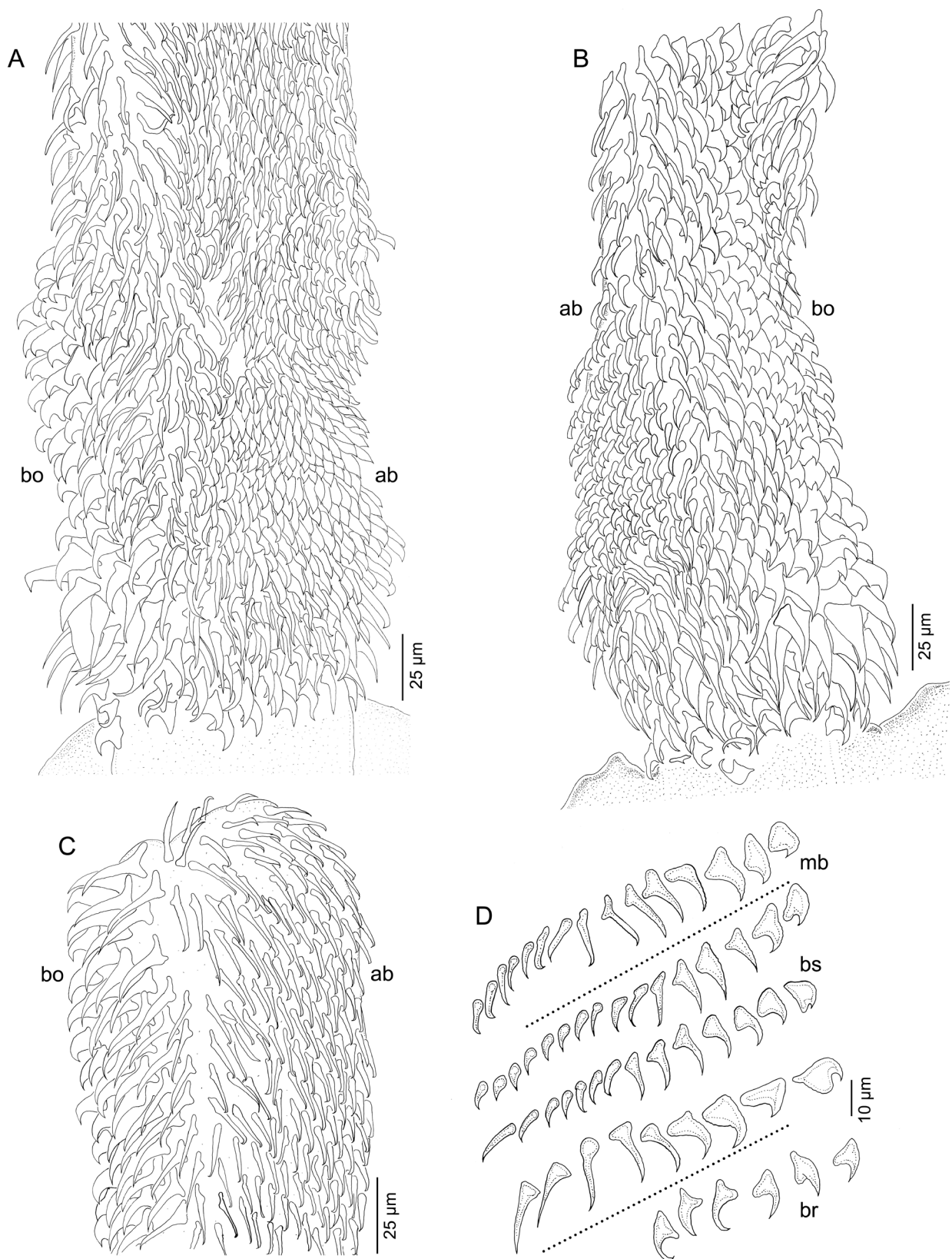
Type locality: Southern Brazilian coast (30°40'S; 53°20'W–50°40'W).

Other localities: Off San Antonio Oeste (40°50'S; 64°58'W), Rio Negro Province, Argentina; off Mar del Plata

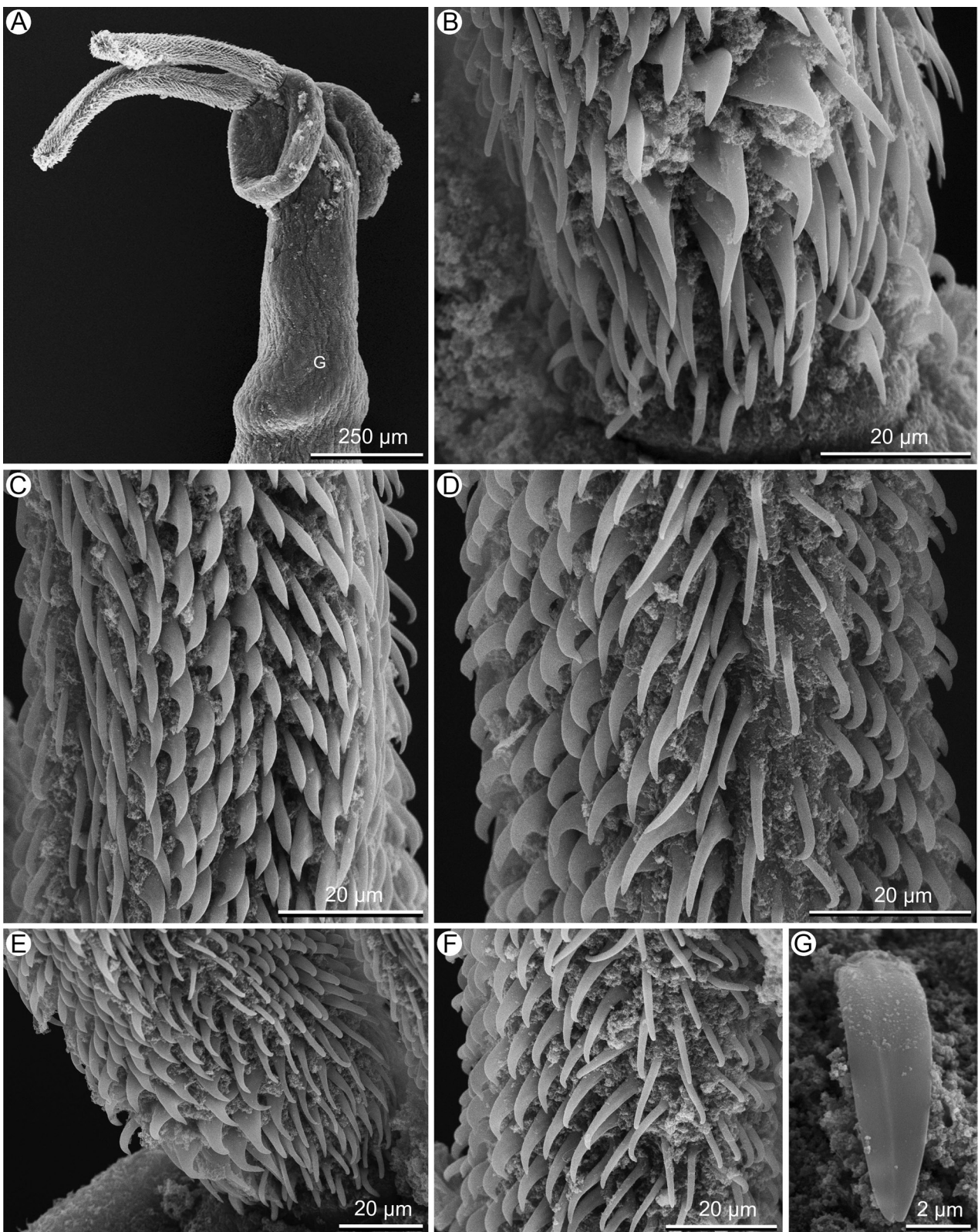




**Fig. 5.** *Dollfusiella vooremi* (São Clemente et Gomes, 1989) from *Mustelus schmitti*. **A** – entire worm (voucher MACN-Pa No. 543/1); **B** – mature proglottid, dorsal view (voucher MACN-Pa No. 543/1); **C** – detail of terminal genitalia, dorsal view (paratype MACN-Pa 543/1); **D, E** – cross sections of a gravid proglottid: at level of testes, anterior to cirrus sac (D), at level of genital pore (E); **F** – unembryonated egg. Circummedullary vitelline follicles not drawn or partially drawn in figures A–C to allow the view of internal organs. *Abbreviations:* cs – cirrus sac; esv – external seminal vesicle; t – testis; u – uterus; vd – vas deferens; vf – vitelline follicle; vg – vagina; vod – ventral osmoregulatory duct.



**Fig. 6.** Tentacular armature of *Dollfusiella vooremi* (São Clemente et Gomes, 1989) from *Mustelus schmitti*. **A** – internal surface; **B** – external surface; **C** – internal surface at distal region of the tentacle; **D** – profiles of hooks on basal and metabasal armature. *Abbreviations:* ab – antibothrial surface; bo – bothrial surface; br – basal row; bs – basal swelling; mb – metabasal hooks.-



**Fig. 7.** Scanning electron micrographs of *Dollfusiella vooremi* (São Clemente et Gomes, 1989) from *Mustelus schmitti*. **A** – partial view of the scolex, small letter indicates location of detail shown in figure G; **B–F** – tentacular armature; **B** – bothrial surface, basal region; **C** – bothrial surface, metabasal region; **D** – external surface, metabasal region; **E** – internal surface, basal region; **F** – internal surface, metabasal region; **G** – surface of scolex peduncle (bifid spinithrix).

**Table 2.** Oncotaxy and hooks measurements of *Dollfusiella vooremi*.

Armature	Surface	Shape	Length	Base	Height	Guard	Toe
Basal							
Rows 1–3		uncinate	10–20 (14 ± 2)	6–13 (9 ± 2)	6–11 (8 ± 1)	2–5 (3 ± 1)	1–5 (3 ± 1)
Rows 4–6		falcate	14–30 (21 ± 4)	4–12 (8 ± 2)	9–21 (14 ± 4)	-	-
Basal swelling	bothrial	uncinate	9–23 (14 ± 2)	7–13 (9 ± 2)	4–15 (8 ± 2)	2–7 (4 ± 1)	1–4 (2 ± 1)
	antibothrial	billhook	9–14 (10 ± 1)	2–4 (3 ± 1)	-	-	-
Metabasal	bothrial	uncinate	17–22 (20 ± 2)	13–17 (14 ± 1)	7–10 (8 ± 1)	1	5–8 (7 ± 1)
	antibothrial	billhook	9–14 (12 ± 2)	3–5 (4 ± 1)	9–12 (11 ± 1)	-	-

(38°00'S; 57°33'W), Buenos Aires Province, Argentina.

Site of infection: Spiral intestine.

Material studied: Holotype CHIOC No. 32566a and paratypes CHIOC No. 32566a,b,d from *Mustelus canis*; paratype CHIOC No. 32566c from *Mustelus schmitti*.

New material: 2 specimens (vouchers, gravid and immature worms) MACN-Pa No. 543/1–2. Additional specimens (whole mounts, histological sections, and specimens prepared for SEM) retained in the collection of Verónica Ivanov.

Prevalence and intensity of infection: 2 of 2 hosts examined; intensity 2–6 specimens per individual examined.

**Remarks.** The specimens described herein were collected from *Mu. schmitti* in Mar del Plata and San Antonio Oeste, Argentina, near the type locality of *D. vooremi*. Although the tentacular armature was not originally described in detail, the hook pattern is consistent in the specimens from different localities. All the specimens have a basal armature consisting of rows of uncinata and falcate hooks, a basal swelling with falcate hooks with recurved tip and uncinata hooks, and a heteroacanthous heteromorphous metabasal armature with billhooks on the antibothrial surface and uncinata hooks on the bothrial surface (Figs. 6, 7B–F, the present study; figs. 2 and 3 in São Clemente and Gomes 1989a).

There are some differences in the terminology used to define hook morphology in the original description and the present study, such as, for example, the subtriangular hooks with enlarged base on the external surface mentioned by São Clemente and Gomes (1989a). We assume that these hooks are uncinata based on figures 2 and 3 in São Clemente and Gomes (1989a). Also, the uncinata hooks of the basal swelling are not mentioned in the original description, but can be observed in their figures 2 and 3 (São Clemente and Gomes 1989a). In the present redescription the tentacular armature is described in detail, including drawings and SEM micrographs of all tentacular surfaces (Figs. 6, 7B–F). Ranges for most measurements are expanded, information on the surface of the peduncle scolex, drawings of the entire worm and cross sections of proglottids are presented for the first time (Figs. 5A, 6, 7G).

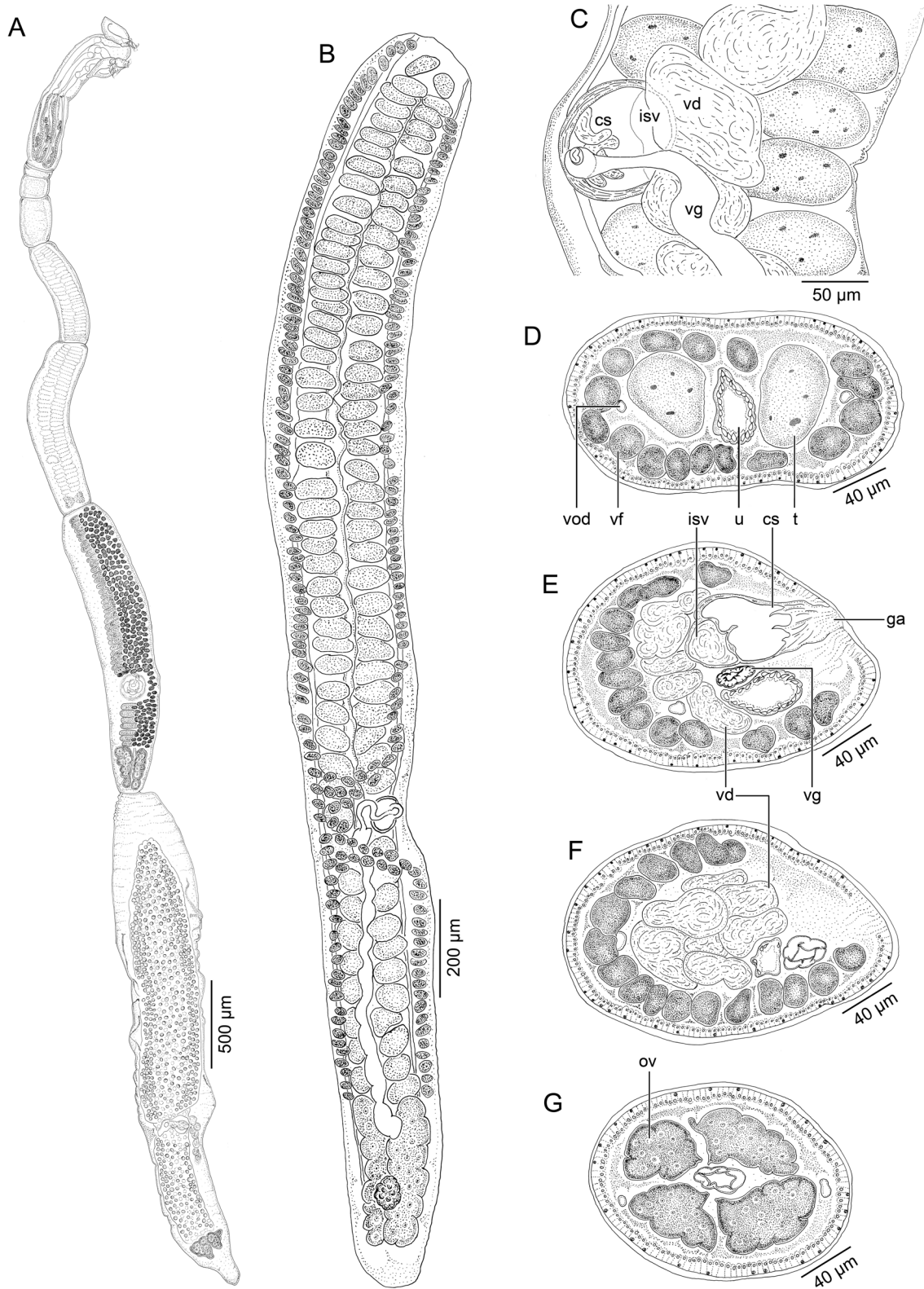
In the key by Schaeffner and Beveridge (2013c), *D. vooremi* grouped with all the species considered to lack enlarged spinitriches on the scolex surface. The

specimens of *D. vooremi* herein studied showed spinitriches along the entire surface of the scolex peduncle. Therefore it closely resembles *D. litocephala* in having a large scolex (more than 4 mm long) and bulbs longer than 2.2 mm. *Dollfusiella vooremi* differs from *D. litocephala* in having heteromorphous rather than homeomorphous metabasal armature (fig. 16 in Heinz and Dailey 1974), more principal hooks per row (16–20 vs about 10), and 3 initial rows of uncinata hooks with broad base and recurved tip that are absent in *D. litocephala* (fig. 15 in Heinz and Dailey 1974).

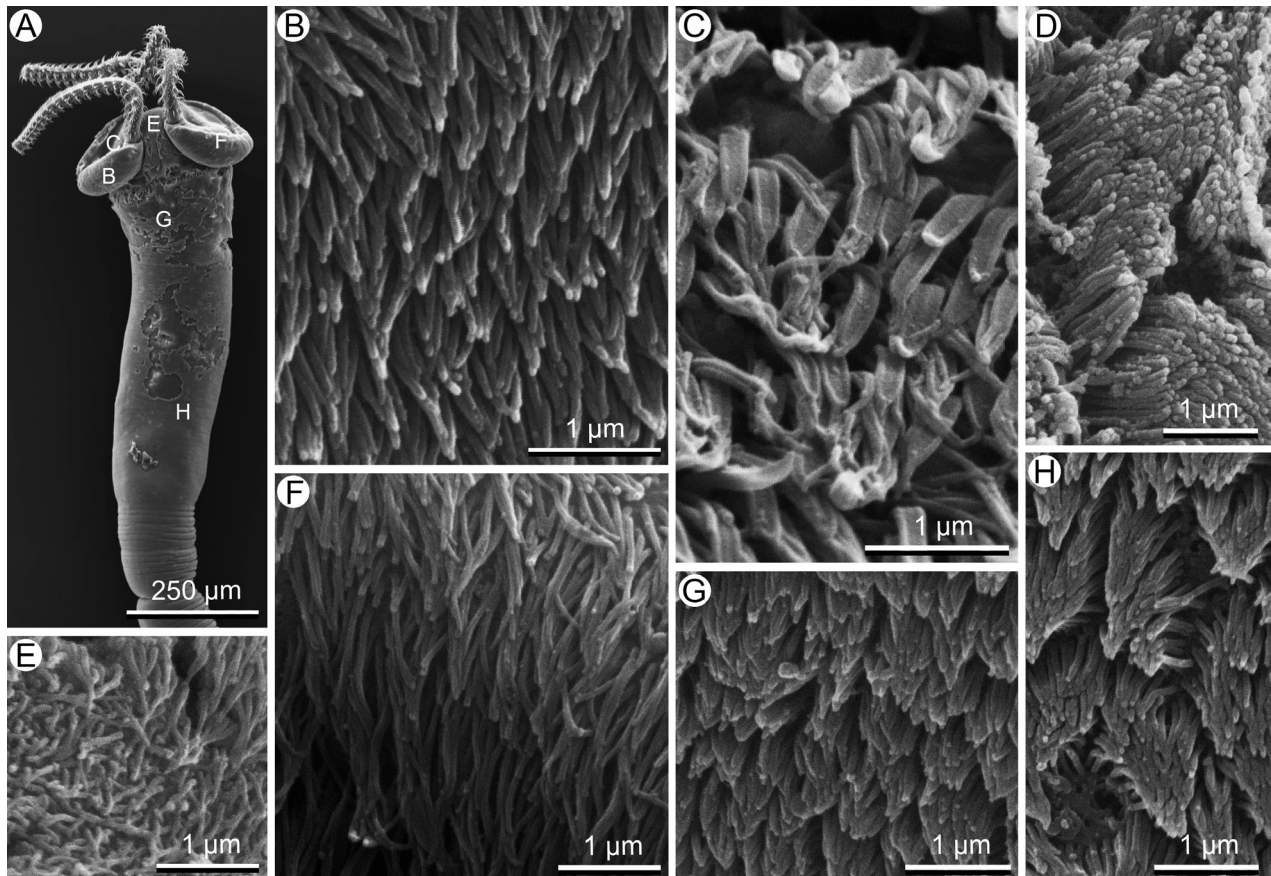
*Parachristianella damiani* sp. n. Figs. 8–11, Table 3

**Description** based on 26 complete worms prepared as follows: 23 whole mounts (19 mature and 4 gravid worms), histological sections of 6 mature proglottids, 3 specimens observed with SEM, and everted tentacles removed from 7 specimens.

Worms apolytic, 3.04–9.20 mm (5.20 ± 1.59 mm, n = 23) long, mature specimens 3.0–6.8 mm (4.6 ± 0.9 mm, n = 22) long, gravid specimens 5.5–9.2 mm (7.6 ± 1.6 mm, n = 4) long, maximum width at level of pars bothrialis or terminal proglottid (Fig. 8A). Proglottids acraspedote, 6–9 (7 ± 1, n = 23) per worm, 5–8 (6 ± 1, n = 23) immature proglottids, 1 mature proglottid, 0–1 gravid proglottid (Fig. 8A,B). Scolex 750–1175 (961 ± 113, n = 23) long, maximum width at level of pars bothrialis, length to width ratio 1.9–4.9 (2.2 ± 0.7, n = 23). Apex of scolex covered with acicular filitriches (Fig. 9E). Two subcircular bothria 160–275 (216 ± 32, n = 21, n = 37) long, 100–220 (149 ± 47, n = 9, n = 13) wide (Figs. 8A, 9A). Proximal bothrial surface covered with acicular filitriches (Fig. 9B). Distal bothrial surface covered with aristate lingulate spinitriches interspersed with capilliform filitriches (Fig. 9C), bothrial margin covered with capilliform filitriches (Fig. 9F). Pars bothrialis 165–280 (227 ± 33, n = 23) long, 185–460 (364 ± 61, n = 23) wide. Pars vaginalis 470–980 (592 ± 128, n = 23) long, 110–310 (233 ± 49, n = 23) wide, covered with acicular filitriches; tentacle sheaths sinuous (Fig. 9G). Pars bulbosa 365–510 (427 ± 46, n = 23) long, 105–290 (172 ± 26, n = 23) wide; covered with acicular filitriches (Fig. 9H). Bulbs elongate, 330–510 (414 ± 44, n = 23, n = 33) long, 55–90 (72 ± 9, n = 23, n = 32) wide, length to width ratio 4.12–7.60 (5.85 ± 0.90, n = 23, n = 32). Prebulbar organ



**Fig. 8.** *Parachristianella damiani* sp. n. from *Myliobatis goodei*. **A** – entire worm (holotype MACN- Pa No. 545/1); **B** – mature proglottid, ventral view (paratype MACN-Pa No. 545/2); **C** – detail of terminal genitalia, ventral view; **D–G** – cross sections of mature proglottid; **D** – at level of testes, anterior to cirrus sac; **E** – at level of genital atrium. **F** – posterior to cirrus sac, showing extensive vas deferens. **G** – at level of ovary, anterior to isthmus. Circummedullary vitelline follicles are not drawn or only partially drawn in figures A–C to allow the view of internal organs. *Abbreviations:* cs – cirrus sac; ga – genital atrium; isv – internal seminal vesicle; ov – ovary; t – testis; u – uterus; vd – vas deferens; vf – vitelline follicle; vg – vagina; vod – ventral osmoregulatory duct.



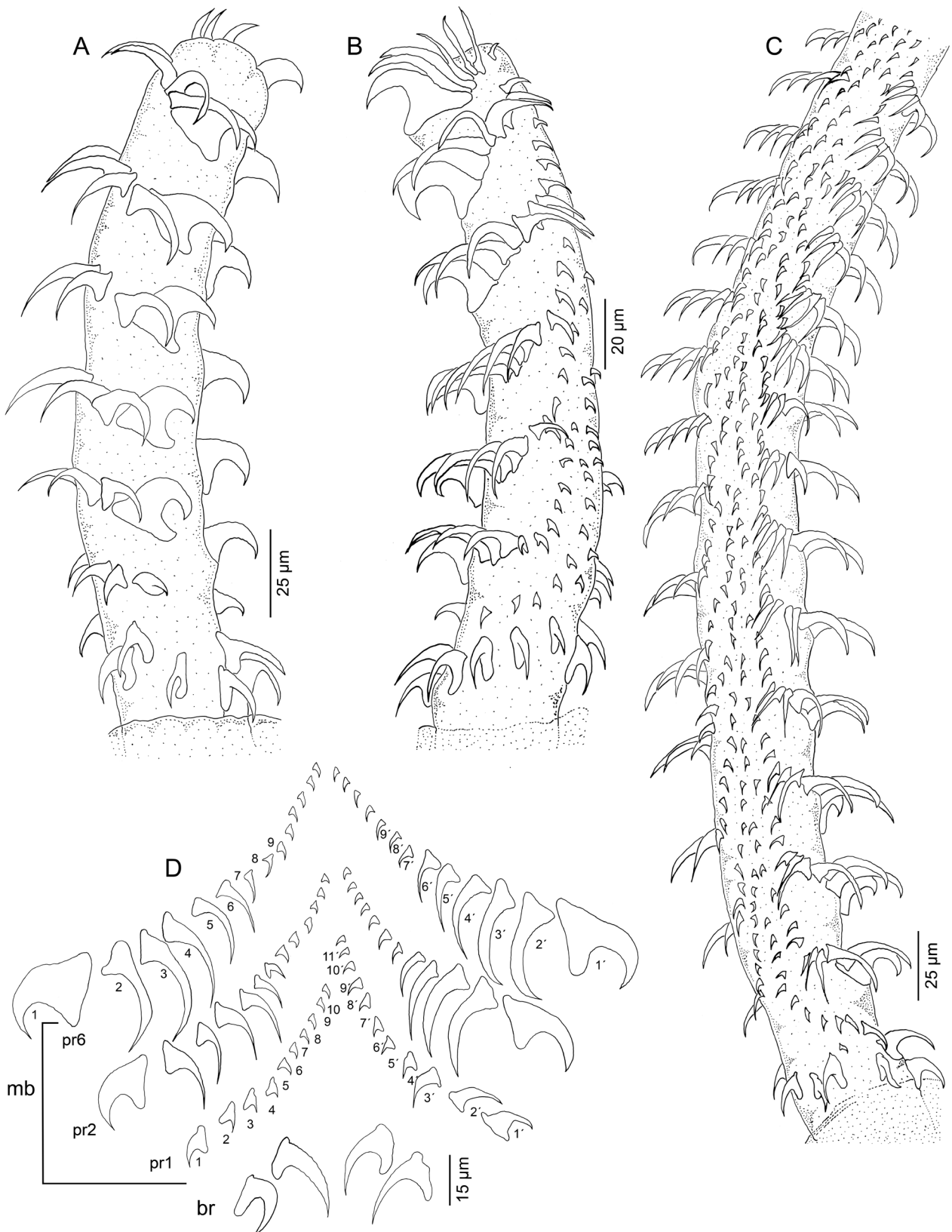
**Fig. 9.** Scanning electron micrographs of *Parachristianella damiani* sp. n. from *Myliobatis goodei*. **A** – scolex, lateral view; small letters indicate locations of details shown in figures B,C, E–H. **B** – proximal bothrial surface (acicular filitriches); **C** – distal bothrial surface (aristate lingulate spinitriches and capilliform filitriches); **D** – surface of terminal proglottid (acicular to capilliform filitriches); **E** – apex of scolex (acicular filitriches); **F** – bothrial margin (capilliform filitriches); **G** – surface of pars vaginalis (acicular filitriches); **H** – surface of pars bulbosa (acicular filitriches).

present, 7–10 ( $9 \pm 1$ ,  $n = 12$ ,  $n = 13$ ) long, 10–22 ( $16 \pm 3$ ,  $n = 12$ ,  $n = 13$ ) wide. Retractor muscle originates at base of bulb, gland-cells surround retractor muscle to middle of bulb. Pars post bulbosa 15–55 ( $33 \pm 11$ ,  $n = 23$ ) long, 160–410 ( $200 \pm 50$ ,  $n = 23$ ) wide. Scolex ratio (pars bothrialis: pars vaginalis: pars bulbosa: pars postbulbosa) 1 : 1.4–3.4 : 1.0–2.4 : 0.1–0.2. Tentacles elongate, without basal swelling, up to 470 long. Diameter at base 25–35 ( $29 \pm 3$ ,  $n = 21$ ,  $n = 24$ ) without hooks, 30–52 ( $40 \pm 6$ ,  $n = 21$ ,  $n = 24$ ) with hooks. Distal diameter of tentacles 23–35 ( $28 \pm 3$ ,  $n = 19$ ,  $n = 20$ ) without hooks, 40–72 ( $60 \pm 9$ ,  $n = 19$ ,  $n = 20$ ) with hooks.

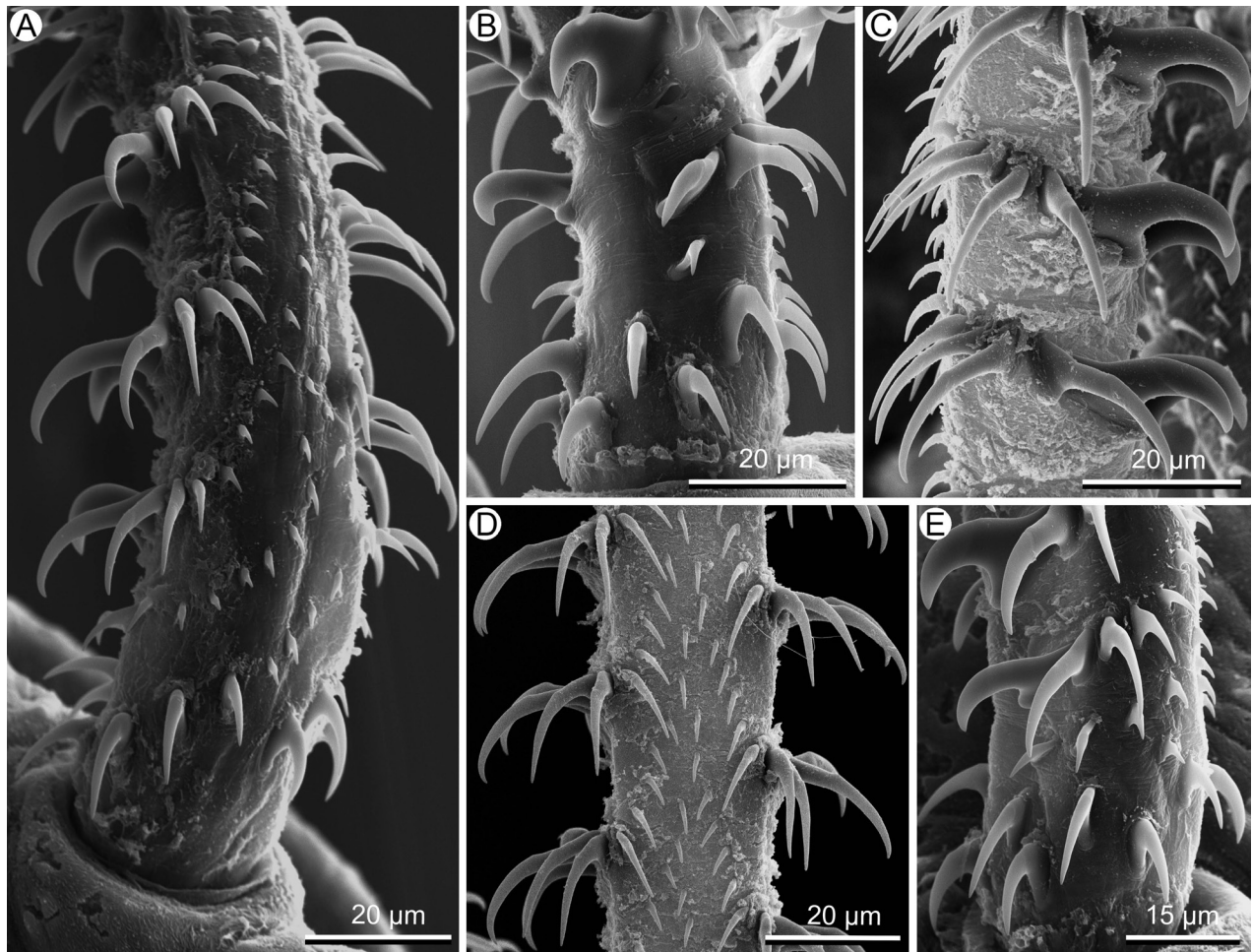
Armature heteroacanthous typical, heteromorphous; hooks solid. Distinctive basal armature and basal swelling absent, initial 2–3 rows of hooks large, uncinata with recurved tip (Figs. 10, 11A,B,E). Metabasal armature arranged in ascending rows beginning on internal surface, terminating on external surface; distinct space between hooks 1 and 1'; 10–14 hooks per principal row (Figs. 10, 11A,B,D). First principal row with small hooks, 10–12 hooks per row, hooks 1(1')–6(6') uncinata, hooks 7(7')–12(12') spiniform (Figs. 10, 11A,B,E; Table

3). Following principal rows with hooks 1(1') uncinata with broad base, hooks 2(2') falcate, hooks 3(3')–5(5') falcate with narrow base, hooks 6(6') spiniform. Hooks 7(7')–14(14') spiniform, hooks gradually diminish in size along row from internal to external surface (Figs. 10, 11A,C,D, Table 3). Hooks in principal rows overlap and alternate on external surface (Figs. 10C,D, 11A,D).

Immature proglottids wider than long, becoming longer than wide with maturity. Mature proglottids longer than wide, 1 050–2 750 ( $1 816 \pm 417$ ,  $n = 20$ ,  $n = 20$ ) long, 180–390 ( $272 \pm 61$ ,  $n = 20$ ,  $n = 20$ ) wide, length to width ratio 4.8–12.1 ( $6.9 \pm 2.1$ ,  $n = 20$ ,  $n = 20$ ) (Fig. 8A,B). Genital pore 30–43% ( $38 \pm 0.2$ ,  $n = 18$ ,  $n = 18$ ) from posterior margin of proglottid. Mature proglottid covered with acicular to capilliform filitriches (Fig. 9D). Testes oval, 60–95 ( $78 \pm 12$ ,  $n = 14$ ,  $n = 98$ ) long, 38–65 ( $47 \pm 6$ ,  $n = 14$ ,  $n = 98$ ) wide, 63–94 ( $79 \pm 9$ ,  $n = 12$ ,  $n = 12$ ) in number, arranged in 2 columns, interrupted at level of cirrus sac on poral side, 25–37 ( $31 \pm 4$ ,  $n = 14$ ) prevaginal, 6–11 ( $8 \pm 1$ ,  $n = 14$ ) postvaginal, 30–49 ( $40 \pm 5$ ,  $n = 14$ ) antiporal (Fig. 8A–D). Cirrus sac globular, thick-walled, 50–105 ( $68 \pm 16$ ,  $n = 17$ ) long, 68–120 ( $69 \pm 17$ ,  $n = 12$ )



**Fig. 10.** Tenticular armature of *Parachristianella damiani* sp. n. from *Myliobatis goodei*. **A** – antibothrial and internal surfaces of tentacle; **B** – bothrial surface of tentacle; **C** – external surface of tentacle; **D** – profiles of hooks on basal and metabasal armature. *Abbreviations:* br – basal rows; mb – metabasal armature; pr1 – first principal row; pr2 – second principal row; pr6 – sixth principal row.



**Fig. 11.** Scanning electron micrographs of tentacular armature of *Parachristianella damiani* sp. n. from *Myliobatis goodei*. **A** – basal and proximal metabasal region, external surface; **B** – basal and proximal metabasal region, internal surface; **C** – distal metabasal region, bothrial surface; **D** – distal metabasal region, external surface; **E** – basal and proximal metabasal region, antibothrial surface.

wide, length to width ratio 0.5–0.8 ( $0.7 \pm 0.1$ ,  $n = 17$ ); cirrus short, unarmed. Vas deferens coiled, extending to mid-proglottid (Fig. 8B,C,E,F). External seminal vesicle not observed, internal seminal vesicle present (Fig. 8C,E). Vagina thin-walled, opening into genital atrium lateral and ventral to cirrus sac, running posteriorly to ootype region (Fig. 8B,C,E). Ovary lobulated, bilobed in dorsoventral view, four-lobed in cross section at level of ovarian isthmus, 135–395 ( $228 \pm 60$ ,  $n = 11$ ) long, 100–170 ( $145 \pm 24$ ,  $n = 11$ ) wide (Fig. 8B,G). Vitelline follicles circummedullary, interrupted dorsally at level of cirrus sac, reaching anterior margin of ovary; vitelline follicles 15–32 ( $21 \pm 5$ ,  $n = 11$ ,  $n = 28$ ) long, 23–47 ( $35 \pm 7$ ,  $n = 11$ ,  $n = 28$ ) wide (Fig. 8A,B,D–F). Mehlis' gland posterior to ovarian isthmus, 60–155 ( $81 \pm 24$ ,  $n = 5$ ) long, 40–135 ( $64 \pm 41$ ,  $n = 5$ ) wide. Ventral osmoregulatory ducts lateral. Gravid proglottids longer than wide, 2070–3525 ( $2985 \pm 623$ ,  $n = 4$ ) long, 390–500 ( $432 \pm 49$ ,  $n = 4$ ) wide, length to width ratio 4.7–9.1 ( $7.0 \pm 1.9$ ,  $n = 4$ ) (Fig. 8A). Genital pore 29–41% ( $33 \pm 2$ ,  $n = 2$ ) from posterior margin

of proglottid. Uterus saccate, 10–18% ( $14 \pm 0.6$ ,  $n = 2$ ) from anterior margin of proglottid, 10–19% ( $15 \pm 0.6$ ,  $n = 2$ ) from posterior margin of proglottid, uterine pore not observed. Intrauterine unembryonated eggs spherical, 38–40 ( $39 \pm 1$ ,  $n = 4$ ) long, 42–44 ( $43 \pm 1$ ,  $n = 4$ ) wide.

**Type host:** *Myliobatis goodei* Garman, southern eagle ray (Myliobatiformes: Myliobatidae) (AMPQ-365).

**Type locality:** Playa Punta Negra (38°61'S; 58°80'W), Necochea, Buenos Aires Province, Argentina.

**Site of infection:** Spiral intestine.

**Specimens deposited:** Holotype (gravid worm) MACN-Pa No 545/1, 3 paratypes (2 mature and 1 gravid worm) MACN-Pa No. 545/2–4, 2 paratypes (1 mature and 1 gravid worm) IPCAS No. C-660. Additional specimens (whole mounts, histological sections, and specimens prepared for SEM) retained in the collection of Verónica Ivanov.

**Prevalence and intensity of infection:** Prevalence 33% (1 of 3 rays examined); intensity more than 50 worms per host.

**Etymology:** This species is named after Damián A. Mar-



**Table 3.** Oncotaxy and hooks measurements of *Parachristianella damiani* sp. n.

Armature	Hooks	Shape	Length	Base	Height	Guard	Toe
Basal							
Rows 1–3		uncinate	13–22 (17 ± 2)	10–17 (12 ± 1)	6–17 (10 ± 3)	4–7 (6 ± 1)	1–3 (2 ± 1)
Metabasal							
First row	1(1')–12(12')	uncinate/spiniform	5–12 (7 ± 2)	3–8 (5 ± 1)	3–7 (4 ± 1)	-	-
From second row	1(1')	uncinate (broad base)	24–31 (26 ± 2)	16–22 (19 ± 1)	10–16 (12 ± 1)	3–6 (4 ± 1)	2–5 (4 ± 1)
	2(2')	falcate	20–31 (27 ± 2)	8–13 (10 ± 1)	16–22 (20 ± 1)	1–3 (2 ± 1)	1–3 (2 ± 1)
	3(3')	falcate	20–30 (26 ± 2)	6–11 (8 ± 1)	16–25 (20 ± 2)	1–2 (1.5 ± 0.5)	1–2 (1.5 ± 0.5)
	4(4')	falcate	19–28 (23 ± 2)	5–9 (7 ± 1)	12–22 (17 ± 3)	1–2 (1.5 ± 0.5)	1–2 (1.5 ± 0.5)
	5(5')	falcate	10–21 (18 ± 3)	4–9 (7 ± 1)	-	-	-
	6(6')	spiniform	7–19 (14 ± 4)	3–7 (5 ± 1)	-	-	-
	7(7')	spiniform	6–16 (11 ± 3)	3–6 (4 ± 1)	-	-	-
	8(8')–14(14')	spiniform	6–11 (8 ± 1)	3–5 (4 ± 1)	-	-	-

tínez Roldán for his genuine friendship.

**Remarks.** All species of *Parachristianella* have 1–3 rows of enlarged hooks around the base of the tentacle (Kovacs and Schmidt 1980, Beveridge 1990, Beveridge et al. 2004, Palm 2004, Campbell and Beveridge 2007). This feature has been treated as a distinctive basal armature (Palm 2004) or as initial rows of hooks in species lacking a distinctive basal armature (Beveridge 1990, Beveridge et al. 2004, Campbell and Beveridge 2007). In addition, *Pa. baverstocki* Beveridge, 1990 and *Pa. indonesiensis* Palm, 2004 have 2–3 enlarged hooks on the external surface of the tentacle, which were also considered by Palm (2004) as part of the distinct basal armature. Therefore, inconsistencies in descriptions are due to different interpretations of a similar hook arrangement. In this study the criteria of Beveridge (1990), Beveridge et al. (2004), and Campbell and Beveridge (2007) have been followed. Thus, *Pa. damiani* sp. n., having 2–3 initial rows of large uncinat hooks with recurved tip, is described as lacking a distinctive basal armature. *Parachristianella damiani* can easily be distinguished from *Pa. baverstocki* and *Pa. indonesiensis* by the lack of enlarged hooks on the external surface of the tentacles.

*Parachristianella damiani* has hooks 1(1')–4(4') much longer than *Pa. caribbensis* Kovacs et Schmidt, 1980, *Pa. dimegacantha* Kruse 1959, *Pa. parva* Campbell et Beveridge, 2007, and *Pa. trygonis* Dollfus, 1946. For example, the hooks 1(1') are 24–31 µm long in *Pa. damiani*, whereas they range from 9 to 21 µm in the other species. Moreover, *Pa. damiani* has conspicuously more testes per proglottid than *Pa. caribbensis* and *Pa. parva* (63–94 vs 8–10 and 32–33, respectively). The number of hooks per principal row is lower in *Pa. damiani* (10–14 hooks per row) compared to *Pa. trygonis* and *Pa. duodecacanthe* Palm, 2004, which have more than 18 hooks per principal row.

*Parachristianella damiani* and *Pa. heteromegacantha* Feigenbaum, 1975 are similar, with hooks 1 and 1' in the second principal row larger than in the first principal row (Fig. 10A,D). However, in *Pa. damiani* sp. n. the size of hooks 1 and 1' remains constant along the tenta-

cle, being slightly shorter only at the tip of the tentacle (Fig. 10C), whereas they are gradually smaller in each row in *Pa. heteromegacantha* along the entire metabasal region (see fig. 230d in Palm 2004).

*Parachristianella damiani* most closely resembles *Pa. monomegacantha* Kruse, 1959 in the arrangement of hooks in the tentacular armature. However, *Pa. damiani* sp. n. has larger hooks (e.g. hooks 1(1') 24–31 µm long in *Pa. damiani* vs 14–22 µm long in *Pa. monomegacantha*), and the vagina runs lateral to the cirrus sac rather than anterior as described in *Pa. monomegacantha* (figs. 149–150 in Beveridge 1990).

## DISCUSSION

The microtrix pattern has been studied in a few eutetrarhynchids. It is partially known in 12 species, including 8 species of *Dollfusiella* and 2 species of *Parachristianella* (see Whittaker et al. 1985, Beveridge et al. 2004, Palm 2004, Friggens and Duszynski 2005, Chervy 2009). The presence of spinitriches covering the surface of the scolex peduncle has been used as a diagnostic feature in species of *Dollfusiella* (see Beveridge et al. 2004, Schaeffner and Beveridge 2013c). The scolex peduncle is completely covered with enlarged spinitriches in *D. cortezensis*, *D. imparispinis*, *D. micracantha*, *D. ocalaghani*, *D. parva*, *D. spinifer*, *D. spinosa*, *D. tenuispinis*, *D. vooremi*, and *D. taminii*, or partially covered (up to the level of the bulbs) in *D. angustiformis*, *D. elongata*, *D. hemispinosa*, *D. owensi*, and *D. spinulifera* (Beveridge 1990, Beveridge et al. 2004, Friggens and Duszynski 2005, Schaeffner and Beveridge 2013c).

However, this character is somewhat unreliable, since the spinitriches can be lost in specimens not properly fixed, as mentioned by Beveridge and Jones (2000) for specimens of *D. spinulifera*. Also, Heinz and Dailey (1974) described 'deciduous hairs' on the scolex peduncle of *D. litocephala*. In most specimens of *D. vooremi* studied herein, these spinitriches were partially lost. In addition, this feature was described as variable in *D. aculeata*, where the distribution of spinitriches in the posterior part of the scolex was observed only in some specimens (Bev-

eridge et al. 2004). Unfortunately, the presence or absence of enlarged spinitriches on the scolex peduncle was used as the first couplet choice in the most recent key to the species of *Dollfusiella* (see Schaeffner and Beveridge 2013c). The collection of well preserved specimens of the 14 species of *Dollfusiella*, for which this character has not been described, is essential to verify the lack of these large spinitriches. Actually, *D. vooremi* was included in the key in the group lacking spinitriches on the scolex peduncle. Our study now provides evidence for the presence of these enlarged spinitriches (Fig. 7G).

These enlarged spinitriches have been referred as 'fine spines' in *D. schmidti* and *D. litocephala*, and 'robust spines' in *D. spinifer*, *D. ocallaghani*, *D. micracantha*, and *D. owensi* (see Beveridge 1990). SEM studies available for 7 species of *Dollfusiella* show that they all share a similar type of spinitrix, being palmate with different number of digits. Thus, *D. cortezensis*, *D. tenuispinis*, *D. spinosa*, and *D. taminii* have actually bifid and trifid spinitriches (2–3 digits), whereas *D. angustiformis*, *D. hemispinosa*, *D. imparispinis* and *D. parva* have palmate spinitriches with 4–14 digits (see fig. 211G in Palm 2004, fig. 11 in Friggens and Duszynski 2005, figs. 3H, 6G, 12G, and 14C in Schaeffner and Beveridge 2013c). The spinitriches on the scolex peduncle of *D. spinulifera* have been described as "deltoid" (Beveridge and Jones 2000). In this case the magnitude of the micrographs (figs. 19–20 in Beveridge and Jones 2000) does not allow for the distinction of their precise shape.

The two species of *Parachristianella* studied at SEM, i.e. *Pa. monomegacantha* and *Pa. damiani*, share a similar pattern, having filitriches on most surfaces and aristate gladiate or lingulate spinitriches covering the distal bothrial surface (Whittaker et al. 1985, Palm 2004, present study). However, *Pa. damiani* lacks palmate spinitriches on the scolex peduncle described in *Pa. monomegacantha*.

Since the erection of *Parachristianella* by Dollfus (1946), Campbell and Beveridge (1994) and Palm (2004) have presented amended diagnoses of the genus with the addition of several characters, some of which need to be amended. Campbell and Beveridge (1994) mentioned that the vagina is anterior to the cirrus sac. However, the vagina is anterior to the cirrus sac and crosses the vas deferens only in *Pa. monomegacantha*, *Pa. baverstocki* and *Pa. indonesiensis*, whereas it is posterior to the cirrus sac in *Pa. caribbensis*, and lateral to the cirrus sac in the remaining species (Beveridge 1990, Palm 2004, Campbell and Beveridge 2007). Palm (2004) included the presence of a uterine pore in the diagnosis of *Parachristianella*, however, this structure has not been mentioned for any species described in the genus so far. Also, the distribution of the vitelline follicles is referred to as anterior to the ovary (Palm 2004), but they are distributed all along the

proglottid, including postovarian follicles, in *Pa. caribbensis* (see description and fig. 10 in Kovacs and Schmidt 1980), and overlap the ovary in *Pa. parva* (see fig. 2 in Campbell and Beveridge 2007).

A recent phylogenetic analysis of the Trypanorhyncha Diesing, 1863 shows a basal split leading to two major lineages formally recognised as suborders, the Trypanobatoidea and the Trypanoselachoida (Olson et al. 2010). One of the most distinctive feature of each suborder is the affinity to rays or sharks, respectively. Species of *Parachristianella* and *Dollfusiella* belong to the Trypanobatoidea mostly parasitising rays (Friggens and Duszynski 2005, Campbell and Beveridge 2007, Schaeffner and Beveridge 2013c). Most species of *Parachristianella* (8 out of 9 species) were found in myliobatiform rays of the families Dasyatidae, Myliobatidae, Urotrygonidae and Urolophidae (Kovacs and Schmidt 1980, Beveridge 1990, Palm 2004, Campbell and Beveridge 2007). Among them, 5 species were only found in Myliobatiformes, whereas 2 species also parasitise Rhinopristiformes, and sharks in Carcharhiniformes and Orectolobiformes (Beveridge 1990, Palm 2004, Campbell and Beveridge 2007). Species of *Dollfusiella* are also well represented in the Myliobatiformes, because 18 of the 28 valid species in the genus have been reported from Dasyatidae, Myliobatidae and Urolophidae (Heinz and Dailey 1974, Beveridge 1990, Beveridge and Jones 2000, Beveridge et al. 2004, Palm 2004, Friggens and Duszynski 2005, Schaeffner and Beveridge 2013c).

However, many species of *Dollfusiella* are parasites of carcharhiniform sharks, i.e. *D. australis*, *D. vooremi*, *D. tenuispinis*, *D. ocallaghani*, *D. musteli*, *D. litocephala*, *D. macrotrachela*, *D. martini* (see Dollfus 1969, Carvajal 1974, Heinz and Dailey 1974, Beveridge 1990, Palm 2004), and a few have also been reported from rhinopristiform and rajiform batoids, and orectolobiform and hexanchiform sharks (Beveridge 1990, Tanzola et al. 1998, Beveridge et al. 2004, Palm 2004, Schaeffner and Beveridge 2013c). The level of specificity for the final host is highly variable in both genera, with a few oioxenous species (i.e. *D. bareldsi*, *D. cortezensis*, *D. imparispinis*, *D. lineata*, *D. micracantha* and *D. musteli*) and most species that have been reported from host species in different genera, families or orders (Beveridge 1990, Beveridge and Jones 2000, Beveridge et al. 2004, Palm 2004, Friggens and Duszynski 2005, Schaeffner and Beveridge 2013c). Such an array of different unrelated hosts that can be parasitised by species of *Dollfusiella* and *Parachristianella* could be explained by multiple events of host switching from a putative plesiomorphic myliobatiform host.

Palm (2004) suggested a life cycle for eutetrarhynchid cestodes that includes 3 hosts, with copepods as first intermediate hosts, other invertebrates as obligatory sec-

ond intermediate hosts, and elasmobranchs as definitive hosts. In fact, the plerocerci of most species of *Dollfusiella* and *Parachristianella* have been found in invertebrates (Feigenbaum 1975, Feigenbaum and Carnuccio 1976, Beveridge 1990, Palm 2004). Some species have been recovered from crustaceans (crabs and shrimps) (e.g. *Pa. heteromegacantha*, *Pa. monomegacantha*, *Pa. trygonis*, *D. carayoni*, and *D. schmidtii*), whereas *Pa. dimegacantha* was also reported from mollusks (Feigenbaum 1975, Feigenbaum and Carnuccio 1976, Beveridge 1990, Palm 2004). Reports of plerocerci of eutetrarhynchids from teleost fishes are rare (Dollfus 1942, Palm 2004). As in most trypanorhynchids the fidelity of species of *Parachristianella* and *Dollfusiella* for their intermediate host is also very low. All plerocerci of *Parachristianella* were found in invertebrates, crustaceans and/or mollusks, with the exception of *Pa. heteromegacantha* that infects hosts in a single genus (Feigenbaum and Carnuccio 1976, Beveridge 1990, Palm 2004). Plerocerci of *Dollfusiella* were found in crustaceans and/or fishes (Dollfus 1942, Palm 2004).

The definitive hosts of the eutetrarhynchids found in the Argentine Sea are mainly carcinophagous, and eventually include some teleost fishes in their diet. In fact, *Mu. schmitti* consumes *Anchoa marinii* Hildebrand (Clupeiformes: Engraulidae), *Cynoscion striatus* (Cuvier) (Perciformes: Sciaenidae), and *Sprattus fuegensis* (Jenyns) (Clupeiformes: Clupeidae) (Olivier et al. 1968, Chiaramonte and Pettovello 2000). *Psammobatis bergi* preys on *Trachurus lathami* Nichols (Perciformes: Carangidae) and *Engraulis anchoita* Hubbs et Marini (Clupeiformes: Engraulidae), and *Mu. goodei* feeds on *Nemadactylus bergi* (Norman) (Perciformes: Cheilodactylidae) (Pozzobon 1987, San Martín et al. 2007, Barbini 2011). During this survey specimens of these teleost species were examined for parasites and no eutetrarhynchid plerocerci were found. It is likely that the species of *Dollfusiella* and *Parachristianella* in the area do not include fishes as intermediate hosts, and follow the transmission pathway observed in other eutetrarhynchids, with benthic invertebrates as obligatory second intermediate hosts.

As occurs with other cestodes, the pattern of distribution of parasites can vary also within hosts with a wide distribution. Thus, the presence of certain parasites in cosmopolitan elasmobranchs can be common in multiple areas, or locally restricted (Beveridge 1990, Palm and Beveridge 2002, Palm 2004, Schaeffner and Beveridge 2013c). For example, migratory sharks such as *Sphyrna zygaena* (Linnaeus), *Carcharhinus plumbeus* (Nardo), *Carcharhinus brachyurus* (Günther), and *Notorynchus cepedianus* (Péron) have been reported as hosts for eutetrarhynchids in the North Atlantic and Indo-Pacific region (Beveridge 1990, Palm 2004, Campbell and

Beveridge 2007). However, no eutetrarhynchids have yet been reported from these hosts in the southwestern Atlantic. Instead, they have been reported as hosts for tentaculid and lacistorhynchids off Brazil (São Clemente and Gomes 1989b, Knoff et al. 2002, Gomes et al. 2005).

So far, only *D. vooremi* has been found in sharks in the southwestern Atlantic (São Clemente and Gomes 1989a, Alarcos et al. 2006). *Dollfusiella vooremi* has been previously reported from *Mu. schmitti* in Argentina during a study on its cestode assemblages (Alarcos et al. 2006), and from the batoid *S. bonapartii* off Bahía Blanca (Argentina) (Tanzola et al. 1998). During the course of this study, 42 specimens of *S. bonapartii* were examined for parasites and none of them was infected with *D. vooremi*. Instead, a yet undescribed eutetrarhynchid has been collected from this host, which can be distinguished from *D. vooremi* in lacking billhooks in the metabasal armature. Unfortunately, none of the specimens reported by Tanzola et al. (1998) have been deposited in a parasitological collection to verify their identity. On the basis of the data recently collected, it is likely that the report of *D. vooremi* in *S. bonapartii* was a result of misidentification. If this is the case, *D. vooremi* is restricted to carcharhiniform hosts. No previous reports of species of *Parachristianella* have been mentioned in the southwestern Atlantic and the present study represents the first record of the genus in this region.

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