

Further study on *Procamallanus (Spirocammallanus) pintoi* (Kohn et Fernandes, 1988) (Nematoda: Camallanidae) in *Corydoras paleatus* and *Corydoras micracanthus* (Siluriformes: Callichthyidae) from Salta, Argentina, with a key to congeneric species from Neotropical Realm

Lorena G. Ailán-Choke^{1,3*}, Geraldine Ramallo² and Dora Davies¹

¹Instituto para el Estudio de la Biodiversidad de Invertebrados, Facultad de Ciencias Naturales, Universidad Nacional de Salta, Av. Bolivia 5150, (4400) Salta, Argentina; ²Instituto de Invertebrados, Fundación Miguel Lillo, Miguel Lillo 251, (4000) San Miguel de Tucumán, Argentina; ³Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

Abstract

This study describes the morphology of *Procamallanus (Spirocammallanus) pintoi* (Kohn et Fernandes, 1988), isolated from the intestine of *Corydoras micracanthus* Regan, 1912 and *C. paleatus* (Jenyns, 1842) (both Callichthyidae, Siluriformes) from Bermejo and Juramento River basins, respectively, province of Salta, Argentina. This is the first record of *P. (S.) pintoi* in *C. micracanthus* from Northwestern Argentina. The light and scanning electron microscopy observations of *P. (S.) pintoi*, revealed a few previously unreported morphological details of the cephalic region, vulva and caudal region of males. In addition, morphometric variability was observed in, mainly body size, glandular oesophagus length and position of the vulva between present specimens and those described in previous studies. A key to the species of *Procamallanus (Spirocammallanus)* from the Neotropical Realm is proposed.

Keywords

Camallanoidea, fish parasite, *Corydoras paleatus*, *Corydoras micracanthus*, Northwestern Argentina

Introduction

The genus *Procamallanus* Baylis, 1923 (Nematoda, Spirurida) comprises numerous parasitic nematode species of the stomach and intestine of marine and freshwater fishes, reported in a broad range of hosts from several geographical regions (Moravec 1998). Currently, 30 species of *Procamallanus* are described in the Neotropical Realm, these belong to three subgenera: *Procamallanus* Baylis, 1923, *Denticamallanus* Moravec et Thatcher, 1997 and *Spirocammallanus* Olsen, 1952 (Moravec *et al.* 2004; Ramallo 2008; Giese *et al.* 2009; Ramallo 2011; Ramallo and Ailán-Choke 2017). Moravec (1998) proposed a key to species of the genus *Procamallanus* parasitic in Neotropical freshwater fishes, however this is outdated, because later new congeneric species were described and others synonymized (Moravec *et al.* 2000; Moravec *et al.* 2004; Giese *et al.* 2009; Ramallo 2008; Ramallo and Ailán-Choke 2017).

In Argentina, seven *Procamallanus* species have hitherto recorded in freshwater fishes: *Procamallanus (Denticamallanus) ana* Ramallo, 2011; *P. (S.) hilarii* Vaz *et al.* 1934, *P. (S.) huacraensis* Ramallo, 2008, *P. (S.) inopinatus* Travassos, Artigas *et al.* 1928, *P. (S.) juana* Ramallo *et al.* 2017, *P. (S.) pintoi* (Kohn et Fernandes, 1988) and *P. (S.) rarus* Travassos, Artigas *et al.* 1928 (Ramallo 2011; Ramallo and Ailán-Choke 2017).

Procamallanus (Spirocammallanus) pintoi is a parasite widely reported in freshwater fishes belonging to the genus *Corydoras* Lacépède, 1803 from Neotropical Realm (Kohn and Fernandes 1988; Moravec *et al.* 1997, 1999; Ito *et al.* 2005; Santana-Piñeros *et al.* 2017), but it has been recorded as well in *Trichomycterus spegazzinii* (Berg, 1897) from Northwestern Argentina (Ailán-Choke *et al.* 2014). Despite of several authors (Kohn and Fernandes 1988; Moravec *et al.* 1997, 1999) studied the morphology specimens of this species, some aspects of the cephalic structures and number and disposition of caudal papillae still insufficiently

*Corresponding author: lorenaailanchoke@gmail.com

known. Therefore, the purpose of this study is to provide a detailed description and add new morphological features of the collected specimens, based on light and scanning electron microscopy examinations and compare it with some congeneric Neotropical species. A taxonomic identification key for the known species of *Procamallanus* (*Spirocammallanus*) in Neotropical Region is provided, modifying the key proposed by Moravec (1998).

Materials and Methods

Parasitological surveys were performed from June 2014 to February 2017. Fifty three specimens of *C. paleatus* (Jenyns, 1842) (standard length 12.00–50.86 mm; weight 0.10–6.70 g) were collected from Arias-Arenales River ($24^{\circ}48'27.73"S$; $65^{\circ}25'56.03"W$) and Arias River ($24^{\circ}47'41.65"S$; $65^{\circ}28'0.72"W$) (Juramento River basin); and 17 of *C. micracanthus* Regan, 1912 (standard length 16.13–35 mm; weight 0.10–2.00 g) from Yacones River ($24^{\circ}40'15.79"S$; $65^{\circ}24'8.96"W$) and Lesser River ($24^{\circ}39'43.56"S$; $65^{\circ}28'49.079"W$) (Bermejo River basin). All fishes were fixed in 10% formalin for 24 h and preserved in 70% ethanol for later helminthological examination. Isolated nematodes from the intestine were preserved in 70% ethanol.

Infection parameters (prevalence and mean intensity) for each host species were estimated based on Bush *et al.* (1997). The examined fishes were deposited in the Colección Ictiológica, Instituto de Bio y Geociencias del Noroeste Argentino (IBIGEO-I), Salta, Argentina.

For light microscopy, the nematodes were cleared with lactophenol. Drawings were made using a camera lucida. Some specimens, from both hosts, were dehydrated throughout an ethanol series, acetone and ether, coated with gold and examined in a Zeiss Supra 55VP SEM. Measurements (minimum and maximum) are given in millimetres (mm) unless otherwise indicated. Nematodes were deposited in the Colección Helmántológica Fundación Miguel Lillo (CH-FML), San Miguel de Tucumán, Argentina.

Results

The description is based on nematodes obtained from *C. paleatus* (9 males, 8 females and 9 first-stage larvae). The morphometry of specimens from *C. micracanthus* (6 males, 10 females) is listed in Tables I and II.

Order Spirurida Chitwood, 1933

Family Camallanidae Railliet et Henry, 1915

Genus *Procamallanus* Baylis, 1923

Subgenus *Spirocammallanus* Olsen, 1952

Procamallanus (*Spirocammallanus*) *pintoi* (Kohn et Fernandes, 1988) (Figs 1, 2)

Syn.: *Spirocammallanus pintoi* Kohn et Fernandes, 1988

General: Medium sized nematodes. Cuticle with fine transverse striations. Oral opening circular, surrounded by eight

submedian cephalic papillae, arranged in two circlets, each circlet formed by four papillae (the papillae of the external circlet are distinctly larger), each papillae accompanied by distinct proximal pore and additional six pores (four submedian and two lateral) present near of the margin of oral opening. Pair of small lateral amphids present (Figs 1D, 2A, B). Buccal capsule orange-brown, thick-walled, barrel-shaped, slightly longer than wide. Two third of inner surface of capsule provided with spiral thickenings (ridges) in lateral view (Figs 1A–C). Basal ring not observed. Muscular oesophagus club-shaped, distinctly shorter than glandular oesophagus, cylindrical, expanded near its posterior end (Figs 1A, B). Small lateral deirids, simple shape and situated just posterior to buccal capsule, projecting from ring-like cuticular pattern (Figs 2C, D). Nerve-ring anterior to middle of muscular oesophagus. Excretory pore slightly below to nerve-ring (Figs. 1A, 2E). Tail conical with rounded tip (Figs 1F, I, 2F, G).

Male (9 specimens): Length of body 2.95–5.35, maximum width 0.15–0.22. Buccal capsule 0.05–0.07 long and 0.05–0.06 wide with 6–8 inner spiral thickenings, the anterior two incomplete (Fig 1B). Muscular oesophagus 0.26–0.32 long, 0.09–0.15 wide. Glandular oesophagus 0.49–0.72 long, 0.07–0.15 wide. Nerve-ring and excretory pore 0.13–0.20 and 0.17–0.27, respectively, from anterior extremity (Fig 1A). Spicules short, similar and subequal with arrow-like tips: right spicule slightly larger than left one: right spicule 0.07–0.15, left spicule 0.06–0.11 (Fig 1I). Gubernaculum absent. Caudal alae lacking. Seven pairs of caudal papillae. Preanal papillae: four pairs of subventral sessile papillae (homogeneously spaced); postanal papillae: 3 pairs of small subventral papillae, the first pair situated at short distance of anus (Figs 1I, 2G). Phasmids absent. Tail conical 0.15–0.20 long (Fig 2G).

Gravid females (6 specimens): Length of body 7.36–13.45, maximum width 0.25–0.65. Buccal capsule 0.05–0.07 long and 0.05–0.06 wide with 7–9 inner spiral thickenings, the anterior two incomplete (Fig. 1C). Muscular oesophagus 0.25–0.29 long, 0.11–0.15 wide. Glandular oesophagus about three times longer than muscular one 0.74–1.03 long, 0.09–0.24 wide. Nerve-ring, excretory pore and deirids 0.15–0.16, 0.20–0.27 and 0.06, respectively, from anterior extremity (Figs 2C, D). Vulva postequatorial, weakly visible (at 66–80% of body length) 1.97–4.27 from posterior end of body (Fig. 1E). Tail conical 0.26–0.30 long (Figs 1F, 2F).

Non-gravid females (2 specimens): Length of body 3.03–3.15, maximum width 0.15. Buccal capsule 0.06 long and 0.06 wide with 7–8 inner spiral thickenings, the anterior two incomplete. Muscular oesophagus 0.25–0.28 long, 0.08–0.10 wide. Glandular oesophagus about two times longer than muscular one 0.47–0.50 long, 0.06–0.08 wide. Nerve-ring and excretory pore 0.13–0.15 and 0.20–0.27, respectively, from anterior extremity. Vulva inconspicuous, postequatorial 1.45 from posterior end of body. Muscular vagina, directed posteriorly from vulva (Fig. 1H). Tail conical 0.17–0.18 long.

First-stage larvae (8 specimens from uterus): Length of body 0.10–0.46, maximum width 0.02. Head is armed with a

Table I. Measurements of males of *Procamallanus (*Spirocammallanus*) pintoi*

Sources	Hosts	Corydoras paleatus	Corydoras reticulatus	Corydoras paleatus	Corydoras micracanthus	Present study	
						n = 1	n = 6
Kohn & Fernandes (1988)	Total body length	4.67	3.09	2.95–5.35	1.87–3.56		
	Body width	0.25	0.20	0.15–0.22	0.11–0.20		
Moravec et al. (1999)	Buccal capsule length	0.05	0.06	0.05–0.06	0.05–0.07		
	Buccal capsule width	0.05	0.06	0.05–0.07	0.04–0.05		
	Nº of spiral thickenings in buccal capsule	6	7	6–8	6–8		
	Muscular oesophagus length	0.23	0.30	0.26–0.32	0.24–0.36		
	Muscular oesophagus width	0.11	0.11	0.09–0.15	0.07–0.13		
	Glandular oesophagus length	0.59	0.53	0.49–0.72	0.37–0.57		
	Glandular oesophagus width	0.12	0.11	0.07–0.15	0.06–0.10		
	Glandular/ muscular oesophagus length ratio	1:2.57	1:1.8	1: 1.62–2.50	1:1.29–1.97		
	Nerve ring—anterior end	0.11	0.14	0.13–0.20	0.14–0.19		
	Excretory pore—anterior end	0.16	0.17	0.17–0.27	0.16–0.22		
	Deirids—anterior end	—	0.06	—	0.08–0.12		
	Right spicule length	0.09	0.11	0.07–0.15	0.07–0.10		
	Left spicule length	0.08	0.11	0.06–0.11	0.06–0.09		
	Pairs of preanal papillae	4	4	4	4		
	Pairs of postanal papillae	2	2	3	3		
	Tail length	0.12	0.21	0.15–0.20	0.11–0.18		
	Locality	Iguazú River, Parana State, Brazil	Peru	Arenales and Arias-Arenales Rivers, Salta, Argentina	Lesser and Yacones Rivers, Salta, Argentina		

Given in mm, minimum value–maximum value

Table II. Measurements of females of *Procamallanus (Spirocammallanus) pintoi*

Sources	Kohn & Fernandes (1988)	Moravec et al. (1997)	Moravec et al. (1999)	Present study			
Hosts	<i>Corydoras paleatus</i>	<i>Corydoras aeneus</i>	<i>Corydoras reticulatus</i>	<i>Corydoras paleatus</i>		<i>Corydoras micracanthus</i>	
Females	n = 3 (gravid)	n = 4 (non-gravid)	n = 2 (non-gravid)	n = 6 (gravid)	n = 6 (non-gravid)	n = 4 (gravid)	n = 6 (non-gravid)
Total body length	21.8–26	3.44–4.66	4.67–6.70	7.36–13.45	3.03–3.15	8.30–13.28	2.15–5.49
Body width	0.95–1.16	0.16–0.19	0.30–0.48	0.25–0.65	0.15	0.56–0.74	0.11–0.41
Buccal capsule length	0.06–0.07	0.08–0.09 ^b	0.08	0.05–0.07	0.06	0.07–0.08	0.06–0.07
Buccal capsule width	0.05–0.06	0.06	0.07–0.08	0.05–0.06	0.06	0.05–0.06	0.05–0.06
Nº of spiral thickenings in buccal capsule	9–10	8–12	8–10	7–9	7–8	7–8	6–8
Muscular oesophagus length	0.27–0.30	0.34–0.39	0.34	0.25–0.29	0.25–0.28	0.31–0.34	0.25–0.33
Muscular oesophagus width	0.11–0.14	0.10–0.11	0.14	0.11–0.15	0.08–0.10	0.12–0.15	0.09–0.13
Glandular oesophagus length	0.87–1.05	0.48–0.60	0.67	0.74–1.03	0.47–0.50	1.13–1.19	0.39–0.89
Glandular oesophagus width	0.22–0.23	0.08–0.10	0.17–0.20	0.09–0.24	0.06–0.08	0.16–0.23	0.06–0.19
Glandular/muscular oesophagus length ratio	1:3.22–3.48	1:1.3–1.7	1:2.00	1:1.70–3.57	1:1.70–2.03	1:3.29–3.85	1:1.60–2.72
Nerve ring – anterior end	0.12–0.16	0.19	0.14–0.19	0.15–0.16	0.13–0.15	0.16–0.19	0.14–0.18
Excretory pore – anterior end	0.30	0.25–0.28	0.26	0.20–0.27	0.20–0.27	0.20–0.26	0.17–0.23
Deirids – anterior end	–	0.13	0.06	0.06	–	0.07–0.09	0.07–0.11
Vulva – posterior end	7.9 ^a	2.80–3.40 ^a	1.24–2.64	1.97–4.27	1.45	1.68–2.84	0.44–1.19
Tail length	0.28	0.18–0.20	0.11–0.23	0.26–0.30	0.17–0.18	0.29–0.34	0.14–0.22
Locality	Iguazú River, Paraná State, Brazil	Suripá River, Barinas State, Venezuela	Arenales and Arias-Arenales Rivers, Salta , Ar- gentina	Lesser and Yacones, Rivers, Salta, Argentina			

Given in mm, minimum value–maximum value. References: ^ameasurement taken from anterior end; ^bmeasurement taken including the basal ring

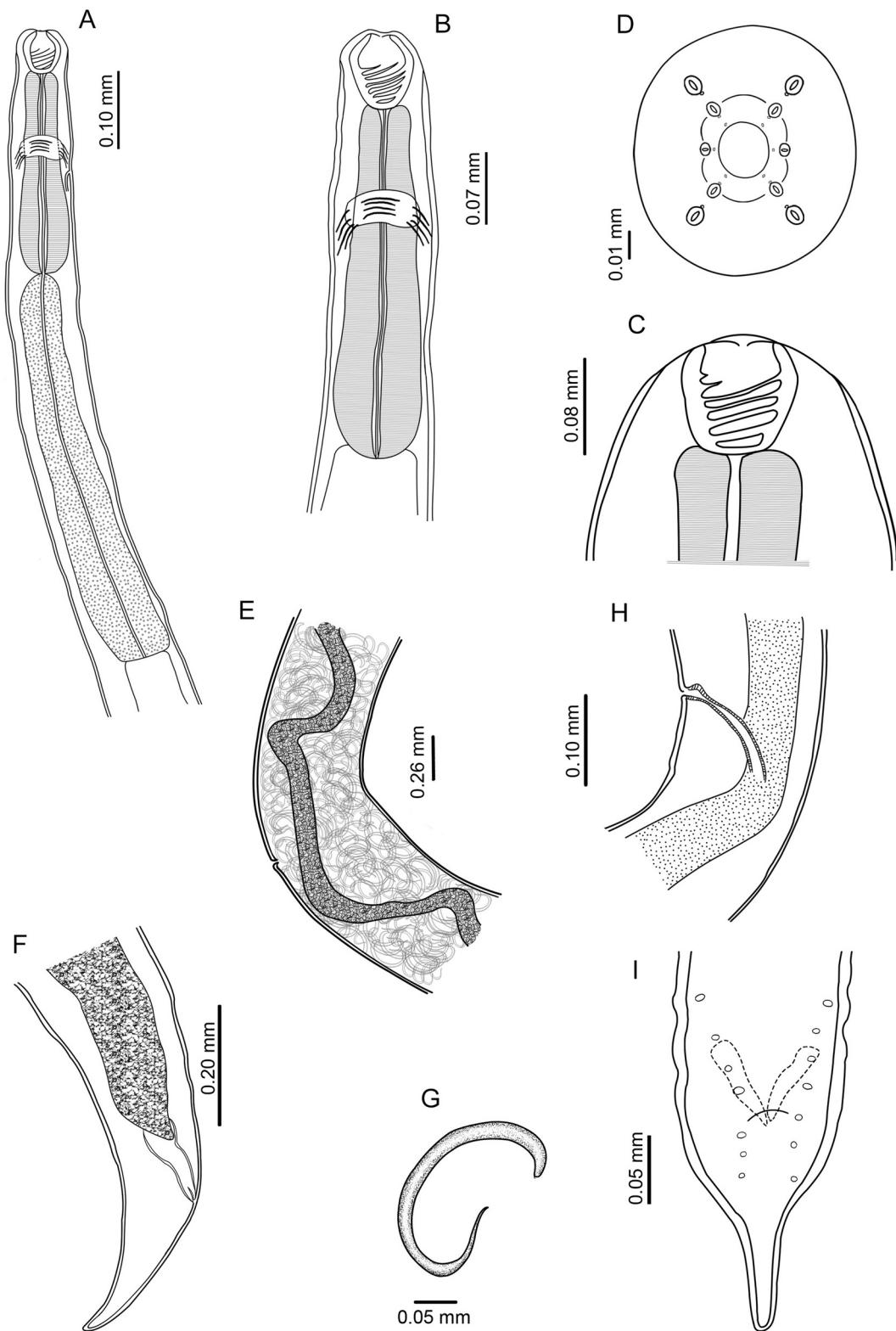


Fig. 1 *Procamallanus (Spirocammallanus) pintoi* (Kohn & Fernandes, 1988). **A** – anterior end of male, lateral view. **B** – anterior end of female, lateral view. **C** – cephalic end of female, lateral view. **D** – cephalic end of male, apical view. **E** – Vulva and uterus containing larvae in gravid female, lateral view. **F** – posterior end of gravid female, lateral view. **G** – First-stage larva. **H** – region of vulva in non-gravid female, lateral view. **I** – posterior end of male, ventral view

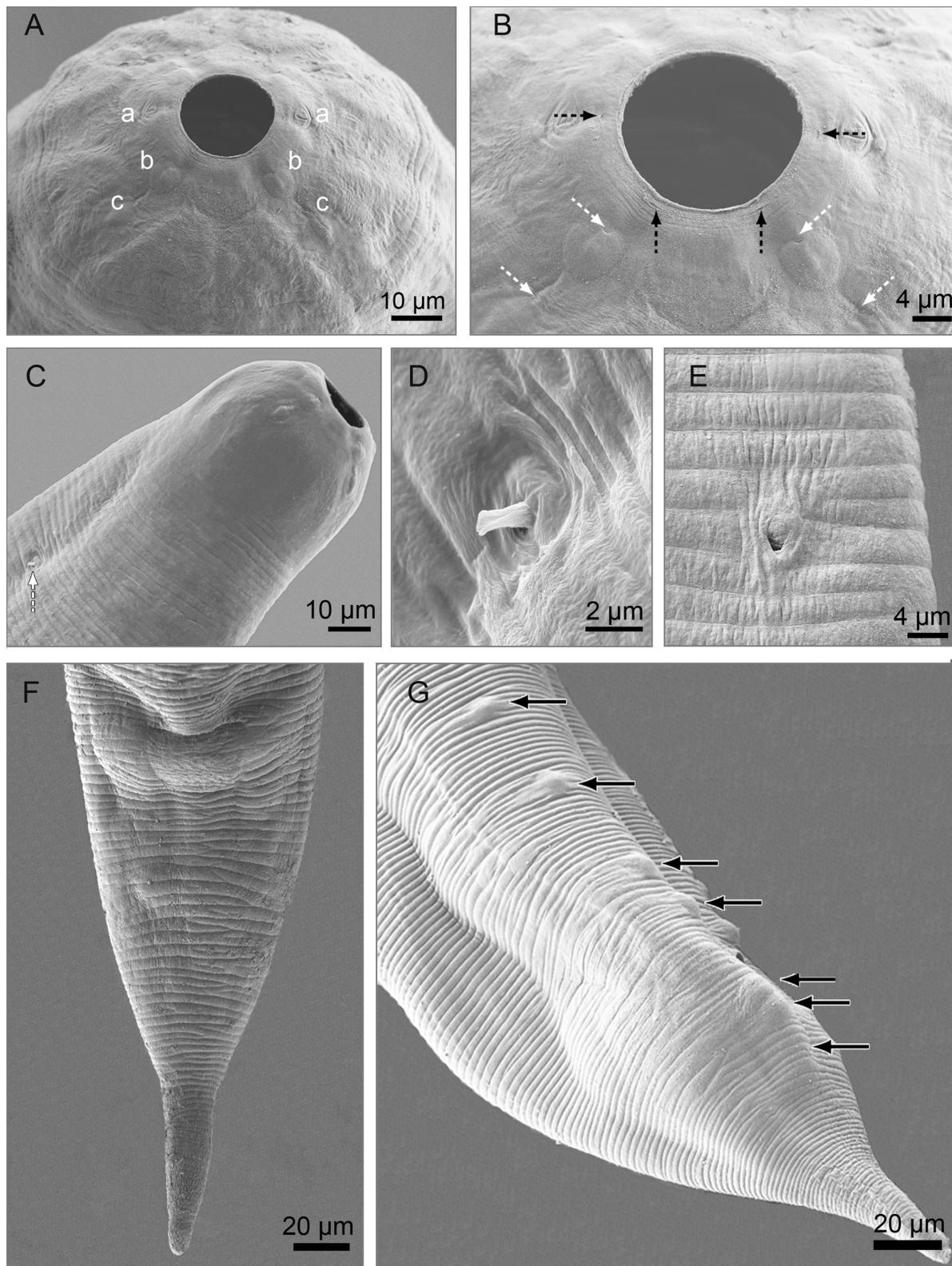


Fig. 2 *Procamallanus (Spirocammallanus) pintoi* (Kohn & Fernandes, 1988), scanning electron micrographs. **A** – cephalic end of male, subapical view. **B** – detail of pores in the cephalic end of male, subapical view (black dotted arrows indicate pores surrounding the oral opening, white dotted arrows indicate cephalic papillae accompanied by a proximal pore). **C** – anterior end of female, sublateral view (dotted arrow indicates deirid). **D** – Deirid. **E** – Excretory pore. **F** – posterior end of female, ventral view. **G** – posterior end of male, ventrolateral view (black arrows indicate caudal papillae). Abbreviations: **a** – amphid; **b** – cephalic papillae of inner circlet; **c** – cephalic papillae of outer circlet

dorsal tooth. Oesophagus cylindrical and not divided in muscular and glandular portions 0.10–0.12 long. Intestine simple. Tail long with a terminal spike 0.05–0.08 long (Fig 1 G).

Taxonomic summary

Hosts: *Corydoras paleatus* (type host) (IBIGEO-I # 458–459) and *C. micracanthus* (IBIGEO-I # 460–461) (both Callichthyidae, Siluriformes, Osteichthyes.).

Site of infection: Intestine.

Localities: *Corydoras paleatus* from Arias-Arenales River (24°48'27.73"S; 65°25'56.03"W) and Arias River (24°47'41.65"S; 65°28'0.72"W), and *C. micracanthus* from Yacones River (24°40'15.79"S; 65°24'8.96"W) and Lesser River (24°39'43.56"S; 65°28'49.079"W), province of Salta, Argentina.

Prevalence: *C. paleatus*, 46% (16 fish infected/35 fish examined) from Arias-Arenales River and 44% (8/18) from Arias River; *C. micracanthus*, 90% (9/10) from Yacones River and 71% (5/7) from Lesser River.

Mean intensity (range): *C. paleatus* 1.4 (1–4) nematodes per fish from Arias-Arenales River and 1.1 (1–2) from Arias River; *C. micracanthus* 1.8 (1–3) from Yacones River and 1.2 (1–2) from Lesser River.

Specimens deposited: voucher specimens (one female and one male) deposited in the Colección Helmintológica de Fundación Miguel Lillo (CH-FML # 7739, 7740), San Miguel de Tucumán, Argentina.

Discussion

*Procamallanus (*Spirocammallanus*) *pintoi** was originally described by Kohn and Fernandes (1988) as *Spirocammallanus pintoi* (Kohn et Fernandes, 1988) from *Corydoras paleatus* (Jenyns, 1842) from Iguazú River, Brazil. Later, Moravec *et al.* (1997) studied conspecific young females collected in *C. aeneus* (Gill, 1858) from the Orinoco River basin and provided the first observations of *P. (S.) pintoi* using SEM, however this study was limited to cephalic end; thus some morphological details have been not observed or overlooked by them, and others are still lacking in those micrographs, e.g. the caudal region of males. Moravec *et al.* (1999) also described specimens of *P. (S.) pintoi* collected in *C. reticulatus* Fraser-Brunner, 1938, ornamental freshwater fishes imported from Peru to Germany. The morphology and measurements of present specimens are very similar to the descriptions of Kohn and Fernandes (1988) and Moravec *et al.* (1997; 1999), consequently we consider that these nematodes specimens belong to *P. (S.) pintoi*. Even though, some small morphological and biometric differences were observed, the specific identify was confirmed.

The body length of gravid females from *C. paleatus* and *C. micracanthus*, is almost half of the length reported by Kohn and Fernandes (1988) (Table II). In addition, the males from *C. paleatus* were slightly larger than those of *C. micracanthus* in the present study (Table I). Kohn and Fernandes (1988) re-

ported 9–10 spiral thickenings in the buccal capsule of the gravid females, while those newly-collected from *C. paleatus*, have a lower number of ridges (7–9). Moravec *et al.* (1997) were the only one to report the buccal capsule with a basal ring well developed and 8–12 spiral ridges in young females from *C. aeneus*. Other difference was the glandular oesophagus length between gravid females of *C. micracanthus* and those examined by Kohn and Fernandez (1988) (see Table II). Kohn and Fernandez (1988) reported that the vulva is slightly posterior to middle of body (at 66% of body length); but in some specimens from *C. paleatus* and *C. micracanthus*, the vulva is observed closer to the posterior end (at 66–80% at body length) (Table II).

Moreover, it was observed that male specimens show one more pair of postanal papillae (three pairs in total), different to that observed by Kohn and Fernandez (1988) and Moravec *et al.* (1999). It is more likely that this difference is an intraspecific variation, since male specimens were properly observed and drawn in lateral and ventral views by Moravec *et al.* (1999).

The morphological and morphometric differences observed here could be considered intraspecific variations between different populations of *P. (S.) pintoi*, resulted by different host species and the wide geographical distribution of this nematode. The biometric variations also could be due to the specimens having been treated with different fixing and clearing agents that could influence in length changes (Fagerholm 1979).

In the present study, the light and scanning electron microscopy observations revealed some morphological details previous unreported or poorly described such as the presence and distribution of pores in the cephalic end of both sexes (pores nearby to each of cephalic papillae and additional six pores surrounding the oral opening), the shape of deirids and the accurate morphology of vulva. Even though previous authors (Kohn and Fernandes 1988; Moravec *et al.* 1997; 1999) reported the relative position of deirids and the vulva, they did not described the morphology of these structures.

Regarding host spectrum, *Procamallanus (*Spirocammallanus*) pintoi* seen to be specific from freshwater fishes belonging to the genus *Corydoras* Lacépède, 1803; since it has been widely reported in *C. aeneus*, *C. metae* Eigenmann, 1914, *C. paleatus* and *C. reticulatus* from Venezuela, Colombia, Brazil and Argentina, and Peru, respectively; (Kohn and Fernandes 1988; Moravec *et al.* 1997, 1999; Ito *et al.* 2005; Santana-Piñeros *et al.* 2017). Nevertheless, this species was recorded as well in *T. spegazzinii*, (Trichomycteridae).

To date, 30 valid species of *Procamallanus* were described from Neotropical freshwater fishes; between these it is possibly distinguished a morphological group characterized by the lack of caudal alae, and having short and similar spicules in males, represented by *P. (S.) belenensis* Giese, Santos et Landolfi, 2009, *P. (S.) chimusensis* (Freitas et Ibañez, 1968), *P. (S.) hilarii* Vaz et Pereira, 1934, *P. (S.) huacraensis* Ramallo, 2008; *P. (S.) inopinatus* Travassos, Artigas et Pereira, 1928, *P. (S.)*

krameri (Petter, 1974), *P. (S.) neocaballeroi* (Caballero-De-loya, 1977), *P. (S.) paraensis* Pinto et Noronha, 1976, *P. (S.) pintoi* and *P. (S.) saofranciscencis* (Moreira, Oliveira et Costas, 1944) (Moravec 1998; Moravec et al. 2004; Ramallo 2008; Giese et al. 2009). Based on the postequatorial position of the vulva and the spiral thickenings limited to two thirds of the buccal capsule in males and females, *P. (S.) pintoi* resembles *P. (S.) belenensis*, *P. (S.) inopinatus* and *P. (S.) saofranciscencis*; but differ in the number of ridges (6–9 vs. 8–13, 8–18 and 11–17, respectively) and pairs of postanal papillae (3 vs. 4–5, 6 and 6 pairs, respectively). Moreover, *P. (S.) belenensis* is the only with two small spike-like projections in the caudal tip of males (Giese et al. 2009).

The present study increased the knowledge on the morphology of *P. (S.) pintoi*, mainly regarding details of the cephalic end of both sexes and the caudal region of males; moreover it is the first record of *P. (S.) pintoi* from *Corydoras micracanthus* from Bermejo River basin (Northwest Argentina). Further studies approaching molecular and morphological data will be useful for revealing population patterns and the phylogenetic relationships of *P. (S.) pintoi* with other congeneric species. The features that differentiate *P. (S.) pintoi* from other species of same subgenus, which are parasitic in Neotropical freshwater fishes, are apparent from the following key.

Key to *Procamallanus (Spirocammallanus)* spp. parasitic in Neotropical freshwater fishes

1. Males with 7 pairs of preanal papillae or more pairs 2
– Males with at most 4 pairs of preanal papillae 4
2. Preanal papillae seven pairs. Spicules short, equal, 0.070–0.090 mm long. Caudal alae absent. Buccal capsule wit 14–16 spiral thickenings in both sexes. Parasitic in Erythrinidae (Characiformes) from Brazil
..... *P. (S.) paraensis* Pinto et Noronha, 1976
- Preanal papillae 8–10 pairs. Spicules large, unequal. Narrow caudal alae present. Buccal capsule with 3–9 spiral thickenings 3
3. Buccal capsule dissimilar in males and females: male with 7–9 spiral thickenings, female capsule with 3–4 spiral thickenings appearing in the optical section to form several anteriorly oriented teeth. Large spicule 0.440–0.550 mm long, small spicule 0.230–0.240 mm long. Recorded in Characiformes and Siluriformes from Brazil and Venezuela
..... *P. (S.) iheringi* Travassos, Artigas et Pereira, 1928
- Buccal capsule of both sexes with 6–8 spiral thickenings. Large spicule 0.440–0.550 mm, small spicule 0.240–0.270 mm long. Parasitic in Anostomidae (Characiformes) from Brazil
..... *P. (S.) amarali* Vaz et Pereira, 1934
4. Males with broad caudal alae present 5
– Males with caudal alae absent or poorly developed 17
5. Buccal capsule with 3–4 spiral thickenings. Four pairs of preanal papillae. Large spicule 0.400–0.640 mm, with ventral outgrowth on distal end, small spicule 0.170–0.280 mm.
Parasitic mainly in Siluriformes, also in Characiformes and Perciformes from Argentina, Brazil, Paraguay and Peru
..... *P. (S.) rarus* Travassos, Artigas et Pereira, 1928
- Buccal capsule with numerous spiral thickenings. Three, exceptionally two pairs of preanal papillae 6
6. Two pairs of preanal papillae. Buccal capsule with 12–17 spiral thickenings. Large spicule 0.430–0.450 mm, small spicule 0.210–0.220 mm. Female with terminal spike, males with terminal digitiform process. Recorded in Siluriformes from Brazil
..... *P. (S.) solani* Pinto, Fabio, Noronha et Rolas, 1975
- Three pairs of preanal papillae. Number of spiral thickenings may be different 7
7. Cervical alae present. Buccal capsule with 9–14 spiral thickenings. Large spicule 0.180–0.200 mm, small spicule 0.150–0.160 mm. Parasitic in Loricariidae (Siluriformes) from Paraguay
..... *P. (S.) cervicalatus* (Petter, 1990)
- Cervical alae absent. Number of spiral thickenings may be different 8
8. Spicules dissimilar and equal to subequal in length, right spicule 0.251–0.325 mm long, small spicule 0.227–0.317 mm long. Buccal capsule wit 12–20 spiral thickenings. Female tail ending in small terminal cuticular spike with finger-like digit. Parasitic in Auchenipteridae (Siluriformes) from Colombia
..... *P. (S.) penneri* (Fusco et Brooks, 1978)
- Spicules unequal in length 9
9. Spicules short and unequal; large spicule 0.100–0.150 mm long, small spicule 0.045–0.070 mm long. Buccal capsule with 18–19 spiral thickenings. Female tail with terminal digitiform appendix 0.060–0.100 mm long. Recorded in Characiformes from Paraguay
..... *P. (S.) paraguayensis* (Petter, 1990)
- Spicules much longer, large spicule not less than 0.300 mm long, small spicule not less than 0.150 mm long 10
10. Tail tip with cuticular spikes 11
- Tail tip simple, without a few cuticular spikes 15
11. Three pairs of postanal papillae. Spicules unequal, large spicule 0.750–0.800 mm long, small spicule 0.260–0.280 mm long. Buccal capsule with 5–7 spiral thickenings occupying whole inner surface of buccal capsule. Parasitic in Siluriformes from Argentina
..... *P. (S.) juana* Ramallo et Ailán-Choke, 2017
- Six pairs of postanal papillae, and additional two pairs of small sessile ventral papillae surrounding cloacal opening. Spiral thickenings more numerous 12
12. Vulva posequatorial. Buccal capsule with 14–18 spiral thickenings. Spicules similar shape and unequal in length, large spicule 0.480–0.525 mm long, small spicule 0.261–0.315 mm long. Parasitic in Cichlidae (Perciformes) from Mexico
..... *P. (S.) rebecae* (Andrade-Salas, Pineda-López et García-Magaña, 1994)
- Vulva preequatorial. Number of spiral thickening may be different 13
13. Buccal capsule with 8–10 spiral thickenings. Large spicule 0.318–0.348 mm long, small spicule 0.156–0.192 mm

- long. Dorsal wall of cloaca forming small sclerotized gubernaculum formation. Tail tip of both sexes with minutes cuticular spikes. Parasitic in Eleotridae (Perciformes) from Mexico..... *P. (S.) gobiomori* Moravec, Salgado-Maldonado et Caspeta-Mandujano, 2000
- Number of spiral thickenings more numerous. Gubernaculum absent 14
14. Buccal capsule with 15–16 spiral thickenings. Large spicule 0.606–0.900 mm long, small spicule 0.282–0.354 mm long. Tail tip of both sexes with minutes cuticular spikes. Parasitic in Mugilidae (Mugiliformes) from Mexico..... *P. (S.) jaliscensis* Moravec, Salgado-Maldonado et Caspeta-Mandujano, 2000
- Buccal capsule with 10–12 spiral thickenings. Large spicule 0.480 mm long, small spicule 0.231 mm. Tail tip of males with a terminal spike, females tail conical without any terminal spike. Parasitic in Cichlidae (Perciformes) from Mexico *P. (S.) mexicanus* Moravec, Salgado-Maldonado et Caspeta-Mandujano, 2000
15. Buccal capsule with 17–19 spiral thickenings. Large spicule 0.465–0.534 mm long, small spicule 0.172–0.214 mm long. Female tail with a terminal conical appendix. Recorded in Siluriformes from Brazil *P. (S.) freitasi* (Moreira, Oliveira et Costa, 1991)
- Buccal capsule with at most 15 spiral thickenings. Spicules longer, large spicule exceeding 0.700 mm long 16
16. Buccal capsule 7–9 spiral thickenings. Large spicule 0.705–0.804 mm long, small spicule 0.258–0.315 mm long. Female tail conical, with narrow rounded tip. Parasitic in Pimelodidae (Siluriformes) from Brazil *P. (S.) pimelodus* Pinto, Fabio, Noronha et Rolas, 1974
- Buccal capsule with 9–12 spiral thickenings. Large spicules 0.730 mm long, small spicules 0.280 mm long. Female tail rounded, with small terminal digitiform process. Parasitic in Mugilidae (Mugiliformes) from Lesser Antilles *P. (S.) dessetae* (Petter, Golvan et Tcheprakoff, 1977)
17. Males with 6 pairs of caudal papillae: 3 pairs preanal and 3 pairs postanal. Buccal capsule with 20 spiral thickenings. Large spicule 0.060 mm, small spicule 0.050 mm. Parasitic in Clupeidae (Clupeiformes) from Brazil *P. (S.) barroslimai* Pereira, 1935
- Males with more pairs of caudal papillae or differently arranged. The number of spiral thickenings may be different 18
18. Buccal capsule dissimilar in males and females 19
- Buccal capsule of similar shape in both sexes 21
19. Spiral thickenings absent from anterior third to half of buccal capsule in males, but covering whole capsule in females; spiral thickenings 10–12 in males and 14–15 in females. Spicules subequal, right spicule 0.075–0.087 mm long, small spicule 0.072–0.087 mm long. Parasitic in Characidae (Characiformes) from French Guiana and Venezuela *P. (S.) krameri* (Petter, 1974)
- Spiral thickenings occupying whole inner surface of buccal capsule with sharply pointed anteriorly oriented teeth in its basal and middle regions of females capsule. Four pairs of preanal papillae. Spicules short and equal 20
20. Spiral thickenings in buccal capsule 4–10 (9–10 in males, 4 in females). Four pairs of postanal papillae. Spicules short, equal 0.144–0.183 mm long. Vulva slightly pre-equatorial. Parasitic in Trichomycteridae (Siluriformes) from Colombia and Peru *P. (S.) chimusensis* (Freitas et Ibañez, 1968)
- Buccal capsule with 3–4 spiral thickenings. Two pairs of postanal papillae. Spicules equal 0.180–0.190 mm long. Vulva postequatorial. Parasitic in Trichomycteridae (Siluriformes) from Argentina *P. (S.) huacraensis* Ramallo, 2008
21. Spiral thickenings occupying whole inner surface of buccal capsule in both sexes 22
- Spiral thickenings occupying about two posterior thirds of buccal capsule 23
22. Males with 3 pairs of preanal, 1–2 pairs of adanal and 3 pairs of postanal papillae. Buccal capsule with 13–18 spiral thickenings. Large spicule 0.070–0.082 mm long, small spicule 0.050–0.062 mm long. Recorded in Characiformes and Siluriformes from Argentina, Brazil and Peru *P. (S.) hilarii* Vaz et Pereira, 1934
- Male with 4 pairs of preanal and 6 pairs of postanal papillae. Buccal capsule with 15–19 spiral thickenings. Spicules equal, 0.065–0.078 mm long. Parasitic mainly in Characiformes from Mexico *P. (S.) neocaballeroi* (Caballero-Deloya, 1977)
23. Males with 3 pairs of preanal papillae. Buccal capsule with 8–13 spiral thickenings. Spicules short and subequal, large spicule 0.058–0.080 mm long, small spicule 0.050–0.075 mm long. Tail tip of males with two small spike-like projections. Parasitic in Auchenipteridae (Siluriformes) from Brazil *P. (S.) belenensis* Giese, Santos et Lanfredi, 2009
- Males with four pairs of preanal papillae. Number of spiral thickenings may be different. Tail tip without any cuticular spikes 24
24. Buccal capsule with 6–10 spiral thickenings. Postanal papillae 2–3. Spicules subequal, large spicule 0.070–0.150 mm long, small spicule 0.060–0.110 mm long. Parasitic mainly in Callichthyidae (Siluriformes) from Argentina, Brazil, Colombia, Peru and Venezuela *P. (S.) pintoi* (Kohn et Fernandes, 1988)
- Buccal capsule with 8–20 spiral thickenings. Six pairs of postanal papillae 25
25. Buccal capsule with 11–17 spiral thickenings, three large conical teeth at bottom. Mouth with 4 (2 dorsal and 2 subventral) retractile teeth. Posterior part of female tail narrowed to form rather long digitiform appendix. Large spicule 0.083–0.095 mm long, small spicule 0.071–0.083 mm long. Parasitic in Characidae (Characiformes) from Brazil *P. (S.) saofranciscensis* (Moreira, Oliveira et Costas, 1944)

- Buccal capsule with 8–20 spiral thickenings, without conspicuous teeth at bottom. Mouth with 2 retractile (dorsal and ventral) teeth. Female tail without distinct terminal appendix. Spicules equal 0.075–0.135mm long. Parasitic in Characiformes, Siluriformes and Perciformes from Argentina, Brazil, Paraguay and Venezuela
..... *P. (S.) inopinatus* Travassos, Artigas et Pereira, 1928

Acknowledgments. The authors wish to thanks to the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET, Argentina) and the Consejo de Investigación de la Universidad Nacional de Salta (CIUNSA, Argentina) for providing financial support; and the Secretaría de Medio Ambiente del Gobierno de la Provincia de Salta for allowing us to make the collection of ichthyologic materials. We are grateful to Daniel Paredes, Florencia Liquín, José Saravia and Federico Soria, for their assistance in the capture of hosts; Fabiana Cancino and Roberto Sánchez for their help with the identification of fishes, Pablo Pereira and José Saravia for help with the digitalization of figures and Nathalia Arredondo for her useful suggestions. We would also like to thank Luciano Martínez and Hernán Esquivel with the staff of the Laboratory of Scanning Electron Microscopy (CIME) (Tucumán, Argentina), for their technical assistance and to the anonymous reviewers for their valuable comments and suggestions.

References

- Ailán-Choke L., Ramallo G., Nieva L., Davies, D. 2014. Nuevos registros de helmintos parásitos en dos especies de peces fluviales, provincia de Salta, Argentina. *Acta Zoológica Lilloana*, 58, 251–255. DOI: 10.15560/10.3.597
- Bush A.O., Lafferty K.D., Lotz J.M., Shostak A.W. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology*, 83, 575–583. DOI: 10.2307/3284227
- Fagerholm P. 1979. Nematode length and preservatives, with a method for determining the length of living specimens. *Journal of Parasitology*, 65, 331–335. DOI: 10.2307/3280182
- Giese E.G., Santos J.N., Lanfredi R.M. 2009. A new species of Camallanidae from *Ageneiosus ucayalensis* (Pisces: Siluriformes) from Pará State, Brazil. *Journal of Parasitology*, 95, 407–412. DOI: 10.1645/ge-1680.1
- Ito K.F., Moreira S.T., Massato Takemoto R., Pavanello G.C. 2005. Ecological aspects of the *Procamallanus (Spirocammallanus) pintoi* parasite of *Corydoras paleatus* (Jenyns, 1842) (Siluriformes: Callichthyidae) in reservoirs of the State of Paraná, Brazil. *Acta Scientiarum Biological Sciences*, 27, 239–242
- Kohn A., Fernandes B.M.M. 1988. Helminth parasites from the hydroelectric power station of Electrosul (Brazil). I- *Procamallanus petterae* n. sp. and *Spirocammallanus pintoi* n. sp. (Nematoda, Camallanidae) from the reservoir of "Salto Ossorio". *Memórias do Instituto Oswaldo Cruz*, 83, 293–298
- Moravec F. 1998. Nematodes of freshwater fishes of the Neotropical Region. Academia, Praha, pp. 464
- Moravec F., Chara J., Shinn A.P. 2004. Two nematodes, *Dentinema trichomycteri* n. g., n. sp. (Cosmocercidae) and *Procamallanus chimusensis* Freitas & Ibáñez, 1968 (Camallanidae), from catfishes *Trichomycterus* spp. (Pisces) in Colombia. *Systematic Parasitology*, 59, 189–197. DOI:10.1023/b:syap.000048098.80098.26
- Moravec F., Prouza A., Royero R. 1997. Some nematodes of freshwater fishes in Venezuela. *Folia Parasitologica*, 44, 33–47
- Moravec F., Salgado-Maldonado G., Caspetá-Mandujano J. 2000. Three new *Procamallanus (Spirocammallanus)* species from freshwater fishes in Mexico. *Journal of Parasitology*, 86, 119–127. DOI: 10.2307/3284921
- Moravec F., Wolter J., Korting W. 1999. Some nematodes and acanthocephalans from exotic ornamental freshwater fishes imported into Germany. *Folia Parasitologica*, 46, 296–310
- Ramallo G. 2008. Nueva especie de *Procamallanus (Spirocammallanus)* (Nematoda, Camallanidae), parásito de *Trichomycterus corduvensis* (Siluriformes: Trichomycteridae), en el Norte de Argentina. *Acta Zoologica Lilloana*, 52, 25–29. DOI: 10.1515/ap-2015-0032
- Ramallo G. 2011. New species of *Procamallanus (Denticamallanus)* (Nematoda: Camallanidae) in *Thoracocharax stellatus* (Pisces: Gasteropelecidae) from Argentina. *Munis Entomology & Zoology Journal*, 6, 301–305
- Ramallo G., Ailán-Choke L.G. 2017. Observations on two *Procamallanus (Spirocammallanus)* species (Nematoda: Camallanidae) from freshwater fishes in Argentina, including description of *Procamallanus (Spirocammallanus) juana* sp. nov. *Zootaxa*, 4323, 286–294. DOI: 10.11646/zootaxa.4323.2.12
- Santana-Piñeros A.M., Cruz-Quintana Y., Castillo Olaya V. 2017. Infection parameters of *Procamallanus (Spirocammallanus) cf. pintoi* in *Corydoras metae* from Villavicencio, Colombia. *La técnica: Revista de las Agrociencias*, 18:49–57

Received: February 13, 2018

Revised: May 2, 2018

Accepted for publication: May 4, 2018