Zoosyst. Evol. 100 (4) 2024, 1315–1331 | DOI 10.3897/zse.100.125466

PENSOFT

für Natur MUSEUM FÜR NATURKUNDE BERLIN

Synonymy, redescription, molecular characterisation, and new distribution data of species of *Stilestrongylus* and *Guerrerostrongylus* (Nematoda, Heligmonellidae) parasitic in sigmodontine rodents from Argentina and Uruguay: a collection-based survey

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https://zoobank.org/DE37DFA9-F0D9-41AD-B021-7F990C241FA3

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Academic editor: Andreas Schmidt-Rhaesa ♦ **Received** 17 April 2024 ♦ **Accepted** 8 August 2024 ♦ **Published** 24 September 2024

Abstract

In this study, we review the taxonomic status of the parasitic nematodes *Stilestrongylus oryzomysi* and *Guerrerostrongylus uruguayensis* (Heligmonellidae), which had been described only once from sigmodontine rodents from Argentina and Uruguay, respectively. To this aim, we examined 38 complete helminth sets deposited in the Helminthological Collection of the Museo de La Plata (MLP-He), Argentina, including type material of *G. uruguayensis*, *S. oryzomysi*, and a closely related species, *Stilestrongylus azarai*. We also examined voucher rodent specimens deposited in the Mammal Collection of the Museo de La Plata (MLP-Mz) to assess the identity of the symbiotypes and other rodent hosts. Based on these observations, *S. oryzomysi* is proposed as a junior synonym of *S. azarai*; the identity of the symbiotype of *S. oryzomysi* and *Trichofreitasia lenti* (Heligmonellidae) is emended from *Oligoryzomys flavescens* to *Akodon azarae*; *G. uruguayensis* is proposed as a junior synonym of *Guerrerostrongylus zeta*; *S. azarai* is redescribed based on type and voucher material; and the latter species and *G. zeta* are molecularly characterised using the ITS+ gene. We extend the geographic distribution of *S. azarai* to include Uruguay and provide a new host record for *T. lenti* (*A. azarae*, type host species), a new host record for *G. zeta* in Argentina (*O. flavescens*), and the first record of helminths for *Oligoryzomys nigripes* in Uruguay.

Key Words

Akodon azarae, *Guerrerostrongylus uruguayensis*, *Guerrerostrongylus zeta*, integrated collections, ITS+, *Oligoryzomys* spp., *Stilestrongylus azarai*, *Stilestrongylus oryzomysi*, *Trichofreitasia lenti*

Introduction

Heligmonellidae is the most speciose family of the Trichostrongylina (Strongylida), with ca. 350 species distributed worldwide, most of which are parasites of rodents. Within this family, the cosmopolitan Nippostrongylinae includes the largest number of species (ca. 230), with rodents of the superfamily Muroidea as main hosts (Beveridge et al. 2014; Durette-Desset et al. 2017). In South America, muroids are mostly represented by the Sigmodontinae, which includes ca. 380 species (D`Elía and Pardiñas 2015). In Argentina, ca. 29 species of Nippostrongylinae have been described from sigmodontines mainly inhabiting the Río de la Plata Basin region (Durette-Desset and Sutton 1985; Sutton and Durette-Desset 1991; Digiani and Durette-Desset 2003a, 2003b; Digiani et al. 2003; Navone et al. 2009; Digiani and Kinsella 2014; Panisse et al. 2017; Gómez-Muñoz et al. 2020; Serrano et

al. 2021). In particular, four of the latter species were described in 1991 from yellow pygmy rice rats, *Oligoryzomys flavescens* (Waterhouse) (commonly known as "colilargo del Plata"), which were collected at two localities in Argentina and Uruguay, distant ca. 400 km from each other and separated by the Uruguay River. These species are *Stilestrongylus oryzomysi* Sutton & Durette-Desset, 1991; *Trichofreitasia lenti* Sutton & Durette-Desset, 1991, from the Argentinean locality; *Stilestrongylus flavescens* Sutton & Durette-Desset, 1991; and *Guerrerostrongylus uruguayensis* Sutton & Durette-Desset, 1991, from the Uruguayan locality.

Subsequently, *S. flavescens* was reported from its type host species and other sigmodontine rodents in the Río de La Plata Basin region in Argentina (Navone et al. 2009; Hancke and Suárez 2018; Serrano 2024). *Trichofreitasia lenti* was found in different eco-regions in Argentina and Brazil, though never from its type host species (Digiani et al. 2007; Simões et al. 2011, 2012b; Panisse et al. 2017). *Stilestrongylus oryzomysi* and *G. uruguayensis* were not recorded again (see, however, Digiani et al. 2007 for records of *Guerrerostrongylus* spp.), despite the intensive sampling effort used in different studies (Navone et al. 2009; Panisse et al. 2017; Gómez-Muñoz et al. 2020; Serrano et al. 2021). Both species were described from a very small number of specimens, and their differential diagnoses against known species were mainly based either on morphometric characters of soft organs or on unspecific or rather ambiguous morphological features.

Stilestrongylus oryzomysi was differentiated from *S. azarai* Durette-Desset & Sutton, 1985, parasitic in *Akodon azarae* (Fischer) from Buenos Aires province, by having a more posterior excretory pore and a more developed genital cone (Sutton and Durette-Desset 1991). However, the authors only provided measurements of the holotypes and allotypes, and therefore no measurement ranges are available for any of the two species.

The remarkable similarity between *S. azarai* and *S. oryzomysi*, together with the fact that the latter has only been reported in its original description, led us to suspect that the specimens described as *S. oryzomysi* could be an infrequent acquisition of *S. azarai* by *O. flavescens*.

Similarly, *Guerrerostrongylus uruguayensis* was differentiated from *Guerrerostrongylus zeta* (Travassos, 1937), parasitic in various sigmodontines from Brazil (concerning the use of the spelling *zeta*, see Digiani et al. 2024), by its larger body size and a widening of the body just anterior to the tail in females, and by details of the bursal rays in males. However, the diagnostic characters proposed for females are taxonomically unreliable because they may vary with age and reproductive status, whereas those for males are ambiguous and subjected to individual variation. In addition, the description of *G. uruguayensis* did not account for morphometric variability since it was based solely on the holotype and allotype.

Within this framework, the main aim of the present study was to review the taxonomic status of *S. oryzomysi* and *G. uruguayensis* based on type material examination and comparison with closely related species. Additionally, our results allowed us to provide a morphological redescription of *S. azarai* based on type and voucher material, as well as a molecular characterisation of this species and of *G. zeta* based on the internal transcribed spacer (ITS) region. Finally, we shed some light on the host spectrum and geographic distribution of the species concerned.

Materials and methods

Type material examined from the Helminthological Collection of the Museo de La Plata, Argentina (MLP-He)

Stilestrongylus azarai

ARGENTINA • ♂, holotype; Buenos Aires Province, Balcarce; 1977–1978; Sutton leg.; *Akodon azarae*; MLP-He 0687-1• ♀, allotype; same data as for holotype; MLP-He 0687-2 • 6 ♂♂, 6 ♀♀, paratypes; same collection data as for preceding; MLP-He 0687-3.

Stilestrongylus oryzomysi

ARGENTINA • 2 ♂♂, 10 ♀♀, paratypes; Buenos Aires Province, Campana, National Route 12 (RN12) Km 100-101; [34°00'27.432"S, 58°58'29.28"W]; Apr. 1989; Sutton leg.; *Akodon azarae*, MLP-Mz 3076, "*Oryzomys flavescens*, 1914"; MLP-He 1914-3.

Guerrerostrongylus uruguayensis

URUGUAY • ♂, holotype; Artigas Department, Bella Unión, Colonia España; [30°21'52"S, 57°38'34"W]; Jul. 1989; Sutton leg.; "*Oryzomys flavescens*"; MLP-He 2046-1 • ♀, allotype; same data as for holotype; MLP-He 2046-2 • 2 ♂♂ (distal fragments), 3 ♀♀, paratypes; same collection data as for preceding; MLP-He 2046-3.

Type material of *G. zeta* was not examined; instead, data were drawn from two published redescriptions, which included the study of syntypes and voucher specimens housed in the Helminthological Collection of the Instituto Oswaldo Cruz (CHIOC), Rio de Janeiro, Brazil (Simões et al. 2012a) and of voucher specimens from Brazil and Argentina (Misiones province) (Digiani et al. 2012).

Other material examined

Additionally, we examined 35 sets of parasitic intestinal helminths in *A. azarae* and *Oligoryzomys* spp. housed in MLP-He for identification. These were selected because they had been collected from the type localities of *S. azarai*, *S. oryzomysi*, and *G. uruguayensis* and from the same sampling events as the type material of these species. The sets were complete, and the worms remained unidentified. Therefore, each set examined corresponded to an

infracommunity of intestinal helminths of either *A. azarae* or *Oligoryzomys* spp. from each of the localities concerned.

From Locality I (type locality of *S. azarai*): MLP-He 674, 675, 676, 683, 686.

From Locality II (type locality of *S. oryzomysi*): MLP-He 1905, 1906, 1907, 1911, 1913, 1915, 1933, 1940.

From Locality III (type locality of *G. uruguayensis*): MLP-He 2047, 2048, 2049, 2050, 2051, 2052, 2054, 2055, 2056, 2057, 2058, 2059, 2061, 2062, 2063, 2064, 2066, 2067, 2068, 2069, 2070, 2072.

Prevalence (P) and mean intensity of infection (MI) were calculated by host and locality according to Bush et al. (1997). We followed Beveridge et al. (2014) for high-level taxonomy (Order to Subfamily).

Hosts

Hosts from Loc. I (Table 1) were collected and identified by mammalogists of the Museo Municipal Lorenzo Scaglia, Mar del Plata, Buenos Aires province, Argentina. Their viscera were submitted for parasitological examination to the División Zoología Invertebrados (Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata) in the framework of an agreement between both institutions in the 1980's. Voucher host specimens of all helminth sets from Loc. II and several sets from Loc. III were deposited in the Mammal Collection of Museo de La Plata (MLP-Mz), thus allowing us to confirm or emend previous host identifications (Tables 2, 3).

Table 1. Helminth sets from Locality I (Balcarce, Argentina, type locality of *Stilestrongylus azarai*). In parentheses, intensity of infection.

Accession N° MLP-He	Host ID	Heligmonellid species	Other intestinal parasites
674	*Akodon azarae*	*Stilestrongylus azarai* (187)	Rictulariidae undet. (3) Cestoda undet. (3) *Trichuris* sp. (23) *Syphacia* sp. (6)
675	*A. azarae*	*S. azarai* (5)	–
676	*A. azarae*	*S. azarai* (14)	*Syphacia* sp. (3)
683	*A. azarae*	*S. azarai* (31)	*Syphacia* sp. (98)
686	*A. azarae*	*S. azarai* (7)	*Syphacia* sp. (15)
687†	*A. azarae*	*S. azarai* (13)	*Trichuris* sp. (44)

†type host of *S. azarai*.

Morphological study

Worms were studied in toto under a light microscope (Leica DM2500 equipped with a drawing attachment). Measurements are provided in micrometres unless stated otherwise, with the range followed by the mean (in parentheses) and the coefficient of variation expressed as a percent value. Transverse body sections were made and mounted for synlophe examination. The sections are oriented with the dorsal side of the worm towards the top of the page and the left side of the worm towards the left of the page.

Table 2. Helminth sets from Locality II (RN 12 Km 100, Campana, Argentina, type locality of *Stilestrongylus oryzomysi*). In parentheses, intensity of infection. The host's identity was confirmed by the re-examination of the voucher specimen. No other taxa were present in the intestine.

Accession N° MLP-He	Host N° in MLP-Mz	Host ID	Heligmonellid species
1905	3072	*Oligoryzomys flavescens*	*Guerrerostrongylus zeta* (10) *Stilestrongylus flavescens* (23)
1906	3090	*O. flavescens*	*G. zeta* (3) *S. flavescens* (76)
1907	3073	*Oligoryzomys nigripes*	*G. zeta* (1) *S. flavescens* (26)
1913	3075	*O. nigripes*	*G. zeta* (1) *S. flavescens* (12) *Stilestrongylus lanfrediae* (1)
1911	3074	*Akodon azarae*	*Stilestrongylus azarai* (93)
1914	3076†	*A. azarae*	*S. azarai* (9) *Trichofreitasia lenti* (16)
1915	3077	*A. azarae*	*S. azarai* (93) *T. lenti* (1)
1933	3078	*A. azarae*	*S. azarai* (13)
1940	3079	*A. azarae*	*S. azarai* (7)

†symbiotype of *S. oryzomysi* and *Trichofreitasia lenti*.

Molecular study

All attempts to obtain DNA from the aged material deposited in the MLP-He were unsuccessful, and DNA had to be extracted from specimens collected in localities other than the type localities (Table 6). These were recovered from *A. azarae* and *Oligoryzomys nigripes* (Olfers) and identified as *S. azarai* and *G. zeta*, respectively, on morphological criteria. The posterior ends of ethanol-fixed males were cut and individually stored in 70% ethanol as voucher specimens (accession numbers MLP-He 8101 to 8104). Genomic DNA was extracted from the remaining part of the body using a commercial kit (Promega) following the manufacturer's instructions. A region of nuclear rDNA including 18S 3'-terminus, ITS1, 5.8S subunit, ITS2, and 28S 5'-terminus (ITS+) was amplified using the primer sets ITS-F (5'-TTG AAC CGG GTA AAA GTC G-3') and ITS-R (5'-TTA GTT TCT TTT CCT CCG CT-3') (Stock et al. 2001), a PCR master mix (Productos Bio-Lógicos, Argentina), and 6 µl of DNA for a final volume of 50 µl under the following PCR conditions: an initial denaturation at 94 °C for 10 min, followed by 45 cycles at 94 °C for 30 s, 54 °C for 40 s, 72 °C for 80 s, and a final extension at 72 °C for 10 min. PCR products were analysed on 1.5% agarose gel electrophoresis, stained with ethidium bromide, and visualised on a UV transilluminator. Amplicons were submitted for sequencing to Macrogen Inc. (South Korea) with the same primers used for amplification.

The obtained sequences ranged between 995 and 1010 bp in length; they were manually edited and compared with those in GenBank using the BLASTn tool (Altschul et al. 1990) to determine their phylogenetic position. Alignments were made with MUSCLE through MEGA v10.2.6 (Kumar et al. 2018) and

Table 3. Helminth sets from Locality III (Bella Unión, Uruguay, type locality of *Guerrerostrongylus uruguayensis*). In parentheses, intensity of infection. In bold, the host's identity was confirmed by a voucher specimen. Otherwise, host identification is based on field notes.

Accession N° MLP-He	Host N° in MLP-Mz	Host ID	Heligmonellid species	Other intestinal parasites
2046	–	"*Oryzomys*" †	*Guerrerostrongylus zeta* (5) *Stilestrongylus flavescens* (57)	
2047	**3080**	***Oligoryzomys nigripes***	*G. zeta* (14) *S. flavescens* (10)	*Syphacia* sp. (1)
2048	**3081**	***Oligoryzomys flavescens***	*G. zeta* (9) *S. flavescens* (16)	–
2049	**3082**	***O. nigripes***	*G. zeta* (7) *S. flavescens* (17)	*Syphacia* sp. (5)
2050	–	No field data	*G. zeta* (19) *S. flavescens* (51)	–
2052	**3083**	***O. nigripes***	*G. zeta* (48) *S. flavescens* (45)	–
2054	–	No field data	*G. zeta* (7) *S. flavescens* (23)	*Strongyloides* sp. (1)
2056	–	"*Oryzomys*"	*G. zeta* (18) *S. flavescens* (5)	*Syphacia* sp. (3)
2057	–	"*Oryzomys*"	*G. zeta* (8)	–
2058	**3084**	***O. nigripes***	*G. zeta* (20) *S. flavescens* (5)	*Syphacia* sp. (7)
2059	–	"colilargo"	*G. zeta* (40) *S. flavescens* (38)	–
2062	–	"*Oryzomys*"	*G. zeta* (13) *S. flavescens* (7)	–
2063	**3085**	***O. nigripes***	*G. zeta* (25) *S. flavescens* (3)	–
2064	**3086**	***O. flavescens***	*G. zeta* (47) *S. flavescens* (12)	*Syphacia* sp. (7)
2067	–	"*Oryzomys*"	*G. zeta* (27) *S. flavescens* (47)	–
2068	**3088**	***O. flavescens***	*G. zeta* (9) *S. flavescens* (20) *Hassastrongylus hoineffae* (1)	–
2069	–	"*Oryzomys*"	*G. zeta* (21) *S. flavescens* (41)	*Syphacia* sp. (3)
2051	–	"*Akodon*"	*S. azarai* (66)	Rictulariidae undet. (2) Cestoda Hymenolepididae (1)
2055	–	"*Akodon*"	*S. azarai* (315)	Physalopteridae undet. (stomach) (1) *Pterygodermatites* sp. (1)
2061	–	"*Akodon*"	*S. azarai* (2)	*Syphacia* sp. (2) Rictulariidae undet. (1)
2066	**3087**	***Akodon azarae***	*S. azarai* (23)	–
2070	**3089**	***A. azarae***	*S. azarai* (67)	*Syphacia* sp. (1)
2072	–	No field data	*S. azarai* (17)	–

†type host of *Guerrerostrongylus uruguayensis* and *Stilestrongylus flavescens*.

further edited with GBlocks (Castresana 2000). The genetic distances were calculated using the p-distance method as implemented in MEGA v10.2.6 with default parameters. The nucleotide substitution model was selected using jModelTest v2.1 based on the best-fitting model indicated by the Bayesian Information Criterion (BIC) (Darriba et al. 2012). Maximum likelihood analysis was performed in MEGA with 1,000 bootstrap replicates. Posterior probabilities of all branches were calculated using Bayesian-based inference as implemented in MrBayes v3.2, and analyses were run for 20,000,000 generations (Ronquist et al. 2012). *Uncinaria lucasi* Stiles, 1901 (Ancylostomatidae) was used as an outgroup. The resulting phylogenetic trees were edited in FigTree v1.4.4.

It is worth mentioning that, despite several attempts, we failed to amplify the mitochondrial cytochrome c oxidase subunit 1 (COI) gene using the primer sets COIintF (5′-TGATTGGTGGTTTTGGTAA-3′) and COIintR (5′-ATAAGTACGAGTATCAATATC-3′) (Casiraghi et al. 2001), LCOI1490 (5'-GGTCAACAAATCATAAAGATATTGG-3'), and HCOI2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994).

Results

Morphological study

Order Strongylida (Railliet & Henry, 1913)
Suborder Trichostrongylina (Leiper, 1908, family) Durette-Desset & Chabaud, 1993
Family Heligmonellidae (Skrjabin & Schikhobalova, 1952 tribe) Durette-Desset & Chabaud, 1977
Subfamily Nippostrongylinae Durette-Desset, 1971

Genus *Stilestrongylus* Freitas, Lent & Almeida, 1937

Figs 1, 2, Table 4

Stilestrongylus azarai Durette-Desset & Sutton, 1985

Redescription. Based on type material (see Material and Methods) and 27 voucher specimens from the same sampling event (14 males, 13 females).

General. Worms small to medium-sized, varying from loosely to tightly coiled, usually with 2–3 spires in anterior portion of body.

Head. Observed in two voucher specimens. Rounded buccal opening surrounded by thin ring; 2 amphids;

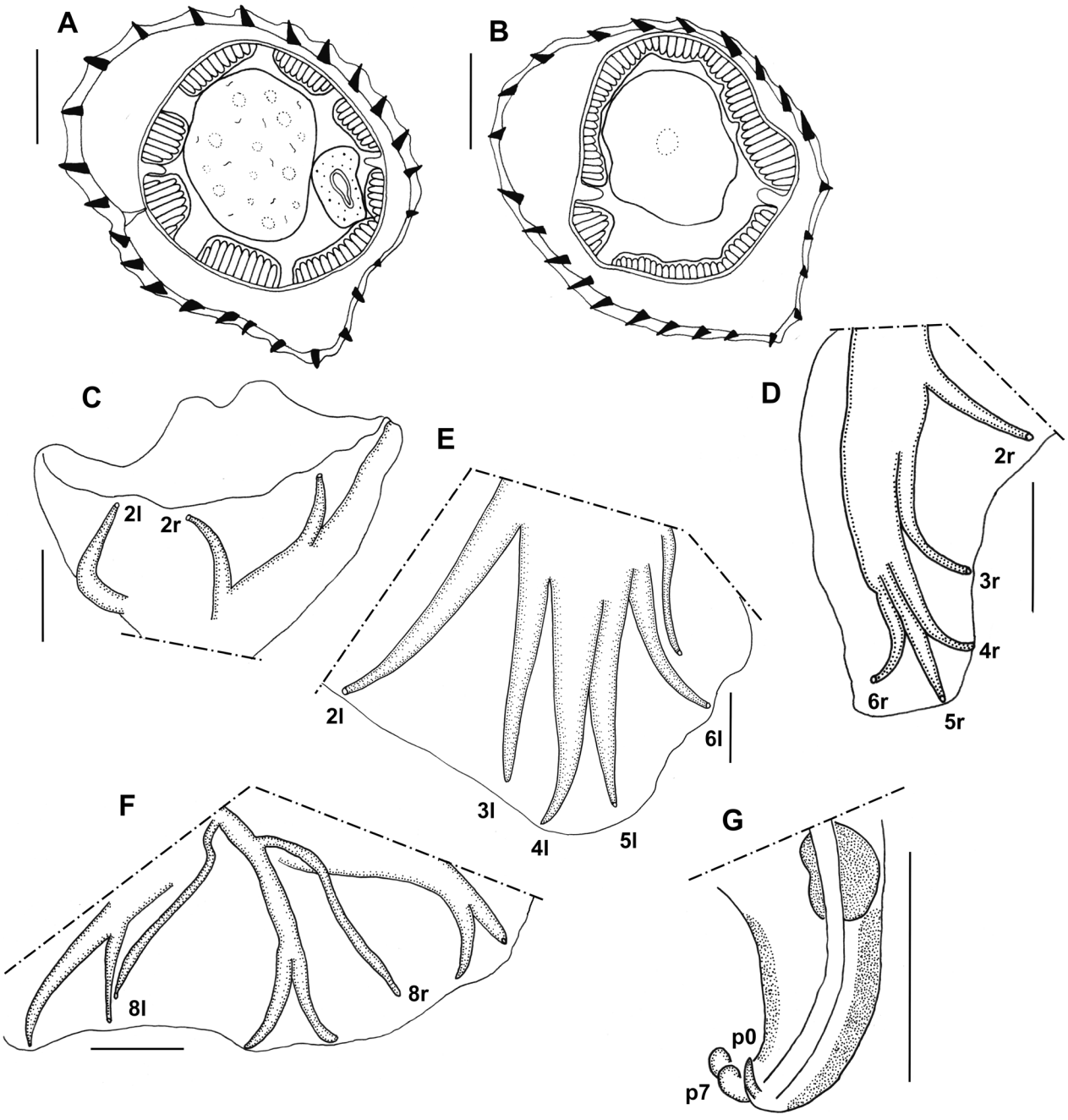

Figure 1. *Stilestrongylus azarai*. **A, B.** Synlophe in transverse section at midbody: **A.** Male; **B.** Female; **C.** Male caudal bursa, ventral view showing papillae 2; **D.** Right lobe of bursa, dorsal view; **E.** Left lobe of bursa, dorsal view; **F.** Dorsal lobe of bursa, dorsal view; **G.** Genital cone, left lateral view. **2l-6l** - left bursal rays 2 to 6; **8l** - left ray 8; **2r-6r** - right bursal rays 2 to 6; **8r** - right ray 8; **p0** - single papilla 0; **p7** - paired papillae 7. Scale bars: 20 µm (**A, B, E**); 50 µm (**C, D, F, G**). **C, G** from paratypes. **A, B**, and **D–F** from other specimens in *A. azarae* from the type locality (Balcarce).

4 externo-labial (2 dorsal, 2 ventral); and 4 cephalic papillae visible; lateral externo-labial papillae probably fused with amphids; each cephalic papilla connected with its contiguous externo-labial papilla by thickening, shaped as arc of circle (see description in Digiani and Durette-Desset 2003c).

Synlophe. Studied in 1 male and 1 female. Identical to that illustrated by Durette-Desset and Sutton (1985). With 25 subequal ridges in both sexes. Double axis of orientation of ridges: right axis inclined at 60° to sagittal axis, left axis at 80°. Twelve dorsal and 13 ventral ridges with respect to axis of orientation (Fig. 1A, B).

Males. Measurements in Table 4. Bursa large, bell-shaped, and dissymmetrical, with dorsal lobe well developed and right lobe markedly larger than left one. Prebursal papillae not observed. Bursa characterised by papillae 2 (ventral) very close (45–50 µm) to each other (Fig. 1C), implying that lobes were studied separately

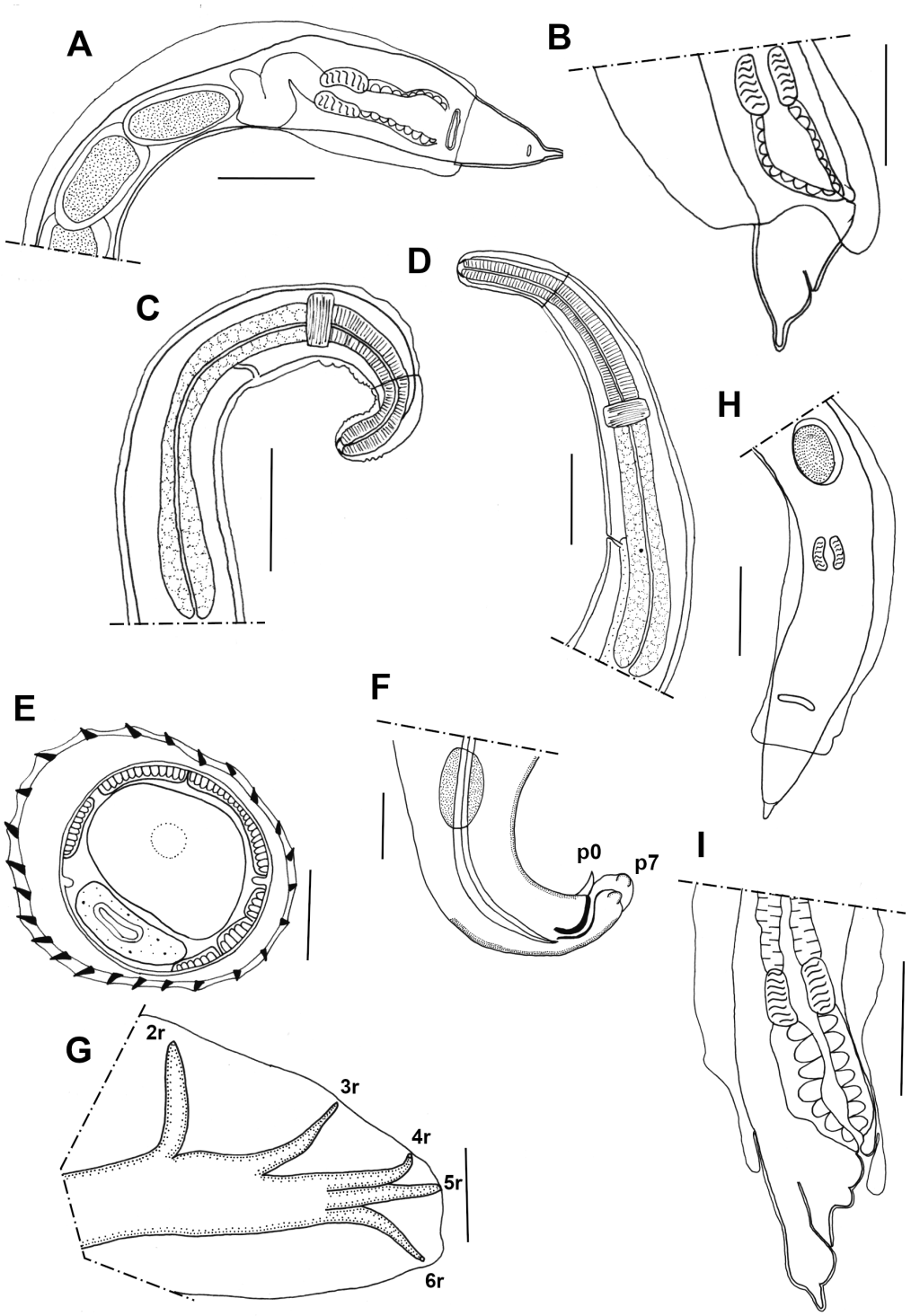

Figure 2. *Stilestrongylus azarai*. **A, B.** Female posterior end: **A.** Ventral view; **B.** Right lateral view; **C, D.** Anterior end: **C.** Curved and wrinkled, right lateral view (male); **D.** Stretched, left lateral view (female); **E.** Female synlophe in transverse section at mid-body; **F, G.** Male: **F.** Genital cone, right lateral view; **G.** Right lobe of caudal bursa, dorsal view; **H, I.** Female, posterior end: **H.** Ventral view; **I.** Right lateral view. **2r-6r** - right bursal rays 2 to 6; **p0** - single papilla 0; **p7** - paired papillae 7. Scale bars: 50 μm (**A–D, G–I**); 20 μm (**E, F**). **A–C** from paratypes of *S. azarai*. **D** from another specimen in *A. azarae* from the type locality (Balcarce). **E, H**, and **I** from a paratype of *S. oryzomysi* from Campana. **F** and **G** from other specimens in *A. azarae* from Campana.

because spreading out the bursa would break them. Right lobe (Fig. 1D): pattern of type 1-4, with ray 2 arising first from long common trunk of rays 3–6. Ray 3 arising at mid-length of common trunk, but distance between papillae 2 and 3 larger than that between papillae 3 and 4. Rays 4–6 diverging nearly at same level at distal quarter of common trunk, forming the characteristic "lateral trident". Ray 6 curved posteriorly, may be slightly longer than rays 4 and 5. Rays 3, 4, 5, and 6 reaching bursal margin. Left lobe (Fig. 1E): pattern of type 2-2-1. Rays 2 and

Table 4. Comparison of measurements of *Stilestrongylus azarai* from Balcarce (type locality), Campana (including paratypes of *Stilestrongylus oryzomysi*), and San Luis City. Measurements are in micrometres, unless otherwise stated.

Locality (Province)	**Balcarce (Buenos Aires)**		**Campana (Buenos Aires)**		**San Luis Capital City (San Luis)**	
Host	***Akodon azarae***		***Akodon azarae***		***Graomys griseoflavus***	
Source	**This work**		**This work**		**Digiani & Durette-Desset (2003c)**	
Body length (mm) (BL)	♂ (n = 23) 2.12–2.75 (2.35) 6%	♀ (n = 19) 2.3–3.8 (3.1) 14.2%	♂ (n = 16) 2.03–3.39 (2.67) 19.4%	♀ (n = 20) 1.88–5.63 (3.33) 40.9%	♂ (n = 10) 3.00–4.00 (3.33)	♀ (n = 10) 4.5–5.7 (5.1)
Body width	50–90 (78) 15%	70–100 (82) 11.4%	50–120 (72) 34.4%	75–130 (106) 19.1%	120–150 (132)	100–140 (120)
Cephalic vesicle length	45–60 (53) 8.4%	55–60 (57) 4.6% (n = 6)	42–60 (54) 10.6%	40–65 (52) 13.5%	55–65 (61)	50–75 (65)
Cephalic vesicle width	18–30 (24) 15.1%	20–28 (25) 11.6% (n = 6)	20–28 (23) 14.4%	14–45 (24) 28.8%	30–40 (33)	35–40 (38)
Oesophagus length (OeL)	230–310 (277) 6.8%	280–330 (298) 5.8%	245–295 (273) 6.7%	210–340 (276) 13.6%	290–310 (300)	320–360 (344)
Nerve ring†	100–135 (113) 9.7% (n = 8)	110–135 (118) 9.8% (n = 5)	110–150 (130) 10.4%	90–170 (124) 14.4%	140–175 (155)	120–170 (150)
Excretory pore† (EP)	170–195 (176) 11% (n = 5)	195–220 (203) 7.1% (n = 3)	185–245 (214) 9.7% (n = 6)	157–250 (197) 16%	220–260 (239)	190–240 (220)
EP/OeL (%)	59.6–70.9 (64) 10.3% (n = 5)	59.1–73.3 (66.6) 10.7% (n = 3)	72.5–83.1 (77.8) 5.1% (n = 6)	61.3–76.9 (69.7) 8.3%	71.0–88.1 (79.2)	54.3–66.7 (61.8)
Deirids†	140–205 (177) 12.9% (n = 10)	195–220 (206) 6.4% (n = 4)	185–245 (219) 9.3% (n = 7)	160–245 (200) 16.2%	220–260 (239)	190–240 (220)
Spicule length (SpL)	310–460 (380) 10.2%	–	290–445 (366) 13.2%	–	440–480 (456)	–
SpL/BL (%)	14.4–18.9 (16.5) 8.7%	–	11.7–16.5 (13.8) 10%	–	11.3–16.0 (13.8)	–
Genital cone length	70–125 (88) 16.3%	–	60–135 (109) 20.7%	–	–	–
Genital cone width	27–50 (40) 16.7%	–	32–50 (42) 14.9%	–	–	–
Vulva‡	–	55–80 (68) 11.6% (n = 9)	–	32–88 (62) 27.5%	–	70–100 (82)
Vestibule length	–	30–65 (48) 22%	–	35–65 (54) 16.3% (n = 9)	–	55–75 (62)
Sphincter length	–	25–30 (27) 7.9%	–	20–30 (28) 12.9%	–	30–40 (38)
Infundibulum length	–	65–85 (77) 8.7% (n = 10)	–	70–80 (78) 6.5% (n = 4)	–	90–110 (104)
Uterus length (UtL)	–	270–880 (460) 31.2%	–	270–1000 (575) 45.4%	–	800–980 (874)
UtL/BL (%)	–	11.2–23.2 (15.5) 22.7%	–	11.3–21.1 (14.8) 22.2%	–	15–19 (17)
Tail length	–	20–35 (28) 16.7% (n = 7)	–	22–45 (34) 25.4% (n = 9)	–	20–25 (23)
Egg number	–	3–24 (9) 61.1%	–	3–12 (7) 42.4%	–	24–43

†distance from apex. ‡distance from posterior extremity.

3 diverging in "V" proximally. Very short common trunk of rays 4–6, with rays 3 and 6 diverging at same level. Rays 4 and 5 diverging last. All rays reach bursal margin. Distance between papillae 2 and 3 slightly larger than that between papillae 5 and 6. Papillae 3, 4, and 5 approximately equidistant from each other. Rays 2 thickest and 6 thinnest. Dorsal lobe well developed, displaced to the left, compensating the reduced size of left lobe. Dorsal ray very long, divided at about its distal quarter into two branches, each one bifurcated distally into two papillae, external rays 9 and internal rays 10. Arising and path of rays 8 markedly dissymmetrical (Fig. 1F). Left ray 8 arising proximally from dorsal ray, nearly at its base; then running close and parallel to left trunk, approaching to and ending near left papilla 6. Right ray 8 arising more distally on dorsal ray, at about its proximal quarter, running between right trunk and dorsal ray, then heading distally towards right ray 6 but ending far from it. Genital cone long, well developed, bulbous at base, strongly curved ventrally in distal part. Distal half of cone with sclerotised walls. Dorsal lip bearing two rounded conspicuous papillae 7; ventral lip with single lappet-shaped papilla 0 (Fig. 1G). Gubernaculum conspicuous. Spicules thin and alate, ending in single sharp tip.

***Females*.** Measurements in Table 4. Reproductive tract monodelphic. Uterus less than 20% of body length; eggs few (3–9). Infundibulum slightly longer than vestibule. Posterior extremity straight or barely curved. Slight cuticular inflation from level of distal uterus up to vulvar aperture. Tail short and stout, ending in mucron (Figs 2A, B). Posterior end moderately retractile.

Voucher material examined. Argentina • 2 ♂♂, 2 ♀♀; Buenos Aires Province, Balcarce; 1977–1978; Sutton leg.; *Akodon azarae*; MLP-He 0674-1 • 3 ♂♂; same collection data as for preceding; MLP-He 0675-1 • 1 ♂, 1 ♀; same collection data as for preceding; MLP-He 0676-1 • 5 ♂♂, 6 ♀♀; same collection data as for preceding; MLP-He 0683-1 • 3 ♂♂, 4 ♀♀; same collection data as for preceding; MLP 0686-1.

Prevalence and mean intensity. P=100% (n=6), MI=42.8 (range 5–187) (Table 1).

Remarks. Worms of the type series showed strong contraction and curvature of the anterior body (Fig. 2C). Indeed, the body portion between the cephalic vesicle and the oesophageal-intestinal junction often appeared considerably wrinkled, hindering measurements of soft organs in this region (Table 4). On the contrary, the posterior body was relaxed, stretched, and easily accessible for measurements. The scarcity of material led us to include additional specimens from other *A. azarae* hosts collected in the same sampling event. We examined a total of five complete helminth sets, all of which were composed of worms assignable to *S. azarai*. Among these, we selected worms with relaxed and stretched anterior ends (Fig. 2D) to take measurements of the proximal part.

Specimens identified as *Stilestrongylus oryzomysi* Sutton & Durette-Desset, 1991

Fig. 2, Table 4

Considerations on the type host species. The rodent with field number 1914, designated as the type host of *S. oryzomysi* and *T. lenti* by Sutton and Durette-Desset (1991), was originally attributed to "*Oryzomys flavescens*" (current name= *Oligoryzomys flavescens*). After re-examination of the voucher (now designated as symbiotype) in MLP-Mz (accession N° 3076), it was found to belong to *A. azarae* (Table 2, Fig. 3). Therefore, *A. azarae* is the actual type host species of *S. oryzomysi*.

Examination of the type series. *Head*. Observed in one female paratype. Identical to that illustrated by Sutton and Durette-Desset (1991).

***Synlophe*.** Based on one female paratype. With 25 subequal ridges, regularly spaced, mostly oriented from right-ventral to left-dorsal quadrant, with axis of orientation inclined at about 60° to sagittal axis. Right-ventral ridges smallest (Fig. 2E).

***Males*.** Proximal part of body loosely coiled. Genital cone long, well developed, strongly curved ventrally in distal part. Distal half of cone with sclerotised walls. Dorsal lip bearing two papillae 7; ventral papilla 0 not observed. Gubernaculum conspicuous. Spicules thin and alate, ending in single sharp tip (Fig. 2F).

***Females*.** Body varying from loosely coiled in 2–3 irregular spirals to tightly coiled in up to 5 spirals. Monodelphic. Uterus less than 20% of body length; eggs few (3–9). Infundibulum longer than vestibule. Posterior extremity mostly straight, sometimes slightly curved ventrally. Cuticular inflation present from level of ovejector up to vulvar aperture. Posterior end retractile into inflation, never completely invaginated. Tail short and stout, ending in mucron (Fig. 2H, I).

Remarks. The worms in the type series of *S. oryzomysi* were relaxed and stretched, and diaphonisation was unnecessary for taking measurements. However, the males showed excessive flattening of the body, hindering the study of the bursa. Additional worms had to be included from the same sampling event due to material scarcity. We examined the complete helminth sets recovered from two *O. flavescens*, two *O. nigripes*, and five *A. azarae*. None of the *Oligoryzomys* spp. harboured worms assignable to *S. oryzomysi*. Instead, they were parasitised by *S. flavescens* (P=100%, MI=34.2) and to a lesser degree, by *Stilestrongylus lanfrediae* Souza, Digiani, Simões, Rodrigues-Silva & Maldonado, 2009 (Table 2). On the other hand, specimens of *A. azarae* were consistently parasitised by worms assignable to *S. azarai* (P=100%, MI=43) (Fig. 2G). Both *A. azarae* and *Oligoryzomys* spp. were also parasitised by nippostrongylines of other genera: two *A. azarae* specimens harboured *T. lenti*, and all *Oligoryzomys* spp. harboured *G. zeta* (P=100%, MI=3.7) (Table 2).

Voucher material examined. Argentina • 11 ♂♂, 10 ♀♀; Buenos Aires Province, Campana, National Route 12 (RN12) Km 100–101; [34°00'27.432"S, 58°58'29.28"W]; Apr. 1989; Sutton leg.; *Akodon azarae*, MLP-Mz 3074; MLP-He 1911-1 • 3 ♂♂; same collection data as for preceding; MLP-Mz 3079; MLP-He 1940-1.

Genus *Guerrerostrongylus* Sutton & Durette-Desset, 1991

Fig. 4, Table 5

Guerrerostrongylus zeta (Travassos, 1937)
Longistriata zeta Travassos, 1937
Hassalstrongylus zeta (Travassos, 1937): Durette-Desset, 1971
Guerrerostrongylus zeta (Travassos, 1937): Sutton & Durette-Desset, 1991

Main diagnostic characters. Body large to very large (males 4.20–8.40, females 5–13.7 mm), uncoiled or coiled irregularly; cephalic vesicle relatively short and stout. Synlophe with numerous (>35) continuous, subequal ridges, oriented from right to left (right, dorsal, and ventral ridges) or perpendicular to body surface (left ridges). Males: 37 to 44 ridges, caudal bursa subsymmetrical, elliptical to rectangular, pattern 2-2-1 tending to 1-3-1, dorsal lobe well developed; rays 6 longest, arising at same level as rays 2; rays 8 arising at proximal 1/4 or

Table 5. Comparison of measurements of *G. zeta* from different sources (including types of *Guerrerostrongylus uruguayensis*). Measurements are in micrometres except otherwise stated.

	Travassos 1937 (description)		Digiani et al. 2012 (redescription, on voucher material)		Simões et al. 2012a (redescription, on syntypes and voucher material)		Werk et al. 2016 (new locality records)		This work	
	♂ (n = ?)	♀ (n = ?)	♂ (n = 23)	♀ (n = 27)	♂ (n = 10)	♀ (n = 10)	♂ (n = 10)	♀ (n = 10)	♂ (n = 22)	♀ (n = 21)
N° of ridges at midbody	?	?	40–44 (n = 4)	35–48 (n = 7)	37 (syntypes, n = 1) 36–42 (vouchers, n = 2)	53 (syntypes, n = 1) 38–42 (vouchers, n = 2)	40–46 (n not specified)		38–53 (n = 4)	40–50 (n = 4)
Body length (mm) (BL)	6400	6800–7300	4.4–8.4 (6.75)	5.5–13.7 (9.17)	4.28–6.90 (5.2)	5.06–12.67 (8.41)	6.6–10.7 (8.5)	10.2–17.9 (14.5)	4.35–8.9 (7.0) 18.3%	4.95–14.9 (9.47) 21.8%
Body width	150	140–150	140–290 (197)	100–290 (197)	80–180	100–320	83–157	157–230	90–250 (176) 24.6%	200–350 (247) 16.1%
Cephalic vesicle length	45–52	45–52	35–70 (56)	35–65 (55)	43–70	40–74	55–64	46–64	40–60 (50) 12.2%	40–70 (49) 17.8%
Cephalic vesicle width	–	32–40 (36)	30–60 (44)	35–60 (43)	20–56	36–67	46–55	46–64	30–70 (47) 23.4%	30–55 (41) 19.6%
Oesophagus length (OeL)	340–470	340–470	345–495 (401)	350–500 (411)	340–716	260–390	369–498	500–672	315–375(348) 8.2% (n = 5)	330–430 (383) 9.9% (n = 6)
Nerve ring†	–	–	190–295 (234)	130–285 (169)	70–233	100–250	182–314	434	120–145 (132) 9.6% (n = 3)	135–210 (178) 21.8% (n = 3)
Excretory pore† (EP)	200	200	250–345 (305))	345–380	229–633	221–402	323–425	455,470	185–225 (203) 9.9% (n = 3)	205–270 (237) 13.7% (n = 3)
EP/OeL (%)	–	–	66–84	75–81 (n = 12)	–	58.8–73.9 (66.1) (n = 5)	–	–	–	58.7–77.1 (66) 14.8% (n = 3)
Deirids†	–	–	250–380 (315)	235–275 (253)	235–327 (267) (n = 4)	200–268 (233) (n = 3)	–	–	230 (n = 1)	330 (n = 1)
Spicule length (SpL)	877	–	750–1420 (1115)	–	580–1160	–	800–1300	–	810–1130 (963) 10.7%	–
SpL/BL (%)	13.7	–	10.6–24.4 (15.5)	–	–	–		–	11.8–18.6 (15) 14.9%	–
Vulva‡	–	112–135	–	112–255 (176)	–	105–233	–	157–277	–	105–145 (130) 10.9% (n = 6)
Uterus length (UtL)	–	–	–	800–1560 (1230)	–	1350–2540	–	–	–	1400–1950 (1622) 14.1%
UtL/BL (%)	–	–	–	9.5–22.4 (16.1)	–	–	–		–	15.4–21.9 (19.2) 11.8% (n = 6)
Tail length	–	43–45	–	40–100 (70)	–	43–97	–	42–61	–	35–60 (49) 18.7% (n = 6)
Egg number	–	–	–	6–50 (28)	–	–	–	>50	–	41–130 (80) 40.1% (n = 6)

†distance from apex. ‡distance from posterior extremity.

1/3 of dorsal trunk. Genital cone moderately developed, telamon V-shaped, spicules long and thin with undulating or winding pattern. Females: 35 to 53 ridges; vestibule as long as infundibulum; uterus ca. 20% of body length; eggs numerous. Posterior extremity straight; tail conical, not retractile. Tail length about 1/3 of distance from vulva to posterior extremity (from Travassos 1937; Digiani et al. 2012; Simões et al. 2012a).

Specimens identified as *Guerrerostrongylus uruguayensis* Sutton & Durette-Desset, 1991

Fig. 4, Table 5

Considerations on the type host species. The rodent with field number 2046, designated as type host of *G. uruguayensis* and *Stilestrongylus flavescens* by Sutton and Durette-Desset (1991), was originally attributed to

Figure 3. *Akodon azarae* MLP-Mz 3076 (field number 1914), symbiotype of *Stilestrongylus oryzomysi* and *Trichofreitasia lenti*.

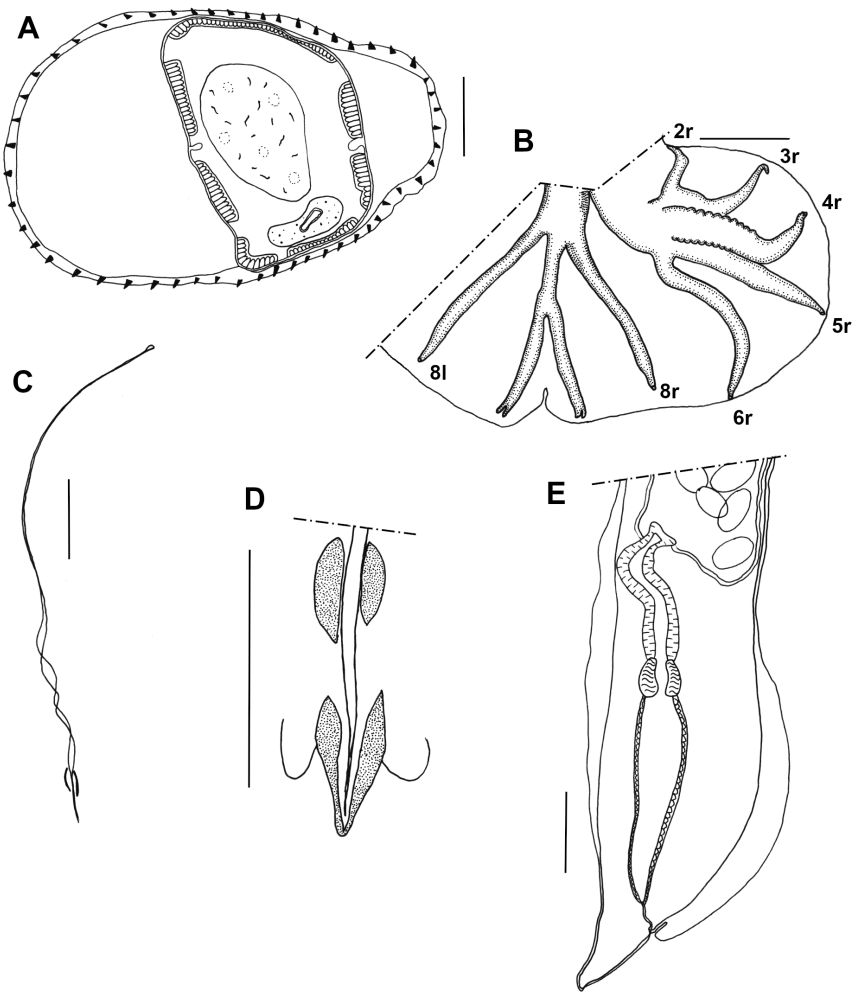

Figure 4. *Guerrerostrongylus zeta*. **A.** Male synlophe in transverse section at midbody; **B.** Male caudal bursa, dorsal view (left lobe omitted); **C.** Spicules, ventral view; **D.** Gubernaculum and genital cone, ventral view; **E.** Female, posterior end, right lateral view. **8l** - left ray 8; **2r-6r** - right bursal rays 2 to 6; **8r** - right ray 8. Scale bars: 50 µm (**A, D**); 100 µm (**B, C, E**). **A, B, D, E** from specimens of *Oligoryzomys nigripes* from Bella Unión. **C** from a paratype of *G. uruguayensis*.

"*Oryzomys flavescens*" (current name= *Oligoryzomys flavescens*). Unfortunately, its specific identity could not be established because no voucher was found in MLP-Mz or in other zoological collections. A symbiotype for these species is therefore lacking.

Examination of the type series. Most of the internal characters of the specimens could not be observed or measured because of their opaque bodies, even after using strong clearing agents. The low number of material prompted us to include more specimens from the same sampling event, and as a result, 16 complete helminth sets from hosts assigned to *Oligoryzomys* spp. were examined. All of them harboured several specimens of *Guerrerostrongylus* sp., which could be studied and measured.

General. Worms large to very large, uncoiled.

Head. Cephalic vesicle short and stout. Apical structures hardly visible. Oral aperture large, triangular, with rounded corners, and surrounded by thick ring. Four externo-labial papillae (dorsal and ventral) observed in one female.

Synlophe. Based on four males and four females. With 38–53 ridges in males (Fig. 4A), 40–50 in females. Ridges continuous, subequal, oriented from right to left (right, dorsal, and ventral ridges), or perpendicular to body surface (left ridges). Two prominent lateral cuticular dilatations, left larger than right one. Synlophe identical to those described by Digiani et al. (2012, figs 3, 4) and (Simões et al. 2012a, figs 4, 5) for *G. zeta*.

Males. Large to very large, uncoiled or coiled irregularly. Bursa subsymmetrical, elliptical, with pattern 2-2-1 tending to 1-3-1. Rays 6 longest, arising at same level as rays 2; rays 8 arising at proximal 1/4 of dorsal trunk. Some specimens show serrated ornamentation on margins of rays 4 or 4–5 and/or thickened bases of dorsal ray and rays 8 (Fig. 4B). Spicules long and thin with undulating pattern (Fig. 4C). Genital cone moderately developed, telamon V-shaped (Fig. 4D).

Females. Large to very large; vestibule as long as infundibulum; uterus ca. 20% of body length; eggs numerous. Posterior extremity straight; tail conical, not retractile. Tail length about 1/3 of distance from vulva to posterior extremity (Fig. 4E).

Voucher material examined. Uruguay • 1 ♂, 2 ♀♀; Artigas Department, Bella Unión, Colonia España; [30°21'52"S, 57°38'34"W]; Jul. 1989; Sutton leg.; *Oligoryzomys nigripes*, MLP-Mz 3080; MLP He-2047-1 • 3 ♂♂, 2 ♀♀; same data as for preceding; MLP-Mz 3084; MLP-He 2058-1 • 2 ♂♂, 2 ♀ ♀; same collection data as for preceding; "*Oryzomys*"; MLP-He 2056-1 • 4 ♂♂, 5 ♀♀; same data as for preceding; MLP-He 2057-1 • 6 ♂♂, 5 ♀♀; same data as for preceding; "colilargo"; MLP-He 2059-1 • 3 ♂♂, 1 ♀; same data as for preceding; *O. flavescens*, MLP-Mz 3086; MLP-He 2064-1.

Prevalence and mean intensity. P=100% (n=17), MI=19.8 (range 5–48) (Table 3).

Remarks. Some helminth sets from this sampling lacked the voucher host in the mammal collection. Only eight of them could be located, which corresponded to the helminth sets MLP-He 2047, 2049, 2052, 2058, and 2063 (*O. nigripes*); MLP-He 2048, 2064, and 2068 (*O. flavescens*) (Table 3). The hosts of the remaining helminth sets were a priori identified in the field and subsequently labelled as "*Oryzomys* sp." or "colilargo" (Table 3). Whether the identity of these hosts was further confirmed or not, they had helminth assemblages composed of *Guerrerostrongylus* spp. showing the features described above and of *S. flavescens* (P=94.1%, MI=21.2). One specimen identified as *O. flavescens* also harboured *Hassastrongylus hoineffae* (Durette-Desset, 1969). In addition, we examined six *A. azarae* from the same sampling event and found that they were parasitised by *S. azarai* (P=100%, MI=81.7), but not by any species of *Guerrerostrongylus* (Table 3).

Molecular study

Sequences of ITS+ were obtained from three specimens of *G. zeta* (970–973 bp) and one of *S. azarai* (950 bp) (Table 6).

After alignment with MUSCLE, we obtained 1056 positions, which were reduced to 910 using GBLOCKS. GTR+G was selected as the best-fit substitution model using MEGA and MRBAYES. The resulting trees show similar topology except for the position of *Nippostrongylus brasiliensis* (Travassos, 1914).

No genetic divergence is found between the sequences of *G. zeta* specimens (Table 7), which cluster together with *Hassalstrongylus* sp., forming a strongly supported monophyletic clade in both phylogenetic reconstructions (Figs 5, 6). In turn, a clade including these two species and *S. azarai* (South American nippostrongylines) was recovered in both phylogenetic analyses, though with lower support.

Discussion and conclusions

Taxonomic aspects

S. azarai / S. oryzomysi

We found no morphological differences among the type series of *S. oryzomysi*, the specimens of *S. azarai* harboured by *A. azarae* from the same sampling event, and the type series of *S. azarai*. The synlophe of a paratype of *S. oryzomysi* was identical to that of *S. azarai* in fig. IIc of Durette-Desset and Sutton (1985). Details of the ovejector and tail in the female and the bursa and genital cone in the male were identical in both type series. Therefore, we propose to consider the relative distances between papillae 2, 3, and 4 of the right lobe, the pathway of rays 8, and the appearance of the papillae on the genital cone as diagnostic characters of *S. azarai*. Moreover, the cephalic structures and arrangements observed by Sutton and Durette-Desset (1991) in worms from the locality of Campana were also observed in voucher specimens of *S. azarai*.

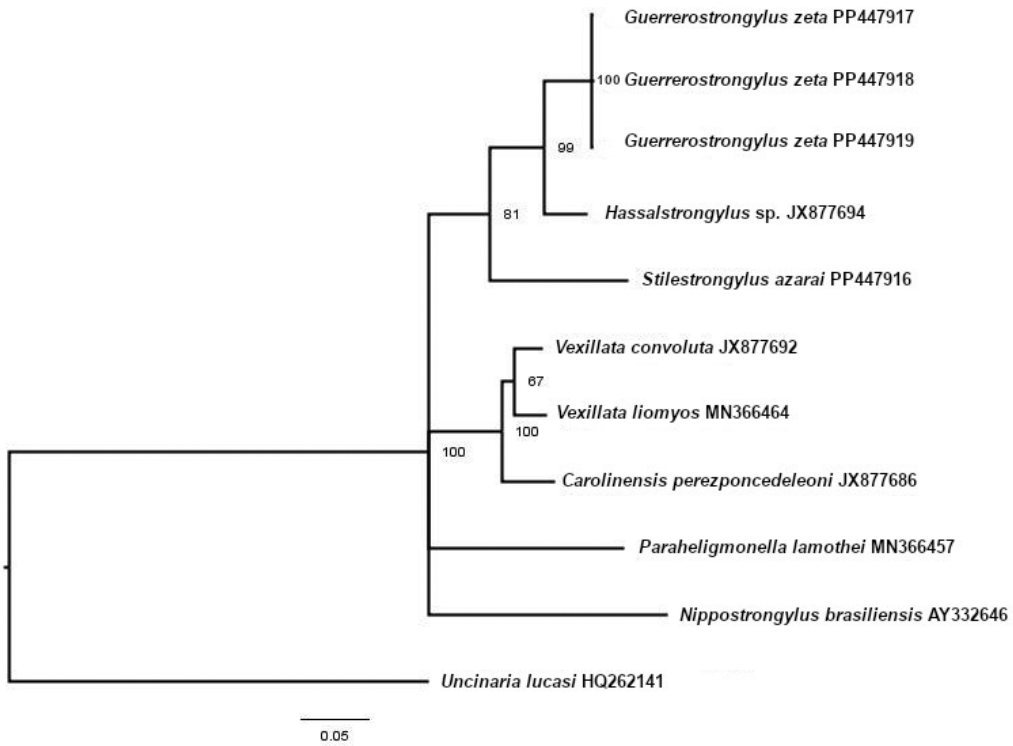

Figure 5. Phylogram resulting from Bayesian inference. The values next to the nodes are posterior probabilities (%). The scale bar represents the number of substitutions per site.

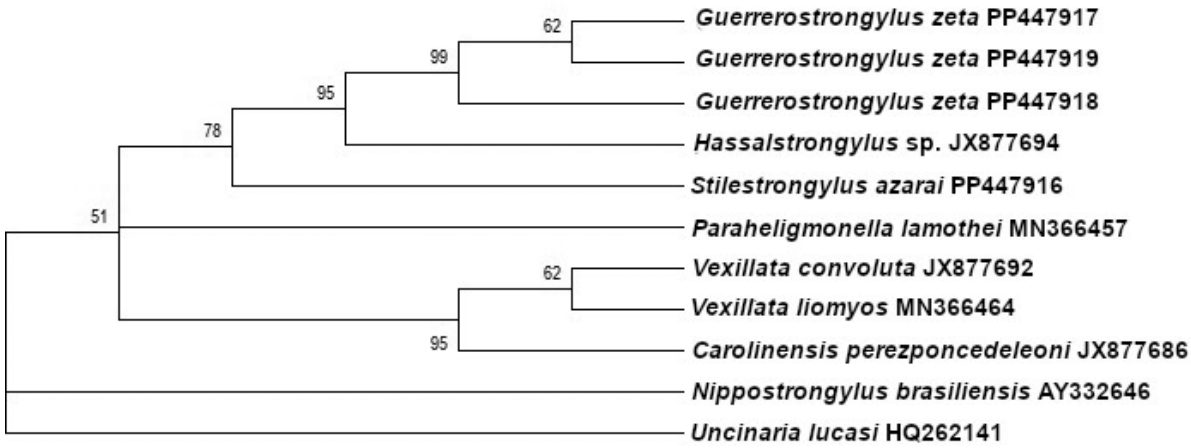

Figure 6. Maximum likelihood bootstrap consensus tree. Values next to the nodes are bootstrap proportions (%).

In regard to morphometry, most of the body length values obtained by us for *S. oryzomysi* were lower than those reported by Sutton and Durette-Desset (1991) (Table 4). *Stilestrongylus oryzomysi* was differentiated from *S. azarai* by the more distal position of the excretory pore (72–74% of the oesophagus length vs. 41–51%) and by the more developed genital cone (90 × 36 μm vs. 80 × 40 μm) (Sutton and Durette-Desset 1991). These characters are of poor diagnostic value in the Trichostrongylina, in which morphometric characters of soft organs may vary even within individual hosts (Durette-Desset et al. 2017). It should be kept in mind that the only measurements reported for both *S. azarai* and *S. oryzomysi* were taken from their holotypes and allotypes, probably accounting for their metric discrepancies. Moreover, the measurements of the anterior organs provided in the original description of *S. azarai* were most likely underestimated because the specimens of the type series were wrinkled. Digiani & Durette-Desset (2003c) also found differences between *S. azarai* specimens parasitising *Graomys griseoflavus* (Waterhouse) from San Luis province, Argentina, and those described in the original description (i.e., larger body measurements, a more distal position of the nerve ring and excretory pore, a larger number of eggs in the uterus) (see Table 4). Notwithstanding these metric discrepancies, the worms from San Luis unequivocally exhibited the diagnostic characters of *S. azarai*. Arc-like structures connecting the cephalic papillae were also present in the helminths of *G. griseoflavus* (figs 26, 33–35 of Digiani and Durette-Desset 2003c).

Table 6. Nematode family and species, host species, collection locality, and GenBank accession number for sequences of ITS+ rDNA used for phylogenetic analysis. In bold, the sequences obtained in this work.

Family	Species	Host	Locality	Accession number
Heligmonellidae	***S. azarai***	***A. azarae***	**Berisso, Buenos Aires province, Argentina**	**PP447916**
	***G. zeta* (1)**	***O. nigripes***	**Campo San Juan, Misiones province, Argentina**	**PP447917**
	***G. zeta* (2)**	***O. nigripes***	**Campo San Juan, Misiones province, Argentina**	**PP447918**
	***G. zeta* (3)**	***O. nigripes***	**Campo San Juan, Misiones province, Argentina**	**PP447919**
	Hassalstrongylus sp.	*Calomys* sp.	Santa Bárbara, Jujuy province, Argentina	JX877694
	Nippostrongylus brasiliensis	Rodents	Brest, France	AY332646
	Carolinensis perezponcedeleoni	*Nyctomys sumichrasti*	Catemaco, Veracruz, Mexico	JX877686
	Paraheligmonella lamothei	*Sylvilagus floridanus*	Chiapas, Mexico	MN366457
Ornithostrongylidae	*Vexillata liomyos*	*Liomys pictus*	Jalisco, Mexico	MN366464
	Vexillata convoluta	*Cratogeomys merriami*	Morelos, Mexico	JX877692
Ancylostomatidae	*Uncinaria lucasi*	*Eumetopias jubatus*	Hazy Island, Southeast AK, USA	HQ262141

Table 7. Genetic divergence among species of Heligmonellidae, estimated through the uncorrected p-distance of the ITS+ rDNA region.

		1	2	3	4	5	6	7	8	9	10	11
1	*Uncinaria lucasi* (outgroup)											
2	*S. azarai*	0.30										
3	*G. zeta* (specimen 1)	0.28	0.13									
4	*G. zeta* (specimen 2)	0.28	0.13	0.00								
5	*G. zeta* (specimen 3)	0.28	0.13	0.00	0.00							
6	*Hassalstrongylus* sp.	0.30	0.13	0.06	0.06	0.06						
7	*Vexillata convoluta*	0.28	0.16	0.14	0.14	0.14	0.14					
8	*Vexillata liomyos*	0.29	0.16	0.15	0.15	0.15	0.14	0.04				
9	*Carolinensis perezponcedeleoni*	0.30	0.16	0.14	0.14	0.14	0.15	0.05	0.06			
10	*Paraheligmonella lamothei*	0.31	0.18	0.17	0.17	0.17	0.17	0.16	0.17	0.17		
11	*Nippostrongylus brasiliensis*	0.33	0.22	0.27	0.27	0.27	0.24	0.21	0.19	0.20	0.24	

In conclusion, both type series appear to be morphologically identical, and after reassigning the symbiotype of *S. oryzomysi* (MLP-Mz 3076) to *A. azarae*, here we propose *S. oryzomysi* as a junior synonym of *Stilestrongylus azarai*.

Stilestrongylus oryzomysi was possibly regarded as a new species because it was described from a host mislabelled as *Oligoryzomys* spp. This assumption is based on the fact that *Oligoryzomys* spp. can be easily distinguished from *A. azarae*, even by non-experts. We believe that this labelling mistake would have been noticed if more hosts from the same sampling were examined at the time of describing the species.

Additionally, since the rodent MLP-Mz 3076 was also the symbiotype of *Trichofreitasia lenti* (Sutton and Durette-Desset 1991), it should be reassigned from *O. flavescens* to *A. azarae*.

G. zeta / *G. uruguayensis*

We found no morphological or metric differences among the type specimens of *G. uruguayensis*, the specimens of *Guerrerostrongylus* harboured by the remaining colilargos from the same sampling, and the specimens of *G. zeta* redescribed by Digiani et al. (2012) and Simões et al. (2012a). Diagnostic characters of *G. zeta*, such as the proportions of the cephalic vesicle, ray pattern of the bursa, details of the genital cone, telamon, and spicules, were observed in all the worms examined from the colilargos from Uruguay. In regard to morphometry, *G. uruguayensis* was differentiated from *G. zeta* by its larger body size. However, the description of *G. uruguayensis* was based only on the holotype and allotype, and it did not account for morphological or morphometric variability. On the other hand, our body length values obtained from the holotype and allotype were lower than those reported by Sutton and Durette-Desset (1991). Additionally, *G. uruguayensis* was differentiated from *G. zeta* by a widening of the body just anterior to the tail in the female; by bursal rays 6 longer than rays 8; by rays 8 arising from the base of the dorsal ray; and by the presence of cuticular ornamentation on rays 4 and 5 in the male (Sutton and Durette-Desset 1991). In females, body size is often related to age and the posterior widening to reproductive status, as gravid specimens bearing numerous eggs in the uterus usually have a widened pre-vulvar region. On the other hand, the bursal characters argued as diagnostic for *G. uruguayensis* are ambiguous and dependent on the degree of spreading of the bursa, or unspecific and subjected to individual variation. The following characters should be dismissed as diagnostic for *G. uruguayensis*: 1) rays 8 arising from the base of the dorsal ray, because all the specimens examined clearly showed a proximal common trunk to rays 8 and the dorsal ray; 2) rays 6 longer

than rays 8, because in the original description of *L. zeta* Travassos (1937) pointed out that rays 6 were the longest; 3) cuticular ornamentation on rays 4 and 5, because it was mostly absent and could be seen on the margins of rays 4 and 5 only in a few males. In addition, males with and without ornamentation coexisted in the same infrapopulation, suggesting that it may be a polymorphic trait or an artefact of fixation.

In conclusion, the comparison of the type series of *G. uruguayensis* against other specimens of *Guerrerostrongylus* from the same sampling event and against all available descriptions of *G. zeta* reported so far confirms that the worms examined herein parasitising *Oligoryzomys* spp. from Uruguay belong to *G. zeta*. This species was originally described as *Longistriata zeta* by Travassos (1937), then transferred to *Hassalstrongylus* by Durette-Desset (1971), and finally to *Guerrerostrongylus* by Sutton and Durette-Desset (1991). The identification of *G. uruguayensis* as a distinct species from that described by Travassos was likely due to the fact that both original descriptions were based on very few specimens, leading to the overestimation of metric differences and morphological variations without specific value. In addition, the description of *G. uruguayensis* was published in 1991, while the synlophe of *G. zeta* remained undescribed until many years later. Further redescriptions of *G. zeta* (Digiani et al. 2012; Simões et al. 2012a) based on paratypes and, especially, on larger sets of voucher specimens provided the description of the synlophe and a range of metric variability broad enough to include Travassos' specimens and the type material of *G. uruguayensis*. Consequently, *G. uruguayensis* is proposed as a junior synonym of *G. zeta*.

The rodent with field number 2046, consigned "*Oryzomys flavescens*" by Sutton and Durette-Desset (1991), is also the type host of *Stilestrongylus flavescens*. Due to the absence of a voucher, the identity of this rodent could not be ratified or rectified (see Table 3), and therefore it must follow the one designated in the original description. Then, the type host species of *S. flavescens* is, according to the current nomenclature, *Oligoryzomys flavescens* (= *Oryzomys flavescens*).

Host range and geographic distribution

The examination of the material has afforded an opportunity to clarify the taxonomic status of two of the examined nippostrongyline species as well as to shed light on the host spectrum and geographic distribution of some others. According to Sutton and Durette-Desset (1991), *O. flavescens* harboured *S. oryzomysi* and *T. lenti* in Argentina, and *S. flavescens* and *G. uruguayensis* in Uruguay. After examining numerous helminth sets, we found not only that this rodent harboured the same nippostrongyline assemblage on both sides of the Uruguay River but also that it was shared with *O. nigripes*. On the other hand, *A. azarae*, which is present in the same sampling localities as above, was strongly parasitised by *S. azarai* and, at least on the Argentinean side and to a lesser degree, by *T. lenti* (see Results and Tables 1, 2). Thus, this study extends the distribution range of *S. azarai* to include Uruguay and reports a new host record for *T. lenti* (*A. azarae*, type host species), a new host record for *G. zeta* in Argentina (*O. flavescens*), and the first record of helminths for *O. nigripes* in Uruguay.

***Stilestrongylus azarai*.** This species seems to be the main component of the helminth community of *A. azarae*. It has been found in most of the rodent's geographic distribution, which ranges from southern Brazil and eastern Paraguay south through Uruguay and central Argentina (Pardiñas et al. 2015). Up to the present, *S. azarai* has been recorded in the Argentinean provinces of Formosa, Chaco, Santa Fe, Entre Ríos, Corrientes, and Buenos Aires, and in Uruguay (Durette-Desset and Sutton 1985; Navone et al. 2009; Miño et al. 2012, 2019; Serrano 2024; this work). It has been rarely found in other hosts, always with relatively low prevalences and intensities of infection, e.g., in *Oligoryzomys fornesi* (Massoia) (P=14%, IM=4, n=7) and *Calomys callosus* (Rengger) (P=33%, IM=1, n=3) both from Chaco province (Serrano 2024). Four out of five *Reithrodon auritus* (Desmarest) from Balcarce (helminth sets housed in the MLP-He) harboured a few *S. azarai* specimens coparasitic with *Stilestrongylus aureus* Durette-Desset & Sutton, 1985 (Digiani pers. obs.). The three latter records were obtained from localities where the respective hosts live in sympatry with *A. azarae*, which is clearly the main host. *Stilestrongylus azarai* was also reported in *Graomys griseoflavus* from San Luis province (P=27.8%, and IM= 16.2, n=18), mainly coparasitic with a species of *Hassalstrongylus* (Digiani and Durette-Desset 2003c). To our knowledge, no other species of *Akodon* have been reported to harbour *S. azarai*. It would be interesting to investigate the role of *Akodon dolores* Thomas as the main host of this parasite in San Luis Province, where it is the only *Akodon* species present (Pardiñas et al. 2015).

On the other hand, *A. azarae* specimens have been rarely found harbouring heligmonellid species other than *S. azarai*, with the exception of *T. lenti*. In Corrientes province, this rodent was reported to be parasitised by *Stilestrongylus stilesi* Freitas, Lent & Almeida, 1937 (P=57%, Gómez-Muñoz et al. 2020) and *Hassalstrongylus dollfusi* (Díaz Ungría, 1963) (P=3.6%, Serrano et al. 2021), neither of which were coparasitic with *S. azarai*.

***Trichofreitasia lenti*.** Although it was not found in the Uruguayan sample, several helminth sets still remain unexamined. Moreover, its presence in Uruguay is expected given the fact that this species has already been reported from different *Akodon* species in Argentina and Brazil (Digiani et al. 2007; Simões et al. 2011, 2012b; Panisse et al. 2017; Cardoso et al. 2018; this work). In Brazil, *T. lenti* has been recorded in other host species, particularly *O. nigripes* (Simões et al. 2011, 2012b; Cardoso et al. 2019; Benatti et al. 2021), but these reports do not include either descriptions or illustrations and may deserve revision. In any case, none of the 22 samples of *Oligoryzomys*

spp. examined in the present survey contained *T. lenti*. Moreover, in another, more extensive survey, Serrano (2024) examined 179 *Oligoryzomys* spp. that were not parasitised by *T. lenti*.

***Guerrerostrongylus zeta*.** Numerous publications have confirmed that the main host of *G. zeta* is *O. nigripes* rather than its type host species, *Nectomys squamipes* (Brants). It was repeatedly reported parasitising *O. nigripes* from Argentina and Brazil (Pinto et al. 1982; Gomes et al. 2003; Simões et al. 2011, 2012a, 2012b; Digiani et al. 2012; Werk et al. 2016; Panisse et al. 2017; Cardoso et al. 2018, 2019; Boullosa et al. 2020; Kersul et al. 2020; Gentile et al. 2022). In Brazil, this species was also recorded in *O. flavescens* (Cardoso et al. 2018), *N. squamipes*, *Cerradomys subflavus* (Wagner), *Galea spixii* (Wagler) (Pinto et al. 1982), *Euryoryzomys russatus* (Wagner), *Akodon cursor* Winge, and *A. montensis* Thomas (Gomes et al. 2003; Simões et al. 2011; Boullosa et al. 2020; Kersul et al. 2020). However, these reports lack descriptions or illustrations. It is possible that at least the worm from *E. russatus* could belong to *Guerrerostrongylus ulysi* Digiani, Notarnicola & Navone, 2012, a species described from *Sooretamys angouya* (Fischer) in Misiones province, Argentina (Digiani et al. 2012) and later found in *E. russatus* in the same province by Panisse et al. (2017).

A special case involves females identified as *Guerrerostrongylus* sp. in *Akodon simulator* Thomas from Tucumán province (northwestern Argentina) (Digiani et al. 2007). These females showed the typical synlophe of *Guerrerostrongylus*, but their opacity precluded the observation of any diagnostic character and thus the identification at the species level. In turn, the males recovered from the same host were identified as *G. uruguayensis* before redescriptions and further reports of *G. zeta* from Argentina were available (Digiani et al. 2007). Although our results suggest that these males would belong to *G. zeta*, the information on their hosts is incomplete and uncertain. Therefore, newly collected material from a larger number of individually identifiable hosts is required for a more accurate identification of *Guerrerostrongylus* spp. associated with *A. simulator*.

Phylogenetic analysis

Despite the wide distribution of South American Nippostrongylinae (SAN) as parasites of sigmodontines, they remain poorly studied from a molecular approach, with only two studies involving molecular phylogenetic reconstructions. Scheibel et al. (2014) mainly focused on the nematode family Viannaiidae and solely included *Hassalstrongylus* sp. as a representative of SAN. Later, Weirich et al. (2016) used a fragment of the mitochondrial gene coding for the large ribosomal subunit RNA (rrnL) to analyse the phylogenetic position of *Guerrerostrongylus marginalis* (Weirich, Catzeflis & Jiménez, 2016), *Hassalstrongylus* sp., and *Stilestrongylus* sp., among other Trichostrongylina. In their phylogenetic tree, these species were clustered in a strongly supported monophyletic clade, though with greater genetic similarity between *Hassalstrongylus* sp. and *Stilestrongylus* sp. In the present study, we confirm, using a nuclear gene, the monophyly of the clade formed by *Stilestrongylus*, *Hassalstrongylus*, and *Guerrerostrongylus*, which are the three most speciose and widely distributed genera of SAN.

In the present study, we provide a significant amount of information on the taxonomy and geographic distribution of three nippostrongyline species obtained from the examination of several lots of material deposited in the Helminthological and Mammal Collections of the Museo de La Plata. Our findings confirm the importance of examining the largest possible number of specimens to describe new taxa and highlight the role of public biological collections as biodiversity repositories.

Acknowledgements

We are grateful to C. Damborenea and V.H. Merlo Alvarez from MLP-He and I. Olivares from MLP-Mz for facilitating access to collection material; to M. Ibañez Shimabukuro and M. Moncada from CEPAVE for molecular laboratory assistance; to M.M. Montes for helping with the phylogenetic analysis; to S. Pietrokovsky for the English revision; and to the three reviewers that helped to improve the first version of the manuscript. Special thanks are due to N. Cazzaniga for helping in the interpretation of the ICZN, to C. Galliari for helping in the identification of the voucher rodents, and to C. Lanzone and E. Soibelzon for providing the rodents harbouring the specimens used for molecular analysis. This research was supported by Agencia I+D+i, Argentina (grant PICT 2019-3535 to MCD) and CONICET, Argentina (grants PIP 2014-0429 and 2010-0006 to MCD). The authors declare that they have no conflict of interest.

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