Research Article

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Trypanorhynch cestodes (Eutetrarhynchidae) from batoids along the coast of Argentina, including the description of new species in *Dollfusiella* Campbell et Beveridge, 1994 and *Mecistobothrium* Heinz et Dailey, 1974

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Abstract: During a recent parasitological survey of elasmobranchs along the coast of Argentina, two new species of eutetrarhynchid cestodes of the genera *Dollfusiella* Campbell et Beveridge, 1994 and *Mecistobothrium* Heinz et Dailey, 1974 were collected from batoids. *Dollfusiella acuta* sp. n. was found in four arhynchobatid skates, i.e. *Sympterygia acuta* Garman (type host), *Sympterygia bonapartii* Müller et Henle, *Atlantoraja castelnaui* (Miranda Ribeiro) and *Atlantoraja platana* (Günther), and *Mecistobothrium oblongum* sp. n. in the eagle ray *Myliobatis goodei* Garman. *Dollfusiella acuta* sp. n. has a tentacular armature consisting of basal rows of uncinata hooks, a distinct basal swelling with uncinata, falcate and bill hooks, and a heteroacanthous metabasal armature with heteromorphous hooks (bothrial uncinata hooks and antibothrial falcate hooks), hooks 1(1') not separated, testes in two columns and an internal seminal vesicle. The tentacular armature of *M. oblongum* sp. n. is characterised by basal rows of uncinata hooks, a basal swelling with uncinata and falcate hooks, a typical heteroacanthous metabasal armature with heteromorphous hooks (uncinata and falcate to spiniform), and hooks 1(1') separated and of a constant size along the tentacle. It also possesses an elongate scolex, numerous testes arranged in 5–6 irregular columns, and an internal seminal vesicle. The discovery of *M. oblongum* in *M. goodei* represents the first record of species of *Mecistobothrium* in the southwestern Atlantic Ocean. An amended description of *Dollfusiella cortezensis* (Friggens et Duszynski, 2005) is also provided to clarify details of the scolex and tentacular armature. Members of *Dollfusiella* in the southwestern Atlantic are specific to a single host species or to a particular host family, while *M. oblongum* was found in a single host species. Although globally some plerocerci of eutetrarhynchids have been found in teleosts, extensive examination of teleosts off the coast of Argentina suggests that the transmission pathways of these species are exclusively based on invertebrates as intermediate or paratenic hosts.

Keywords: *Dollfusiella acuta* sp. n., *Mecistobothrium oblongum* sp. n., *Myliobatis*, *Atlantoraja*, *Sympterygia*

Eutetrarhynchidae is one of the most diverse families in Trypanorhyncha (Cestoda), with 92 species out of the 309 currently recognised in the order (Palm 2004, Campbell and Beveridge 2006a,b, 2007, Schaeffner and Beveridge 2012a,b, 2013a,b,c, Menoret and Ivanov 2014, Schaeffner 2014). Molecular phylogenies for Trypanorhyncha suggest that the Eutetrarhynchidae and some eutetrarhynchid genera are paraphyletic (i.e. *Parachristianella* Dollfus, 1946, *Dollfusiella* Campbell et Beveridge, 1994 and *Prochristianella* Dollfus, 1946) (Palm et al. 2009, Olson et al. 2010). However, these results have been based on less than the 25% of the species currently described in the family and need to be verified with a larger sample of taxa.

Eutetrarhynchids are characterised by the presence of a heteroacanthous metabasal armature (Campbell and Beveridge 2006b, Beveridge 2008, Schaeffner and Beveridge 2012a,b), with the exception of *Poecilorhynchus* Schaeffner et Beveridge, 2013 with a poecilorhynchous armature (Schaeffner and Beveridge 2013a). Metabasal hooks are heteromorphous in most genera, being relatively homeomorphous or slightly heteromorphous in *Eutetrarhynchus* Pintner, 1913, *Dollfusiella*, *Oncomegas* Dollfus, 1929, and *Paroncomegas* Campbell, Marques et Ivanov, 1999 (Campbell and Beveridge 2006b, Schaeffner and Beveridge 2012a,b, 2013a, Schaeffner 2014). A distinctive basal armature and/or basal swelling are present in all 15

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genera of eutetrarhynchids, with the exception of *Mobulocestus* Campbell et Beveridge, 2006 (Campbell and Beveridge 2006b, Beveridge 2008, Schaeffner and Beveridge 2012a,b, 2013a).

The genitalia are quite variable among eutetrarhynchids, but as a general pattern most genera have seminal vesicles (internal, external or both), testes arranged in two columns, ovary four-lobed in cross sections and circum-medullary vitelline follicles (Campbell and Beveridge 1994, Palm 2004). In particular, the presence and position of seminal vesicles are difficult to observe in some species, e.g. *Dollfusiella musteli* (Carvajal, 1974), *Dollfusiella cortezensis* (Friggens et Duszynski, 2005), *Mecistobothrium myliobati* (Heinz et Dailey, 1974), *Paroncomegas myliobatis* Palm, 2004 and *Parachristianella dimegacantha* Kruse, 1959. Therefore, these features need to be verified in the species that have not been studied with cross sections.

Recently, keys for the identification of species in *Eutetrarhynchus* and *Dollfusiella* were provided by Schaeffner (2014) and Schaeffner and Beveridge (2013b), and the diagnoses of *Eutetrarhynchus* and *Parachristianella* have been formally amended (Menoret and Ivanov 2014, Schaeffner 2014).

In the southwestern Atlantic only three species of eutetrarhynchids have been reported so far, i.e. *Dollfusiella taminii* Menoret et Ivanov, 2014, *Dollfusiella vooremi* (São Clemente et Gomes, 1989), and *Parachristianella damiani* Menoret et Ivanov, 2014 (see Alarcos et al. 2006, Menoret and Ivanov 2014). All of them seem to be quite specific for their definitive host, being found in the arhynchobatid skate *Psammobatis bergi* Marini, in the carcharhiniform shark *Mustelus schmitti* Springer and the myliobatiform eagle ray *Myliobatis goodei* Garman, respectively.

During a recent parasitological survey of elasmobranchs along the coast of Argentina, two new species of eutetrarhynchids of the genera *Dollfusiella* and *Mecistobothrium* Heinz et Dailey, 1974 were collected from batoids. The new species of *Dollfusiella* was collected from species of *Sympterygia* Müller et Henle and *Atlantoraja* Menni (Rajiformes, Arhynchobatidae), and *Mecistobothrium* was found in *M. goodei* (Myliobatiformes, Myliobatidae).

Dollfusiella is the most speciose genus in the family, with 28 valid species (Schaeffner and Beveridge 2013b, Menoret and Ivanov 2014, Schaeffner 2014). The genus is widely distributed, with most species reported in the Indopacific (Palm 2004, Schaeffner and Beveridge 2013b, Menoret and Ivanov 2014). Most species are parasites of batoids, essentially Myliobatiformes and Rajiformes, whereas a few have been found in carcharhinid and orectolobid sharks (Beveridge 1990, Palm 2004, Friggens and Duszynski 2005, Schaeffner and Beveridge 2013b, Menoret and Ivanov 2014).

Mecistobothrium includes five species distributed in the North Atlantic and Indopacific. Adults are parasites of myliobatiforms, with some members restricted to a single host species or a single family (Heinz and Dailey 1974, Campbell and Carvajal 1975, Beveridge and Campbell 1998, Palm 2004).

Based on the material recently collected from batoids captured off the shelf of Argentina, we describe here the new species of *Dollfusiella* and *Mecistobothrium*, this being the first record of species of *Mecistobothrium* in the southwestern Atlantic, and the first report of trypanorhynchids for the batoids *Sympterygia acuta* Garman, *Atlantoraja castelnaui* (Miranda Ribeiro) and *Atlantoraja platana* (Günther). An emended description of *Dollfusiella cortezensis* is also provided, to clarify some features of the scolex and genitalia.

MATERIALS AND METHODS

Cestodes examined in this study were collected from *Myliobatis goodei*, *Sympterygia acuta*, *Sympterygia bonapartii* Müller et Henle, *Atlantoraja castelnaui* and *Atlantoraja platana*. A single individual of *M. goodei* (host field number PD3-155) was caught in March 2011 off Punta Mejillón in Río Negro Province (41°11'S; 64°03'W). Five specimens of *S. acuta* were caught off Buenos Aires Province (39°55'S; 62°03'W) (PD7-534, PD7-541, PD7-562) and off Punta Mejillón (PD7-458, PD7-459) in March 2013. Four specimens of *S. bonapartii* (AMPQ-140, AMPQ-155, AMPQ-171, VIPQ-062) were caught during 2001–2009 off Puerto Quequén, Buenos Aires Province (38°37'S; 58°53'W). One specimen of *A. castelnaui* (AMPQ-166) was collected off Puerto Quequén and one specimen of *A. platana* (PD3-171) was caught off Punta Mejillón. Hosts labelled as PD3 and PD7 were caught with bottom trawls on board of the Oceanographic Vessel 'Puerto Deseado' (CONICET). Hosts labelled as AMPQ and VIPQ were caught by commercial trawlers.

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, dehydrated in a graded ethanol series, and dried using hexamethyldisilazane. After dehydration, the 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. 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' hematoxylin, counterstained with eosin and mounted in Canada balsam. At least one tentacle was removed from the scolex of the specimens examined and temporarily mounted in glycerine to study the tentacular armature in detail. Terminology for the morphology of hooks 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). Host specificity

ty categories follow Palm and Caira (2008). All measurements are in micrometres (μm) unless otherwise stated. Features and measurements of the scolex were based on immature, mature and gravid specimens; worm length, maximum width and number of proglottids are referred only to mature and gravid worms. Museum abbreviations used are as follows: IPCAS – Institute of Parasitology, Czech Academy of Sciences, České Budějovice, Czech Republic; MACN-Pa – Museo Argentino de Ciencias Naturales, Colección Parasitológica, Buenos Aires, Argentina; USNPC – Department of Invertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

RESULTS

Dollfusiella acuta sp. n. Figs. 1–4, Table 1

ZooBank number for species:

urn:lsid:zoobank.org:act:998372F6-1946-41D4-A6BE-A5205F465C27

Description (based on 24 worms prepared as follows: whole mounts of 19 entire worms – 4 immature, 8 mature and 7 gravid worms; 3 specimens with partial strobilae – 2 mature and 1 immature worms; 3 strobilae without scolex and 6 detached gravid proglottids, histological sections of 2 gravid proglottids, 2 mature specimens observed with SEM, and tentacles removed from 12 specimens). Worms apolytic, gravid worms 12.4–23.0 mm ($17.5 \text{ mm} \pm 5.0$, $n = 6$) long, mature worms 5.6–10.2 mm ($7.8 \text{ mm} \pm 1.4$, $n = 7$) long, maximum width at level of posterior proglottids. Proglottids acraspedote, 11–18 (14 ± 2 , $n = 19$) per worm, 9–14 (11 ± 2 , $n = 19$) immature proglottids, 1–3 (2 ± 1 , $n = 19$) mature proglottids, 1–3 (2 ± 1 , $n = 19$) gravid proglottids (Fig. 1A).

Scolex 870–1350 (1049 ± 125 , $n = 21$) long, maximum width at level of pars bothriialis, length to width ratio 4.1–9.8 (6.3 ± 0.6 , $n = 22$) (Figs. 1B, 2A,B). Apex of scolex covered with capilliform filitriches (Fig. 2H). Two subcircular bothria 125–226 (176 ± 25 , $n = 19$, $n = 28$) long, 100–200 (134 ± 34 , $n = 9$, $n = 10$) wide (Figs. 1B, 2A,B). Proximal bothrial surface covered with trifid spinitriches interspersed with acicular filitriches (Fig. 2D). Distal bothrial surface covered with coniform spinitriches interspersed with capilliform filitriches (Fig. 2E). Pars bothriialis 150–250 (190 ± 27 , $n = 21$) long, 120–285 (182 ± 48 , $n = 21$) wide. Pars vaginalis 400–780 (536 ± 113 , $n = 21$) long, 95–255 (132 ± 41 , $n = 21$) wide; tentacle sheaths sinuous; pars bulbosa 380–580 (484 ± 52 , $n = 21$) long, 90–210 (139 ± 29 , $n = 21$) wide; pars postbulbosa 20–80 (50 ± 19 , $n = 15$) long, 80–190 (119 ± 34 , $n = 15$) wide (Fig. 1B). Scolex peduncle covered with trifid spinitriches interspersed with acicular filitriches from between bothria to posterior part of pars bulbosa in most specimens, covering pars postbulbosa in some specimens (Figs. 1B, 2C,F,G). Bulbs elongate, 380–580 (484 ± 52 , $n = 20$, $n = 34$) long, 40–80 (53 ± 10 , $n = 20$, $n = 34$) wide, length to width ratio 5.87–13.50 (9.19 ± 1.70 , $n = 20$, $n = 34$). Prebulbar organ present; retractor muscle originates at base of bulb; gland-cells surround retractor muscle in posterior

half of bulb (Fig. 1B). Scolex ratio (pars bothriialis : pars vaginalis : pars bulbosa : pars postbulbosa) 1 : 2.04–4.00 : 2.02–3.18 : 0.08–0.43.

Tentacles slender, up to 420 long, with prominent basal swelling (Figs. 3A,B, 4A). Diameter at base 15–22 (18 ± 2 , $n = 15$, $n = 20$) without hooks, 20–27 (24 ± 2 , $n = 15$, $n = 20$) with hooks. Diameter at basal swelling 19–27 (22 ± 3 , $n = 11$, $n = 15$) without hooks, 27–37 (33 ± 4 , $n = 11$, $n = 15$) with hooks. Distal diameter of tentacles 13–18 (16 ± 2 , $n = 7$, $n = 8$) without hooks, 18–25 (21 ± 3 , $n = 7$, $n = 8$) with hooks.

Tentacular armature heteroacanthous typical. Hollow hooks arranged in ascending half spirals originating on antibothrial surface of tentacle, terminating on bothrial surface (Fig. 3A,B). Distinctive basal armature present, initial 3 rows of uncinuate hooks with recurved tips, followed by 3 rows of falcate hooks (Figs. 3A,B, 4A). Basal swelling with 9–10 rows of hooks, 7–11 hooks per half spiral (Figs. 3A,B, 4A); rows on antibothrial surface V-shaped, with billhooks projecting perpendicularly from surface of tentacle, densely packed, gradually changing in shape to uncinuate hooks on bothrial surface; rows on bothrial surface form inverted Vs.

Metabasal armature (from row 16–17 to tip of tentacle) heteroacanthous, heteromorphous, with 7–8 hooks per half spiral, hooks 1 and 1' not separated (Figs. 3A–D, 4B,C). Rows on antibothrial surface V-shaped, rows on bothrial surface in inverted Vs. Transitional zone in proximal metabasal armature from row 16–17 to row 19–22 (Fig. 3A,B). Rows on antibothrial surface with falcate hooks, rows on bothrial surface with uncinuate hooks (Fig. 3A,B). Hooks on internal surface falcate to spiniform. External surface with hooks gradually changing in shape from uncinuate on bothrial surface to falcate on antibothrial surface (Fig. 3A,B). Principal rows (from row 20–23 to tip of tentacle) with falcate erect hooks on antibothrial surface, uncinuate hooks with large base on bothrial surface (Figs. 3A–D, 4B–E). Mid-internal and mid-external surfaces with short falcate hooks (Figs. 3C,D, 4B–E). Hooks 1(1')–3(3') falcate, erect, hooks 4(4')–5(5') short, falcate, hooks 6(6')–8(8') uncinuate (Fig. 3C,D, Table 1).

Immature proglottids wider than long to longer than wide with maturity. Mature proglottids longer than wide, 0.77–3.88 mm ($2.16 \text{ mm} \pm 0.73$, $n = 18$, $n = 28$) long, 140–480 (241 ± 94 , $n = 18$, $n = 28$) wide, length to width ratio, 3.9–19.4 (9.9 ± 4.5 , $n = 18$, $n = 28$) (Fig. 1A,C); covered with capilliform filitriches (Fig. 2I). Genital pore 24–38% (30 ± 3 , $n = 13$, $n = 16$) from posterior margin of proglottid. Testes oval, 40–85 (59 ± 14 , $n = 7$, $n = 16$) long, 30–45 (35 ± 5 , $n = 7$, $n = 16$) wide, 70–102 (85 ± 8 , $n = 18$) in number, arranged in 2 columns, 1 layer deep (Fig. 1C,E). Testes distributed as follows: 30–43 (35 ± 3 , $n = 16$) prevaginal testes, 5–8 (7 ± 1 , $n = 16$) postvaginal testes, 34–52 (43 ± 5 , $n = 16$) antiporal testes (Fig. 1C). Cirrus sac oval, thin-walled, 108–255 (176 ± 41 , $n = 16$, $n = 18$) long, 80–195 (129 ± 33 , $n = 16$, $n = 18$) wide; containing long, unarmed cirrus. Vas deferens coiled, extending to mid-proglottid (Fig. 1D). Internal seminal vesicle present, external seminal vesicle absent (Fig. 1C,D).

Fig. 1. *Dollfusiella acuta* sp. n. from *Sympterygia acuta* Garman. **A** – entire worm (holotype MACN-Pa No. 575/1); **B** – scolex (holotype MACN-Pa No. 575/1); **C** – mature proglottid, dorsal view (paratype MACN-Pa No. 575/2); **D** – detail of terminal genitalia, dorsal view; **E–G** – cross sections of a mature proglottid; **E** – at level of cirrus sac; **F** – at level of vagina near genital atrium; **G** – at level of ovary anterior to isthmus. Circum-medullary vitelline follicles not drawn or partially drawn in figures A, C, D to allow the view of internal organs. *Abbreviations:* cs – cirrus sac; isv – internal seminal vesicle; ov – ovary; t – testis; u – uterus; vf – vitelline follicle; vg – vagina; vod – ventral osmoregulatory duct.

Fig. 2. Scanning electron micrographs of *Dollfusella acuta* sp. n. **A** – scolex, from *Sympterygia acuta* Garman; small letters indicate locations of details shown in figures B, C, G; **B** – partial scolex, from *S. acuta*; small letters indicate locations of details shown in figures D–F, H; **C** – posterior region of pars bulbosa and first immature proglottids; **D** – proximal bothrial surface (trifid spinitriches interspersed with acicular filitriches), from *S. acuta*; **E** – distal bothrial surface (coniform spinitriches interspersed with acicular filitriches), from *Sympterygia bonapartii* Müller et Henle; **F** – surface of scolex proper (trifid spinitriches interspersed with acicular filitriches), from *S. bonapartii*; **G** – surface of pars bulbosa (trifid spinitriches interspersed with acicular filitriches), from *S. bonapartii*; **H** – surface of the apex of scolex (capilliform filitriches), from *S. bonapartii*; **I** – surface of immature proglottid (capilliform filitriches), from *S. acuta*.

Vagina thick-walled, opening into genital atrium posterior to cirrus sac, running posteriorly to ootype region (Fig. 1D). Ovary lobulated, 2-lobed in dorsoventral view, 4-lobed in cross section at level of ovarian isthmus, 115–390 (250 ± 76 , $n = 15$, $n = 23$) long, 113–320 (182 ± 69 , $n = 16$, $n = 20$) wide (Fig. 1C,G). Vitelline follicles circum-medullary, extending from anterior margin of proglottid to ovarian isthmus, interrupted at level of genital atrium and cirrus sac (dorsally and ventrally) (Fig. 1C–G), follicles 28–55 (41 ± 8 , $n = 10$, $n = 24$) long, 17–50 (29 ± 9 , $n = 10$, $n = 24$) wide. Mehlis' gland posterior to ovarian isthmus, 40–75 (59 ± 12 , $n = 6$, $n = 10$) in diameter. Uterus median, tubular.

Gravid proglottids longer than wide, 2.43–7.03 mm ($4.12 \text{ mm} \pm 1.20$, $n = 8$, $n = 18$) long, 350–800 (595 ± 141 , $n = 8$, $n = 18$) wide, length to width ratio 3.0–19.0 (7.1 ± 3.7 , $n = 8$, $n = 18$) (Fig. 1A). Genital pore 15–27% (21 ± 4 , $n = 8$, $n = 18$) from posterior margin of proglottid. Detached gravid proglottids longer than wide, 2.96–9.25 mm

($5.64 \text{ mm} \pm 262$, $n = 6$) long, 475–700 (542 ± 81 , $n = 6$) wide, length to width ratio 5.48–16.92 (10.31 ± 4.29 , $n = 6$). Uterus saccate, lacking uterine pore.

Type host: *Sympterygia acuta* Garman, bignose fanskate (Rajiformes: Arhynchobatidae) (PD7-458, PD7-459, PD7-534, PD7-541, PD7-562).

Additional hosts: *Sympterygia bonapartii* Müller et Henle, smallnose fanskate (Rajiformes: Arhynchobatidae) (AMPQ-140, AMPQ-155, PD3-140, VIPQ-062); *Atlantoraja castelnaui* (Miranda Ribeiro), spotback skate (Rajiformes: Arhynchobatidae) (AMPQ-166); *Atlantoraja platana* (Günther), La Plata skate (Rajiformes: Arhynchobatidae) (PD3-171).

Type locality: Off Punta Mejillón ($41^{\circ}11'S$; $64^{\circ}03'W$), Río Negro Province, Argentina.

Other localities: Off Puerto Quequén, Buenos Aires Province ($38^{\circ}37'S$; $58^{\circ}53'W$); off Río Colorado ($39^{\circ}55'S$; $62^{\circ}03'W$), Buenos Aires Province, Argentina.

Site of infection: Spiral intestine.

Specimens deposited: Holotype (gravid worm) MACN-

Fig. 3. Tentacular armature of *Dollfusiella acuta* sp. n. **A** – basal and metabasal armatures, external surface, from *Sympterygia acuta* Garman; **B** – basal and metabasal regions, antibothrial surface (tentacle slightly rotated showing external surface to the tip), from *S. acuta*; **C** – metabasal region, internal surface, from *Atlantoraja platana* (Günther); **D** – metabasal region, external surface, from *A. platana*. Abbreviations: ab – antibothrial surface; bo – bothrial surface; ex – external surface; in – internal surface.

Fig. 4. Scanning electron micrographs of the tentacular armature of *Dollfusiella acuta* sp. n. **A** – basal armature, external surface, from *Sympterygia acuta* Garman; **B** – metabasal armature, external surface, from *S. acuta*; **C** – metabasal region, internal surface, from *Atlantoraja platana*; **D** – metabasal region, bothrial hooks, from *Sympterygia bonapartii* Müller et Henle; **E** – metabasal region, anti-bothrial hooks, from *S. bonapartii*. Abbreviations: ab – antibothrial surface; bo – bothrial surface.

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

Armature	Surface	Shape	Length	Base	Height	Guard	Toe
Basal							
row 1 to row 3		uncinate	6–7 (6.5 ± 0.5, n = 13)	4–5 (4.5 ± 0.5, n = 13)	5–7 (6 ± 1, n = 13)	1–2 (1.5 ± 0.5, n = 10)	1–2 (1.5 ± 0.5, n = 10)
row 4 to row 6		falcate	7–9 (8 ± 1, n = 13)	3–4 (3.5 ± 0.5, n = 13)	9–21 (14 ± 4, n = 13)	-	-
basal swelling	bothrial	uncinate	9–23 (14 ± 2, n = 15)	7–13 (9 ± 2, n = 15)	4–15 (8 ± 2, n = 15)	2–7 (4 ± 1, n = 10)	1–4 (2 ± 1, n = 10)
	antibothrial	billhook	9–14 (10 ± 1, n = 10)	2–4 (3 ± 1, n = 10)	-	-	-
Metabasal							
row 16–17 to row 19–22			5–6 (5.5 ± 0.5, n = 8)	2–4 (3 ± 1, n = 8)	4–5 (4.5 ± 0.5, n = 8)	-	-
row 23 to row 60	bothrial	uncinate	5–6 (5.5 ± 0.5, n = 20)	3–4 (3.5 ± 0.5, n = 20)	4–5 (4.5 ± 0.5, n = 18)	1–2 (1.5 ± 0.5, n = 15)	1–2 (1.5 ± 0.5, n = 15)
	antibothrial	falcate	6–7 (6.5 ± 0.5, n = 23)	1–2 (1.5 ± 0.5, n = 23)	-	-	-

Pa No. 575/1 ex *S. acuta*, 3 paratypes (mature and 2 gravid worms) ex *S. acuta*, MACN-Pa No. 575/2–4, 2 paratypes (mature and gravid worms) IPCAS C-700. 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 20% in *S. acuta* (5 hosts infected out of 25 specimens examined), 3–9 worms per host; prevalence 8% in *S. bona-*

partii (4 hosts infected out of 50 specimens examined), 3–6 worms per host; prevalence 6% in *A. castelnaui* (1 host infected out of 18 specimens examined), 5 worms per host; prevalence 33% in *A. platana* (1 host infected out of 3 specimens examined), 2–4 worms per host.

E t y m o l o g y : This species is named after its type host, *Sympterygia acuta*.

Remarks. The worms recovered from species of *Sympterygia* and *Atlantoraja* belong to *Dollfusiella* because of

their possession of hollow hooks arranged in a distinctive basal armature with a basal swelling, heteroacanthous metabasal armature with heteromorphous hooks, principal rows beginning on the antiothrial surface and terminating on the bothrial surface, and hooks 1(1') not separated.

By having an heteromorphous metabasal armature, *Dollfusiella acuta* sp. n. differs from *D. aculeata* Beveridge, Neifar et Euzet, 2004, *D. aetobati* (Beveridge, 1990), *D. angustiformis* Schaeffner et Beveridge, 2013, *D. bareldsi* (Beveridge, 1990), *D. carayoni* (Dollfus, 1942), *D. geraschmidtii* (Dollfus, 1974), *D. hemispinosa* Schaeffner et Beveridge, 2013, *D. martini* (Beveridge, 1990), *D. michiae* (Southwell, 1929), *D. micracantha* (Carvajal, Campbell et Cornford, 1976), *D. musteli*, *D. ocallaghani* (Beveridge, 1990), *D. owensi* (Beveridge, 1990), *D. schmidtii* (Heinz et Dailey, 1974), *D. spinifer* (Dollfus, 1969), *D. spinosa* Schaeffner et Beveridge, 2013, *D. spinulifera* (Beveridge et Jones, 2000), *D. taminii* and *D. tenuispinis* (Linton, 1890).

Dollfusiella acuta can be distinguished from *Dollfusiella lineata* (Linton, 1909) by having fewer hooks per half spiral on the basal swelling (7–11 vs more than 20), fewer hooks per half spiral on the metabasal armature (7–8 vs 11–12), and by having hooks 1(1') abutting rather than separated (see Palm 2004). In addition, *D. acuta* sp. n. has fewer proglottids (11–18 vs 33–34), and the seminal vesicle is internal instead of external as in *D. lineata*.

Whereas the shape of the hooks of the principal rows changes gradually from falcate (antiothrial surface) to uncinat (bothrial surface) in *D. acuta*, in *D. imparispinis* Schaeffner et Beveridge, 2013 the change in shape is abrupt, having all hooks falcate (beginning on antiothrial surface) and only one uncinat hook on the bothrial surface. Also, the size of the hooks diminishes gradually from antiothrial to bothrial surface in *D. acuta*. This character also aids in the distinction of *D. acuta* from *D. elongata* Beveridge, Neifar et Euzet, 2004 that has the largest hooks on the external and internal surfaces, being hooks 4(4') the longest out of 7 principal hooks.

Dollfusiella acuta has fewer hooks per principal row than *D. australis* (Prudhoe, 1969), *D. litocephala* (Heinz et Dailey, 1974), *D. macrotrachela* (Heinz et Dailey, 1974), *D. parva* Schaeffner et Beveridge, 2013 and *D. vooremi* (7–8 vs 14–15, 16–18, 17–20, 12–15 and 16–22 hooks, respectively). Moreover, *D. acuta* sp. n. has the testes arranged in 1 layer different to *D. australis* and *D. litocephala*, which have testes in two layers. In addition, *D. acuta* differs in size (worm length and number of proglottids) from *D. macrotrachela*, *D. parva*, *D. vooremi* and *D. cortezensis*. *Dollfusiella parva* and *D. cortezensis* are smaller worms (1.2–1.9 mm and 2.5–6.8 mm, respectively vs 12.4–23.0 mm long in *D. acuta* sp. n.) and have fewer proglottids (2–4 and 3–9 vs 11–18) than *D. acuta* sp. n. In contrast, *D. macrotrachela* and *D. vooremi* are larger worms than *D. acuta* (37.3–120.3 mm and 39.7–44.8 mm vs 12.4–23.0 mm long, respectively) and have more proglottids (21–51 and 40–51 vs 11–18, respectively).

Dollfusiella cortezensis (Fruggens et Duszynski, 2005) Fig. 5, Table 2

Syn. *Eutetrarhynchus cortezensis* Fruggens et Duszynski, 2005

Amended description of the tentacular armature (based on the holotype – gravid worm, and genitalia based on the holotype and 7 paratypes – entire gravid and mature worms). Scolex peduncle covered with spinitriches from between bothria to anterior half of pars bulbosa (Fig. 5A). Diameter of tentacles at base without hooks 20–22 (21, $n = 1$, $n = 2$), with hooks 24–25 (22, $n = 1$, $n = 2$). Diameter at basal swelling without hooks 27–29 (28, $n = 1$, $n = 2$), with hooks 30–37 (34, $n = 1$, $n = 2$). Distal diameter of tentacles without hooks 23–25 (24, $n = 1$, $n = 2$), with hooks 31–33 (32, $n = 1$, $n = 2$).

Tentacular armature heteroacanthous typical. Hollow hooks, arranged in ascending half spirals originating on antiothrial surface of tentacle, terminating on bothrial surface (Fig. 5B). Distinctive basal armature present, initial 4 rows of uncinat hooks with recurved tips, followed by 3 rows of falcate hooks (Fig. 5B, Table 2). Basal swelling with 10 rows (from row 8 to row 17) of heteromorphous hooks, 8–10 hooks per half spiral; hooks on antiothrial surface falcate, projecting perpendicularly from surface of tentacle, densely packed, gradually changing in shape to uncinat hooks on bothrial surface. Spiral rows ascending from antiothrial to bothrial surface (Fig. 5B, Table 2).

Metabasalar armature (from row 18 to tip of tentacle) heteromorphous, with 6–8 hooks per half spiral. Rows on antiothrial surface V-shaped, rows on bothrial surface in inverted Vs. Transitional zone in proximal metabasalar armature consists of 4 half spirals of hooks (from row 18 to row 21). Metabasalar armature (from row 22 to tip of tentacle) having falcate erect hooks on antiothrial surface, slender uncinat hooks on bothrial surface (Fig. 5B, Table 2). Hooks on external surface gradually changing in shape from falcate (antiothrial surface) to enlarged uncinat (bothrial surface).

Mature proglottids longer than wide, 630–1175 (796 ± 176 , $n = 8$, $n = 8$) long, 130–240 (167 ± 37 , $n = 8$, $n = 8$) wide, length to width ratio, 3.37–7.58 (4.90 ± 1.31 , $n = 8$, $n = 8$). Genital pore 32–47% (41 ± 6 , $n = 8$, $n = 8$) from posterior margin of proglottid. Testes oval, arranged in 2 columns, 1 layer deep. Cirrus sac oval, thin-walled, containing long, unarmed cirrus. Seminal vesicle surrounded by wall with dark cells similar to cirrus sac wall (internal seminal vesicle?) (Fig. 5C). Vagina thick-walled, opening into genital atrium posterior to cirrus sac, running posteriorly to ootype region (Fig. 5C). Ovary lobulated, H-shaped in dorsoventral view. Mehli's gland posterior to ovarian isthmus. Vitellaria circum-medullar, from anterior margin of proglottid to anterior margin of ovary, interrupted at level of cirrus sac (holotype). Postovarian vitelline follicles in some paratypes. Uterus saccate in gravid proglottids, not observed in mature proglottids.

Fig. 5. *Dollfusiella cortezensis* (Friggens et Duszynski, 2005) from *Urobatis halleri* Cooper (holotype USNPC No. 92215). **A** – scolex; **B** – basal and metabasal regions of the tentacle, external surface; **C** – detail of terminal genitalia, gravid proglottid. Abbreviations: ab – antibothrial surface; bo – bothrial surface; ex – external surface.

Table 2. Oncotaxy and hook measurements of *Dollfusiella cortezensis* (Friggens et Duszynski, 2005)

Armature	Hooks	Shape	Length	Base	Height
Basal					
row 1 to row 4		uncinate	5–7 (6 ± 1 , $n = 4$)	4–5 (4.5 ± 0.5 , $n = 4$)	4–6 (5 ± 1 , $n = 4$)
row 5 to row 7		falcate	6–8 (7 ± 1 , $n = 6$)	2–3 (2.5 ± 0.5 , $n = 6$)	6–8 (7 ± 1 , $n = 6$)
basal swelling	bothrial	uncinate	5–6 (5.5 ± 0.5 , $n = 5$)	4–5 (4.5 ± 0.5 , $n = 5$)	3–4 (3.5 ± 0.5 , $n = 5$)
	antibothrial	falcate	7–8 (7.5 ± 0.5 , $n = 5$)	1–3 (2 ± 1 , $n = 5$)	6–7 (6.5 ± 0.5 , $n = 5$)
Metabasal					
row 14 to row 20	bothrial	uncinate	5–6 (5.5 ± 0.5 , $n = 4$)	4–5 (4.5 ± 0.5 , $n = 4$)	3–4 (3.5 ± 0.5 , $n = 4$)
	antibothrial	falcate	6–7 (6.5 ± 0.5 , $n = 4$)	2–3 (2.5 ± 0.5 , $n = 4$)	6–7 (6.5 ± 0.5 , $n = 4$)
row 21 to row 41	bothrial	uncinate	4–5 (4.5 ± 0.5 , $n = 6$)	3–4 (3.5 ± 0.5 , $n = 6$)	4–5 (4.5 ± 0.5 , $n = 6$)
	antibothrial	falcate	6–8 (7 ± 1 , $n = 5$)	2–3 (2.5 ± 0.5 , $n = 5$)	6–7 (7 ± 1 , $n = 5$)

Type host: *Urobatis halleri* Cooper, Haller's round ray (Myliobatiformes: Urolophidae).

Type locality: Puerto Peñasco (31°18'27"N; 113°32'52"W), Sonora, Mexico.

Site of infection: Spiral intestine, chambers 1–12.

Examined material: Holotype USNPC No. 92215 (gravid worm with evaginated tentacles) and 7 paratypes (mature and gravid worms with invaginated tentacles) selected on slide USNPC No. 92216 containing 18 worms).

Remarks. *Dollfusiella cortezensis* was originally described in the genus *Eutetrarhynchus* by Friggens and Duszynski (2005). Later, Schaeffner (2014) transferred the species to *Dollfusiella*, mainly based on the arrangement of testes (in two columns) and the presence of an external seminal vesicle. In fact, Friggens and Duszynski (2005) described the seminal vesicle as external, yet we observed that the vesicle is surrounded by a thick wall with dark cells similar to the cirrus sac wall in the type specimens (USNPC No. 92215, and six worms in USNPC No. 92216), giving the impression of being internal rather than external (Fig. 5C). However, histological sections will be required to corroborate this feature. If this is the case, the only unequivocal character that supports the placement of this species in *Dollfusiella* is the distribution of the testes.

In addition, the presence of a basal swelling in the tentacular armature was confirmed in the type specimens (Fig. 5B). This feature was included in the original description, but ignored by Schaeffner (2014) in the diagnosis of *D. cortezensis*. Also, the principal hooks begin on the antibothrial surface with falcate hooks and terminate on the bothrial surface with slender uncinuate hooks, rather than beginning on the internal and terminating on the external surface (see figures 15–17 in Friggens and Duszynski 2005). Friggens and Duszynski (2005) mentioned that the microtriches covered the entire scolex, including the pars bulbosa. However, it was noted in the type material that the spinitriches partially cover the pars bulbosa (Fig. 5A).

Mecistobothrium oblongum sp. n. Figs. 6–9, Table 3

ZooBank number for species:

urn:lsid:zoobank.org:act:74C82DEE-DF8C-41F0-A01F-4F104D752DE7

Description (based on 3 complete gravid worms prepared as follows: whole mounts of entire worms – 1 scolex partially removed and prepared for observation with SEM, 1 tentacle of each worm removed and studied in temporary mounts, and histological sections of 2 gravid proglottids). Worms apolytic, 40.4–59.4 mm (47.9 mm $\pm$ 10.1, $n = 3$) long, maximum width at level of last gravid proglottid; strobila 36.5–57.7 mm (47.3 mm $\pm$ 10.1, $n = 3$) long. Proglottids craspedote, 68–72 (70 $\pm$ 2, $n = 3$) in number, 58–61 (59 $\pm$ 1, $n = 3$) immature, 5–7 (6 $\pm$ 1, $n = 3$) mature, and 3–5 (4 $\pm$ 1, $n = 3$) gravid proglottids per worm (Fig. 6A). Scolex 1.53–1.93 mm (1.70 mm $\pm$ 175, $n = 3$) long, maximum width at level of pars bothrialis, length to width ratio 2.9–4.4 (3.6, $n = 2$) (Figs. 6B, 7A). Apex of scolex covered with coniform spinitriches. Two subcircular bothria 325–430 (371 $\pm$ 44, $n = 3$, $n = 4$) long, 340

($n = 1$) wide (Figs. 6B, 7A). Distal bothrial surface covered with hamulate spinitriches (Fig. 7B,C). Pars bothrialis 325–435 (368 $\pm$ 60, $n = 3$) long, 340–570 (453 $\pm$ 113, $n = 3$) wide, tentacle sheaths sinuous. Pars vaginalis 840–1337 (1084 $\pm$ 239, $n = 3$) long, 340–470 (403 $\pm$ 63, $n = 3$) wide, covered with coniform spinitriches (Fig. 7D). Pars bulbosa 474–530 (500 $\pm$ 24, $n = 3$) long, 380–480 (433 $\pm$ 41, $n = 3$) wide. Bulbs elongate, 457–515 (480 $\pm$ 22, $n = 3$, $n = 7$) long, 100–120 (110 $\pm$ 10, $n = 3$, $n = 7$) wide, length to width ratio 3.8–5.3 (4.4 $\pm$ 0.6, $n = 3$, $n = 7$). Pars postbulbosa 140–200 (167 $\pm$ 32, $n = 3$) long, 315–465 (400 $\pm$ 65, $n = 3$) wide. Pintner's cells prominent (Fig. 6B). Prebulbar organ present, 10–13 (11 $\pm$ 1, $n = 3$, $n = 5$) long, 6–8 (7 $\pm$ 1, $n = 3$, $n = 5$) wide. Retractor muscle originates at base of bulb; gland-cells surround retractor muscle at posterior half of bulb (Fig. 6C). Ratio of pars bothrialis: pars vaginalis: pars bulbosa: pars postbulbosa 1 : 2.6–3.2 : 1.2–1.5 : 0.4–0.6.

Tentacles partially evaginated, up to 165 long, basal swelling present. Diameter at base without hooks 27–47 (36, $n = 2$), with hooks 32–52 (41, $n = 2$). Diameter at basal swelling without hooks 36–57 (44, $n = 2$), with hooks 51–67 (57, $n = 2$). Distal diameter of tentacles without hooks 27–37 (31, $n = 2$), with hooks 37–45 (40, $n = 2$).

Tentacular armature heteroacanthous typical, hooks hollow. Hooks arranged in ascending half spirals originating on antibothrial surface of tentacle, terminating on bothrial surface (Figs. 8A,D, 9C). Distinctive basal armature, initial 2–3 rows of uncinuate hooks. Basal swelling (from row 3–4 to row 8), 7–9 hooks per half row; rows on antibothrial surface V-shaped with hooks falcate and falcate with recurved tip, gradually changing in shape to uncinuate on bothrial surface (Figs. 8A,D,E, 9A,B,E).

Metabasal armature (from row 9 to tip of tentacle) heteroacanthous, heteromorphous, 8–9 hooks per principal row; hooks 1 and 1' separated (Figs. 8B,C,E, 9D,F). Proximal metabasal armature (from row 9 to row 12) consists of 3–4 rows of uncinuate hooks, with robust hooks on antibothrial surface and slender hooks on bothrial surface. Principal rows with hooks 1(1') large, uncinuate, hooks 2(2')–3(3') uncinuate to falcate, hooks 4(4')–9(9') falcate with narrow base to spiniform (Figs. 8B,C,E, 9D, Table 3). Hooks in principal rows do not overlap on bothrial surface.

Immature proglottids wider than long to longer than wide with maturity. Mature proglottids longer than wide, 1.49–2.25 mm (1.74 mm $\pm$ 220, $n = 3$, $n = 18$) long, 335–660 (512 $\pm$ 99, $n = 3$, $n = 18$) wide, length to width ratio 2.5–5.5 (3.5 $\pm$ 1.0, $n = 3$, $n = 17$) (Fig. 6A). Genital pore 40–53% (46 $\pm$ 4, $n = 3$, $n = 18$) from posterior margin of proglottid. Testes oval, arranged in 5–6 irregular columns, 2 layers deep, 85–115 (97 $\pm$ 8, $n = 3$, $n = 50$) long, 50–80 (67 $\pm$ 7, $n = 3$, $n = 50$) wide, 80–108 (94 $\pm$ 7, $n = 3$) in number, 25–38 (33 $\pm$ 5, $n = 3$) prevaginal testes, 9–14 (12 $\pm$ 2, $n = 3$) postvaginal testes, 38–57 (49 $\pm$ 5, $n = 3$) antiporal testes (Fig. 6D–G), extending from anterior margin of proglottid to anterior margin of ovary, interrupted dorsally and ventrally at level of cirrus sac, some testes in between ovarian lobes (Fig. 6D–G). Cirrus sac globular, thick-walled, 100–235 (202 $\pm$ 30, $n = 3$, $n = 24$) long, 125–160 (144 $\pm$ 12, $n = 3$, $n = 25$) wide, containing short, unarmed cirrus. Vas

Fig. 6. *Mecistobothrium oblongum* sp. n. from *Myliobatis goodei* Garman. **A** – entire worm (holotype MACN-Pa No. 576/1); **B** – scolex (holotype MACN-Pa No. 576/1); **C** – bulb (paratype MACN-Pa No. 576/2); **D** – terminal gravid proglottid, dorsal view (holotype MACN-Pa No. 576/1); **E–G** – cross sections of a gravid proglottid; **E** – at level of the anterior third of the proglottid; **F** – at level of the cirrus sac; **G** – at level of ovary anterior to isthmus; Circum-medullary vitelline follicles not drawn or partially drawn in figures A–B to allow the view of internal organs. *Abbreviations:* cs – cirrus sac; gp – genital pore; isv – internal seminal vesicle; ov – ovary; t – testis; u – uterus; vd – vas deferens; vf – vitelline follicle; vg – vagina; vod – ventral osmoregulatory duct.

Fig. 7. Scanning electron micrographs of *Mecistobothrium oblongum* sp. n. from *Myliobatis goodei* Garman. **A** – scolex, small letters indicate locations of details shown in figures B–D; **B** – distal bothrial surface, lateral margin (hamulate spinitriches); **C** – distal bothrial surface, central zone (hamulate spinitriches); **D** – surface of pars vaginalis (coniform spinitriches).

deferens coiled, extending to mid-proglottid, from anterior margin of cirrus sac to ovarian isthmus (Fig. 6D,F). Internal seminal vesicle 60–115 (92 ± 16 , $n = 3$, $n = 16$) long, 40–95 (72 ± 15 , $n = 3$, $n = 16$) wide (Fig. 6D,F).

Vagina thin-walled, opening into genital atrium lateral and dorsal to cirrus sac, running posteriorly to ootype region (Fig. 6D,F,G). Ovary lobulated, 2-lobed in dorsoventral view, 4-lobed in cross section at level of ovarian isthmus, 340–550 (463 ± 53 , $n = 3$, $n = 25$) wide, ovarian lobes 230–560 (387 ± 87 , $n = 3$, $n = 24$) long (Fig. 6D,G). Vitelline follicles Circum-medullary, extending throughout entire proglottid from anterior margin of proglottid to ovarian isthmus, interrupted dorsally at level of cirrus sac; follicles 25–55 (41 ± 7 , $n = 3$, $n = 56$) long, 15–35 (25 ± 5 , $n = 3$, $n = 56$) wide (Fig. 6D–G). Mehlis' gland posterior to

ovarian isthmus, 85–155 (109 ± 21 , $n = 3$, $n = 13$) in diameter. Uterus not observed in mature proglottids.

Gravid proglottids longer than wide, 1.95–2.83 mm ($2.36 \text{ mm} \pm 0.30$, $n = 3$, $n = 11$) long, 520–675 (629 ± 45 , $n = 3$, $n = 11$) wide, length to width ratio 2.9–5.4 (3.8 ± 0.7 , $n = 3$, $n = 11$) (Fig. 6A,D). Genital pore 41–53% (45 ± 3 , $n = 3$, $n = 10$) from posterior margin of proglottid. Ventral osmoregulatory ducts lateral, poral duct slightly deviates to mid-proglottid at level of cirrus sac. Uterus saccate, uterine pore not observed.

Type host: *Myliobatis goodei* Garman, southern eagle ray (Myliobatiformes: Myliobatidae) (PD3-155).

Type locality: Off Punta Mejillón ($41^{\circ}11'S$; $64^{\circ}03'W$), Río Negro Province, Argentina.

Site of infection: Spiral intestine.

Fig. 8. Tentacular armature of *Mecistobothrium oblongum* sp. n. from *Myliobatis goodei* Garman. **A** – basal and metabasal regions, antithoracic surface (tentacle slightly rotated showing external surface to the tip); **B** – metabasal armature, external surface; **C** – metabasal armature, internal surface; **D** – basal and metabasal regions, antithoracic surface; **E** – profiles of hooks of basal and metabasal armature. *Abbreviations:* ab – antithoracic surface; bo – bothrial surface; br – basal rows; bs – basal swelling; ex – external surface; in – internal surface; mb – metabasal hooks.

Prevalence and intensity of infection: Prevalence 20% (1 of 5 rays examined); intensity, 3 worms per host.

Specimens deposited: Holotype (gravid worm) MACN-Pa No. 576/1, 2 paratypes (gravid worms), MACN-Pa No. 576/2–3. Additional material (histological sections and material prepared for SEM) is retained in the personal collection of Verónica Ivanov.

Etiology: The specific name ‘*oblongum*’ relates to the

elongated scolex of this species of *Mecistobothrium*.

Remarks. The tentacular armature of the specimens recently collected from *M. goodei* is consistent with *Mecistobothrium* by a having basal swelling, a heteroacanthous metabasal armature with heteromorphous hollow hooks, 8–9 hooks per principal row, hooks 1(1') enlarged and uncinat, and the remainder of the hooks smaller (un-

Fig. 9. Scanning electron micrographs of the tentacular armature of *Mecistobothrium oblongum* sp. n. from *Myliobatis goodei* Garman. **A** – basal region, internal surface; **B** – basal region, bothrial surface; **C** – basal region, antibothrial surface; **D** – metabasal region, external surface; **E** – basal region, external surface; **F** – basal swelling and proximal metabasal region, internal surface. *Abbreviations:* ab – antibothrial surface; bo – bothrial surface; ex – external surface; in – internal surface.

cinate, falcate and spiniform hooks). In addition, they have a craspedote strobila, numerous testes arranged in 5–6 irregular columns, an internal seminal vesicle, and the vagina running lateral and dorsal to the cirrus sac at level of the genital pore.

Mecistobothrium oblongum sp. n. can be distinguished from *M. paucioortesticulatum* Palm, 2004 and *M. johnstonei* (Southwell, 1929) by having an elongate scolex (twice as long as wide) rather than robust (as long as wide). Also, these species lack a distinct basal armature and basal swell-

ing, which are present in *M. oblongum* sp. n. In addition, *M. oblongum* sp. n. has fewer hooks per principal row than *M. pauciortesticulatum* (8–9 vs 12) and the hooks 1(1') are of constant size along the tentacle, whereas they decrease in size proximally and distally from mid-tentacle in *M. pauciortesticulatum*. Beveridge and Campbell (1998) described an external seminal vesicle in *M. johnstonei*, which is absent in *M. oblongum*, and more testes per proglottid (ca 300 vs 80–108).

As with *M. oblongum*, *M. brevispine* (Linton, 1897), *M. myliobati* and *M. penaeus* (Feigenbaum, 1975) have a slender scolex. However, *M. oblongum* has conspicuously more hooks in the basal swelling than *M. brevispine* (4–5 rows with 7–9 hooks per row vs 4 rows with 5–6 hooks per row), and fewer hooks per basal rows (5 vs 6–7). In addition, *M. brevispine* is smaller than *M. oblongum* (10–12 mm vs 40.4–59.4 mm long), with fewer proglottids (up to 50 vs 68–72), a shorter pars bulbosa (320–340 vs 480–530), and smaller mature proglottids (900–950 vs 1487–2250 long).

The scolex of *M. oblongum* is much longer than in *M. myliobati* (1525–1925 vs 490–830), having the pars vaginalis three times longer than the pars bothrials, whereas in *M. myliobati* these parts are of similar length. *Mecistobothrium oblongum* has fewer hooks per principal row than *M. myliobati* (8–9 vs 10–12 hooks), and larger hooks in the external surface (6–11 vs 3.7–4.5 in length). Additionally, *M. oblongum* is a larger worm than *M. myliobati*, and has more proglottids (40.4–59.4 mm long with 68–72 proglottids vs up to 27.6 mm long with 22–55 proglottids, respectively).

Finally, *M. oblongum* can clearly be distinguished from *M. penaeus* in the relative size of the hooks in the principal rows. Thus, in *M. penaeus* the hooks 2(2')–3(3') are the longest hooks in the row, and in *M. oblongum* sp. n. the hooks 1(1') are larger than the remaining hooks, which decrease in size towards the external surface.

DISCUSSION

The genus *Dollfusiella* seems to be well represented in the southwestern Atlantic, *D. acuta* being the third species reported in the area (São Clemente and Gomes 1989, Alarcos et al. 2006, Menoret and Ivanov 2014). *Dollfusiella* was created to include species of *Eutetrarhynchus* without internal seminal vesicles, testes distributed in two columns, and tentacles with distinct basal armature and basal swelling (Campbell and Beveridge 1994). Later on, Palm (2004) modified the diagnosis of *Dollfusiella* including the presence of internal seminal vesicles. Therefore, both genera, *Dollfusiella* and *Eutetrarhynchus*, could have an internal seminal vesicle, an external seminal vesicle, both or none of them. More recently, Schaeffner (2014) amended the diagnosis of *Eutetrarhynchus*, including in this genus species with 1–2 internal seminal vesicles and without an external seminal vesicle. As a result, 15 species of *Eutetrarhynchus* have been transferred to *Dollfusiella* (Campbell and Beveridge 1994, Beveridge et al. 2004). Even so, the proper generic placement of some species should be revised. For example, the observations made on the type specimens of

D. cortezensis in the present study confirm its placement in *Dollfusiella* only on the basis of testis distribution, because the position of the seminal vesicle is dubious (most likely internal).

The discovery of *Mecistobothrium oblongum* in *Myliobatis goodei* represents the first record of *Mecistobothrium* in the southwestern Atlantic. This genus was originally described by Heinz and Dailey (1974), and its diagnosis has been subsequently amended by Campbell and Beveridge (1994) and Palm (2004). However, some diagnostic features are in need of revision, e.g. the relationship between the length of pars bothrials, pars bulbosa and pars vaginalis, the surface of the tentacle where the principal hooks begin in the metabasal armature, and the presence of internal and external seminal vesicles.

For example, not all the species in the genus have the pars bothrials longer than the pars bulbosa, as indicated in the generic diagnosis by Heinz and Dailey (1974) (see Feigenbaum 1975). Actually, in *M. penaeus* the pars bothrials and the pars bulbosa are of the same length and in *M. oblongum* the bothria are slightly shorter than the bulbs. Similarly, the relationship in length between the pars vaginalis and the pars bothrials is also variable among the members of the genus, the pars vaginalis being shorter than the pars bothrials in *M. pauciortesticulatum*, and *vice versa* in all the remaining species.

There has been some controversy in describing the tentacular metabasal region in species of *Mecistobothrium*. Whereas in *M. brevispine*, *M. pauciortesticulatum* and *M. penaeus* the principal rows begin on the internal surface (Campbell and Carvajal 1975, Feigenbaum 1975, Palm 2004), Heinz and Dailey (1974) described hooks 1(1') on the external surface in *M. myliobati*. In the present study, the tentacular armature of *M. oblongum* observed using SEM and light microscopy, allowed us to confirm that the hooks 1(1') are on the antibothrial surface (see Fig. 8A–E). Therefore, it would be interesting to verify this feature in all other species of *Mecistobothrium* to provide an unequivocal characterisation of its oncotaxy. In addition, *M. pauciortesticulatum* and *M. oblongum* have only an internal seminal vesicle, rather than both (internal and external seminal vesicles) as mentioned in the diagnosis of *Mecistobothrium* by Palm (2004).

Elasmobranchs and benthic invertebrates play an important role in the transmission of eutetrarhynchid cestodes as definitive and intermediate hosts, respectively (Campbell and Beveridge 1994, Palm 2004). A few plerocerci have been found in teleosts (Sciaenidae, Batrachoididae and Platycephalidae) (Palm 2004, Pereira and Boeger 2005). Species of *Dollfusiella* include a wide array of elasmobranchs as definitive hosts (i.e. myliobatiform and rajiform batoids, and carcharhiniform, hexanchiform, and orectolobiform sharks), with a variable host specificity ranging from oioxenous to metastenoxenous (Menoret and Ivanov 2014, Schaeffner and Beveridge 2014). Plerocerci have been described for four species found in decapods (i.e. *D. carayoni*, *D. martini* and *D. schmidtii*) and perciform teleosts (i.e. *D. lineata* and an unidentified species of

Dollfusiella) (Gurney et al. 2004, Palm 2004, Pereira and Boeger 2005).

Members of *Dollfusiella* in the southwestern Atlantic have shown specificity to a single host species (i.e. *D. tamini* in *Psammobatis bergi*), or to a particular host family (i.e. *D. acuta* in arhynchobatid skates and *D. vooremi* in triakid sharks) (Menoret and Ivanov 2014). The definitive hosts for the species of *Dollfusiella* off the coast of Argentina feed on teleosts and crustaceans (Cousseau et al. 2007, Schwingel and Assunção 2009, Barbini 2011). Since more than 65 species of teleosts have been examined for trypanorhynchids in the same area (Menoret and Ivanov 2012) and none of them was infected with *Dollfusiella*, it is likely that its life cycles includes only invertebrates as intermediate and paratenic hosts.

Transmission pathways of species of *Mecistobothrium* include myliobatiforms as definitive hosts and shrimps as intermediate hosts (Feigenbaum 1975, Palm 2004). The specificity for the definitive host is variable, from oioxenous (i.e. *M. brevispine* and *M. paucioortesticulatum*) to euryxenous (i.e. *M. myliobati*) (Beveridge and Campbell 1988, Palm 2004, Heinz and Dailey 1974), whereas the plerocerci of *M. penaeus* are restricted to shrimps of the genus *Penaeus* (Feigenbaum 1975, Feigenbaum and Carnuccio 1976).

In the North Atlantic, the cownose ray *Rhinoptera bonasus* (Mitchill) is the definitive host of *M. brevispine* (see Campbell and Carvajal 1975). It feeds mainly on crustaceans including shrimps that have been reported as intermediate hosts for *M. penaeus* in the same area (Feigenbaum 1975, Feigenbaum and Carnuccio 1976, Collins et al. 2007). However, adults of *M. penaeus* were not found in *R. bonasus*, nor plerocerci of *M. brevispine* in shrimps of the genus *Penaeus*. This fact would reinforce the idea of a strict specificity of *M. penaeus* and *M. brevispine* for their respective hosts.

In the southwestern Atlantic *M. oblongum* is a parasite of *M. goodei*, and co-occurs with *Pa. damiani* in the same

host species (see Menoret and Ivanov 2014). The food items of *M. goodei* are teleosts (Cheilodactylidae), batoids (Narcinidae), bivalves, amphipods and polychaetes (Pozzobon 1987, Molina and Lopez Cazorla 2015). During the present study, 53 specimens of *Nemadactylus bergi* (Norman) (Cheilodactylidae) and 50 specimens of *Discopyge tschudii* (Heckel) (Narcinidae) were examined for trypanorhynchids (Menoret and Ivanov 2012, 2013) and plerocerci of *Mecistobothrium* were not detected. Since plerocerci of none of these eutetrarhynchids have been found in a large sample of teleosts that included 68 species caught between depths of 20–2000 meters deep along the coast of Argentina, it is likely that their transmission pathways are also based on invertebrates as intermediate hosts.

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