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VERSITA

Strongyloides myopotami in ctenomyid rodents: Transition from semi-aquatic to subterranean life cycle

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Abstract

Strongyloides myopotami, a parasite of *Myocastor coypus* (nutria or coypu), was found during an extensive parasitological survey carried out on parasitic helminths of 5 species of subterranean rodents (tuco-tucos) belonging to the genus *Ctenomys* from Argentina and Uruguay. *Strongyloides myopotami* became known by causing "marsh itch" (also called "nutria itch" or "swimmer's itch"), a severe rash caused by larvae that enter the skin in humans, and it is recognised as a zoonosis for people handling nutria fur. In the present study *S. myopotami* was found in 2 of the 5 examined species of *Ctenomys* (*C. talarum* from Argentina and *C. pearsoni* from Uruguay), both inhabiting the vicinity of water courses. Population descriptors of *S. myopotami* in *C. talarum* showed that a population of this parasite is well established in this rodent. The development of infective filariform larvae from eggs in the faeces of *C. talarum* and the prevalence of gravid parasitic females in this host can be considered as evidence of the establishment of a population of *S. myopotami* independent of the source population parasitizing *M. coypus*. Therefore, the presence of *S. myopotami* in these species of tuco-tucos indicates a change from a semi-aquatic to subterranean life cycle. Evidence that tuco-tucos are reservoirs for these nematodes and therefore may be a risk to human health in the areas studied is provided.

Keywords

Strongyloides myopotami, nutria, *Myocastor coypus*, subterranean rodents, *Ctenomys talarum*, *C. pearsoni*

Introduction

Parthenogenetic adults females of *Strongyloides myopotami* Artigas et Pacheco, 1933 are intestinal parasite of *Myocastor coypus* Molina, 1782 (nutria or coypu), inhabiting the small intestine, whereas free living adults and larvae are only known from nutria faecal cultures (Little 1966).This nematode was originally described as a parasite of nutria with no reference to the locality from which hosts were obtained (Artigas and Pacheco 1933). Since its original description, this parasite has been reported in nutria from some countries in America: United States (Babero and Lee 1961), Brazil (Vicente *et al.* 1997) and Argentina (Roveda and Mazzini 1949, Boero and Boehringer 1967, Sutton 1974, Martinez *et al*. 2004), whereas there are no records of this species from Uruguay.

Myocastor coypus is a South American semi-aquatic rodent with a wide geographical distribution from middle Bolivia and southern Brazil to Tierra del Fuego (Argentina), and as a result of escapes and liberations from fur farms, feral populations now occur in Europe, Asia, and North America (Woods *et al*. 1992). Similar geographical distribution have the species of the genus *Ctenomys* Blainville, 1826 (commonly termed as tuco-tucos), subterranean rodents, whose distribution ranges from Bolivia to Tierra del Fuego, inhabiting a great variety of soils and living in individual burrow systems (Reig *et al*. 1990). Because most of the life of tuco-tucos is spent underground, certain phases of their life history and ecology are poorly studied, especially their fauna of endoparasites.

During an extensive parasitological survey carried on helminths of 5 species of South American subterranean rodents of the genus *Ctenomys*, nematodes referable to *S. myopotami* were found. These parasites are described herein and the possible modes of infection to novel hosts are discussed.

Materials and methods

Five species of *Ctenomys* (tuco-tuco) from Argentina and Uruguay were studied. In the field, inhabited burrow systems were distinguished by the presence of conspicuous mounds of

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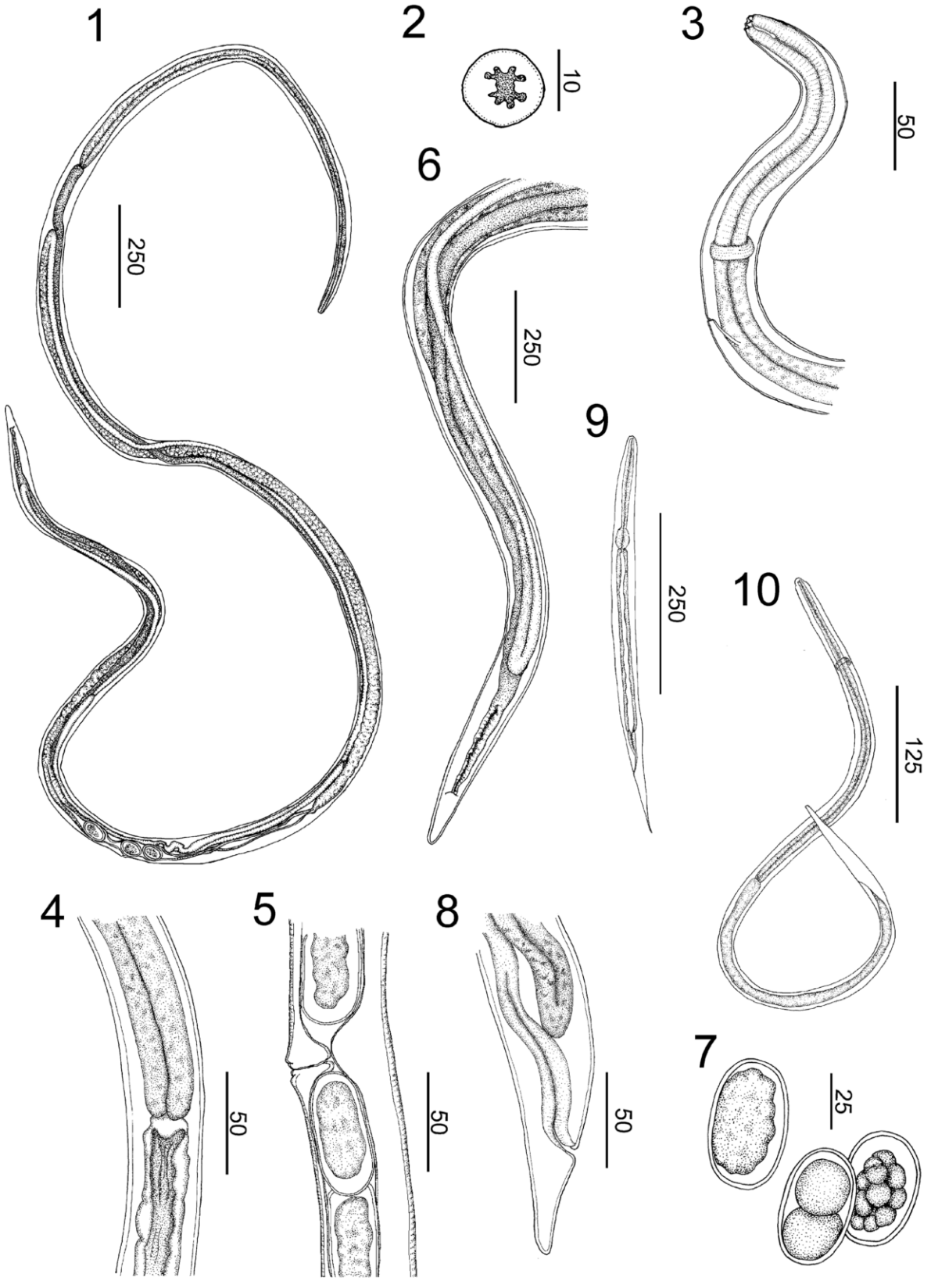

Figs 1–10. *Strongyloides myopotami* Artigas et Pacheco, 1933. **1–8.** Parasitic female. **1.** Female. **2.** Stoma (apical view). **3.** Anterior end. **4.** Oesophago-intestinal junction. **5.** Vulvar region. **6.** Posterior end. **7.** Eggs. **8.** Caudal end. **9–10.** Free living larvae. **9.** Rhabditoid larva. **10.** Filariform larva

fresh earth brought to the surface during burrowing activities of the rodents. Live traps were placed in these burrows and checked every hour throughout the day during each trapping session.

A total of 87 specimens of tuco-tuco was caught in Argentina, 42 *Ctenomys talarum* Thomas, 1898 from Mar de Cobo, Buenos Aires Province (37°58´S, 57°34´W) and 45 *C. australis* Rusconi, 1934 from Necochea (Paraje Las Grutas), Buenos Aires Province (38°33´S, 58°45´W). Samples from Uruguay comprised 40 specimens of each of the following species: *C. pearsoni* Lessa et Langguth, 1983, from Penino, Departamento de San José (34°68´S, 56°25´W); *C. torquatus* Lichtenstein, 1830 from San Gregorio de Polanco, Depto. Tacuarembó (32°36.97´S, 55°50.6´W); and *C. rionegrensis* Langguth et Abella, 1970 from El Rincón, Depto. Río Negro (33°20.43´S, 58°17.45´W).

Rodents were killed by ether inhalation in the laboratory. Then they were dissected and the small intestine was examined for parasites using stereoscopic microscopy. Living nematodes were fixed in 4% formaldehyde solution and preserved in 70% ethanol. Specimens were cleared in lactophenol, studied and measured under a light microscope. Drawings were made using a drawing tube. All measurements are given in micrometres, unless otherwise indicated. The means followed by SD and the range in parentheses in Table I. Prevalence and mean intensity were calculated according to Bush *et al*. (1997). The studied material was deposited in the Helminthological Collection of the Museo de La Plata (CHMLP), La Plata, Argentina (Coll. No. 5870) and the Helminthological Collection of Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (BP11151-11160).

For scanning electron microscopy (SEM), specimens were dehydrated using a series of ethanol washes, dryed by evaporation with hexamethyldisilazane, coated with gold-palladium and scanned in a Jeol T100 SEM.

Viability of eggs and larvae was assessed by culture of fresh faeces of *C. talarum* collected in the field, and the larvae were collected weekly by the Baermann technique. This technique relies on larvae moving trough the faecal mass, passing into water and falling to the bottom of a tube (Speare and Tinsley 1986).

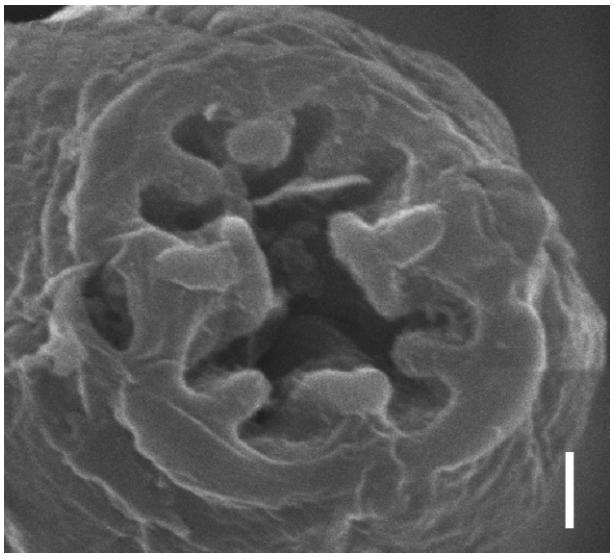

Fig. 11. *Strongyloides myopotami* Artigas et Pacheco, 1933: Stoma (apical view), SEM photomicrograph. Scale bar = 1 μm

Results

Only two out of the five species of *Ctenomys* examined harbored nematodes belonging to the genus *Strongyloides*. A total of 59 and 48 parasitic females were collected from the small intestine of 11 of 42 *C. talarum* (prevalence 26.2%, mean intensity 5.36, range 1–30) and 1 of 40 *C. pearsoni* (prevalence 2.5%, intensity 48), respectively.

Parasitic female (general description): Small and slender nematodes (Fig. 1), cuticle thin and transversely striated. Stoma complex, mouth surrounded by 8 lobes: 1 dorsal, 1 ven-

Table I. Morphometry of parasitic female *Strongyloides myopotami* parasites of *Ctenomys talarum* and *C. pearsoni*

Host	***S. myopotami* parasite of *Ctenomys talarum***	***S. myopotami* parasite of *Ctenomys pearsoni***	***S. myopotami* parasite of "coypu or nutria" (Little 1966)**
N	10	10	14
Total length (mm)	3.96 ± 0.12 (3.79–4.13)	4.74 ± 0.25 (4.47–5.18)	4.12 (3.10–5.2)
Width at midbody	44 ± 4 (40–52)	43 ± 4 (37–48)	37 (30–42)
Nerve ring to anterior end	127 ± 0.19 (97–150)	120 ± 23 (106–153)	–
Excretory pore to anterior end	164 ± 0.27 (112–200)	230 ± 37 (170–260)	–
Oesophagus length	1.21 ± 0.78 (1.10–1.28)	0.98 ± 0.10 (0.80–1.10)	1.09 (0.8–1.3)
Vulva to posterior end (mm)	1.16 ± 0.89 (0.97–1.26)	1.41 ± 0.10 (1.26–1.56)	1.27 (0.90–1.60)
Uterus length	419 ± 59 (275–540)	614 ± 113 (483–681)	–
Number of eggs	1–7	4–14	–
Eggs, length × width	59 ± 3 (55–62) × 29 ± 4 (25–37)	58 ± 6.7 (48–70) × 26 ± 3.4 (18–30)	58 × 25
Tail length	71 ± 9 (62–90)	65 ± 1 (55–79)	57 (40–75)

Values are means ± SD with range in parentheses; N – number of measured worms.

tral, 2 lateral, 2 latero-ventral, 2 latero-dorsal (Figs 2 and 11), lateral lobes larger and with amphids (Fig. 11). Deirids difficult to observe. Oesophagus with a primarily muscular part, anterior to nerve ring, and a mainly glandular posterior part (Figs 3 and 4). Didelphic (Fig. 5), ovaries long and straight, directly recurrent; anterior ovary running parallel to the intestine, in most specimens distal and proximal arms crossing the intestine at its anterior third; posterior ovary mirrors the distribution of the anterior one (Fig. 6). Uterus short; eggs "in uterus" at different development stages, from uncleaved to morula stage (Fig. 7), eggs also at these different cleavage stages when passed in faeces. Vulva with prominent lips (Fig. 5). Anus subterminal (Fig. 8). Tail conical with rounded tip (Fig. 8). Measurements of specimens from both host species are given in Table I.

Free living stages (rhabditoid and filariform larvae) of *S. myopotami* were obtained from faeces of *C. talarum*. Rhabditoid larva (Fig. 9): collected 6–7 days post culture. Whitish in colour, total body size 516 (467–530) × 29 (27–30) wide. Oesophagus rhabditoid, 134 (100–152) long. Intestine tubular and straight. Rectum short and muscular. Tail 88.8 (80–95) long. Filariform larva (Fig. 10): collected 10–12 days after culture. Transparent, total body length 729 (712–752) × 15 wide. Oesophagus filariform, 305 (276–325) long. Nerve ring situated at 95 (93–100) from anterior end of body. Intestine straight and tubular. Tail 85 (80–90) long with a notched tip.

Discussion

The diagnostic features used to distinguish between the parasitic females of the genus *Strongyloides* include the shape of the stoma, the type of ovary, the shape of the tail and the developmental stage of larvae in eggs released in the host's faeces (Little 1966). *Strongyloides myopotami* is characterized by having a complex stoma with 8 lobes and an ovary running parallel to the intestine (Artigas and Pacheco 1933, Sato *et al*. 2008). The morphology of the stoma and ovary, as well as all morphometric features of specimens found in the small intestine of *C. talarum* and *C. pearsoni* agree with those of *S. myopotami*, and are therefore considered as conspecific. Some morphometric differences such as total body length, maximum body width, length of oesophagus and tail length were found between parasitic females from both host species. This variability might be due to the differential immune response among host species, as has been demonstrated for other species of *Strongyloides* in hosts after experimental alteration of their immune system (Dawkins 1989, Baek *et al*. 2003). The morphometry of larvae given by Little (1966) also agrees with those obtained from culture in the present study.

Strongyloides myopotami is recognised as a zoonotic agent (Ruano *et al*. 2005, Schwartz and Mordechai 2008) known by causing "marsh itch" (also called "nutria itch" or "swimmer's itch"), which is a severe rash caused by larvae that enter the skin of people handling nutria fur (Burks and Jung 1960, Little 1966, LeBlanc 1994). Accidental and intentional release of nutria has led to the establishment of widespread and localized populations in various wetlands throughout the world (Burks and Jung 1960). Consequently, *S. myopotami* became established in these new geographic regions, such as Poland (Scheuring 1990) and Japan (Matsudate *et al*. 2003, Asakawa 2005). Its establishment probably was facilitated by its direct life cycle (Little 1966). However, and in spite of its potential infectivity to other hosts, such as humans, no hosts other than nutria have been reported for this parasite.

Two filters constrain the parasite establishment of host species (Combes 1991) an encounter filter and a compatibility filter, the latter excludes all host individuals in which the parasites can not survive due to physiological, morphological or immunological causes. Therefore, the possibility of colonising a new host declines with an increase of the phylogenetic distance among host species. Indeed, studies on host specificity of a related species, *Strongyloides ratti*, a natural parasite of rats (*Rattus rattus*), showed that it can complete its life-cycle in laboratory mice (*Mus musculus*), but with a decreased reproductive success, due to lower establishment rates, earlier expulsion of established parasites and reduced *per capita* fecundity in mice (Gemmill *et al*. 2000). The authors failed to find the factors underlying the differences in *S. ratti* fitness among rats and mice, and no evidence for interactions between host and parasite genotypes has been found in later studies (Paterson 2005). However, the dispersion of *S. ratti* to wild populations of mice seems unlikely, because there have been only two reports of *Strongyloides* spp. (one of them as *S. ratti*) in wild-caught mice since the late nineteenth century (Gemmill *et al*. 2000).

On the other hand, related species of hosts are known to harbor a single species of *Strongyloides*. As an example, eight species of squirrels commonly harbor *S. robustus* in North America (Bartlett 1995, Pauli *et al*. 2004). Although diverse degrees of detrimental effects are caused by the parasite among the different species of squirrels (Pauli *et al.* 2004), the compatibility filter has not prevented the colonization of these phylogenetically related host species. Similarly, nutrias and tuco-tucos belong to closely related families of hystricomorph rodents, Myocastoridae and Ctenomydae, respectively (Opazo 2005) and compatibility factors seem to have not excluded tuco-tucos as suitable hosts.

Unfortunately, there are no data on population attributes of *S. myopotami* in nutrias to allow a comparison of suitability of tuco-tucos for sustaining populations of the parasite, although differences in prevalence between *C. talarum* and *C. pearsoni* suggest possible differences among both species as adequate hosts. The presence of a single infection of *C. pearsoni* by this nematode could represent a case of accidental infection. On the other hand, the development of infective filariform larvae from eggs in the faeces of *C. talarum* and the prevalence of parasitic females in this host can be considered as an evidence of the establishment of a population of *S. myopotami*, independent of the source population parasitizing *M. coypus*.

The encounter filter (Combes 1991) excludes potential hosts that parasites cannot encounter and colonize for behavioral or ecological reasons. Despite their phylogenetic relatedness, nutrias and tuco-tucos live in completely different habitats with contrasting environmental conditions. Whereas nutrias are semi-aquatic, living in permanent water courses or pools (Nowak 1991, Woods *et al*. 1992), tuco-tucos inhabit permanently sealed individual burrow systems and most of their activities are restricted to the tunnel system. Individuals of both sexes and of all ages (except preweaned young that occupy their mother's burrow system) are sedentary and territorial (Busch *et al*. 1989, Malizia and Busch 1997). Especially, the Mar de Cobo population is characterized by high densities, strong intraspecific aggregation levels, skewed sex ratio favoring females and predominantly male dispersal (Malizia and Busch 1991). However, nutria also make runways through the grass and wander within a radius of about 180 meters of their dens (Doncaster and Micol 1989, Nowak 1991, Woods *et al*. 1992) and tuco-tucos make brief excursions to the surface to collect plant material (Comparatore *et al*. 1992). Therefore, there could have been encounter events of ctenomyids with infective stages in the narrow overlapping zone between in the home range of both hosts, which resulted in the establishment of a subterranean population of the parasite. This is supported by the fact that only two out of the five species of *Ctenomys* herein studied, which live near water courses inhabited by *M. coypus,* were parasitized by *S. myopotami*. However, in the present study some infected specimens of *C. talarum* were caught in burrows located ca. 1 km from the pond inhabited by nutrias in Mar de Cobo. This distance surpasses the home range of both host species. Therefore, the tuco-tucos could not have been infected by direct contact with nutria faeces, but must have been infected by contact with larvae from other tuco-tucos, indicating that an independent parasite population has been established in this population of *C. talarum*. In fact, viable infective larvae were obtained from faeces of *C. talarum* from Mar de Cobo.

The shift from a semi-aquatic life-cycle to a subterranean one, occurring in sandy soils, constitutes a clear example of colonization of a new habitat, and this is probably facilitated by the conditions of high humidity in the burrow systems of ctenomyids (Reig *et al*. 1990, Nevo 1999).

The two localities where *S. myopotami* was found in ctenomyids are urban areas, with a resident human population. The present findings provide evidence that tuco-tucos are reservoirs for *S. myopotami*, constituting therefore a risk for human health in the studied areas.

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