New host, geographic records, and histopathologic studies of Angiostrongyulus spp (Nematoda: Angiostrongylidae) in rodents from Argentina with updated summary of records from rodent hosts and host specificity assessment

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To date, 21 species of the genus Angiostrongyulus (Nematoda: Angiostrongylidae) have been reported around the world, 15 of which are parasites of rodents. In this study, new host, geographic records, and histopathologic studies of Angiostrongyulus spp in sigmodontine rodents from Argentina, with an updated summary of records from rodent hosts and host specificity assessment, are provided. Records of Angiostrongyulus costaricensis from Akodon montensis and Angiostrongyulus morerai from six new hosts and geographical localities in Argentina are reported. The gross and histopathologic changes in the lungs of the host species due to angiostrongylosis are described. Published records of the genus Angiostrongyulus from rodents and patterns of host specificity are presented. Individual Angiostrongyulus species parasitise between one-19 different host species. The most frequent values of the specificity index (STD) were between 1-5.97. The elevated number of host species (n = 7) of A. morerai with a STD = 1.86 is a reflection of multiple systematic studies of parasites from sigmodontine rodents in the area of Cuenca del Plata, Argentina, showing that an increase in sampling effort can result in new findings. The combination of low host specificity and a wide geographic distribution of Angiostrongyulus spp indicates a troubling epidemiological scenario although, as yet, no human cases have been reported.

Key words: Angiostrongyulus - histopathology - host specificity - rodents - Sigmodontinae - Argentina

The main definitive hosts of angiostrongylid nematodes of the superfamily Metastrongyloidea are carnivores and rodents and the known intermediate hosts are molluscs (e.g., Acha & Szyfres 2003). To date, 21 species of the genus Angiostrongyulus Kamensky 1905 have been reported around the world. Six species have been described infecting carnivores: Angiostrongyulus vasorum Baillet 1866, Angiostrongyulus raiillieti Travassos 1927, Angiostrongyulus gubercanulatus Dougherty 1946, Angiostrongyulus chabaudi Biocca 1957, Angiostrongyulus daskalovi Yanchev & Genov 1988, and Angiostrongyulus felineus Vieira et al. 2013, and the remainder from rodents: Angiostrongyulus tateronae Baylis 1928, Angiostrongyulus cantonensis (Chen 1935), Angiostrongyulus sciarri Merdevenci 1964, Angiostrongyulus mackerrasae Bhaiublaya 1968, Angiostrongyulus sandarsae Alicata 1968, Angiostrongyulus petrovii Tarzhanimova & Chertkova 1969, Angiostrongyulus dujardini Drozd & Doby 1970, Angiostrongyulus schmidtii Kinsella 1971, Angiostrongyulus costaricensis Morera & Césedes 1971, Angiostrongyulus malaysiensis Bhaiublaya & Cross 1971, Angiostrongyulus ryjikovi (Jushkov 1971), Angiostrongyulus andersoni (Petter 1972), Angiostrongyulus siamensis Ohbayashi, Kamiya & Bhaiublaya 1979, Angiostrongyulus morerai Robles, Navone & Kinsella, 2008, and Angiostrongyulus lenzii Souza et al. 2009 (Baillet 1866, Travassos 1927, Baylis 1928, Dougherty 1946, Mackerras & Sandars 1955, Biocca 1957, Merdivenci 1964, Alicata 1968, Bhaiublaya 1968, Tarzhanimova & Chertkova 1969, Bhaiublaya & Cross 1971, Doby et al. 1971, Jushkov 1971, Kinsella 1971, Morera & Césedes 1971, Petter 1972, Ohbayashi et al. 1979, Yanchev & Genov 1988, Robles et al. 2008, Souza et al. 2009, Vieira et al. 2013, Spratt 2015). Except for two species, A. costaricensis and A. siamensis, which infect the mesenteric arteries of the caecum, all species inhabit the pulmonary arteries and right ventricle of the heart.

Among rodents, species of Angiostrongyulus are distributed in the Cricetidae, Echimyidae, Gliridae, Heteromyidae, Muridae, and Sciuridae. The best studied and most widely distributed species are A. cantonensis and A. costaricensis, which are primarily parasites of rodents but carnivores, marsupials and primates have also been recorded as definitive hosts (Maldonado et al. 2012) as well as abnormal/aberrant hosts (Spratt 2015). Both species are recognised as zoonotic; the first is the cause of the disease eosinophilic meningonecephalitis from different continents and the second of abdominal angiostrongyliasis from the Americas (Acha & Szyfres 2003, Maldonado et al. 2012, Spratt 2015).

The life cycles of eight species parasitising rodents have been studied: A. andersoni, A. cantonensis, A. costaricensis, A. dujardini, A. mackerrasae, A. malaysiensis, A. ryjikovi, A. tateronae, and A. vasorum. Both species are recognised as zoonotic; the first is the cause of the disease eosinophilic meningonecephalitis from different continents and the second of abdominal angiostrongyliasis from the Americas (Acha & Szyfres 2003, Maldonado et al. 2012, Spratt 2015).

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siensis, A. siamensis, and A. Schmidtii. In those species inhabiting the pulmonary arteries, eggs deposited by adults develop to first stage larvae in the lungs which move up the airways, are swallowed and pass in the faeces. This developmental pathway is exemplified by A. andersoni, A. djayardini, and A. Schmidtii (Kinsella 1971, Bhaiubulya 1975, Mota & Lenzi 2005, Spratt 2015). The resultant pathology has been described in species such as A. cantonensis, A. costaricensis, A. Mackerrasiae, A. morerai, A. sandarsiae, A. Schmidtii, and A. siamensis (Mackerras & Sandars 1955, Alicata 1968, Kinsella 1971, Tesh et al. 1973, Obhayashi et al. 1979, Mota & Lenzi 2005, Robles et al. 2012).

One of the most important properties characterising a parasite taxon is its host specificity. It is indicative of intrinsic biological characteristics of both host and parasite and an emergent property of their ecological and evolutionary relationship (Dick & Patterson 2007). Host specificity can be defined as the extent to which a parasite taxon is restricted in the number of host species used at a given stage in the life cycle (Poulin 2007).

In this paper, we provide new host and geographical records for two species of Angiostrongylus from sigmodontine rodents in Argentina and describe the gross and histopathologic changes in the lungs of the host species due to angiostrongyllosis. Moreover, we present comprehensive data on all the records of the genus Angiostrongylus from rodents and evaluate patterns of host specificity.

MATERIALS AND METHODS

Cricetid rodents were trapped during different field studies between 2007-2012 (see acknowledgements and financial support) and the following species were examined for angiostrongyliid nematodes: eight specimens of Deltamys kempi Thomas 1917 from Reserva Natural de la Costanera Sur (34º36'S 58º27'W), Ciudad Autónoma de Buenos Aires and La Balandra (34º56'S 57º42'W), Partido de Berisso, province of Buenos Aires, 11 specimens of Akodon montensis Thomas 1913 from RP2, 6 km NE, Arroyo Paraíso, (27º12'47.7"S 54º01'59.9"W) and Salto El Paraíso, Arroyo Paraíso (27º13'49.8"S 54º02'24.3"), conducted with the aid of a drawing tube. Each of the five lobes of the lungs was trimmed in the subterminal transversal part, processed, sectioned at 5 µm (+ 25 sections per slide), stained with haematoxylin and eosin (H&E), and examined microscopically. Quantitative parameters of prevalence (P = specimens parasitised/specimens examined x 100) was calculated according to Bush et al. (1997) for each host species and locality.

Records of species of Angiostrongylus from rodents were compiled from the literature (scientific papers and book sections). When necessary, scientific names of mammal hosts have been updated following Edwards et al. (1993), Wilson and Reeder (2005), Weksler et al. (2006), and Srinivasulu and Srinivasulu (2011). In order to evaluate host specificity, the specificity index (S_t) by Poulin and Mouillot (2003) was calculated. This index measures the average taxonomic distinctness of all host species used by a parasite species. All mammal species included were fitted into a taxonomic structure with six hierarchical levels above species, i.e., genus, subfamily, family, superfAMILY, order, and class (Mammalia). The range of index can vary between 1-6, and since the index cannot be computed for parasites exploiting a single host species, the value of zero is assigned to reflect strict host specificity. The value of this index is inversely proportional to host specificity. The asymmetries in the taxonomic distribution of host species were calculated through variance in taxonomic distinctness (VarS_t) (Poulin & Mouillot 2003). A record was defined as the finding of a parasite species on a definitive host and, at a given locality, regardless of the number of host sampled and of nematodes collected on a particular host. The aberrant host species reported (Maldonado et al. 2012, Spratt 2015) which showed signs of disease were included in the calculation of host specificity, but not the experimentally infected or accidental host species.

Adult specimens and H&E stained sections (slides) of lung were deposited in the Helminthological Collection of the Museo de La Plata (CHMLP A. costaricensis 7052 and A. morerai 7053-7059, respectively) and the hosts were deposited in the Mastozoological Collections of the Centro Nacional Patagónico (CNP 1968, 2338, 3004, 3723, 4079, 4080, 4027, 4602, field number CG 70, 78, RR 33), Puerto Madryn, Chubut, Argentina.

Ethics - The research has been conducted according to Argentine laws. Sample collection was carried out during fieldwork under official permits granted by Fauna and Flora of the Province of Buenos Aires (expedient 22500-7981/10), Ministry of Industry and Environment of the Province of Formosa (authorisation n/n; transit guide: 004076), Ministry of Ecology, Renewable Natural Resources, and Tourism of Misiones (authorisation 24 and 27, transit guides: 000316 and 000371). This study was carried out in accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health. The specimens obtained with methods for live capture were studied and humanely sacrificed following the procedures and protocols approved by national laws (Animal Protection National law 14.346 and references in the provincial permits) and Ethical Committee for Research on Laboratory Animals, Farm, and Obtained from Nature of National Council of Scientific and Technical Research (resolution 1047, section 2, annex II), and subsequently...
RESULTS

A single male specimen of *Angiostrongylus* found in the caecal mesenteric arteries of *Akodon montensis* from El Soberbio was identified as *A. costaricensis*. Adult specimens found in the pulmonary arteries and heart of *D. kempi* from La Balandra and Reserva Natural de la Costanera Sur, *A. montensis* and *S. angouya* from Refugio Moconá, and *A. azarae*, *C. callosus*, and *N. lasiurus* from Reserva El Bagual were identified on the basis of the morphology of the bursa, spicules, and diagnostic measurements as *A. morerai* (Fig. 1).

Table I lists prevalence of infections for all hosts examined. The prevalence of *A. costaricensis* was very low (9%). The highest prevalence of *A. morerai* was recorded in *D. kempi*. The region with the most records of this nematode was La Pampa ecoregion (P = 62.5%) in the province of Buenos Aires. The Selva Paranaense (province of Misiones) and Chaco Húmedo (province of Formosa) ecoregions showed similar values (P = 20% and 17.4%, respectively) (Table I).

| Host species                  | Locality                      | Prevalence by population (%) | Prevalence by ecoregion (%) |
|-------------------------------|-------------------------------|------------------------------|-----------------------------|
| *Angiostrongylus costaricensis* |                               |                              |                             |
| *Akodon montensis*            | Arroyo Paraíso                | 1/11 (9)                     | Selva Paranaense (9)        |
|                               |                               |                              |                             |
| *Angiostrongylus morerai*     |                               |                              |                             |
| *Deltamys kempi*              | La Balandra                   | 1/4 (25)                     | La Pampa (62.5)             |
|                               | Reserva Natural de la Costanera Sur | 4/4 (100)                  |                             |
| *A. montensis*                | Refugio Moconá                | 4/27 (14.8)                  | Selva Paranaense (20)       |
| *Sooretamys angouya*          | Refugio Moconá                | 2/3 (66)                     |                             |
| *Akodon azarae bibianae*      | Reserva El Bagual             | 2/11 (18.18)                 | Chaco Húmedo (17.4)         |
| *Calomys callosus*            | Reserva El Bagual             | 1/10 (10)                    |                             |
| *Necromys lasiurus liciae*    | Reserva El Bagual             | 1/2 (50)                     |                             |
Specimens of *A. morerai* were present in heart chambers (Fig. 2A) and in pulmonary arteries sometimes showing the complete obliteration of the lumen (Fig. 2B). The infected rodents showed macroscopic lesions (firm nodules) of verminous pneumonia in three, four, or five lobes. Each lung lobe contained multiple small yellowish nodules scattered throughout the parenchyma (Fig. 2C).

Additionally, histopathology examination of tissue fragments showed multiple nodules in the vessels, interstitium, and alveoli. Nodules were formed by larvae surrounded by an elevated number of granulocyte and mononuclear cells (Fig. 2M). The vessels, interstitium, and alveoli contained nematode larvae with mild to moderate interstitial fibrosis (Fig. 2F-M). Worms were
approximately 80-200 µm long and contained numerous discrete basophilic and eosinophilic granules (Fig. M). Numerous nodules (set of eggs and larvae) surround by granulomatous reactions were situated under the pleural surface (Fig. 2F, J). Several damaged capillaries and small arterioles were observed (Fig. 2D-H).

The lobe with the greatest intensity of larvae proportionally was the left upper followed by the right lower and right medium lobes, the right upper and left lower lobes, had similar, but smaller, intensities of infection. As estimation about one-five larvae per 200 µm² x 5 µm thickness could be observed in the left upper lobe. In the other lobes, the nodules were more scattered. The host with the most nodules (set of larvae) surrounded by granulomatous reactions was *C. callosus* (Fig. 2J, K).

Number of host species for all *Angiostrongylus* species found in rodents and values of $S_{TD}$ and $VarS_{TD}$ for each species are shown in Table II and depicted in Fig. 3. The distribution of number of host species was skewed considering only the natural infection by angiostrongylosis (Fig. 3). The figures clearly show that most *Angiostrongylus* species parasitise between one-19 different host species: five *Angiostrongylus* species were associated with a single species, *A. andersoni* and *A. sandarsae* were found in two host species, *A. dujardini* and *A. mackerrasae* in four host species, *A. morerai* and *A. siamensis* in six host species, and the rest in more than 10 host species. The values of $S_{TD}$ were between 1-5.97. The value of zero was assigned for five species to reflect the strict host specificity. *A. andersoni*, *A. sandarsae*, *A. mackerrasae*, *A. morerai*, and *A. siamensis* parasite species hosts that belong to different subfamilies ($S_{TD} = 1-2$), *A. dujardini* to different families ($S_{TD} = 2-3$), *A. malaysiensis* to different superfamilies ($S_{TD} = 3-4$), and *A. cantonensis* and *A. costaricensis* to different orders ($S_{TD} = 5-6$).

**DISCUSSION**

This is the first record of *A. morerai* from *A. montensis*, *C. callosus*, *D. kempi*, *N. lasiurus*, and *S. angouya* expanding its geographic distribution to the south and northwest of the provinces of Buenos Aires, Misiones, and Formosa. *A. costaricensis* is recorded for first time in *A. montensis* and in Argentina. The presence of *Angiostrongylus* spp in these hosts indicates the ingestion of unknown intermediate hosts, which are apparently frequent in the diet of rodents of the tribe Akodontini (e.g., *Akodon*, *Necromys*, *Deltamys*).

With respect to the gross and histopathologic changes in the lungs of the host species, a different degree of pathogenicity was observed among the hosts, with the highest being in *C. callosus* (Phyllotini). This is the first record of *Angiostrongylus* sp. in this tribe of sigmodontine rodents. As demonstrated in Robles et al. (2012), in *A. morerai*, the resulting immune reaction can cause interstitial fibrosis and the destruction of small capillaries and arterioles. In that study and here, extensive lesions were apparently caused by a single male and female (Fig. 2A, B). Macroscopic lesions of verminous pneumonia in the lungs were similar to those described for *A. mackerrasae* by Mackerras and Sandars (1955) and *A. sandarsae* by Alicata (1968). Histopathological examination revealed nodules formed as a result of larvae being surrounded by granulocytes and mononuclear cells (Fig. 2C-M).

Of the 15 species of *Angiostrongylus* parasitic in rodents, detailed descriptions of histopathologic changes are available for seven (*A. cantonensis*, *A. costaricensis*, *A. mackerrasae*, *A. morerai*, *A. sandarsae*, *A. siamensis*, and *A. schmidti*) and the life cycles of eight species have been studied (*A. andersoni*, *A. cantonensis*, *A. costaricensis*, *A. dujardini*, *A. mackerrasae*, *A. malaysiensis*, *A. siamensis*, and *A. schmidti*) (Mackerras & Sandars 1955, Ali-
| Parasite species                        | Host species                          | $S_{TD}$ and Var$S_{TD}$ | Country                                      | Site infection                                  | References                                                                 |
|----------------------------------------|---------------------------------------|--------------------------|----------------------------------------------|------------------------------------------------|---------------------------------------------------------------------------|
| *Angiostrongylus andersoni* (Petter 1972) | Gerbilliscus kempi*, Taterillus gracilis* | 2 and 0                  | Upper Volta (Africa)                         | Large abscesses in the lungs                      | Petter (1972)                                                             |
| *Angiostrongylus cantonensis* (Chen 1935) | Bandicota indica, Diplophrix legata, Melomys burtoni, Melomys cervinipes, Podomys floridanus*, Rattus rattus, Rattus norvegicus, No rodents, Canis lupus familiaris, Didelphis virginiana, Equus caballus, Homo sapiens, Pteropus poliocephalus, Pteropus alecto, Suncus murinus, Varecia variegata | 5.97 and 3.55            | China (Asia); Asian and Pacific Islands and Australia (Oceania); Brazil, Cuba, Haiti, Jamaica, Puerto Rico, United States of America (USA) (America) | Lungs and heart (central nervous system)                                   | Chen (1935), Mackerras & Sandars (1955), Cross (1979), Aguiar et al. (1981), Andersen et al. (1986), Alicata (1988), Wright et al. (1991), Cooke-Yarborough et al. (1999), Barrett et al. (2002), Kim et al. (2002), Lindo et al. (2002), Raccurt et al. (2003), Smales et al. (2004), Simões et al. (2011), Lunn et al. (2012), Maldonado et al. (2012), Ma et al. (2013), Morton et al. (2013), Okano et al. (2014) |
| *Angiostrongylus costaricensis* Morera & Cáspedes 1971 | Akodon montensis, Liomys adspersus, Melanomys caliginosus*, Oligoryzomys fulvescens*, Oligoryzomys nigripes, Oxymycterus hispidus*, Nephomys albigularis*, Proechimys sp., R. rattus, R. norvegicus, Sigmodon hispidus, Sooretamys angouya*, Zygodontomys revicaudas*, No rodents, Nasua narica, Saginus mystax, Symphalangus syndactylus*, Aotus nancymaeae, Procyn lotor, D. virginiana | 5.37 and 4.28            | Brazil, Colombia, Costa Rica, Dominican Republic, Ecuador, Mexico, Panama, Peru, Puerto Rico, USA, Venezuela, Argentina (America) | Caecum mesenteric arteries (intestinal wall)                               | Morera (1970), Tesh et al. (1973), Monge et al. (1978), Ubelaker & Hall (1979), Malek (1981), Andersen et al. (1986), Teixeira et al. (1990), Vargas et al. (1992), Juminer et al. (1993), Miller et al. (2006), Maldonado et al. (2012) |
| Parasite species                  | Host species                      | S<sub>tr</sub> and VarS<sub>tr</sub> | Country                      | Site infection                  | References                                                                 |
|----------------------------------|-----------------------------------|-------------------------------------|------------------------------|-------------------------------|----------------------------------------------------------------------------|
| *Angiostrongylus dujardini*      | *Apodemus sylvaticus*             | 2.67 and 0.22                      | France, Portugal, Hungary, Finland (Europe) | Lungs and heart               | Dróżdź & Doby (1970), Doby et al. (1971), Mézáros (1972), Tenora et al. (1983) |
| Drożdź & Doby 1970               | *Apodemus flavicolis*             |                                    |                              |                               |                                                                            |
|                                  | *Microtus subterranus*<sup>1</sup> |                                    |                              |                               |                                                                            |
|                                  | *Myodes glareolus*<sup>2</sup>     |                                    |                              |                               |                                                                            |
|                                  | *Myodes glareolus*<sup>2</sup>     |                                    |                              |                               |                                                                            |
|                                  | *Myodes glareolus*<sup>2</sup>     |                                    |                              |                               |                                                                            |
|                                  | *Myodes glareolus*<sup>2</sup>     |                                    |                              |                               |                                                                            |
|                                  | *Myodes glareolus*<sup>2</sup>     |                                    |                              |                               |                                                                            |
| *Angiostrongylus lenzii*         | *A. montensis*                    | 0                                  | Brazil (America)             | Lungs and heart               | Souza et al. (2009)                                                       |
| Souza et al. 2009                 |                                   |                                    |                              |                               |                                                                            |
| *Angiostrongylus mackerrasae*     | *Rattus fuscipes*                 | 1.67 and 0.22                      | Queensland, New South Wales, Tasmania (Oceania) | Lungs and heart               | Bhaibulaya (1968, 1975), Stokes et al. (2007)                              |
| Bhaibulaya 1968                   | *Rattus latreolus*                |                                    |                              |                               |                                                                            |
|                                  | *R. norvegicus*                   |                                    |                              |                               |                                                                            |
| *Angiostrongylus malaysiensis*    | *Berylmys bowersi*<sup>W</sup>     | 3.2 and 5.61                       | Malaysia, Indonesia, Thailand (Asia-Oceania) | Lungs and heart (central nervous system) | Bhaibulaya & Cross (1971), Bhaibulaya & Techasophonmani (1972), Carney & Stafford (1979), Cross (1979), Lim & Ramachandran (1979), Pipitgool et al. (1997) |
| Bhaibulaya & Cross 1971           | *Leopoldamys sabanus*<sup>e</sup> |                                    |                              |                               |                                                                            |
|                                  | *Maxomys surifer*<sup>e</sup>      |                                    |                              |                               |                                                                            |
|                                  | *Maxomys whitehead*<sup>e</sup>   |                                    |                              |                               |                                                                            |
|                                  | *Niviventer cremoriventer*<sup>e</sup> |                                  |                              |                               |                                                                            |
|                                  | *Rattus argentiventer*            |                                    |                              |                               |                                                                            |
|                                  | *Rattus exulans*                  |                                    |                              |                               |                                                                            |
|                                  | *R. norvegicus*                   |                                    |                              |                               |                                                                            |
|                                  | *Rattus rattus diardii*           |                                    |                              |                               |                                                                            |
|                                  | *Rattus tiomanicus*               |                                    |                              |                               |                                                                            |
|                                  | *Sundamys muelleri*<sup>e</sup>   |                                    |                              |                               |                                                                            |
|                                  | No rodents                        |                                    |                              |                               |                                                                            |
|                                  | *S. murinus*                      |                                    |                              |                               |                                                                            |
|                                  | *Tupaia glis*                     |                                    |                              |                               |                                                                            |
| *Angiostrongylus morerai*         | *Akodon azarae*                   | 1.86 and 0.12                      | Argentina (America)          | Lungs and heart               | Robles et al. (2008, 2012)                                                |
| Robles, Navone & Kinsella 2008    | *Akodon dolores*                  |                                    |                              |                               |                                                                            |
|                                  | *Apodemus montensis*              |                                    |                              |                               |                                                                            |
|                                  | *Calomys callosus*                |                                    |                              |                               |                                                                            |
|                                  | *Delamys kempi*                   |                                    |                              |                               |                                                                            |
|                                  | *Necromys lasiurus*               |                                    |                              |                               |                                                                            |
|                                  | *S. angouya*                      |                                    |                              |                               |                                                                            |
|                                  | *Tupaia glis*                     |                                    |                              |                               |                                                                            |
| *Angiostrongylus petrovii*        | *Dryomys nitedula*                | 0                                  | Azerbaidzhazh (Asia)         | Lungs and heart               | Tarzhimanova & Chertkova (1969), Spratt (2015)                            |
| (Tarzhimanova & Chertkova 1969)   |                                   |                                    |                              |                               |                                                                            |
| *Angiostrongylus ryjikovi*        | *Myodes rutilus*<sup>v</sup>      | 0                                  | Soviet Union (Eurasia)       | Lungs and heart               | Jushkov (1971), Spratt (2015)                                              |
| Jushkov 1971                      |                                   |                                    |                              |                               |                                                                            |
| *Angiostrongylus sandarsae*       | *Gerbill tatera*<sup>r</sup>      | 0-1                                | Mozambique, Kenya (Africa)   | Lungs and heart               | Alicata (1968), Kamiya & Fukumoto (1988), Spratt (2015)                    |
| Alicata 1968                      | *Mastomys natalensis*<sup>v</sup> |                                    |                              |                               |                                                                            |
| *Angiostrongylus schmidtii*       | *Oryzomys palustris*              | 0                                  | USA (America)                | Lungs and heart               | Kinsella (1971)                                                           |
| Kinsella 1971                     |                                   |                                    |                              |                               |                                                                            |
| Parasite species         | Host species                          | STD and VarSTD Country Site |
|-------------------------|---------------------------------------|------------------------------|
| Angiostrongylus sciuri  | Sciurus vulgaris                       | Lungs and heart, 1.93 ± 0.06 |
| Angiostrongylus tateronae| Tatera kempi, Taterillus rufescens, Neotoma floridanus | Lung and heart, 0 |
| Angiostrongylus siamensis| L. sabanus, Maxomys surifer, R. rattus | Nigeria (Africa), Albania (Europe) |
| Angiostrongylus costaricensis| Oryzomys caliginosus, Oryzomys fulvescens, Oxymycterus judex, Oryzomys albigularis, Zygodontomys microtinus | 17.4% |
| Angiostrongylus mackerrasae| Pitymys subterranus, Clethrionomys glareolus, Rattus bowersi | 0 |
| A. cantonensis          | Belocaulus angustipes, Phyllocaulis soleiformis | 20% |
| A. schmidti             | Achatina fulica, Bowdichia caniculata, Achatina fulica, Phylocaulis variegatus, Phylocaulis soleiformis | 17.4% |
| A. costaricensis         | A. cantonensis, A. schmidti           | 17.4% |
| A. andersoni             | A. schmidti                            | 17.4% |
| A. muelleri             | A. schmidti                            | 17.4% |
| A. rufogriseus          | A. schmidti                            | 17.4% |
| A. alecto               | A. schmidti                            | 17.4% |
| A. leucopus             | A. schmidti                            | 17.4% |
| A. cf. congicus         | A. schmidti                            | 17.4% |

**References**

Parasite species Host species STD References

Angiostrongylus sciuri Sciurus vulgaris B. indica Bandicota savilei Berylmys berdmorei Merdevenci 1964
Ohbayashi, Kamiya & Bhaibulaya 1979

Angiostrongylus siamensis Kamiya et al. (1980)

Angiostrongylus tateronae Tatera kempi; Taterillus rufescens; Neotoma floridanus; Oryzomys caliginosus; Oryzomys fulvescens; Oxymycterus judex; Oryzomys albigularis; Zygodontomys microtinus; Pitymys subterranus; Clethrionomys glareolus; Rattus bowersi; Rattus sabanus; A. cantonensis in North and South American rodents: there been no cases of eosinophilic meningoencephalitis or abdominal angiostrongylosis in Argentina to date. However, to know the complete pathogenicity and potential transmission of each parasitic species, studies on intermediate hosts and the reaction of the larvae in the affected organs must be completed.

The presence of *A. morerai* in Argentina in different ecoregions indicates that environmental features may have little influence on geographic distribution, although it is interesting to note that apparently these can influence frequency and abundance. Prevalence in the La Pampa ecoregion was considerably higher than Selva Paranaense (20%) and Chaco Húmedo (17.4%). The question is whether the differences in the frequency and abundance of *Angiostrongylus* spp may be due to the sampling effort and/or to the distribution of definitive and intermediate hosts and/or to the susceptibility of both. For example, with respect to the latter, Combes (2001) proposed different filters of parasite-host association; encounter filters (biodiversity and behaviour) and compatibility filters (resource and density).

Five species of *Angiostrongylus* have been reported in North and South American rodents: *A. cantonensis*, *A. costaricensis*, *A. lenzii*, *A. morerai*, and *A. schmidti*. Notably, the snails *Achatina fulica* (Bowdich 1822), *Pomacea canaliculata* (Lamarck 1828), *Phyllocaulis variegatus* (Semper 1885), *Phyllocaulis soleiformis* (Orbigyn 1835), *Belocaulus angustipes* (Heynemann 1885) are recorded from the area studied in this survey, and have all been previously recorded as intermediate hosts of *A. cantonensis* and/or *A. costaricensis* (Teixeira et al. 1993, Diaz et al. 2013, Gregoric et al. 2013). Accordingly, the low host specificity of these *Angiostrongylus* spp is puzzling that there been no cases of eosinophilic meningoencephalitis or abdominal angiostrongylosis in Argentina to date. Spratt (2015) partly answer to a similar situation, since the reports in the literature of many species of *Angiostrongylus* in rodents reflect lack of opportunity or interest in examining nonurban and nonagricultural hosts (Table II).

The elevated number of host species (*n* = 7) of *A. morerai* with a $S_{TR} = 1.86$ is a reflection of multiple systematic studies of parasites from sigmodontine rodents in the area of Cuenca del Plata Argentina, showing that an increase in sampling effort can result in new findings. Therefore, a low number of host species used by other *Angiostrongylus* species may be an artifact caused by lack of sampling effort.

This is the first attempt to describe general patterns of host specificity of *Angiostrongylus* from rodents through a quantitative approach. Host specificity values did not include the hosts recorded as part of experimental infections or accidental hosts (Table II). Those hosts include *Taterillus cf. congicus* for *A. andersoni*, *Aepyprymnus rufescens* and *Macropus rufogriseus* for *A. cantonensis*, *Pteropus alecto* for *A. mackerrasae*, *Meriones unguiculatus*, *Mesocricetus auratus*, *Mus musculus*, *Peromyscus leucopus*, *Rattus norvegicus*, and *Signodont hispidus* for *A. schmidti* (Kinsella 1971, Petter & Cassone 1975, McKenzie et al. 1978, Higgins et al. 1997, Barrett et al. 2002). However, those studies support the conclusions of this survey, since the addition of hosts from other families and orders would only increase the $S_{TR}$ values.
In conclusion, the distribution of Angiostrongyulus spp shows no environmental limits, demonstrates low host specificity, and indicates that their host range has probably been underestimated. In addition, there are other host records of some species of Angiostrongyulus which need to be confirmed by morphological and molecular analysis (Robles et al. 2012). Moreover, it is necessary to explore the different degrees of pathogenicity in various hosts, mainly in those cases that are phylogenetically more distant (different host family) to analyse which are the filters (meeting, immunological, etc.) that determine host distribution. These results would allow anticipating contingencies and prevention planning for diseases caused by angiostrongylosis.

There is a need to increase awareness in the human population about the risk of contracting angiostrongylosis and healthcare providers should consider these parasites on the South American continent when making medical diagnoses. Moreover, surveillance and control of intermediate and definitive hosts as well as health education should be done to avoid human infections.

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Angiostrongylus spp in rodents • María del Rosario Robles et al.

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