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http://doi.org/10.11646/zootaxa.4168.1.8 http://zoobank.org/urn:lsid:zoobank.org:pub:C4A37ED0-54C8-4279-8C8F-4CE71B85703B

First record of Viannaiidae (Nematoda: Trichostrongylina) in fossorial rodents (*Ctenomys* spp.) from Central Argentina, with description of a new genus and species

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Abstract

A new genus and species of Viannaiidae (Trichostrongylina, Heligmosomoidea), *Ischilinema baldoi* **n. gen. et sp.** is described parasitizing two species of tuco-tucos, *Ctenomys bergi* and *Ctenomys rosendopascuali* (Rodentia, Hystricomorpha, Ctenomyidae) from Córdoba province, Central Argentina. No helminths were previously known from these two host species. The new genus is defined by the following characters: synlophe with 15 continuous ridges subequal in size, presence of left cuticular dilatation, a gap between ridges 1' and 2', bursa asymmetrical with dorsal ray hypertrophied and displaced to the right, and spicules not twisted. This is the first record of Viannaiidae from the Ctenomyidae, enlarging the host range of these parasites to five out of the 12 extant families of caviomorphs.

Key words: Nematoda, Heligmosomoidea, *Ischilinema baldoi* n. gen. et sp., synlophe, asymmetrical bursa, *Ctenomys bergi, Ctenomys rosendopascuali*, Argentina

Introduction

The genus *Ctenomys* Blainville, 1826 (Rodentia: Ctenomyidae), includes the fossorial rodents known as tucotucos, which are distributed in southern South America from the Peruvian Altiplano, beneath 10°S to Tierra del Fuego, with representatives in Bolivia, Chile, Argentina, Paraguay, Uruguay and SE Brazil (Bidau 2006). The genus comprises 60 recognized species originated by an explosive speciation process promoted mainly by chromosomal rearrangements (Bidau *et al.* 1996); most of these species (42) are found in Argentina (Bidau 2006, Woods & Kilpatrick 2005).

Several species of *Ctenomys* have been subjects of intense research in numerous aspects of morphology, phylogeny, biogeography, physiology, ethology, genetics and genomics (see Vassallo & Antenucci 2015). However, relatively few species have been subjects of endoparasitological studies. In Argentina, species whose endoparasitic fauna have been more or less well studied are *Ctenomys talarum* Thomas (seven reports), *Ctenomys australis* Rusconi (three reports), and *Ctenomys azarae* Thomas (one report). From these hosts, which are mainly distributed in the provinces of Buenos Aires and La Pampa, six species of nematodes have been described: *Trichuris pampeana* Suriano & Navone, 1994 (Trichuridae) in *C. azarae, C. australis* and *C. talarum; Graphidioides subterraneus* Rossin, Timi & Malizia, 2005 (Trichostrongylidae) in *C. talarum; Pudica ctenomydis* Rossin, Timi & Malizia, 2006 (Heligmonellidae) in *C. talarum* and *C. australis; Paraspidodera uncinata* Rudolphi, 1819 (Aspidoderidae) in *C. talarum; Trichostrongylus duretteae* Rossin, Timi & Malizia, 2006 (Trichostrongylidae) in *C. talarum; Strongyloides myopotami* Artigas & Pacheco, 1933 (Strongyloidiae) in *C. talarum*, and one metacestode, identified as *Taenia talicei* Dollfus, 1960 (Taeniidae) in *C. australis* and *C. talarum* (Suriano & Navone 1994, Rossin & Malizia 2005, Rossin *et al.* 2004, 2005, 2006a, 2006b, 2009, 2010a, 2010b). Outside of Argentina, there are the reports of *Trichuris fulvi* Babero & Murúa, 1987 and *Trichuris robusti* Babero & Murúa, 1990 both in *Ctenomys fulvus* Philippi from Chile; *P. uncinata* and *S. myopotami* in *Ctenomys torquatus*

Lichtenstein and *Ctenomys pearsoni* Lessa & Langguth, respectively, both from Uruguay, and *P. uncinata* in *Ctenomys opimus* Wagner from Bolivia (Babero & Murúa 1987, 1990, and see Rossin *et al.* 2004, 2009).

We had the opportunity of examining the viscera of several *Ctenomys* spp. from different populations in the province of Córdoba (Central Argentina). Tuco-tucos of two species were found parasitized with an undescribed species of Viannaiidae (Trichostrongylina, Heligmosomoidea), a species which, in addition, could not be assigned to any known genus in the family. A new genus and species is then proposed for these specimens. The new taxon is described and discussed herein.

Materials and methods

The viscera of ten tuco-tucos, three *Ctenomys bergi* Thomas, 1902 and seven *Ctenomys rosendopascuali* Contreras, 1995, captured in different localities in the North of Córdoba province, Argentina, between March and May, 1996, were sent to the División Zoología Invertebrados of the Museo de La Plata (La Plata, Argentina), where they were examined for helminths by about 1999. The hosts had been captured in the course of a study on the allozymic polymorphism of two populations assigned to these two species (Bortoluzzi *et al.* 2001). Necropsies yielded several specimens of nematodes, which were fixed, stored in 70% ethanol, and deposited in the Helminthological Collection of the Museo de La Plata (MLP-He) where they remained unidentified until about 2015.

The synlophe was studied following Durette-Desset (1985) and the nomenclature referring to the axis of orientation follows Durette-Desset & Digiani (2005). Ridges are numbered from left to right, from 1 to *n* for dorsal ridges and from 1' to *n*' for ventral ridges. Ridges are considered as dorsal or ventral with respect to the axis of orientation and not in relation to the lateral hypodermal cords. The nomenclature used for the study of the caudal bursa (pattern of lateral lobes and symmetry) follows Durette-Desset & Digiani (2012). Measurements are provided in micrometres, except otherwise stated. SpL/BL and UtL/BL mean the proportion of the spicule length to the body length and of the uterus length to the body length, respectively. Type and voucher specimens of parasites are deposited in the Helminthological Collection of the Museo de La Plata (MLP-He), La Plata, Argentina. Voucher specimens of hosts are deposited in the Museo de Zoología de la Universidad de Córdoba (MZUC), Córdoba, Argentina. The nomenclature for parasites above the family group follows Durette-Desset & Chabaud (1993) and that of the hosts follows Woods & Kilpatrick (2005) at the family level and Bidau (2006) at the species level.

Results

Ischilinema gen. n.

Definition: Trichostrongylina: Heligmosomoidea: Viannaiidae: Viannaiinae. Synlophe with 14–15 uninterrupted ridges, subqual in size. Gap free of ridges on left side between ridges 1' and 2'. Caudal bursa asymmetrical, with right lobe more developed and dorsal ray thick and displaced towards right lobe. Bursal pattern of type 1–4 on right lobe, atypical 1-1-3 on left lobe. Spicules long, not twisted, with no marked differentiation of handle and lamina, ending in simple, rounded tips. Spicular alae visible. Parasites of Ctenomyidae (Rodentia, Hystricomorpha).

Type and sole species: Ischilinema baldoi gen. n. sp. n.

Hosts: Ctenomyidae (Rodentia).

Host site: Small intestine.

Etymology: From "Ischilín", the administrative department of Córdoba province to which the type locality belongs.

Ischilinema baldoi gen. n. sp. n.

(Figs. 1-14)

Description. General: Small nematodes, mostly uncoiled. Excretory pore situated slightly before or behind

oesophago-intestinal junction in males (84–106% of oesophagus length), more proximally in females (mostly within 71–93% of oesophagus length). Deirids minute, hardly visible, situated at level of excretory pore (Fig. 1).

Head: Cephalic vesicle present. In apical view, triangular buccal opening with rounded corners, surrounded by thick ring. Six externo-labial and four submedian cephalic papillae visible (Fig. 2).

Synlophe: (studied in 2 males and 2 females). In both sexes cuticle bearing longitudinal, uninterrupted ridges appearing posterior to cephalic vesicle. Number of ridges at oesophago-intestinal junction: 14 in male, 15 in female (Figs. 3, 4); at mid-body and posterior third of body: 14–15 in male, 15 in female (Figs. 5, 6). Size of ridges: at mid-body, ridges small, subequal, with those on left-ventral quadrant slightly larger, gradient in ridge size absent. Ridges with cuticular struts, oriented from right-ventral to left-dorsal quadrant. Axis of orientation of ridges single, inclined at about 65–70° in both sexes, determining two groups of 7–8 dorsal ridges and 7 ventral ones. On left side, presence of a cuticular dilatation supported by 3–4 ridges, cuticle between ridges 1' and 2' reinforced. Ridges small and subequal in size, mostly perpendicular to body surface; left dilatation supported by 5 ridges. Ridges supporting dilatation more spaced to each other than the other ridges (Figs. 7, 8, 9). Disappearance of ridges at about 100 mm before caudal bursa in males (Fig. 10), at ovejector level in females.

Males (n= 19 except where indicated) (syntypes from *Ctenomys bergi*): 2.00–2.95 (2.54) mm long and 50–90 (66) wide at mid-body. Cephalic vesicle 28–45 (36) long and 18–28 (22) wide. Nerve ring, excretory pore and deirids situated at 100–150 (128) (n=11), 215–260 (234) (n=5) and 240–255 (248) (n=2) from apex, respectively. Oesophagus 220–260 (238) long.

Caudal bursa asymmetrical. Right lobe more developed than left one (Fig. 11). Right lobe with pattern of type 1–4, with right ray 2 arising first from the common trunk of rays 2–6. Ray 3 thicker and longer than ray 2, both supporting ventral margin of lobe. Common trunk of rays 4–6 long, rays 6 diverging first, rays 4 and 5 apposed up to extremities (Figs. 11, 12). Left lobe with atypical pattern of type 1-1-3, with rays 2 and 3 of similar size, short and arising separately on the common trunk of rays 2–6. Thick common trunk of rays 4–6, supporting left-dorsal angle of the bursa. Left rays 4–6 small, diverging distally from common trunk (Figs. 11, 12). Dorsal lobe short. Dorsal ray thick and displaced towards right lobe. Branches of dorsal ray dissymmetrical, well separated, arising just posterior to arising of rays 8, left branch arising proximally. Each branch divided into two sub-branches, bearing papillae 9 (external) and 10 (internal). Rays 8 of similar length, arising dissymmetrically from dorsal ray, left ray 8 arising proximally. Both rays 8 reaching bursal margin (Fig. 11). Spicules subequal, alate, not twisted, 215–320 (268) long, ending each in a rounded tip, enclosed in a membrane. SpL/BL 9.2–12.2 (10.6)%. Spicular alae visible (Fig. 13). Gubernaculum not observed. Genital cone inconspicuous, not measured, papillae on genital cone not observed.

Females (n= 10 except where indicated) (syntypes from *Ctenomys bergi*): 2.66–4.15 (3.59) mm long and 70–100 (84) wide at mid-body. Cephalic vesicle 22–46 (38) long and 20–40 (24) wide. Nerve ring, excretory pore and deirids situated at 100–140 (118), 200–266 (219) (n=4) and 243 (n=1) from apex, respectively. Oesophagus 200–275 (234) long. Monodelphic. Vulva situated at 58–80 (66) from caudal extremity (n=8). Vagina vera 9–12 (11) long (n=7), vestibule 50–85 (67) (n=8), sphincter 20–27 (24) long and 23–37 (30) wide, infundibulum 75–120 (92). Uterus 650–1240 (965) long, containing 10–16 (14) eggs, 55–75 long and 32–42 wide. UtL/BL 20.2–31.6% (26.5%). Tail conical, 25–45 (33) long (Fig. 14).

Type-host. Ctenomys bergi Thomas, 1902 (Rodentia, Hystricomorpha, Ctenomyidae), MZUC 100436.

Type-locality. Las Toscas, Salinas Grandes, Departamento Ischilín, Córdoba, Argentina (30°09'23.75"S-64°55'36.24"W).

Prevalence and intensity of infection. 2 out of 3 hosts examined (P=66.6%) were parasitized with 218 and 8 worms, respectively.

Type material. 29 syntypes (19 males, 10 females) MLP-He 3504-1.

Other material studied. 1 male, 1 female MLP-He 3503-1 (same host species and locality, host not deposited).

Etymology. the species is dedicated to Mgr. Jorge Baldo (VICAM -CONICET) who captured and identified the hosts.

Other hosts and or localities. *Ctenomys rosendopascuali* Contreras, 1995 (Rodentia, Ctenomyidae). Xanaes River mouth, Mar Chiquita (30°57'15.91"S–62°43'44.60"W), and lands of Milanesio family, Miramar (30°55'51.34"S–62°41'53.42"W), both in Departamento San Justo, Córdoba, Argentina.



FIGURES 1–10. *Ischilinema baldoi* **gen. n. sp. n.** 1, female, anterior extremity, right lateral view. 2, female, head, apical view. 3-11, synlophe in transverse sections of the body: 3, 4, at oesophago-intestinal junction, 3, male, 4, female; 5-6, at mid-body, 5, male, 6, female; 7-10, within distal third of body length, 7, male at 500 μ before caudal bursa, 8, female at 500 μ from posterior extremity, 9, male at beginning of spicules, 10, male, at 100 μ before caudal bursa. Abbreviations: R, right, V, ventral. All sections oriented as in Figure 3.



FIGURES 11–14. *Ischilinema baldoi* gen. n. sp. n. 11–12, male, caudal bursa, 11, bursa spread out, ventral view, 12, bursa folded, left lateral view, right branch of dorsal ray omitted. 13, male, spicules in situ, showing spicular alae. 14, female, posterior extremity, left lateral view. Abbreviations: 2r-8r, right rays 2 to 8; 21-81: left rays 2 to 8.

Site. Small intestine, secondarily in large intestine.

Prevalence and intensity of infection. 3 out of 7 *C. rosendopascuali* examined (P=42.8%) were parasitized with 3–65 (MI=26.6) worms, respectively.

Material deposited. 1 male, 2 females MLP-He 3498-1 (host MZUC 100430), 1 male, 11 females MLP-He 3501 (host MZUC 100434), 18 males, 47 females MLP-He 3505 (host not deposited).

Measurements of 10 (except where indicated) males from *C. rosendopascuali.* 1.80–2.50 (2.16) mm long and 55–70 (59) wide at mid-body. Cephalic vesicle 26–45 (36) long and 20–35 (26) wide. Nerve ring, excretory pore and deirids situated at 100–140 (124), 170–250 (206) (n=7) and 210–250 (229) (n=4) from apex, respectively.

Oesophagus 200–240 (218) long. Spicules 230–262 (248) long, SpL/BL 10.4–13.9 (11.5)%. Gubernaculum not observed. Genital cone inconspicuous, not measured, papillae on genital cone not observed.

Measurements of 18 (except where indicated) females from *C. rosendopascuali.* 2.35–3.35 (2.79) mm long and 60–80 (68) wide at mid-body. Cephalic vesicle 30–40 (37) long and 20–33 (26) wide. Nerve ring, excretory pore and deirids situated at 90–145 (114) (n=11), 163–200 (178) (n=7) and 166–200 (180) (n=4) from apex, respectively. Oesophagus 210–240 (226) long (n=11). Vulva situated at 48–57 (54) from caudal extremity (n=10). Vagina vera 7–12 (9) long (n=8), vestibule 50–80 (61) (n=8), sphincter 20–30 (26) long and 25–40 (30) wide (n=9), infundibulum 70–110 (84) (n=7). Uterus 540–860 (689) long, containing 7–17 (13) eggs, 60–85 long and 30–45 wide. UtL/BL 18.3–31.6% (24.5%).Tail 20–30 (24) long.

Differential diagnosis. The presence of a cephalic vesicle and a synlophe with an axis of orientation not bilaterally symmetrical, places these specimens into the superfamily Heligmosomoidea, as redefined by Durette-Desset (1983) and Durette-Desset & Chabaud (1993), which is composed of six families. Among these, the Herpetostrongylidae and the Nicollinidae are readily excluded: both families are characterized morphologically by having well developed buccal capsules and lips; in addition both have fairly restricted host and geographical distributions: saurians, monotremes and marsupials in the Australasian region (Durette-Desset 1985, Beveridge *et al.* 2013). The lack of a spine on the female tail, and the axis of orientation of the ridges oblique and directed from the right-ventral to the left-dorsal quadrant, allow readily excluding the families Heligmosomidae and Ornithostrongylidae, respectively (see Beveridge *et al.* 2013).

The other two families of Heligmosomoidea, i.e. Heligmonellidae and Viannaiidae, are both well represented in South American Hystricognathi rodents (or Caviomorpha). The Heligmonellidae parasitic in caviomorphs belong to two subfamilies, the Heligmonellinae and the Pudicinae. The Heligmonellinae are characterized by synlophes with the left ridge and the right ridge (the single ridges situated just opposite to the lateral cords) distinct and well developed, whereas the Pudicinae possess either a well developed careen (left cuticular dilatation supported by two hypertrophied ridges) or comaretes (large ridges derived from the fusion of two or more ridges) (Beveridge *et al.* 2013). The specimens studied here clearly lack these characters and show ridges which are subequal in size, preventing their inclusion in the Heligmonellidae.

The last family of Heligmosomoidea, the Viannaiidae, is at present composed of seven genera, three of which are parasitic in marsupials and four in caviomorph rodents: *Viannella* Travassos, 1918, *Avellaria* Freitas & Lent, 1934, *Hydrochoerisnema* Arantes & Artigas, 1980 and *Oswaldonema* Travassos, 1927. The main character grouping the Viannaiidae of caviomorphs is the synlophe, which combines ridges subequal in size, an oblique axis of orientation and ridges absent on the lateral sides (Durette-Desset 1971, 1983, Beveridge *et al.* 2013). The synlophe of the present specimens partly conform to this pattern, by having at mid-body an axis of orientation inclined at about 65–70° to the sagittal axis, and a distinct gap free of ridges on the left side, between ridges 1' and 2'. In view of this, we have opted to include these specimens in the family Viannaiidae, though some particular characters of the synlophe and caudal bursa do not allow their inclusion in any of the known genera.

The genus *Viannella* comprises eight species described from five families of caviomorphs and a primate from Brazil and Argentina: *Viannella hydrochoeri* (Travassos, 1914) (type species), *Viannella argentina* Freitas, Lent & Almeida, 1937, *Viannella brevispicula* (Lent & Freitas, 1936), *Viannella dubia* (Travassos, 1921), *Viannella lenti* Durette-Desset, 1968, *Viannella travassossi* Pinto, 1935, *Viannella trichospicula* Durette-Desset, Gonçalves & Pinto, 2006, and *Viannella viscaciae* Goodey, 1925. All these species differ from our specimens mainly by having subsymmetrical bursae with well developed dorsal lobes, spicules short and twisted, and synlophes (known only in 5 species) with ridges in two distinct groups (dorsal and ventral or right-dorsal and left-ventral), more or less separated by left and right gaps (Travassos 1937, Durette-Desset 1971, Durette-Desset *et al.* 2006).

The genus *Avellaria* is composed of two species described from Cuniculidae and Dasyproctidae in Brazil (Freitas & Lent 1934, Durette-Desset *et al.* 2006). They share with our specimens relatively long spicules not twisted, but with synlophes with ridges separated into two distinct groups, like some species of *Viannella*, and subsymmetrical bursae with the dorsal lobe reduced. In addition, species of *Avellaria* are characterized by having didelphic females (Durette-Desset *et al.* 2006), a character which separates them clearly from the specimens studied here.

The monotypic *Hydrochoerisnema anomalobursata* Arantes & Artigas, 1980 is a parasite of capybaras *Hydrochoerus hydrochaeris* (L.) (Caviidae). It is characterized by a bursa with the left lobe strongly chitinized, with rays 3 to 6 appearing as fused, and a synlophe with dorsal and ventral ridges in two distinct groups, separated in the female by two lateral cuticular thickenings without ridges, and in the male only by two lateral gaps (Arantes

& Artigas 1983). These differences in the bursa and the synlophe allow the differentiation of *H. anomalobursata* from the present specimens. The erection of the subfamily Hydrochoerisnematinae to accommodate this single taxon (Arantes & Artigas 1983) seems poorly justified and was contested by Beveridge *et al.* (2013), who also questioned the taxonomic validity of the genus.

The genus Oswaldonema (= Heligmoskrjabinia Freitas & Lent, 1937) is at present composed of two closely related species, Oswaldonema cruzi Travassos, 1927 and Oswaldonema skrjabini (Freitas & Lent, 1937), both coparasitic in Cuniculus paca (L.) (Cuniculidae) from Brazil. Both species share a strong asymmetry of their caudal bursae, involving the lateral lobes, the rays 8 and the dorsal lobe. In both species the right ray 8 appears hypertrophied and displaced to the right whereas the left ray 8 is associated with the left trunk of rays 3-6 rather than with the dorsal lobe. The dorsal lobe, which emerges from the right ray 8, is atypically composed of three branches, all three forked at different levels and bearing papillae whose homologies with papillae 9, 10 and phasmids are not clear. In addition, in both species the pattern on the right lobe is of type 3–2; that on the left lobe being more variable, but with the characteristic of the left ray 8 incorporated into the common trunk of rays 3-6 (Travassos 1937, Freitas & Lent 1937). The asymmetry of the bursa of our specimens, involving mainly the elements of the dorsal lobe, evokes the species of Oswaldonema, however in these latter the dissimilar development of both rays 8 and the arising and position of the dorsal ray are significant differences with respect to these specimens. The pattern of the lateral lobes is also different, with a predominant pattern of type 3-2 on the right lobe in Oswaldonema spp. versus a pattern of type 1-4 in these specimens. Concerning the synlophe, only that of O. skrjabini is known: it shows 9 unequal ridges: three right-dorsal, five mid-ventral, plus one isolated, minute ridge, situated on the left, just above the left lateral field (Durette-Desset & Pinto 1977). We consider these differences in the bursa and the synlophe enough for separating our specimens also from species of Oswaldonema.

The difficulty of assigning these specimens to any of the known genera of Viannaiidae requires the erection of a new genus. We propose for the new taxon the name of *Ischilinema baldoi* gen n. sp. n. A key to the genera of Viannaiidae parasitic in caviomorphs is proposed below.

Key to the genera of Viannaiidae parasitic in caviomorphs

1	Bursa with right ray 8 hypertrophied, left ray 8 incorporated in left trunk of rays 2-6. Dorsal ray tripartite and arising from
	right ray 8. Parasites of Cuniculidae
-	Rays 8 and dorsal ray not as above
2	Bursa asymmetrical, with dorsal ray hypertrophied and displaced rightwards. Right lobe more developed than left one. Syn-
	lophe with gap only on left side, between ridges 1' and 2'. Parasites of Ctenomyidae Ischilinema gen. n.
-	Bursa subsymmetrical or slightly dissymmetrical, dorsal ray not displaced. Synlophe with gaps on both lateral sides, left gap
	between ridges 1 and 1'
3	Left rays 3-6 of bursa fused, with convergent extremities. Parasites of Caviidae, Hydrochoerinae
-	Rays of bursa not fused
4	Dorsal lobe well developed. Spicules twisted. Female monodelphic. Parasites of Caviidae (Caviinae and Hydrochoerinae),
	Dasyproctidae, Chinchillidae
-	Dorsal lobe short. Spicules not twisted. Female didelphic or semi-monodelphic (posterior uterine branch atrophied). Parasites
	of Cuniculidae and Dasyproctidae

Discussion

The new taxon shows, in the synlophe as well as in the caudal bursa, some peculiar characters not observed in other genera of Viannaiidae. Concerning the synlophe, one particular character is the presence of a gap free of ridges only on the left side, between ridges 1'and 2', coincidently with a reinforcement of the cuticle at this level, whereas on the right side, at least at mid-body, there is no special separation between ridges. Comparatively, the synlophe in the other Viannaiidae of caviomorphs is characterized by having two distinct groups of ridges (dorsal/ventral, or right-dorsal/left-ventral), separated by two similar lateral gaps. Depending on the species, the gaps may be relatively short (species of *Avellaria*), or occupy more than 50% of the circumference of the section (*Viannella lenti*, *V. trichospicula*). In the new taxon, only the sections within the posterior part of the body (Figs. 8, 9) show a more or less evident separation of the ridges into two groups, evoking other synlophes of Viannaiidae such as *Avellaria* Durette-Desset, Gonçalves & Pinto, 2006.

The other striking difference compared to the other Viannaiidae of caviomorphs is that in the latter the ridges of the two groups separated by the gaps are oriented in opposite directions, which means that the axis of orientation of the ridges passes through the gaps. On the contrary, in the new taxon the gap appears between two ridges pointing in the same direction (1' and 2'), which means that the axis of orientation of the ridges does not pass through the gap on the left side, but more dorsally.

With respect to the caudal bursa, the majority of species of Viannaiidae show subsymmetrical bursae, with the exception of species of *Oswaldonema*. The differences of these latter with respect to the specimens described were treated in the differential diagnosis of the genus. In the Heligmosomoidea parasitic in rodents, asymmetrical bursae (in the sense of Durette-Desset & Digiani 2012), i. e. bursae where the axis of the dorsal ray does not pass through the sagittal axis of the worm, are found sporadically in all four subfamilies of Heligmonellidae as well as the Viannaiidae. In any case, an asymmetry involving mainly a thickening and displacement of the trunk of the dorsal ray has not been observed previously.

This finding enlarges the known morphological diversity of the Viannaiidae, as well as confirms that the diversity of the Heligmosomoidea parasitizing caviomorphs is far from being well known. This is not surprising, particularly among octodontoids, which represent 75% of the living species of caviomorphs (Ojeda *et al.* 2015), some 190 species, of which barely 20 species have been investigated for endoparasites. This contrasts with the second most speciose groups of caviomorphs, the cavioids, of which more than 60% of the extant species (approximately 20 of 32) have been reported as hosts of helminths.

With respect to the host range, Viannaiidae of caviomorphs have been reported to date from the Caviidae, Dasyproctidae, Cuniculidae (Cavioidea) and Chinchillidae (Chinchilloidea). This report from two species of Ctenomyidae enlarges the host range of these parasites to five out of 12 extant families of caviomorphs, but also to the lineage of the Octodontoidea, to which the tuco-tucos belong. Viannaiidae are then present in three out of the four recognized clades of living caviomorphs (Upham & Patterson 2015), suggesting that the association of viannaiids and caviomorphs preceded the divergence and differentiation of these main lineages. However, available parasitological data are still fragmentary and much more work should be done, especially on the most speciose and less studied groups such as the octodontoids, in order to have a better understanding of the diversity of Heligmosomoidea parasitic in caviomorphs and the relationships with their hosts.

Acknowledgments

The authors express their gratitude to Mgr. Jorge Baldo (VICAM-CONICET), Dr. Mario R. Cabrera and Dr. Ricardo Torres (MZUC) who provided essential information on the specimens of tuco-tucos subject of this study; to Lic. Paulina Hernández (División Entomología, Facultad de Ciencias Naturales y Museo, UNLP), who performed the rodent necropsies during her activity as a technician at the División Zoología Invertebrados; and to the staff of the MLP-He (curator-in-chief M.C. Damborenea, curator L.I. Lunaschi and technician V.H. Merlo Alvarez) for facilitating the access to the material. This work was supported by grants PIP 0006 from CONICET and N751 from SeCyT, UNLP to MCD.

References

- Arantes, I.G. & Artigas, P.T. (1983) Hydrochoerisnema anomalobursata Arantes & Artigas, 1980 (Nematoda; Trichostrongyloidea) parasito de capivara (Hydrochoerus hydrochoeris hydrochoeris) Linnaeus, 1766. Estabelecimento de nova subfamília: Hydrochoerisnematinae. Arquivos do Instituto de Biologia de São Paulo, 50, 39–49.
- Babero, B.B. & Murúa, R. (1987) The helminth fauna of Chile. X. A new species of whipworm from a Chilean rodent. *Transactions of the American Microscopical Society*, 106, 190–193. http://dx.doi.org/10.2307/3226320

Babero, B.B. & Murúa, R.B. (1990) A new species of whipworm from a South American hystricomorph rodent. *Memórias do Instituto Oswaldo Cruz*, 85, 211–213.

http://dx.doi.org/10.1590/S0074-02761990000200012

Beveridge, I., Spratt, D. & Durette-Desset, M.-C. (2013) Order Strongylida (Railliet & Henry, 1913). In: Schmidt-Rhaesa, A. (Ed.), Handbook of Zoology. A Natural History of the Phyla of the Animal Kingdom. 2. Nematoda. De Gruyter, Berlin, pp. 557–612.

http://dx.doi.org/10.1515/9783110274257.557

- Bidau, C.J., Giménez, M.D. & Contreras, J.R. (1996) Especiación cromosómica y la conservación de la variabilidad genética: el caso del género *Ctenomys* (Rodentia, Caviomorpha, Ctenomyidae). *Mendeliana*, 12, 25–37.
- Bidau, C.J. (2006) Familia Ctenomyidae. *In:* Barquez, R., Díaz, M.M. & Ojeda, R. (Eds.), *Mamíferos de Argentina: Sistemática y distribución.* SAREM Sociedad Argentina para el Estudio de los Mamíferos, San Miguel de Tucumán, pp. 212–231.
- Bortoluzzi, A., Gutiérrez, M., Baldo, J. & Gardenal, N.C. (2001) Protein polymorphism in two species of *Ctenomys* (Rodentia, Ctenomyidae) from Córdoba province, Argentina. *Mammalian Biology*, 66, 308–311.
- Durette-Desset, M.-C. (1983) Keys to genera of the Superfamily Trichostrongyloidea. N°10. *In*: Anderson, R.S. & Chabaud, A.G. (Eds.), *CIH Keys to the Nematode Parasites of Vertebrates*. Commonwealth Agricultural Bureaux, Fairham Royal, Bucks, pp.1–68.
- Durette-Desset, M.-C. (1971) Essai de classification des Nématodes Héligmosomes. Corrélation avec la paléobiogéographie des hôtes. *Mémoires du Muséum national d'Histoire naturelle, nouvelle série*, Série A (Zoologie), 49, 1–126.
- Durette-Desset, M.-C. (1985) Trichostrongyloid nematodes and their vertebrate hosts: reconstruction of the phylogeny of a parasitic group. Advances in Parasitology, 24, 239–306. http://dx.doi.org/10.1016/S0065-308X(08)60564-3
- Durette-Desset, M.-C. & Chabaud, A.G. (1993) Nomenclature des Strongylida au-dessus du groupe famille. Annales de Parasitologie humaine et comparée, 68, 111–112.
- Durette-Desset, M.-C. & Digiani, M.C. (2005) The axis of orientation of the synlophe in the Heligmosomoidea (Nematoda, Trichostrongylina): a new approach. *Parasite*, 12, 195–202. http://dx.doi.org/10.1051/parasite/2005123195
- Durette-Desset, M.-C. & Digiani, M.C. (2012) The caudal bursa in the Heligmonellidae (Nematoda: Trichostrongylina). Characterization and hypothesis on its evolution. *Parasite*, 19, 3–18. http://dx.doi.org/10.1051/parasite/2012191003
- Durette-Desset, M.-C. & Pinto, R.M. (1977) Nouvelles données morphologiques sur des Nématodes Trichostrongyloïdes des collections de l'Institut Oswaldo Cruz. *Bulletin du Muséum national d'Histoire naturelle*, 3ème Série, 469 (Zoologie), 326, 755–764.
- Durette-Desset, M.-C., Gonçalves, A.Q. & Pinto, R.M. (2006) Trichostrongylina (Nematoda, Heligmosomoidea) coparasites in *Dasyprocta fuliginosa* (Rodentia, Dasyproctidae) from Brazil with the re-establishment of the genus *Avellaria* Freitas and Lent and the description of two new species. *Revista Brasileira de Zoologia*, 23, 509–519. http://dx.doi.org/10.1590/S0101-81752006000200026
- Freitas, J.F.T. & Lent, H. (1934) Novo nematódeo da sub-familia Heligmosominae Travassos, 1914, parasito de Agouti paca (L.): Avellaria avellari n. g., n. sp. Memórias do Instituto Oswaldo Cruz, 28, 577–583. http://dx.doi.org/10.1590/S0074-02761934000400003
- Freitas, J.F.T. & Lent, H. (1937) Sur deux genres de Heligmosominae (Nematoda: Strongyloidea). Annais da Academia Brasileira de Sciencias, 9, 41–47.
- Gonçalves, A.Q., Durette-Desset, M.-C. & Pinto, R.M. (2007) Parasitism of two zoonotic reservoirs *Dasyprocta leporina* and *D. fuliginosa* (Rodentia) from Amazonas, with Trichostrongylina nematodes (Heligmonellidae): description of a new genus and a new species. *Memorias do Instituto Oswaldo Cruz, Rio de Janeiro*, 102, 763–768. http://dx.doi.org/10.1590/S0074-02762007000600017
- Ojeda, R.A., Novillo, A. & Ojeda, A.A. (2015) Large-scale richness patterns, biogeography and ecological diversification in caviomorph rodents. *In:* Vassallo, A.I. & Antenucci, C.D. (Eds.), *Biology of Caviomorph Rodents: Biodiversity and Evolution. SAREM Series A.* Mammalogical Research, Buenos Aires, pp. 121–138.
- Rossin, M.A. & Malizia, A.I. (2005) Redescription of *Trichuris pampeana* (Nematoda: Trichuridae) from the South American subterranean rodent *Ctenomys talarum* Thomas, 1898 (Rodentia: Octodontidae). *Journal of Parasitology*, 91, 127–130. http://dx.doi.org/10.1645/GE-3383.1
- Rossin, M.A., Malizia, A.I, Timi, J.T. & Poulin, R. (2010a) Parasitism underground: determinants of helminth infections in two species of subterranean rodents (Octodontidae). *Parasitology*, 137, 1569–1575. doi:10.1017/S0031182010000351
- Rossin, M.A., Timi, J.T. & Hoberg, E.P. (2010b) An endemic Taenia from South America: validation of T. talicei Dollfus, 1960 (Cestoda: Taeniidae) with characterization of metacestodes and adults. *Zootaxa*, 2636, 49–58.
- Rossin, M.A., Timi, J.T. & Malizia, A.I. (2004) Redescription and new host record of *Paraspidodera uncinata* (Rudolphi, 1819) (Nematoda, Aspidoderidae) from the South American subterranean rodent *Ctenomys talarum* (Rodentia, Octodontidae). *Acta Parasitologica*, 4, 325–331.
- Rossin, M.A., Timi, J.T. & Malizia, A.I. (2005) Graphidioides subterraneus n. sp. (Nematoda: Trichostrongyloidea) from the South American subterranean rodent Ctenomys talarum Thomas, 1898 (Rodentia: Octodontidae). Parasite, 12, 145–149. http://dx.doi.org/10.1051/parasite/2005122145
- Rossin, M.A., Timi, J.T. & Malizia, A.I. (2006a) New Pudicinae (Trichostrongylina, Heligmosomoidea), *Pudica ctenomydis* n. sp. parasite of *Ctenomys talarum* (Rodentia: Octodontidae) from Argentina. *Parasitology International*, 55, 83–87. http://dx.doi.org/10.1016/j.parint.2005.10.004
- Rossin, M.A., Timi, J.T. & Malizia, A.I. (2006b) A new species of Trichostrongylus (Nematoda, Trichostrongyloidea)

parasitizing the subterranean rodent *Ctenomys talarum* (Rodentia, Octodontidae) from Mar de Cobo, Argentina. *Acta Parasitologica*, 51, 286–289.

http://dx.doi.org/10.2478/s11686-006-0043-3

Rossin, M.A., Varela, G. & Timi, J.T. (2009) *Strongyloides myopotami* in ctenomyid rodents: Transition from semi-aquatic to subterranean life cycle. *Acta Parasitologica*, 54, 257–262.

http://dx.doi.org/10.2478/s11686-009-0033-3

- Suriano, D.M. & Navone, G.T. (1994) Three new species of the genus *Trichuris* Roederer, 1761 (Nematoda: Trichuridae) from Cricetidae and Octodontidae rodents in Argentina. *Research and Reviews in Parasitology*, 1, 39–46.
- Travassos, L. (1937) Revisão da familia Trichostrongylidae Leiper, 1912. Monographias do Instituto Oswaldo Cruz, 1, 1-512.
- Upham, N.S. & Patterson, B.D. (2015) Evolution of Caviomorph rodents: a complete phylogeny and timetree for living genera. *In:* Vassallo, A.I. & Antenucci, C.D. (Eds.), *Biology of Caviomorph Rodents: Biodiversity and Evolution*, SAREM Series A, Mammalogical Research, Buenos Aires, pp. 63–120.
- Vassallo, A.I. & Antenucci, C.D. (2015) Caviomorph rodents: an Introduction. In: Vassallo, A.I. & Antenucci, C.D. (Eds.), Biology of Caviomorph Rodents: Biodiversity and Evolution. SAREM Series A. Mammalogical Research, Buenos Aires, pp. 1–10.
- Woods, C.A. & Kilpatrick, C.W. (2005) Infraorder Hystricognathi. In: Wilson, D.E. & Reeder, D.A.M. (Eds.), Mammal species of the world. A taxonomic and geographic reference. 3rd Edition. Johns Hopkins University Press, Baltimore, Maryland, pp. 1538–1600.