A new species of *Pseudocrepidobothrium* (Cestoda: Proteocephalidea) from *Pseudoplatystoma reticulatum* (Pisces: Siluriformes) in the Paraná River basin (Argentina)

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Abstract: This study describes the proteocephalidean tapeworm *Pseudocrepidobothrium chanaorum* sp. n. (Proteocephalidae: Proteocephalinae), which was found in the intestine of *Pseudoplatystoma reticulatum* (Eigenmann et Eigenmann) from the Colastiné River, a tributary of the Paraná River. The new species differs from the two other species of the genus, *P. eirasi* (Rego et de Chambrier, 1995) and *P. ludovici* Ruedi et de Chambrier, 2012, parasites of *Phractocephalus hemiliopterus* (Bloch et Schneider) from the Amazon River in Brazil, in having fewer proglottides (4–8 without ventral appendages vs 7–12 with ventral appendages and 20–36 without ventral appendages, respectively), a smaller scolex (350–450 µm wide vs 495–990 µm and 515–1020 µm wide, respectively), in the total number of testes (21–25 vs 21–51 and 37–79, respectively), a cirrus-sac usually directed anteriorly if the vagina is posterior to the cirrus-sac vs transversely situated in the known species. The study of the tegumental surface of *Pseudocrepidobothrium* spp. revealed the presence of four types of microtriches: papilliform, acicular and capilliform filitriches, and gladiate spinitriches. The three species have a similar microthrix pattern, with minor differences on the immature proglottis surface. *Pseudocrepidobothrium chanaorum* sp. n. is the ninth proteocephalid reported from *P. reticulatum*.

Keywords: Proteocephalinae, taxonomy, morphology, microthrix pattern, *Pseudocrepidobothrium chanaorum*, surubí atigrado, South America

Rego and Ivanov (2001) created the genus *Pseudocrepidobothrium* Rego et Ivanov, 2001 to allocate *Crepidobothrium eirasi* Rego et de Chambrier, 1995 based on a unique combination of morphological features of the scolex and strobila. The five species of *Crepidobothrium* Monticelli, 1900 are parasites of Neotropical snakes (de Chambrier 1988, 1989a, b), whereas *Pseudocrepidobothrium* is found in siluriform fishes (Rego and de Chambrier 1995, Ruedi and de Chambrier 2012).

During a survey of proteocephalideans of freshwater fishes in the middle Paraná River basin (Argentina), a new species belonging to *Pseudocrepidobothrium* was discovered parasitising *Pseudoplatystoma reticulatum* (Eigenmann et Eigenmann). These tapeworms could not be assigned to either of the two known species. The purpose of this work is to describe the new specimens, including the microthrix pattern. In addition, the microthrix pattern for *Pseudocrepidobothrium eirasi* (Rego et de Chambrier, 1995) and *P. ludovici* Ruedi et de Chambrier, 2012 are described to complete their characterisation.

MATERIALS AND METHODS

Eleven specimens of *Pseudoplatystoma reticulatum* were caught in the Colastiné River, a tributary of the Paraná River (Santa Fe Province, Argentina) during December 2001, 2003 and 2010. All intestinal worms encountered were detached, fixed in hot 4% formaldehyde solution and subsequently stored in 70% ethanol. Entire tapeworms were stained with Langeron's alcoholic hydrochloric carmine (Langeron 1949), differentiated in acid ethanol, dehydrated through a graded ethanol series, cleared in beechwood creosote and mounted in Canada balsam.

Details of the internal anatomy were determined from thick, hand-cut, transverse serial sections of proglottides stained with Langeron's alcoholic hydrochloric carmine. Intrauterine eggs were studied in distilled water for drawings. Unfortunately, no specimens were fixed for molecular study. The holotype and two paratypes were deposited in the Natural History Museum, Geneva, Switzerland (MHNG-PLAT); five paratypes in the Parasitological Collection of the Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina (MACN-Pa); and two paratypes in the Institute of Parasitology České Budějovice, Czech Republic (IPCAS).

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For comparative purpose, the following tapeworms were studied: type (holotype MHNG-PLAT 18299, paratypes 18301–18310) and voucher (MACN-Pa 568/1–4) specimens of *Pseudocrepidobothrium eirasi*; type (paratype MHNG-PLAT 22000) and voucher (MHNG-PLAT 22047, MACN-Pa 520/1–3) specimens of *P. ludovici*; both species are parasites of *Phractocephalus hemiliopterus* (Bloch et Schneider) and were found in Itacoatiara, Amazon River, Brazil.

Five specimens of the new species, 3 of *Pseudocrepidobothrium eirasi* and 2 of *P. ludovici* were prepared for scanning electron microscopy (SEM) as follows: worms were post-fixed in 1% osmium tetroxide, dried with hexamethyldisilazane (Riedel-De Haën, Steinheim, Germany), mounted on stubs with adhesive tape, sputter coated with ~40 nm of gold-palladium in a Thermo VG Scientific Polaron SC 7630 and examined with a Philips XL 30 scanning electron microscope housed at Museo Argentino de Ciencias Naturales 'Bernardino Rivadavia', Buenos Aires, Argentina.

The types and distribution of microtriches were studied on the scolex, proliferation zone (neck) and immature proglottides. Measurements of the microtriches were taken from photomicrographs. Microtrich terminology follows Chervy (2009). Unless otherwise stated, all measurements are given in micrometres, with the range followed in parentheses by the mean and total number of observations (n). For two-dimensional measurements, length is given before width. The relative size of the ovary was calculated according de Chambrier et al. (2012). Illustrations were made with the aid of a camera lucida attached to a Zeiss Axioscope microscope equipped with differential interference contrast optics.

RESULTS

Pseudocrepidobothrium chanaorum sp. n.

Figs. 1–3, Table 1

Description (based on 12 tapeworms and measurements on 9 gravid specimens, and pieces of strobila as cross sections; 5 tapeworms studied with SEM): Proteocephalidae, Proteocephalinae. Testes and ovary medullary, vitelline follicles medullary and paramuscular, uterine stem cortical, uterine diverticula medullary. Small worms 1.2–4.1 mm (2.7 mm) (n = 7) long (Fig. 2A). Strobila acraspedote, anapolytic, flattened dorsoventrally with 4–7 (5) (n = 8) proglottides. Immature proglottides 2–3 (3) (n = 8) in number, mature proglottis 1 (n = 8) in number, gravid proglottides 1–4 (2) (n = 7) in number. Proglottides without ventral posterior appendage on each side (Figs. 1C,D, 2A).

Scolex massive, quadrangular 200–250 (230) (n = 7) × 350–450 (405) (n = 7), without metascolex, wider than proliferation zone. Apex of scolex slightly dome-shaped, with minute gland cells, without apical organ. Suckers uniloculate, notched at posterior margin, 100–160 (140) × 130–215 (165) (n = 21) (Figs. 1A, 2A, 3A,B). Proliferation zone very short, 135–220 (155) × 210–360 (270) (n = 8) (Figs. 1A, 2A, 3A).

Apex of scolex surface covered only with capilliform filitriches (Fig. 3C). Acetabular rim surface and distal

acetabular surface covered with capilliform filitriches interspersed with gladiate spinitriches (Fig. 3D,E). Proximal acetabular surface and proliferation zone surface (PZS) covered with acicular filitriches interspersed with gladiate spinitriches (Fig. 3F–H), with the latter decreasing in size and density antero-posteriorly on the PZS (Table 1). Immature proglottis surface covered only with acicular filitriches (Fig. 3I).

Immature proglottides wider than long to longer than wide, 60–320 (170) × 180–420 (265) (n = 19), length/width ratio 1 : 0.2–1.3. Mature proglottides longer than wide, 350–630 (505) × 215–310 (290) (n = 5), length/width ratio 1 : 1.1–2.0. Gravid proglottides longer than wide, 450–1 080 (675) × 270–500 (400) (n = 8), length/width ratio 1 : 1.0–3.0 (Figs. 1C,D, 2A). Terminal proglottides, 1 240–1 290 × 250–270 (n = 2), length/width ratio 1 : 4.7–5.0.

Internal longitudinal musculature weakly developed, arranged in one row of small isolated bundles of muscle fibres (Fig. 2B–E). Osmoregulatory canals medullary lying between testes and vitelline follicles. Dorsal canal 5–15 (10) (n = 9) in diameter; ventral canal, 10–30 (15) (n = 9) in diameter, with short secondary canal situated at posterior end of each proglottis or unusually between proglottides, opening on ventral surface; both canals usually overlapping each other along proglottides, sometimes overlapping testes and ovary (Figs. 1C,D, 2A–E).

Testes medullary, oval to spherical, 30–85 (60) × 30–75 (50) (n = 17), 21–25 (23) (n = 7) in number per mature proglottis, distributed in single slightly irregular dorsal field, overlapping vaginal canal and uterus, not overlapping cirrus sac and ovary (Figs. 1B–D, 2A–D). Cirrus sac small, pyriform, usually anteriorly directed if vagina posterior to cirrus sac, with thin muscular wall, 75–115 (100) × 45–60 (50) (n = 6), occupying 34–36% (35%) (n = 6) of proglottis width in mature proglottides, usually not surpassing body midline. Cirrus 50–90 (65) (n = 6) long, occupying 55–75% (65%) (n = 6) of cirrus sac length in mature proglottides. Vas deferens coiled, 15–25 (20) (n = 6) in diameter, surpassing body midline in mature proglottides (Figs. 1B–D, 2A,C). Genital atrium present. Genital pores irregularly alternating, 13–26% (20%) (n = 7) from anterior margin of mature proglottides and 11–32% (19%) (n = 9) from anterior margin of gravid proglottides (Figs. 1B–D, 2A).

Ovary medullary, bilobed, butterfly-shaped, slightly lobulate, 90–200 (135) × 135–200 (160) (n = 5), occupying 46–65 % (55%) (n = 6) of proglottis width in mature proglottides and 53–70% (59%) (n = 9) in gravid proglottides; relative size of ovary 9.8–13.0% (11.5%) (n = 5). Posterior margin of ovary sometimes not reaching posterior margin of proglottides (Figs. 1C,D, 2A,E). Mehlis' gland situated slightly posterior to ovarian isthmus, 35–60 (45) × 30–50 (40) (n = 5). Vaginal canal thin-walled, 10 in diameter, straight or sometimes slightly sinuous; vagina

Fig. 1. *Pseudocrepidobothrium chanaorum* sp. n. from *Pseudoplatystoma reticulatum*. **A** – scolex, dorsoventral view; holotype (MHNG-PLAT 86873); **B** – detail of terminal genitalia, dorsal view; paratype (MACN-Pa 567/1); **C** – mature proglottis, dorsal view; paratype (MHNG-PLAT 86874); **D** – gravid proglottis, ventral view; paratype (MHNG-PLAT 86874). *Abbreviations:* cs – cirrus-sac; doc – dorsal osmoregulatory canal; ga – genital atrium; gc – gland cells; nt – notch; t – testis; ut – uterus; vc – vaginal canal; vd – vas deferens; vf – vitelline follicle; voc – ventral osmoregulatory canal; vs – vaginal sphincter; vsc – ventral secondary canals.

anterior (48%) (n = 21) or posterior (52%) (n = 21) to cirrus sac. Anterior vagina overlaps vas deferens. Vaginal sphincter terminal, 25–30 × 15–25 (n = 3) (Figs. 1B–D, 2A). Vitelline follicles medullary; some follicles paramuscular in cross sections, 25–30 (27) × 20–25 (23) (n = 8), few in number, arranged in one lateral band on each proglottis margin, occupying 68–81% (74%) (n = 6)

of mature proglottis length on aporal side and 60–75% (68%) (n = 6) of mature proglottis length on poral side, usually absent in preporal region (Figs. 1B–D, 2A,B,D,E).

Uterus preformed, uterine stem in ventral cortex; uterine diverticula develop in medulla occupying entire length of gravid proglottides, uterus of type 1 (*sensu* de Chambrier et al. 2004a). Uterus occupying 20–49%

Fig. 2. *Pseudocrepidobothrium chanaorum* sp. n. from *Pseudoplatystoma reticulatum*. **A** – entire worm, ventral view; holotype (MHNG-PLAT 86873); **B** – transverse section of mature proglottis at level of cirrus sac; paratype (MACN-Pa 567/5); **C** – transverse section of gravid proglottis at level of cirrus sac; paratype (MHNG-PLAT 86874); **D** – transverse section of gravid proglottis at level of testes; paratype (MHNG-PLAT 86874); **E** – transverse section of gravid proglottis at level of ovary; paratype (MHNG-PLAT 86874); **F** – egg. *Abbreviations:* cs – cirrus sac; doc – dorsal osmoregulatory canal; em – embryophore; lh – larval hooks; lm – longitudinal musculature; oe – outer envelope; on – oncosphere; ov – ovary; t – testis; ut – uterus; vc – vaginal canal; vd – vas deferens; vf – vitelline follicle; voc – ventral osmoregulatory canal.

(31%) (n = 7) of proglottis width, with 11–19 (15) (n = 3) poral diverticula and 10–18 (14) (n = 3) aporal diverticula. Uterine slit present (Figs. 1D, 2A–E). Uteroduct not observed. Intrauterine eggs spherical; hyaline outer envelope

partially collapsed 30–40 (n = 2) in diameter; embryophore bilayered, external layer spherical, 15–20 (n = 5); oncosphere 9–10 (n = 5) in diameter; hooks not measured because were not longitudinally situated (Fig. 2F).

Fig. 3. *Pseudocrepidobothrium chanaorum* sp. n. from *Pseudoplatystoma reticulatum*; scanning electron micrographs. **A** – scolex, dorsoventral view; black arrows show notch at posterior margin of suckers; letters C–I indicate surfaces shown at high magnification in C–I; **B** – detail of sucker showing posterior notch; **C** – capilliform filitriches on apex of scolex; **D** – capilliform filitriches and gladiate spinitriches on acetabular rim surface; **E** – capilliform filitriches and gladiate spinitriches on distal acetabular surface; **F** – capilliform filitriches and gladiate spinitriches on proximal acetabular surface; **G** – acicular filitriches and gladiate spinitriches on anterior proliferation zone surface; **H** – acicular filitriches and scarce gladiate spinitriches on posterior proliferation zone surface; **I** – acicular filitriches on immature proglottis surface.

Type host: *Pseudoplatystoma reticulatum* (Eigenmann et Eigenmann) (Siluriformes: Pimelodidae). Common names ‘surubí atigrado’ or ‘cachorro’ (juvenile) in Argentina.

Type locality: Colastiné River (tributary of Paraná River) (31°40'S; 60°46'W), near Barrio Colastiné Sur, Santa Fé Province, Argentina.

Site of infection: Anterior and middle intestine.

Infection rate: Prevalence 36% (4/11); intensity 2–7 tapeworms per fish, mean intensity 4, abundance 1.45.

Deposition of specimens: Holotype MHNG-PLAT 86873 (entire worm, on one slide); 2 paratypes MHNG-PLAT 86874 (entire worm, with transverse section, on one same slide), MHNG-PLAT 86875 (entire worm on one slide); 5 paratypes: MACN-Pa 567/1 (entire worm on one slide), MACN-Pa 567/2 (entire worm on one slide), MACN-Pa 567/3 (entire worm with transverse section on same slide), MACN-Pa 567/4 (entire worm on one slide), MACN-Pa 567/5 (worm with transverse section, on one slide, scolex used for SEM); 2 paratypes IPCAS C-648 (entire worm, with

Table 1. Microthrix pattern of the three species of *Pseudocrepidobothrium* from South American siluriform fishes. Range with mean in parentheses followed by the number of measurements (n).

<i>Pseudocrepidobothrium</i>	Surface	Microthrix type	Size	Figs.
<i>P. chanaorum</i> sp. n.	ASS	CF	0.85–1.41 (1.11) × 0.05–0.11 (0.07) (n = 7)	3C
	ARS	CF/GS	0.68–0.94 (0.84) × 0.08–0.13 (0.10) (n = 6) / 0.79–1.14 (1.04) × 0.20–0.53 (0.33) (n = 9)	3D
	DAS	CF/GS	0.78–1.29 (1.03) × 0.08–0.12 (0.10) (n = 13) / 0.77–1.00 (0.88) × 0.28–0.31 (0.30) (n = 6)	3E
	PAS	CF/GS	- / 0.98–1.63 (1.34) × 0.28–0.62 (0.47) (n = 10)	3F
	PZS	AF/GS	0.30–0.48 (0.35) × 0.10–0.16 (0.13) (n = 12) / 1.26–1.86 (1.52) × 0.48–0.71 (0.57) (n = 10)	3G,H
	IPS	AF	0.25–0.46 (0.35) × 0.11–0.14 (0.13) (n = 9)	3I
<i>P. eirasi</i>	ASS	CF	-	-
	ARS	CF/GS	0.78–0.97 (0.86) × 0.19–0.25 (0.23) (n = 4) / 1.17–1.25 (1.21) × 0.22–0.26 (0.24) (n = 3)	-
	DAS	CF/GS	0.82–1.16 (1.02) × 0.08–0.18 (0.12) (n = 5) / 1.01–1.11 (1.06) × 0.21–0.29 (0.24) (n = 3)	-
	PAS	CF/GS	0.38–0.72 (0.57) × 0.12–0.16 (0.14) (n = 4) / 0.59–0.74 (0.66) × 0.22–0.24 (0.23) (n = 3)	-
	PZS	AF/GS	0.78–0.95 (0.85) × 0.08–0.15 (0.13) (n = 5) / 1.18–2.07 (1.60) × 0.21–0.82 (0.49) (n = 7)	-
	IPS	PF/AF	0.15–0.20 (0.17) × 0.08–0.10 (0.10) (n = 5) / 0.19–0.32 (0.26) × 0.08–0.12 (0.10) (n = 8)	-
<i>P. ludovici</i>	ASS	CF	-	-
	ARS	CF/GS	0.68–0.92 (0.76) × 0.08–0.11 (0.09) (n = 5) / 1.03–1.19 (1.10) × 0.21–0.26 (0.23) (n = 5)	-
	DAS	CF/GS	0.99–1.28 (1.10) × 0.09–0.11 (0.10) (n = 4) / 0.95–1.15 (1.08) × 0.28–0.32 (0.30) (n = 3)	-
	PAS	CF/GS	0.80–1.07 (0.91) × 0.09–0.13 (0.11) (n = 5) / 1.16–1.53 (1.36) × 0.36–0.54 (0.45) (n = 7)	-
	PZS	AF/GS	0.15–0.31 (0.23) × 0.06–0.19 (0.11) (n = 14) / 0.77–1.35 (1.02) × 0.36–0.49 (0.42) (n = 8)	-
	IPS	PF/AF	0.16–0.20 (0.18) × 0.10–0.14 (0.12) (n = 6) / 0.22–0.24 (0.23) × 0.09–0.11 (0.10) (n = 4)	5E

ASS – apex of scolex surface; ARS – acetabular rim surface; DAS – distal acetabular surface; PAS – proximal acetabular surface; PZS – proliferation zone surface; IPS – immature proglottis surface; AF – acicular filitriches; CF – capilliform filitriches; GS – gladiate spinitriches; PF – papilliform filitriches (measurements in micrometres).

Fig. 4. *Pseudocrepidobothrium eirasi* (Rego et de Chambrier, 1995) from *Phractocephalus hemioliopertus*. **A** – transverse section at level of testes, gravid proglottis, voucher (MACN-Pa 568/4); **B** – transverse section at level of ovary, gravid proglottis, voucher (MACN-Pa 568/4). *Abbreviations:* doc – dorsal osmoregulatory canal; lm – longitudinal musculature; mg – Mehlis' gland; ov – ovary; t – testis; ut – uterus; vc – vaginal canal; vf – vitelline follicle; voc – ventral osmoregulatory canal.

transverse section, on one slide and entire worm on another slide).

E t y m o l o g y : The species is dedicated to the ancient Chaná People who originally inhabited the middle and lower Paraná River basin.

Remarks. The new species is placed in *Pseudocrepidobothrium* because of its small size and few proglottides; the presence of four uniloculate, posteriorly notched

suckers (inverted heart-shaped suckers *sensu* Rego and de Chambrier 1995, Ruedi and de Chambrier 2012), a weakly developed internal longitudinal musculature, testes distributed in a single field, a vagina anterior or posterior to the cirrus sac, a butterfly-shaped ovary, a cortical uterine stem, a uterus of type 1 (*sensu* de Chambrier et al. 2004a), occupying the entire length of gravid proglottides and having short medullary diverticula, and by the absence of vitelline follicles in the preporal region of proglottis (Rego and Ivanov 2001, Ruedi and de Chambrier 2012).

Pseudocrepidobothrium currently includes two species, *P. eirasi* and *P. ludovici* (Figs. 4, 5A,D) both of which are parasites of *Phractocephalus hemioliopertus*, a pime-lodid catfish endemic to the Amazon and Orinoco River basins (Froese and Pauly 2014). *Pseudocrepidobothrium chanaorum* can be easily discriminated from *P. eirasi* by the absence of paired appendages at the ventral posterior edges of each proglottis and the morphology of the eggs (without polar structures).

The new species and *P. ludovici* lack ventral posterior appendages in the proglottides and share the morphology of the eggs (typical of proteocephalids, i.e. without polar structures). However, *P. chanaorum* can be distinguished from *P. ludovici* in having a fewer testes (21–25 vs 37–79), fewer proglottides (4–7 vs 20–36), an overall smaller body (1.2–4.1 mm vs 7–23 mm), a narrower scolex width (350–450 µm vs 515–1 020 µm) and a shorter proliferation zone (135–220 µm vs 620 µm). Additionally, *P. chanaorum* is a parasite of *P. reticulatum*, which is widespread to the Central Amazon, Orinoco, Paraguay and Paraná River basin in Argentina, Brazil, Paraguay

Fig. 5. *Pseudocrepidobothrium eirasi* (Rego et de Chambrier, 1995) and *P. ludovici* Ruedi et de Chambrier, 2012 from *Phractocephalus hemioliopertus*, scanning electron micrographs. **A** – *P. eirasi*, scolex and anterior portion of strobila showing ventral posterior appendages, ventral view; black arrows show notches at posterior margin of suckers, white arrowhead shows opening of osmoregulatory canal at the tip of the appendage (also in B and C); **B** – *P. eirasi*, gravid proglottides showing posterior ventral appendages; **C** – detail of posterior ventral appendages on immature proglottis; **D** – *P. ludovici*, scolex, latero-dorsoventral view; **E** – papilliform and acicular filitriches on immature proglottis surface; black arrows show the scarce acicular filitriches.

and Uruguay (Buitrago-Suárez and Burr 2007, Torrico et al. 2009).

DISCUSSION

Recently, many phylogenetic studies have been conducted aimed at separating cestodes into natural groups on the basis of morphological and molecular evidences (e.g. Bray et al. 1999, Hoberg et al. 1999, Olson et al. 2001, Waeschenbach et al. 2007, 2012). Thus, for example, the Pseudophyllidea emerged as a paraphyletic group, eventually leading to the erection of two new orders:

Bothriocephalidea Kuchta, Scholz, Brabec et Bray, 2008 and Diphyllbothriidea Kuchta, Scholz, Brabec et Bray, 2008 (Mariaux 1998, Bray et al. 1999, Kodedová et al. 2000, Brabec et al. 2006, Kuchta et al. 2008).

Likewise, the Tetraphyllidea was found to be paraphyletic (e.g. Olson et al. 2001, Waeschenbach et al. 2007) and thus was split into three orders: Litobothriidea Dailey, 1969, Cathetocephalidea Schmidt et Beveridge, 1990 and Rhinebothriidea Healy, Caira, Jensen, Webster et Littlewood, 2009 (Dailey 1969, Schmidt and Beveridge 1990, Olson and Caira 2001, Caira et al. 2005, Healy et

al. 2009). Each of these orders was erected on the basis of both molecular and morphological data, and showed at least a single unifying synapomorphy for the whole group. Nonetheless, the classification of cestodes is yet to be resolved. In this regard, the relationships between the Proteocephalidea and some members of the tetraphyllidean family Onchobothriidae Braun, 1900 is a particularly interesting issue (Olson et al. 2001, de Chambrier et al. 2004a, Waeschenbach et al. 2007, 2012).

In a most recent study, Caira et al. (2014) placed the Proteocephalidea together with some members of the family Onchobothriidae in a new order termed Onchoprotocephalidea. However, they draw some controversial conclusions that require further discussion. A major point is that there is no synapomorphy characterising the proposed new order. Caira et al. (2014) hypothesise that the presence of gladiate spinitriches on the cephalic peduncle in Onchobothriidae and the proliferation zone (neck) in Proteocephalidea could be a synapomorphy. However, they state that the homology between the cephalic peduncle and the proliferation zone or neck has not been proven yet (see Caira et al. 2014). It is worth to mention that several proteocephalidean species lack gladiate spinitriches on the proliferation zone, such as *Luciaella ivanovae* Gil de Perterra, 2009; *Proteocephalus membranacei* Troncy, 1978; *P. synodontis* Woodland, 1925; *Ritacestus ritaii* (Verma, 1926); *Sandonella sandoni* (Lynsdale, 1960); and *Spatulifer maringaensis* Pavalelli et Rego, 1989 (see Arredondo and Gil de Perterra 2008, de Chambrier et al. 2008, 2011a,b, Gil de Perterra 2009).

The inclusion of some members of the Onchobothriidae within the proposed order is also a subject of controversy. According to molecular phylogenetic analyses conducted by Caira et al. (2014), *Megalonchos* Baer et Euzet, 1962 is placed in a different clade from that of onchoprotocephalideans; however, the authors conclude that it belongs to the proposed order. They also included the genera *Acanthobothroides* Brooks, 1977, *Onchobothrium* de Blainville, 1828 and *Pinguicollum* Riser, 1955 on the basis of morphological rather than molecular characters. In fact, they justified their inclusion by the scolex morphology, the presence of gladiate spinitriches on the cephalic peduncle and the host. The monophyly of the Proteocephalidea has been confirmed (Zehnder and Mariaux 1999, de Chambrier et al. 2004a), whereas the Onchobothriidae was found to be paraphyletic (Olson et al. 2001, Caira et al. 2005, Waeschenbach et al. 2007, 2012). In this line of reasoning, the molecular-based phylogenetic analysis should encompass all the genera of this family, and the possible inclusion of each genus in the proposed new order should be made after the molecular study rather than before. Until then, it seems appropriate to retain the order Proteocephalidea for *Pseudocrepidobothrium chanaorum* sp. n. Finally, it is highly desirable that an important change in terms of taxonomy and systematics, such as the one proposed by Caira et al. (2014), is sup-

ported by phylogenies inferred not only from molecular but also from morphological characters.

The three species of *Pseudocrepidobothrium* have a small body-size with a reduced number of proglottides, a weakly developed internal longitudinal musculature arranged in a single row of isolated bundles of muscle fibres, ventral osmoregulatory canals with a short lateral secondary branch at the posterior end of each proglottis, a vagina anterior or posterior to the cirrus sac and with sphincter, and a butterfly-shaped ovary, whereas they lack vitelline follicles in the preporal region of proglottides (see Rego and Chambrier 1995, Ruedi and de Chambrier 2012, the present study). For comparative purposes, *P. eirasi* and *P. ludovici* were re-examined and missing data were completed. Results obtained were as follows: the three species have minute gland cells at the apex of the scolex, a similar relative ovarian size (11.5% *P. chanaorum*, 11.0% *P. eirasi* and 12.1% *P. ludovici*), and a cortical uterine stem; additionally, *P. eirasi* has a type 1 uterus (see Fig. 4A,B the present study).

Based on scolex morphology, *P. eirasi* was first included in the genus *Crepidobothrium* (Proteocephalinae). However, *Pseudocrepidobothrium* and *Crepidobothrium* differ in several characters, such as small body size with few proglottides vs large body size with numerous proglottides; absence of an apical organ at the apex of the scolex vs presence; few testes vs numerous testes; butterfly-shaped ovary vs bilobed and mostly reticulate ovary; absence of preporal follicles vs their presence; and a uterus occupying the entire length of the gravid proglottis vs ending at the anterior margin of the ovary. Rego and Ivanov (2001) demonstrated the monophyly of *Crepidobothrium* and created *Pseudocrepidobothrium* to allocate *P. eirasi*.

As a side note, it is interesting to highlight that *P. eirasi* bears posterior ventral appendages that are unique among Cestoda in that they are conical in shape and contain a branch of the ventral osmoregulatory canal opening at each tip (Fig. 5A–C). There are posterior lacinations or lappets (velum) surrounding the proglottis in other cestode groups, including a few proteocephalideans such as *Scholzia emarginata* (Diesing, 1850), *Zygobothrium megacephalum* Diesing, 1850 and *Nomimoscolex piraeba* Woodland, 1934 (see Woodland 1933, de Chambrier and Vaucher 1997, de Chambrier et al. 2005). The conical shape and branching of the ventral osmoregulatory canal within the appendages of *P. eirasi* makes it reasonable to assume that they are not homologous to the lacinations or lappets in other cestodes.

Ammann and de Chambrier (2008) and de Chambrier et al. (2012) studied the relative ovarian size of proteocephalidean cestodes of reptiles throughout the world (mainly data from snakes). They found that the relative ovarian size in species of *Ophiotaenia* La Rue, 1911 is smaller than that of *Proteocephalus* Weinland, 1858 from fishes (both Proteocephalinae). Similarly, the relative size

of the ovary of *Crepidobothrium* from snakes is smaller (4.0–6.5%, calculated in this work from all five valid species) than that of *Pseudocrepidobothrium* from fishes (11.0–12.1%). An exception to this is *Margaritaella gracilis* Arredondo et Gil de Perterra, 2012, a proteocephalidean from fish, which has the smallest relative size of the ovary (0.6–1.8%) (Arredondo and Gil de Perterra 2012).

The microthrix pattern of *P. eirasi* was not studied and that from *P. ludovici* was only partially studied (Rego and de Chambrier 1995, Ruedi and de Chambrier 2012). The tegument surface of the three known species was observed in the present study, and four types of microtriches were found (papilliform, acicular and capilliform filitriches, and gladiate spinitriches). Therefore, *P. eirasi* and *P. ludovici* share the same microthrix pattern, whereas *P. chanaorum* differs slightly in the type of microtriches that cover the immature proglottis surface (acicular and papilliform filitriches vs acicular filitriches, respectively) (Figs. 3I, 5E, Table 1). The three known species of *Pseudocrepidobothrium* have the same distribution of microtriches on the scolex and proliferation zone, whereas *P. chanaorum* differs from the two others in the distribution of microtriches on the immature proglottis. In conclusion, the microthrix pattern of the three species is very homogeneous.

Usually, the uterus of proteocephalidean cestodes from fishes does not occupy the entire length of the gravid proglottis. Exceptionally, the uterus is found occupying the entire length in a few genera that belong to different subfamilies, for example *Amazotaenia* de Chambrier, 2001 (Peltidocotylineae), *Brooksiella* Rego, Chubb et Pavanelli, 1999 (Zygobothriinae), *Cangatiella* Pavanelli et Machado dos Santos, 1991 (Proteocephalinae), some species of *Proteocephalus* Weinland, 1858 (Proteocephalinae) (e.g. *P. sophiae* de Chambrier et Rego, 1994), and *Rudolphiella* Fuhrmann, 1916 (Rudolphiellinae) (see de Chambrier and Rego 1994, Gil de Perterra and Viozzi 1999, Gil de Perterra and de Chambrier 2000, de Chambrier 2001, de Chambrier et al. 2004b). *Pseudocrepidobothrium* is another genus with the uterus occupying the entire length of the gravid proglottis. Further study will be needed to determine whether this character is phylogenetically informative.

The morphology of a given type of scolex may be common to different genera of the same subfamily as in *Crepidobothrium* and *Pseudocrepidobothrium* (Proteocephalinae) (a scolex with uniloculate suckers, notched at

posterior margin), or *Harriscolex* Rego, 1987 and *Houssayella* Rego, 1987 (Zygobothriinae) (scolex with uniloculate suckers bearing small cone-shaped projections on each corner at anterior margin). On the other hand, the scolex can also be shared by genera belonging to different subfamilies, as for example *Harriscolex* and *Houssayella* with *Euzetiella* de Chambrier, Rego et Vaucher, 1999 of the Proteocephalinae, and these three with *Regoella* Arredondo, de Chambrier et Gil de Perterra, 2013 of the Monticelliinae (de Chambrier et al. 1999, de Chambrier and Scholz 2005, Gil de Perterra and de Chambrier 2013, Arredondo et al. 2013). Likewise, *Macrobothriotaenia* Freze, 1965 and *Thaumasioscolex* Cañeda-Guzmán, de Chambrier et Scholz, 2001 (both Proteocephaliinae) show a similar scolex morphology (formed by four lobes, with each lobe containing an unilocular, pincer-shaped sucker), but in fact they are not closely related species as demonstrated by Scholz et al. (2013); the similarity in the morphology of both scoleces has been explained as an adaptation to the morphology of the hosts' intestine (Scholz et al. 2013). In the case of the other above-mentioned genera, it will be interesting to clarify whether the similar shape of the scolex is an evidence of relationship or represents a homoplastic character as a result of convergent evolution.

The genus *Pseudoplatystoma* Bleeker comprises two species in Argentina: *P. corruscans* (Spix et Agassiz), which is present in the Paraná and São Francisco River basins, and *P. reticulatum*, which occurs in the Paraná River basin and the Central Amazon River (see Buitrago-Suárez and Burr 2007, Torrico et al. 2009). *Pseudoplatystoma reticulatum* from the Colastiné River (Middle Paraná River basin) of Argentina harbours the following proteocephalidean species: *Choanoscolex* cf. *abscisus* Riggenbach, 1895; *Monticellia* cf. *spinulifera* Woodland, 1934; *Nomimoscolex lopesi* Rego, 1990; *N. sudobim* Woodland, 1935; *Peltidocotyle rugosa* Diesing, 1850; *Regoella brevis* Arredondo, de Chambrier et Gil de Perterra, 2013; *Spatulifer rugosa* (Woodland, 1935) (see Gil de Perterra 2005, 2009, de Chambrier et al. 2006, Arredondo and Gil de Perterra 2008); *Pseudocrepidobothrium chanaorum* is thus the eighth species reported from this fish host.

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