

# Description of *Litomosoides ysoguazu* n. sp. (Nematoda, Onchocercidae), a parasite of the tuft-toed rice rat *Sooretamys angouya* (Fischer) (Rodentia: Cricetidae), and a first record of *L. esslingeri* Bain, Petit & Berteaux, 1989 in Paraguay

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**Abstract** Paraguay is a small landlocked country whose mammalian fauna is among the least studied in South America, as well as their parasites. As a result of a study of the effects of habitat fragmentation on small mammal biodiversity in eastern Paraguay, we have collected some parasites of cricetid rodents. Herein, we describe a new species of *Litomosoides* Chandler, 1931 parasitising the body cavity of the tuft-toed rice rat *Sooretamys angouya* (Fischer) and *Litomosoides esslingeri* Bain, Petit & Diagne, 1989 parasitising *Oligoryzomys nigripes* (Olfers), thus expanding its geographical distribution into Paraguay. *Litomosoides ysoguazu* n. sp. is characterised by the large size of the females (92.2–117.6 mm long) and by having buccal capsule with an anterior widening with rounded edges on the chitinous segment and a rounded widening at the base; male tail with a single pair of adcloacal papillae, three to five pairs of asymmetrical postcloacal papillae, and one or two unpaired papillae in the

median ventral line; spicules corresponding to the “*sigmodontis*” species group; and microfilaria with a sheath stuck to the body and visible in the anterior extremity. We also describe a fourth-stage female larva. *Oligoryzomys nigripes* is a new host record of *L. esslingeri*; this enlarges the host record to eight species highlighting the low specificity of this species.

## Introduction

Paraguay is a small landlocked country in the south-central region of South America. The country includes five major ecoregions: the Atlantic Forest and Cerrado in eastern Paraguay, the Dry Chaco and Pantanal to the west and the Humid Chaco in the centre subdivided by the Rio Paraguay (Olson et al., 2001). The history of mammalogy is among the earliest of South America with mammalian records as early as 1550 to 1770 by the Jesuit missionaries of the region (López-González et al., 2014). However, the mammalian fauna of Paraguay is still among the least studied and understood in the continent (Myers et al., 2002; López-González et al., 2014) as indicated by the number of recent new and noteworthy records from this country (de la Sancha et al., 2007, 2009, 2011; D’Elía et al., 2008; de la Sancha & D’Elía, 2015; among others) many of which reflect new recent collections.

The current knowledge of the parasite fauna of small mammals in Paraguay is even more scarce; there

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are few records of helminths scattered both in space and time including nematodes of bats (Lent et al., 1946; Durette-Desset & Vaucher, 1999), dasypodids (Lent & Teixeira de Freitas, 1942; Masi Pallarés, 1970, 1990; Fujita et al., 1995) and marsupials (Masi Pallarés et al., 1976). For rodents there is only a single record of the oxyurid *Passalurus ambiguus* (Rudolphi, 1819) from *Cavia aperea* Erxleben, also reported from the lagomorph *Sylvilagus* sp. (Masi Pallarés et al., 1976).

As a result of a recent study of the effects of habitat fragmentation on the biodiversity of small mammals in eastern Paraguay (de la Sancha, 2010, 2014), we have collected parasite samples in several cricetid rodents. Herein, we describe a new species of *Litomosoides* Chandler, 1931 (Nematoda, Onchocercidae) parasitising the body cavity of the tuft-toed rice rat *Sooretamys angouya* (Fischer). Additionally, we include a noteworthy record of *Litomosoides esslingerii* Bain, Petit & Berteaux, 1989 in *Oligoryzomys nigripes* (Olfers) thus expanding the data on host and geographical range of this species.

## Materials and methods

The newly collected material is a product of sampling conducted within the largest remnants of Interior Atlantic Forest (IAF) left in eastern Paraguay, during December 2006 to March 2009. The IAF of eastern Paraguay is home to small mammal assemblages different from other portions of the coastal Brazilian Atlantic Forest (de la Sancha, 2014; de la Sancha et al., 2014).

The trapping consisted of 40 equally-sized grids in four reserves and included pitfall traps, snap traps, and Sherman live traps (de la Sancha, 2014). All mammalian samples trapped were collected as museum vouchers and were prepared as dry skin or specimens fixed in ethanol to be deposited at The Field Museum of Natural History, Chicago, Illinois, and the Natural Science Research Laboratory (NSRL), Texas Tech University, Lubbock, Texas, USA. Viscera were fixed in 10% formalin and stored in 70% ethanol. All applicable institutional, national and international guidelines for the care and use of animals were followed.

Filarial worms were cleared in lactophenol and the morphology examined using an Olympus BZ51 microscope. To examine the disposition of head papillae, a drawing was prepared from one female specimen in apical view. The lateral cuticular internal

ridges were used to identify lateral fields and the Y-shaped section of the lumen of the oesophagus was used to identify the dorsal side. Cross sections of a female, posterior to the vulva, were cut with a razor blade and mounted in glycerin. Microfilariae were obtained from the uterus of one female. Illustrations were made with the aid of a drawing tube. All measurements are in micrometres unless otherwise indicated and are given as the range followed by the mean in parentheses. Type- and voucher specimens were deposited at the Colección de Helminthos Museo de la Plata (MLP-he), La Plata, Argentina and the Harold Manter Laboratory of Parasitology (HWML), Division of Parasitology, University of Nebraska State Museum, Lincoln, Nebraska, USA. Host species nomenclature and synonymy follow Weksler et al. (2006).

### *Litomosoides ysoguanu* n. sp.

*Type-host*: *Sooretamys angouya* (Fischer) (Rodentia, Cricetidae); field number TK129367, adult male, collected on 11.xii.2007, deposited at The Field Museum of Natural History, Chicago, Illinois, USA, FMNH 226738.

*Type-locality*: San Rafael Managed Resource Reserve (26°32'39"S, 55°44'16"W), Department of Itapúa, Paraguay.

*Type-material*: Holotype (male) (MLP-he 6820), allotype (female) (MLP-he 6821), paratypes: 5 males, 15 females, 8 anterior extremities, 5 posterior extremities (MLP-he 6822), and 1 fourth-stage female larva (MLP-he 6823).

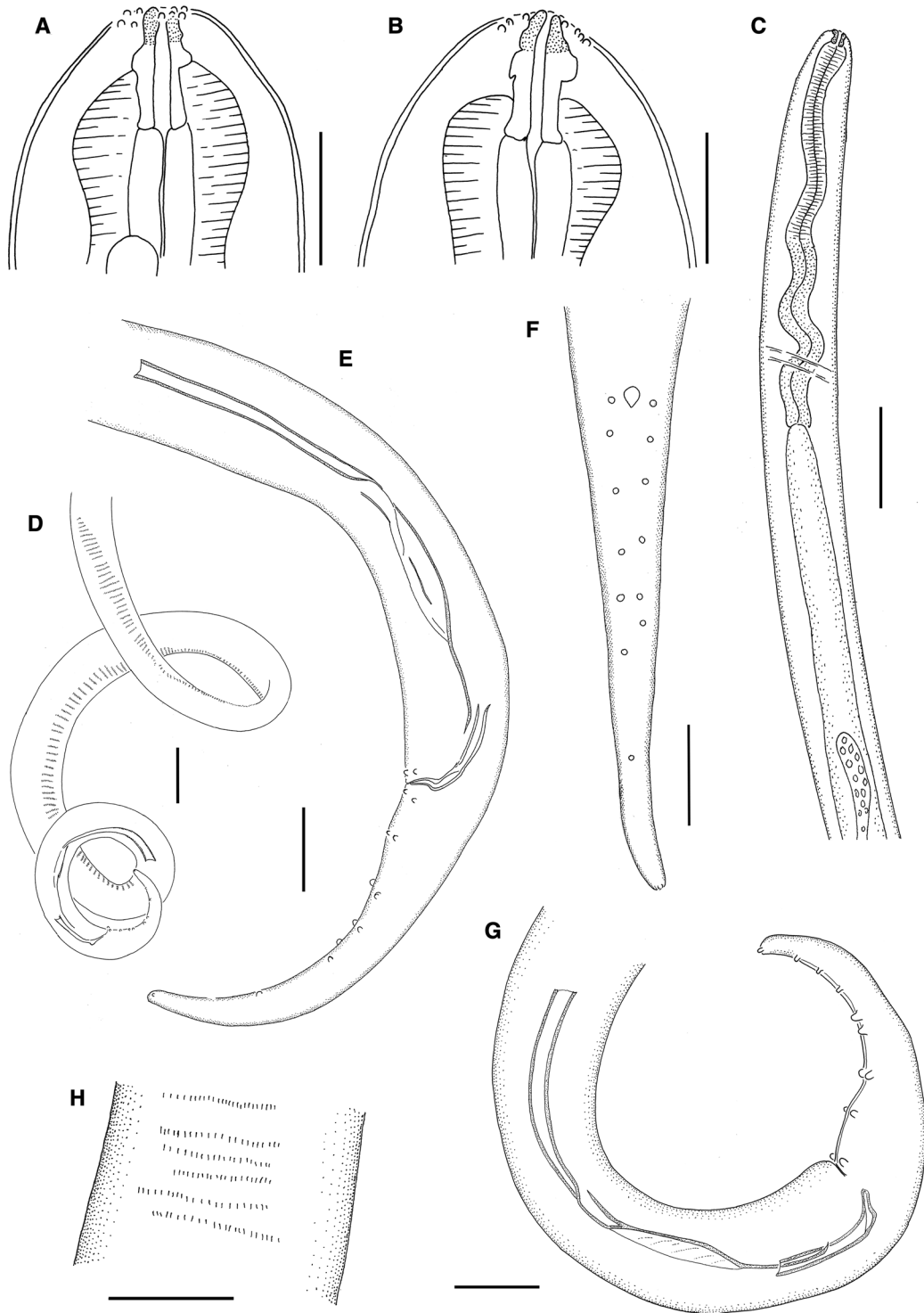
*Site in host*: Abdominal cavity, between the intestinal mesentery and testis.

*Prevalence and intensity*: One of two hosts infected; 32 adult worms and 1 fourth-stage female larva.

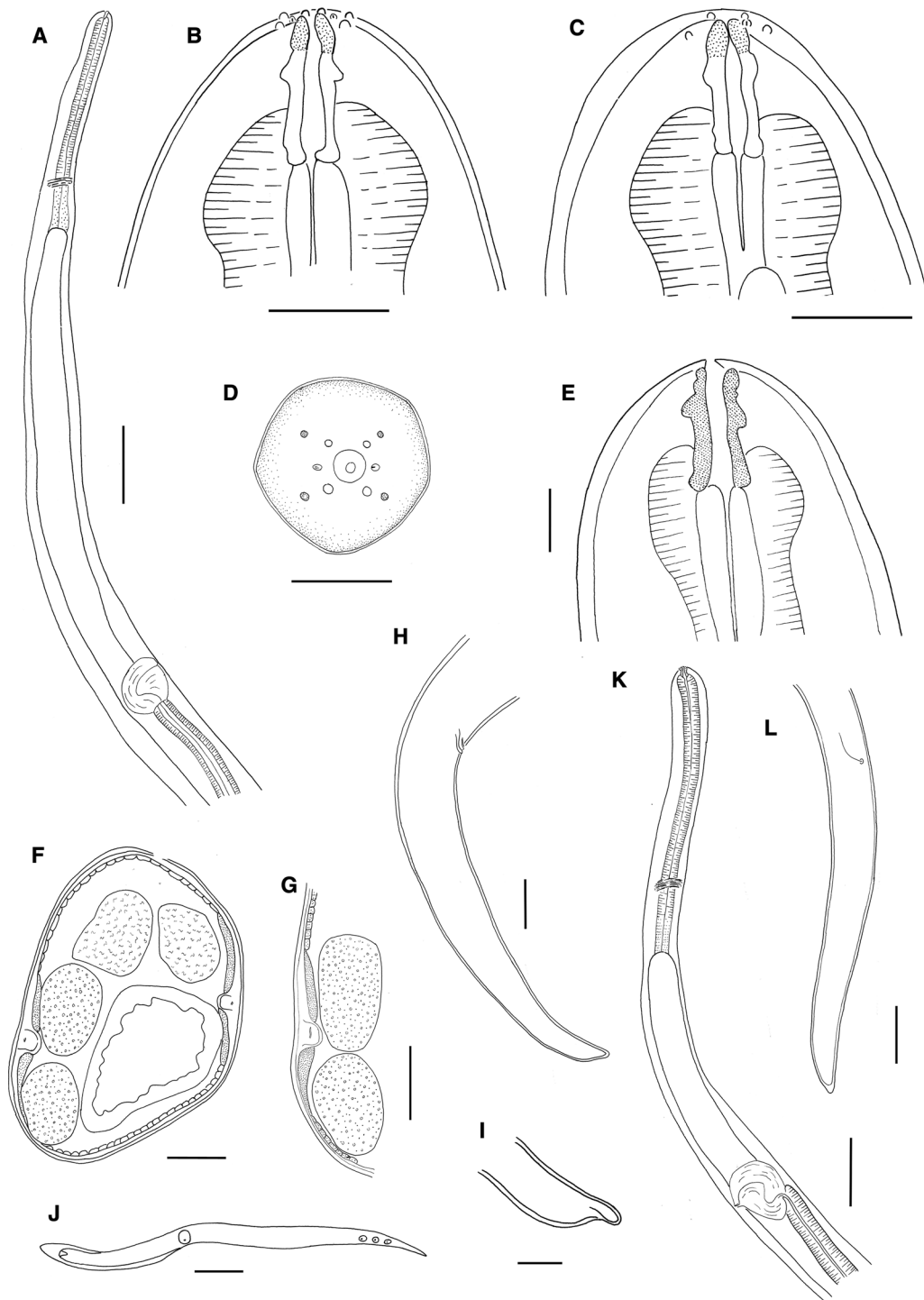
*Etymology*: The species name means big worm: *iso* is a general name for parasitic worms in Guarani, one of Paraguay's official and indigenous languages and *guan* means big in Guarani.

### Description (Figs. 1, 2)

*General*. Females large, males c.4.6× shorter than females. Cephalic extremity rounded. In apical view, head papillae symmetrically arranged, 4 externo-labial papillae and 4 cephalic papillae, both circles of



**Fig. 1** *Litomosoides ysoguazu* n. sp. Male. A, Anterior extremity, lateral view; B, Anterior extremity, median view; C, Anterior region showing the tip of the testis; D, Posterior region; E, Paratype, tail in lateral view; F, Paratype, tail in ventral view; G, Holotype, tail with spicules, lateral view; H, Area rugosa at mid-length. Scale-bars: A, B, 20  $\mu$ m; C, D, 100  $\mu$ m; E–H, 50  $\mu$ m



**Fig. 2** *Litomosoides ysoguazu* n. sp. Female. A, Anterior region, lateral view; B, Anterior extremity, median view; C, Anterior extremity, lateral view; D, Anterior extremity, apical view; E, Fourth-stage female larva, anterior extremity; F, Transverse section posterior to the vulva; G, Detail of the lateral chord; H, Tail, lateral view; I, Tail extremity showing the amphids; J, Uterine microfilaria; K, Anterior region of fourth-stage female larva, lateral view; L, Tail of fourth-stage female larva, lateral view. Scale-bars: A, 200 µm; B–D, 20 µm; E, I, J, 10 µm; F–H, L, 50 µm; K, 100 µm

papillae situated at dorso- and ventro-lateral lines (Fig. 2D); amphids lateral, not salient. Buccal capsule embedded in oesophagus, longer than broad, with transparent anterior segment followed by chitinous segment; chitinous segment possessing anterior widening with rounded edges and rounded widening at base (Figs. 1A, B, 2B, C); buccal cavity smooth, wider near base. Oesophageal apex dilated, with muscular anterior and slightly differentiated glandular posterior portion. Vulva posterior to oesophago-intestinal junction. Tail attenuated.

**Male** [Based on 6 specimens]. Posterior region coiled, with 2 to 3 loops (Fig. 1D). Left spicule with handle shorter than blade (handle longer than blade in some specimens); blade constituted by membranous folded ala and terminal filament (Fig. 1E, G). Right spicule with poorly cuticularised heel (Fig. 1E, G). Tail attenuated, with single pair of adcloacal papillae, 3–5 pairs of asymmetrical postcloacal papillae, and 1 or 2 unpaired papillae in median ventral line (Fig. 1E, G). Area rugosa consisting of transverse ridges made of small longitudinal crests, extends through coiled region (Fig. 1D, H).

Measurements: Holotype: Body length 23.5 mm; width at mid-body 170, at oesophago-intestinal junction 70, at anus 70; buccal capsule 20 long, external diameter 9; buccal cavity 3 wide; oesophagus 545 long; nerve-ring at 210 from anterior extremity; tail 212 long; left spicule 312 long, handle 150 long; right spicule 90 long; spicular ratio 1:3.4; area rugosa 1,300 long, extending from 675 to 1,975 from posterior extremity, ridges *c.* 4 in height, spaced 6–12. Paratypes (n = 5): Body length 18.6–26.0 (22.8) mm; width at mid-body 132–165 (154); buccal capsule 20–23 (21) long, external diameter 6–10 (8); oesophagus 440–640 (544) long; nerve-ring at 200–350 (287) from anterior extremity; tail 200–275 (231) long; left spicule 253–335 (311) long, handle 121–170 (150) long; right spicule 80–110 (93) long; spicular ratio 1: 2.6–4.1 (1: 3.4); area rugosa 880–1,560 (1,285) long, extending from 600–950 (721) to 1,500–2,200 (2,011) from posterior extremity.

**Female** [Based on 12 specimens.] Vulva far posterior to oesophago-intestinal junction. Vagina globular or sub-globular, ovejector muscular directed posteriad (Fig. 2A). Tail slender (Fig. 2H), anus difficult to observe. Phasmids small, divergent (Fig. 2I). In a

transverse section posterior to the vulva, lateral hypodermal chords broad and flattened; internal cuticular ridges square-shaped (Fig. 2F, G).

Measurements: Allotype: Body length 100.5 mm; width at mid-body 270, at oesophago-intestinal junction 110, at level of vulva 180; buccal capsule 22 long, with external diameter 10, buccal cavity 3; oesophagus 600 long; nerve-ring not visible; vulva at 1,950 from anterior end, located 1,300 from oesophago-intestinal junction; vagina sub-globular, 110 × 100; ovejector 1,200 long; tail 395 long. Paratypes (n = 9): Body length 92.2–117.6 (106.3) mm, width at mid-body 220–380 (284), at oesophago-intestinal junction 100–120 (112), at level of vulva 160–230 (197); buccal capsule 18–24 (22) long, with external diameter 10–12 (10); oesophagus 480–700 (598) long; nerve-ring at 120–530 (404) from anterior extremity; vulva 1,500–2,600 (2,024) from anterior extremity, located 880–1,950 (1,410) from oesophago-intestinal junction; tail (n = 3) 550–560 (553) long.

**Microfilaria.** Body fusiform, slender, 67–77 (73) long, 4–5 (4.5) wide (n = 3). Anterior extremity with small visible hook, tail attenuated, with nuclei at 12 from tip tail. Sheath present, stuck to body, visible at anterior extremity (Fig. 2J).

**Fourth-stage female larva.** Immature female short; body length 13.68 mm; width at mid-body 110, at oesophago-intestinal junction 50, at level of vulva 90. Buccal capsule 19 long, with external diameter 10. Oesophagus muscular becoming slightly glandular near oesophago-intestinal junction, 430 long (Fig. 2K). Nerve-ring 330 from anterior extremity. Vulva close to anterior extremity compared with mature females, at 800 from anterior end and 380 from oesophago-intestinal junction; vagina globular, 85 × 95. Tail slender, 290 long (Fig. 2L).

#### Remarks

*Litomosoides ysoguzu* n. sp. belongs to the “*sigmodontis*” group of parasitic worms (Bain et al., 1989; Notarnicola et al., 2000; Bain et al., 2003) based on the morphological characteristics of both spicules. The left spicule has a handle shorter or as long as the blade, and the blade is divided into anterior membranous folded ala, with a terminal filament; the heel of right spicule is not heavily cuticularised. The “*sigmodontis*” group is

comprised of 19 species found in rodents, marsupials and bats, with distinctive characters that make them different from the new species.

*Litomosoides ysoguanu* n. sp. can be differentiated from the three species parasitising bats, i.e. *L. leonilavasquezae* Caballero, 1939, *L. fosteri* Caballero, 1947 and *L. teshi* Esslinger, 1973, in having larger females, longer tail in both sexes, and a more posteriorly located vulva. Moreover, the new species possesses a robust buccal capsule, different from that of *L. leonilavasquezae* and *L. fosteri*, which is thinner, and from that of *L. teshi*, which possesses a dorsal thickening (Caballero, 1939, 1947; Esslinger, 1973).

*Litomosoides ysoguanu* n. sp. differs from *L. barretti* Muller, 1980, a parasite of the marsupial *Micoureus demerarae* (Thomas) (syn. *Marmosa cinerea*) from Brazil, in having females with a shorter oesophagus and a more posteriorly located vulva and males with a shorter right spicule (80–90 vs 100–120  $\mu\text{m}$ ), and in having asymmetrically placed cloacal papillae instead of symmetrical (Muller, 1980).

In comparison with other species found in rodents, the new species differs from *L. ctenomyos* Brant & Gardner, 1997 in having a shorter oesophagus, a longer tail in the male and a more attenuated tail in the female, and in the presence of cephalic papillae, absent in *L. ctenomyos* (Brant & Gardner, 1997); from *L. hoplomys* Esslinger, 1973, a parasite of echimyd rodents from Colombia, in that *L. ysoguanu* n. sp. is a larger species, with an attenuated tail, and with a larger buccal capsule (females: 22 vs 19  $\mu\text{m}$ ; males: 21 vs 17  $\mu\text{m}$ ) with thicker walls (Esslinger, 1973). The new species differs from *L. sigmodontis* Chandler, 1931 in having a buccal capsule with a rounded thickening instead of irregular walls, and a shorter microfilaria (67–77 vs 84  $\mu\text{m}$ ) with a sheath visible at the anterior extremity instead of a long sheath visible at both extremities (Forrester & Kinsella, 1973; Bain et al., 1989).

Body length of females of *L. ysoguanu* n. sp. (92–117 mm) is distinctly larger than that of females of *L. patersoni* (Mazza, 1928) (43 mm); *L. oxymycteri* Notarnicola, Bain & Navone, 2000 (43.0–70.8 mm); *L. anguyai* Notarnicola, Bain & Navone, 2002 (53.6–69.1 mm); *L. nasuti* Notarnicola & Navone, 2009 (37.4–47.9 mm); *L. navonae* Notarnicola, 2005 (44.8–72.3 mm); *L. taylori* Guerrero & Bain, 2011 (mean 54.3 mm); and *L. circularis* (von Linstow, 1899) (65 mm). Moreover, the new species can be

differentiated from *L. patersoni* in having a buccal capsule with a thickening instead of irregular walls, and by the slender microfilaria instead of a stout one (Notarnicola et al., 2010); from *L. oxymycteri* by the absence of a precloacal papilla (Notarnicola et al., 2000); from *L. anguyai* and *L. nasuti* in having no salient amphids and a complete set of head papillae (Notarnicola et al., 2002; Notarnicola & Navone, 2009); from *L. navonae* in having a more posteriorly located vulva (mean 2,023 vs 1,359  $\mu\text{m}$  from the anterior extremity) and microfilaria with a sheath visible only at the anterior extremity (Notarnicola, 2005); from *L. taylori* by the presence of a thickening in the buccal capsule instead of irregular walls (Guerrero et al., 2011); and from *L. circularis* by a shorter right spicule (mean length 80–110 vs 98–121  $\mu\text{m}$ ) and different spicular ratio (mean 3.5 vs 2.8) (Guerrero & Bain, 2011).

*Litomosoides ysoguanu* n. sp. also differs from *L. legerae* Bain, Petit & Bertheaux, 1980, a parasite of *Oxymycterus quaestor* Thomas from Brazil, in having a shorter oesophagus in both sexes (males: 440–640 vs 720–800  $\mu\text{m}$ ; females: 400–700 vs 1,040–1,240  $\mu\text{m}$ ), a buccal capsule without irregular walls, and lateral hypodermic chord broad and flattened instead of narrow and tall (Bain et al., 1980); from *L. galizai* Bain, Petit & Diagne, 1989 in possessing a buccal capsule with wider walls, and a different arrangement of the cloacal papillae (Bain et al., 1989); from *L. chagasfilhoi* Moraes Neto, Lanfredi & De Sousa, 1997 by a longer tail in males (200–275 vs 143–187  $\mu\text{m}$ ) and a buccal capsule without smooth walls (Moraes Neto et al., 1997; Notarnicola et al., 2000); and from *L. esslingeri* Bain, Petit & Diagne, 1989 by the absence of a constricted tail tip in the female (Esslinger, 1973; Notarnicola et al., 2012). The new species differs from *L. kohnae* Bain, Petit & Diagne, 1989 in having females with a tail curved ventrally instead of curved dorsally (Bain et al., 1989).

Finally, there is a group of *Litomosoides* spp., including five species parasitising bats, for which the males are unknown. The descriptions are based on females for three species and only on microfilaria for two species. These species can be separated from the new species as follows. Females of *L. ysoguanu* n. sp. are distinct from those of *L. solarii* Guerrero, Martin, Gardner & Bain, 2002, a parasite of *Trachops cirrhosus* Spix in Peru, in having a more posteriorly located vulva (2,024 vs 910  $\mu\text{m}$  from anterior



extremity) and also distant from the oesophago-intestinal junction, and in having a tail without a sharpened point in the microfilaria as described in *L. solarii* (see Guerrero et al., 2002). Females of the new species are larger than those of *L. artibeii* Esslinger, 1973, possess a thicker buccal capsule lacking anterior enlargements, and the vulva is distant from the oesophago-intestinal junction (Esslinger, 1973). The new species differs from *L. chitwoodi* Bain, Guerrero & Rodriguez, 2003 in being larger (mean 106.3 vs 15 mm) and in having a longer buccal capsule and a more posteriorly located vulva (Chitwood, 1938; Bain et al., 2003). The microfilariae of *L. ysoguanu* n. sp. are shorter than those described for *L. colombiensis* Esslinger, 1973, a parasite of *Platyrrhinus dorsalis* (Thomas) (recorded as *Vampyrops dorsalis*), and *A. jamaicensis* (Leach) from Colombia (67–77 vs 100–125 µm); and the caudal terminal nucleus does not reach the tail tip and is not markedly elongate as in *L. colombiensis* (see Esslinger, 1973). Finally, the microfilariae of *L. ysoguanu* n. sp. are longer than those of *L. caliensis* Esslinger, 1973 (67–77 vs 53–65 µm) with an attenuated tail instead of rounded, and the terminal nucleus is not spheroid and does not reach the tail tip (see Esslinger, 1973).

### *Litosomoides esslingeri* Bain, Petit & Diagne, 1989

**Host:** *Oligoryzomys nigripes* (Olfers) (Rodentia, Cricetidae), field number TK129461, adult male, captured on 13.iii.2008, deposited at the Natural Science Research Laboratory (NSRL), Texas Tech University, Lubbock, Texas USA, TTU-M 118813.

**Locality:** Limoy Biological Reserve (24°43'51"S, 54°24'42"W) Alto Paraná Department, Paraguay.

**Site in host:** Abdominal cavity.

**Prevalence and intensity:** One of three hosts infected; 11 worms.

### Description

**General.** Males one-third length of females. Cephalic extremity rounded; buccal capsule tubular, with irregular thickenings throughout and smooth buccal cavity; posterior part embedded in oesophagus. Cephalic papillae 4, situated at dorso- and ventrolateral lines; labial papillae 4, forming rectangle

elongated in dorso-ventral plane. Oesophagus differentiated in muscular anterior portion and glandular posterior portion. Tail slender.

**Male** [Based on 3 specimens.] Body length 20.7–25.0 (23.3) mm; width at mid-body 120–140 (128). Buccal capsule 19–23 (21) long, external diameter 7–8 (8). Oesophagus 390–580 (503) long. Nerve-ring from anterior extremity 200–390 (270). Posterior region coiled. Tail 212–255 (227) long, with 4–6 pairs of cloacal papillae. Left spicule 280–330 (307) long, with handle 140–170 (153) long, shorter than blade; blade with anterior membranous alae and distal filament; right spicule 80–100 (90) long with heel not heavily cuticularised. Spicular ratio 1:3.3–3.5 (1:3.4). Area rugosa consisting of transverse ridges of small longitudinal crests.

**Female** [Based on 3 specimens.] Body length 60.0–82.5 (74.7) mm; width at mid-body 192–270 (234), at oesophago-intestinal junction 60–82 (75), at level of vulva 80–190 (133). Buccal capsule 22–25 (24) long, with external diameter 9–10 (10). Oesophagus 500–680 (582) long. Nerve-ring 310–520 (403) from anterior extremity. Vulva posterior to oesophago-intestinal junction, at 1,400–1,750 (1,550) from anterior extremity and 720–1,200 (953) from oesophago-intestinal junction. Vagina globular. Tail 600–870 (703) long, with constricted tip; width at anus 75–90 (82).

**Microfilaria** [Based on 5 intrauterine worms.] Body fusiform, slender, 60–70 (66) long, 3–6 (4) wide.

### Remarks

*Litosomoides esslingeri* was originally described in *Melanomys caliginosus* Tomes (reported as *Oryzomys caliginosus*) from Colombia (Esslinger, 1973), and more recently reported from *Oligoryzomys microtis* Allen, *Oligoryzomys* sp., *Eligmodontia puerulus* (Philippi), *Calomys lepidus* (Thomas), *Holochilus sciureus* Wagner, *Oecomys mamorae* (Thomas) and *Ctenomys opimus* Wagner from Bolivia (Notarnicola et al., 2012) and from *E. puerulus* in northern Argentina (Notarnicola et al., 2012). This study provides the first record of *L. esslingeri* in Paraguay and a new host record.

Most of the diagnostic characters of the specimens collected in Paraguay match with those described by

Esslinger (1973) and Notarnicola et al. (2012). The shape of the buccal capsule is uniform among all the specimens, as well as the shape of the spicules and the tail tip of the females. All these features are diagnostic traits for the species.

Notarnicola et al. (2012) recognised two different morphs in females of *L. esslingeri*: one includes females possessing a slender anterior extremity, with width <100 µm at the level of the oesophago-intestinal junction and <180 µm at the level of the vulva. The second, more robust morph includes females possessing a robust anterior extremity, with width >120 µm at the oesophago-intestinal junction and >200 µm at level of the vulva. Among our specimens, we also found females corresponding to both, the slender and robust morph.

## Discussion

Helminth fauna of rodents in Paraguay is poorly studied. Herein, we report the first onchocercid parasitising the tuft-toed rice rat *S. angouya* and provide a new host (*O. nigripes*) and geographical (Paraguay) record for *L. esslingeri*.

The fourth-stage (J4) female larva of *L. ysoguzi* n. sp. found in *S. angouya* adds information on the ontogenesis of *Litomosoides* spp. The oesophagus to body length ratio increases from J4 stage to the adult (mean 32 in J4 vs 178 in adults) as well as the vulva to body length ratio (mean 17 in J4 vs 52.5 in adults), similarly to the observations on *L. brasiliensis*, *L. sigmodontis*, *L. legerae*, and *L. navonae* (see Bain et al., 1980; Maréchal et al., 1996; Guerrero et al., 2002; Notarnicola, 2005). The female larva can be assigned to the new species because it shares the diagnostic features; however the body length was 7.7 times smaller than the length of adults.

The finding of *L. esslingeri* in a different cricetid species, not reported before, expands the data on host range to eight host species and demonstrates the low specificity of this filaria. Five of the 26 species of *Litomosoides* parasitising rodents and marsupials and three of the 15 species parasitising bats exhibit low specificity, e.g. *L. brasiliensis* is recorded in six host species, *L. navonae* in five host species, *L. pardinasi* in four host species, *L. hoplomys*, *L. sigmodontis*, *L. chandleri* and *L. hamletti* in two host species. It seems that the species of *Litomosoides* with low host

specificity also show a wide geographical distribution whereas those species reported in a single host have a restricted geographical distribution. Additional studies are needed, as this will certainly increase the diversity of the genus and the known geographic distribution of its species.

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