

Description of adult and fourth-stage larva of *Litomosoides navonae* n. sp. (Nematoda: Onchocercidae), a parasite of five species of sigmodontine rodents from northeastern Argentina

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Abstract

This study describes a new species of *Litomosoides* Chandler, 1931, parasitic in five different sigmodontine rodents from Misiones, Chaco and Formosa provinces of Argentina. The fourth-stage (L4) larva (male and female) is also described. *L. navonae* n. sp. exhibits: a bottle-shaped buccal cavity; a buccal capsule with irregularly crenate external walls; four externo-labial papillae and one ventral cephalic papilla; a well differentiated oesophagus; and *sigmodontis*-type spicules. The microfilaria is fusiform, with a large sheath. The L4 has a buccal capsule which is relatively longer than that of the adults, with narrower walls and a bottle-shaped lumen. It was observed in this species that the oesophagus/body-length ratio increases from larva to adult (female ratio 26.2–28.3 in larva; 88.4 in adults), and the vulva appears to move further posterior to the oesophago-intestinal junction (200–300 μm in larvae vs a mean of 600 μm in adults). *L. navonae* was found parasitising: *Nectomys squamipes* from the Reserve UNLP Valle del Arroyo Cuñá Pirú, Misiones; *Oligoryzomys chacoensis*, *Holochilus chacarius* and *Akodon azarae bibianae* from the marshes of Arroyo Bellaco, El Colorado, Formosa; and *O. fornesi* and *H. chacarius* from Selvas del Río de Oro (Chaco). Both *N. squamipes* and *H. chacarius* harbour other filarioids species, i.e. *L. kohnae* Bain, Petit & Diagne, 1989 and *L. patersoni* (Mazza, 1928), respectively, throughout their range, but these filarioids are readily differentiated from *L. navonae*. These well-differentiated filarial species found in *Nectomys* and *Holochilus* could indicate how isolated the populations of rodents are and could be interpreted either as: (a) an early point in the speciation processes that could be taking place in these hosts; or (b) extra support for the capture phenomenon theory of the evolution of *Litomosoides*. New regions, such as southern Brazil and northern Argentina, need to be studied in order to clarify these alternatives.

Introduction

Species of *Litomosoides* Chandler, 1931 are parasites from the thoracic and abdominal cavities of bats (Vespertilionidae, Phyllostomidae, Molossidae and Mormoopidae) (Esslinger, 1973; Guerrero et al., 2003), marsupials (Didelphidae) (Muller, 1980; Guerrero et al., 2002), and rodents (Muridae, Ctenomyidae, Sciuridae and Echimyidae) (Bain et al., 1989; Notarnicola et al., 2000). Although

most species of *Litomosoides* are parasites of small Neotropical and Nearctic mammals, *L. sigmodontis* Chandler, 1931 has been used as a model for understanding immunological phenomena and for providing a comparison with the agents of human filariasis (Bain et al., 1991; Martin et al., 2001).

Larval stages (L1 to L4) of only five of the more than 30 described species of *Litomosoides* are currently known, and most of these are forms from rodents and marsupials (Scott et al., 1951; Bain et al., 1980; Diagne et al., 1989). Thus, larval

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stages in bats are still unknown, with the exception of a larva of *L. brasiliensis* Lins de Almeida, 1936 found in the abdominal cavity of *Anoura caudifer* (E. Geoffroy) (Guerrero et al., 2002), plus a larva of *Litomosoides* sp. (probably *L. chandleri* Esslinger, 1973) obtained from an experimentally infected *Ornithonyssus bacoti* fed on *Artibeus jamaicensis* Leach (Bain et al., 2002).

This study describes a new species of *Litomosoides* parasitic in five different sigmodontine rodents from Misiones, Chaco and Formosa provinces in Argentina. The L4 is also described.

Materials and methods

Three localities were sampled. The nature reserve Universidad Nacional de La Plata (UNLP) Valle del Arroyo Cuñá Pirú (Departamento Cainguas, province of Misiones), which belongs to the Paranaense Biogeographical Province, is covered with semi-deciduous primary and secondary rainforests. The other two localities, Selvas del Río de Oro (Departamento Libertador General San Martín, province of Chaco) and El Colorado (Departamento Pirane, province of Formosa), belong to the Chaqueña Biogeographical Province, have a mixture of semi-deciduous xerophic forest mixed with palms, savannas and frequently flooded grassland or swamps (Cabrera, 1994).

Fifteen species of rodents (Muridae, Sigmodontinae) were trapped alive as outlined by Notarnicola & Navone (2002). In July, 1999 and March and September, 2000, 10 *Nectomys squamipes* (Brants) were captured near the Cuñá Pirú stream (27°05'15"S, 54°57'09"W), Reserve UNLP Valle del Arroyo Cuñá Pirú, Cainguas (Misiones). In July, 2000, 15 *Holochilus chacarius* Thomas and 40 *Oligoryzomys fornesi* Massoia were trapped in Selvas del Río de Oro (26°48'15"S, 58°57'25" W) (Libertador Gral. San Martín, Chaco), and in July, 2001, 4 *H. chacarius*, 15 *Oligoryzomys chacoensis* (Myers & Carleton) and 34 *Akodon azarae bibianae* Massoia were caught in the marshes of Arroyo Bellaco, in the Estancia La Marcela (26°14'09" S, 59°07'04" W), El Colorado (Pirane, Formosa). The hosts were or will be deposited in the Mammal Collection Museo de la Plata (CMMLP), Buenos Aires, and Mammal Collection Centro Nacional Patagónico, Puerto Madryn, Argentina (Ulyses Pardiñas field numbers, UP, CP and RORO).

The thoracic and abdominal cavities of the rodents were checked for parasites. The worms were recovered from the abdominal cavity, fixed in 10% formalin, preserved in 70% ethanol, and cleared in lactophenol for light microscopy. An apical view of the head and a cross-section of the female at the level of the vulva were prepared following Notarnicola et al. (2000). Microfilariae were obtained from the uteri of fixed females and from blood samples (see Notarnicola et al., 2000). Illustrations were prepared with the aid of a drawing tube. Measurements are given in micrometres unless otherwise stated; if measurements of more than four paratypes are given, the mean values and standard deviations are presented with the ranges in parentheses, plus the CV (coefficient of variation); data for two or three paratypes are separated by semicolons.

Litomosoides navonae n. sp.

Type-host: *Nectomys squamipes* (Brants) (Rodentia: Muridae) male, CMMLP Argentina No. 16.VIII.02.6. Other hosts deposited as CMMLP 16.VII.02.2 and 16.VII.02.6; field numbers C137; CP02; and CP06.

Site of infection: Abdominal cavity.

Type-locality: Arroyo Cuñá Pirú, Reserva Natural UNLP Valle del Arroyo Cuñá Pirú (27°05'15"S, 54°57'09"W), Cainguas, Misiones, Argentina.

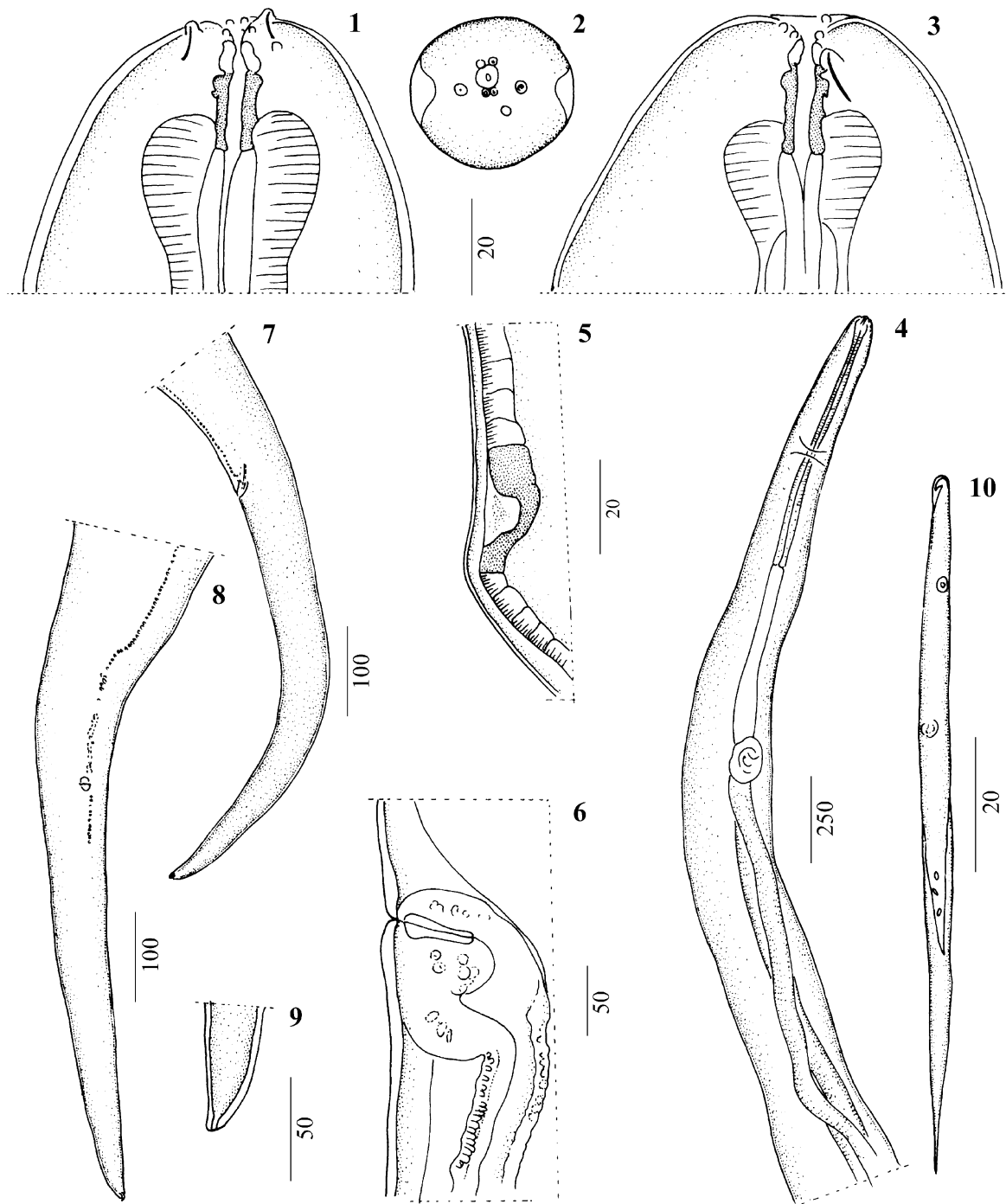
Specimens deposited: Holotype (male), allotype (female), 7 paratypes at the Helminthological Collection Museo de La Plata, Argentina (CHMLP) No. 5392, 5393 and 5394, respectively.

Prevalence and mean intensity: 6/10 hosts parasitised (60%); 6.5 (1–13).

Etymology: The species is named for Graciela T. Navone, in recognition of her contributions to the knowledge of nematodes from rodents, marsupials and xenarthrans in Argentina.

Description (Figures 1–19)

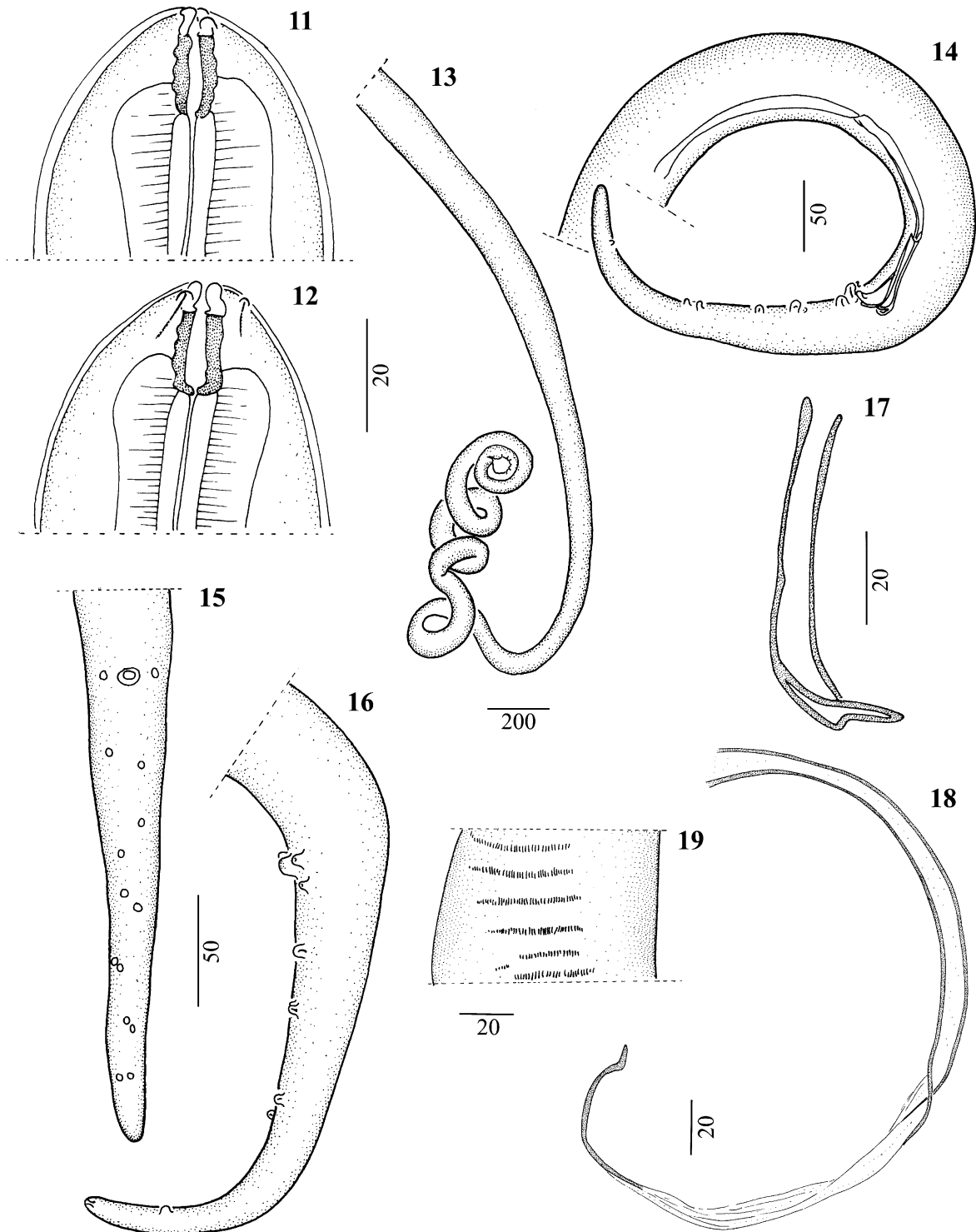
General morphology (based on 13 males and 22 females). Males 1/3 length of females. Anterior region generally robust, but slender in some specimens. Cephalic extremity rounded. Amphids slightly salient, with conspicuous channel. Four externo-labial papillae arranged in rectangle aligned dorso-ventrally and 1 ventral cephalic papilla (Figure 2). Buccal cavity tubular, bottle-



Figures 1–10. *Litomosoides navonae* n. sp. Female. (Host: *Nectomys squamipes*). 1–3. Head, ventral, apical and lateral views. 4. Anterior region, ventral view. 5. Detail of the lateral chord in cross-section, posterior to the vulva. 6. Detail of the vulva. 7, 8. Tail, lateral and ventral views. 9. Distal extremity. 10. Uterine microfilaria.

shaped. Buccal capsule with transparent anterior region and with posterior 2/3 strongly cuticularised; external margins of walls irregularly crenate.

Oesophagus divided, with glandular portion slightly wider than muscular portion. Tail attenuated in both sexes.



Figures 11–19. *Litomosoides navonae* n. sp. Male (Host: *Nectomys squamipes*). 11,12. Head, lateral and median views. 13. Posterior region. 14. Tail, lateral view. 15,16. Male tail showing the caudal papillae, ventral and lateral views. 17. Right spicule. 18. Left spicule. 19. Detail of area rugosa, ventral view.

Male

Posterior region thinner than rest of body, with 3–4 coils (Figure 13). Left spicule with handle shorter than lamina; lamina with distal region comprising membranous alae and terminal filament. Right spicule not heavily cuticularised, with membranous distal extremity supported by 2 parallel rods. Testis posterior to oesophagus. Cloacal aperture slightly protruded, rounded in ventral view with cuticularised ring. Caudal papillae conspicuous; 1 pair adcloacal and 5–6 asymmetrical pairs postcloacal (Figures 15, 16). Area rugosa beginning anterior to cloaca and composed of transverse ridges of small longitudinal crests.

Holotype Length 15.27 mm; width 150. Buccal capsule 19 long and 8 in external diameter. Nerve-ring 381 from anterior extremity. Oesophagus 459 long. Tail 240 long. Left spicule 260 long, with handle 155 long; right spicule 85 long; spicule ratio 3.05. Area rugosa 800 long, beginning at 2,415 from tip of tail and extending to 615; crests 1–2 long, reaching $c.25$ –40 in width; distance between 2 consecutive ridges 7–12.

Paratypes ($n = 12$). Length 22.2 ± 2.1 (19.1–25.6) mm, CV = 9.5; width 144 ± 12.6 (126–164), CV = 8.8. Buccal capsule 19 ± 1.7 (16–21) long, CV = 9.4; maximum diameter 8.5 ± 1 (7–10), CV = 12.5. Nerve-ring 416 ± 77.5 (309–550) from anterior extremity, CV = 18.6. Oesophagus 577 ± 107.7 (420–760) long, CV = 18.6. Tail 213 ± 26.2 (177–248) long, CV = 12.3. Left spicule 304 ± 44.7 (240–370) long, CV = 14.6; handle 136 ± 31.4 (100–190) long, CV = 22.9; right spicule 94 ± 10.6 (85–120) long, CV = 11.2. Area rugosa $2,066 \pm 341.4$ (1,530–2,700) long, CV = 16.5, beginning at $2,762 \pm 333.7$ (2,253–3,400), CV = 12, and extending to 689 ± 114 (483–831) from tip of tail, CV = 16.5.

Female

Vulva post-oesophageal; vagina globular (Figure 6). Ovijector oriented posteriorly; in some specimens first passing anteriorly and then posteriorly. Tail slightly curved ventrally or straight. Phasmids parallel or divergent. In cross-section near level of vulva, lateral chords square in shape (Figures 5, 25); ventral chord at level of vulva and anus with visible cells (Figures 7, 8).

Allotype Length 64.02 mm; width 276. Buccal capsule 22 long, with external diameter 9. Nerve-ring 384 from anterior extremity. Oesophagus 702

long. Vulva 1,227 from anterior extremity; 525 from oesophago-intestinal junction. Tail 456 long.

Paratypes ($n = 21$). Length 64.84 ± 8.9 (44.88–72.13) mm, CV = 13.8; width 269 ± 37.5 (195–328), CV = 13.9. Buccal capsule 22.5 ± 2.2 (20–28) long, CV = 10, and 9.7 ± 0.8 (8–11) in external diameter, CV = 8.4. Nerve-ring 469 ± 65.4 (372–600) from anterior extremity, CV = 13.9. Oesophagus 733 ± 107.4 (552–980) long, CV = 14.6. Vulva $1,359 \pm 218.1$ (987–1,800) from anterior extremity, CV = 16; 600 ± 196.2 (270–1,000), CV = 32.6. from oesophago-intestinal junction. Tail 600 ± 121.2 (440–856) long, CV = 20.2.

Microfilaria. Sheath present, much larger than body, attenuated posteriorly. Body fusiform. Cephalic hook salient. Tail anucleated, not attenuated (Figure 10). Measurements of uterine microfilariae from 2 different female paratypes ($n = 7$): 70 ± 7.1 (62–85) long, CV = 10.2; 3.8 ± 0.3 (3.5–4.5) wide, CV = 10; sheath 81 ± 9 (75–92), CV = 11.1. Blood microfilariae ($n = 9$): 68 ± 2 (65–72) long, CV = 2.9; 4.2 ± 0.4 (4–5) wide, CV = 10.

Differential diagnosis

Litomosoides navonae n. sp. belongs to the *sigmodontis*-group of Bain et al. (1989) and is readily differentiated from other species within this group.

From the *sigmodontis*-group species that are known to occur in bats, *L. navonae* differs from *L. hamletti* Sandground, 1934 by its larger size, longer tail, buccal capsule with thicker walls, different number of postcloacal papillae and a vulva that opens posteriorly to the oesophago-intestinal junction (Sandground, 1934); from *L. leonilavazquezae* Caballero, 1939 in having longer spicules, thinner buccal capsule with irregular internal walls and longer microfilariae (Caballero, 1947); and from both *L. fosteri* Caballero, 1947 and *L. teshi* Esslinger, 1973 in having a buccal capsule that is different in size and shape (Caballero, 1947; Esslinger, 1973).

Five species parasitic in bats and not yet assigned to either the *carinii*- or *sigmodontis*-groups (because the males are still undescribed) can also be differentiated from *L. navonae*. From *L. solari* Guerrero, Martin, Gardner & Bain, 2002, the new species differs in having a divided oesophagus, the

vulva located posterior to the oesophago-intestinal junction, a tail not rounded at the tip and microfilariae without a strongly attenuated posterior end (Guerrero et al., 2002). The buccal capsule and the microfilariae of *L. navonae* are shorter than those of *L. artibeii* Esslinger, 1973 (Esslinger, 1973). Specimens of *L. navonae* exhibit a buccal capsule that is longer than that of *L. chitwoodi* Bain, Guerrero, Rodriguez, Babayan & Jouvenet, 2003. Microfilariae of the new species are smaller than those of *L. colombiensis* Esslinger, 1973 and lack an elongated terminal nucleus; and they are longer than those of *L. caliensis* Esslinger, 1973, which has an attenuated tail (Esslinger, 1973).

In relation to species from marsupials, *L. navonae* differs from *L. barretti* Muller, 1980 in having a different arrangement of the cephalic papillae, a narrower buccal cavity and asymmetrically distributed caudal papillae (Muller, 1980).

In relation to species from rodents, the new species differs from *L. ctenomyos* Brant & Gardner, 1997, a parasite of *Ctenomys opimus*, in having a narrower buccal capsule with smooth internal walls, a greater number of head papillae and a divided oesophagus (Brant & Gardner, 1997). Specimens of *L. navonae* are larger than those of *L. hoplomyis* Esslinger, 1973, a parasite of echimyids (Esslinger, 1973). The new species also differs from *L. circularis* (Linstow, 1899) because the tail and right spicule are shorter (Linstow, 1899); from *L. esslingeri* Esslinger, 1973 in having a longer oesophagus and smooth internal walls of the buccal capsule (Bain et al., 1989); and from *L. galizai* Bain, Petit & Diagne, 1989 in having a different arrangement of head and caudal papillae (Bain et al., 1989). *L. patersoni* (Mazza, 1928), a parasite of *Holochilus chacarius* (as *H. vulpinus*) from Salta, Argentina, also differs from *L. navonae*: its right spicule and the microfilaria are longer (85 vs 50 and 65–72 vs 35–46 μm , respectively) (Mazza, 1928). *L. navonae* also differs from *L. legerae* Bain, Petit & Berteaux, 1980, *L. chagasfilhoi* Moraes Neto, Lanfredi & De Souza, 1997, *L. oxymycteri* Notarnicola, Bain & Navone, 2000 and *L. anguyai* Notarnicola & Navone, 2002, because these species exhibit a muscular oesophagus and longer microfilariae. Moreover, *L. legerae* has a complete set of cephalic papillae and a buccal capsule with two rings (Bain et al., 1980); *L. chagasfilhoi* has two dorsal cephalic papillae (Moraes Neto et al., 1997; Notarnicola et al., 2000); and these papillae are

ventral in both *L. oxymycteri* and *L. anguyai*. The right spicule of *L. navonae* is longer than that in *L. anguyai* (mean 94.5 vs 83 μm) and the tail lacks a pair of precloacal papillae and caudal lappets (Notarnicola et al., 2002). *L. navonae* differs from *L. kohnae* Bain, Petit & Diagne, 1989, a parasite of *Nectomys squamipes* from São Paulo, Brazil, in having a longer buccal capsule, a divided oesophagus and a vulva which opens closer to the anterior end of the body (Bain et al., 1989).

Both males and females of *L. navonae* and *L. sigmodontis* have a similarly shaped buccal capsule and tail, and the sheath of the microfilaria is large in both species; but, the new species differs from *L. sigmodontis* in having one ventral cephalic papilla and an oesophagus with a differentiated glandular region (Bain et al., 1989).

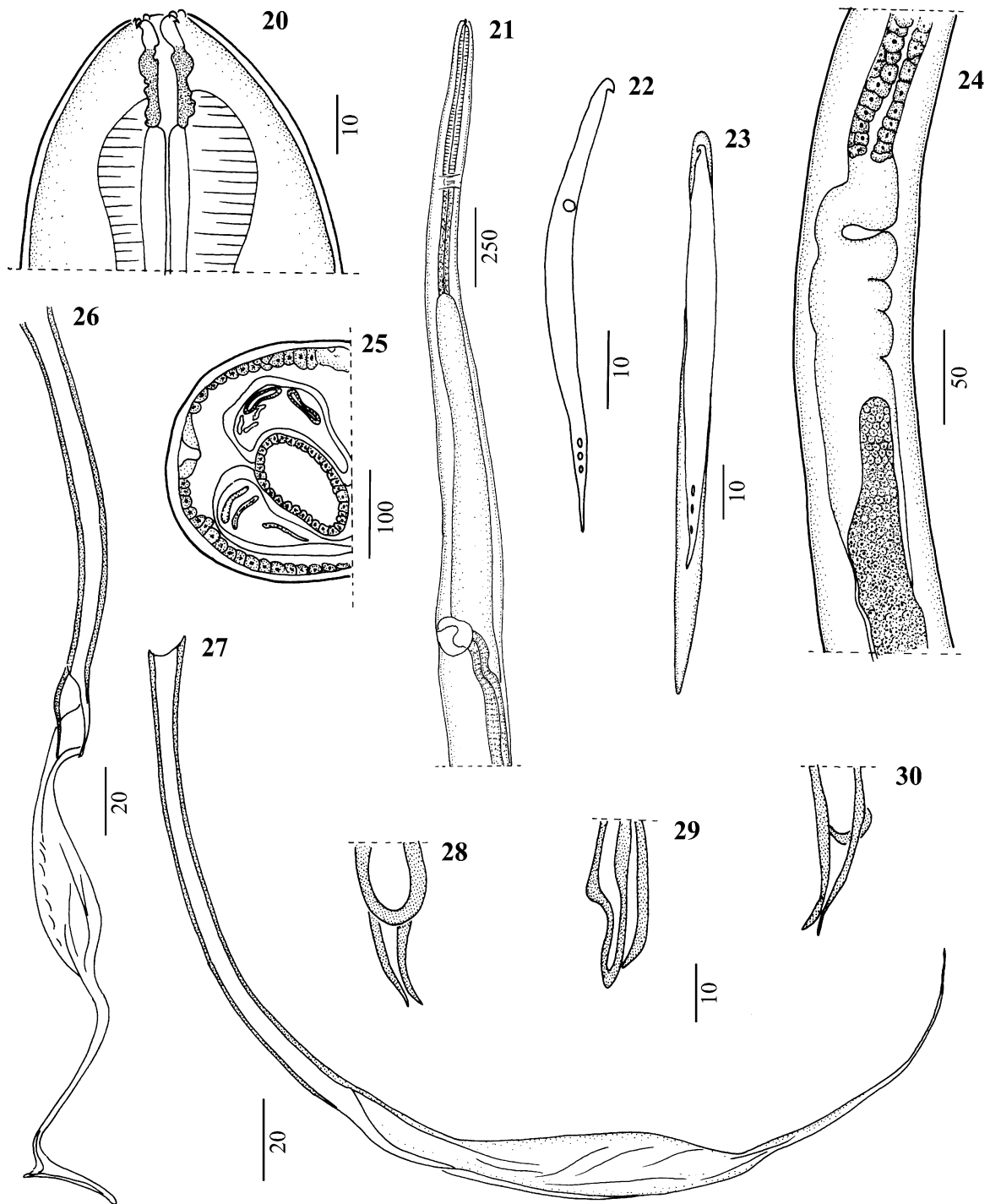
Other hosts and localities (Figures 20–36)

Litomosoides navonae n. sp. was also found in the abdominal and pleural cavities of: *Oligoryzomys cf. chacoensis* (Myers & Carleton) (host UP185 male; filarioids deposited: 2 males, 2 females CHMLP No. 5395); the abdominal cavity of *Holochilus chacarius* Thomas (host UP179 female); and *Akodon azarae bibiana* Massoia (hosts MLP19.VI.02.1 female; MLP19.VI.02.5 female; UP192 male; filarioids deposited: 1 male, 2 females CHMLP No. 5397) from the marshes of Arroyo Bellaco, Estancia La Marcela (26°14'09" S, 59°07'04" W), El Colorado (Pirane, Formosa).

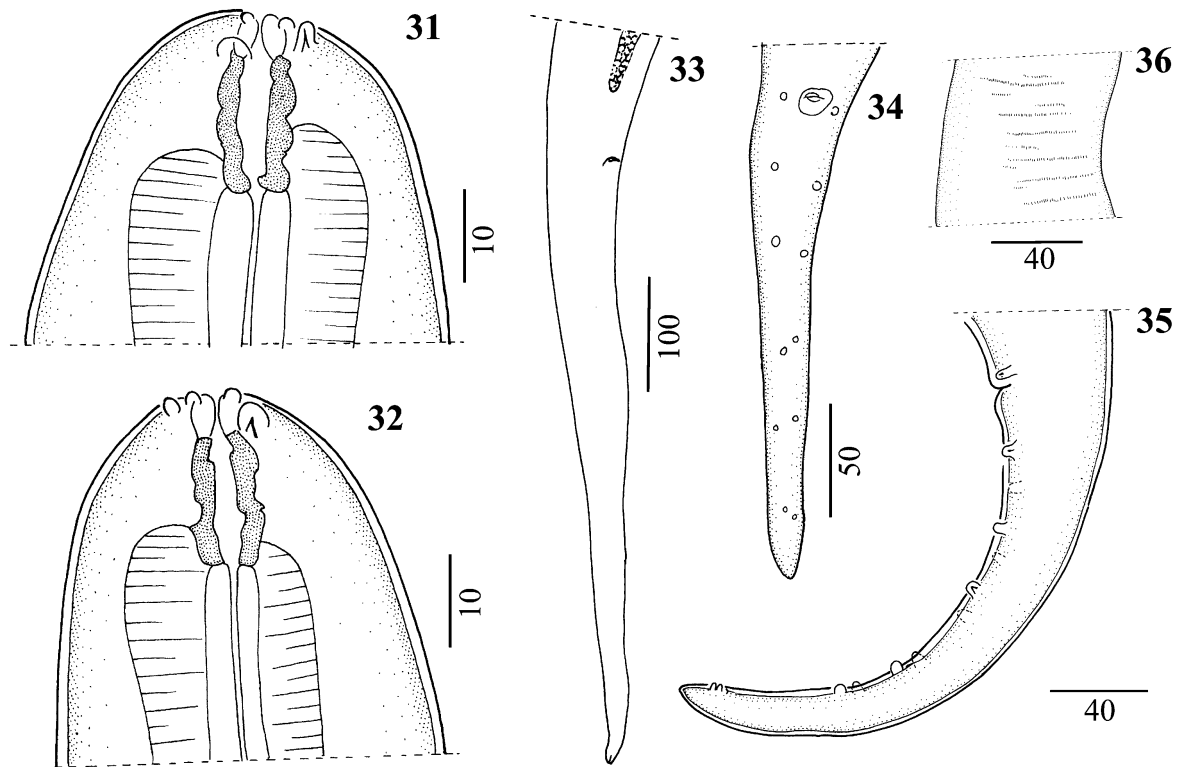
In Selvas del Río de Oro (26°48'15" S, 58°57'25" W), Libertador Gral. San Martín, Chaco, *L. navonae* was found parasitising the abdominal cavity of *O. fornesi* Massoia (MLP27.XI.01.16 male) and *H. chacarius* (hosts RORO046 male; RORO009 female; filarioids deposited: 2 males, 2 females CHMLP No. 5396).

Tables 1 and 2 show the measurements of the new species and also provide additional information on the localities and hosts.

In Formosa, of 15 *O. chacoensis*, 1 was parasitised (prevalence 6.6%) and harboured 16 worms. Of 4 *H. chacarius*, 1 (25%) was parasitised and harboured 6 filarioids. Of 34 *A. a. bibiana*, 3 (9%) were parasitised and the mean intensity was 3 (3–5). In Chaco, 1 of 24 *O. fornesi* was parasitised (4.1%) with an intensity of 6. Of 15 *H. chacarius*, 2 (13.3%) were infected and the mean intensity was 5 (1–10).



Figures 20–30. *Litomosoides navonae* n. sp. (Hosts: 20,21,25,26,28–30 *Oligoryzomys chacoensis*; 23,24,27 *Holochilus chacarius*; 22 *Akodon azarae bibiana*). 20. Female head, median view. 21. Female anterior region. 22. Uterine microfilaria. 23. Blood microfilaria. 24. Anterior region of the male showing the oesophago-intestinal junction and the extremity of the testis. 25. Cross-section of a female, posteriorly to the vulva. 26. Left spicule dissected. 27. Left spicule, lateral view. 28–30. Detail of the extremity of the right spicule dissected, dorsal, lateral and ventral views.



Figures 31–36. *Litomosoides navonaen.* sp. (Hosts: 31,32,34–36 *Holochilus chacarius*; 33 *Akodon azarae bibiana*). 31. Female head, lateral view. 32. Male head, median view. 33. Female tail. 34. Male tail, ventral view. 35. Male tail, another specimen, lateral view. 36. Detail of the area rugosa, ventral view.

Microfilariae

Uterine microfilaria

From *O. chacoensis* (UP185 male) (n = 9): 74.5 ± 5.1 (66–80) long, 4 wide; from *A. a. bibiana* (UP192): 65; 62; 70 long, 3; 3; 3.5 wide; from *O. fornesi*: 84; 83; 83; 84 long, 4 wide.

Blood microfilaria

From *H. chacarius* (RORO009) 73.55 ± 0.42 (71–78) long, 4.25 ± 0.42 (4–5) wide; sheath 90.89 ± 3.82 (83–95) long (n = 10).

Late larval stages of Litomosoides navonae n. sp. (Figures 37–44)

Three clearly smaller specimens were found (in three different hosts) along with the remaining adults which shared the diagnostic features of the new species, except that the cuticle of the anterior end of the male and one female was roughened. Thus, it was assumed that they were starting the moulting process from L4 to the adult stage (see

Guerrero et al., 2002). The other specimen is an immature adult female, whose L4 moult has finished and the vulva was open.

Fourth-stage larval male (Figures 39–44).

From *H. chacarius* (RORO009, Selvas del Río de Oro, Chaco; filarioid deposited CHMLP No. 5400): Buccal capsule narrow; anterior external wall with ring and internal walls smooth; buccal cavity bottle-shaped. Amphids conspicuous. Oesophagus with differentiated posterior glandular region. Size and shape of spicules similar to adults. Cloacal papillae as follows: 1 pair of adcloacal plus 4 pairs of postcloacal papillae distributed in anterior 2/3 and 1 pair on distal extremity.

Measurements: Length 8.3 mm; width 88; buccal capsule 20 long, 7 wide; nerve-ring 270 from anterior extremity; oesophagus, tail and right spicule 520, 280 and 85, respectively; left spicule 260, handle 130; area rugosa 1,020 long, extending from 1,635 to 615 from tip of tail; testis 1,152 from anterior extremity.

Table 1. Measurements of males of *Litomosoides navonae* n. sp. from different host species in Formosa and Chaco provinces.

Measurements	Selvas del Río de Oro, Chaco			
	El Colorado, Formosa	<i>Holochilus chacarius</i> (n = 2)	<i>Akodon azarae bibianae</i> (n = 1)	<i>Oligoryzomys fornesi</i> (n = 1)
Host species	<i>Oligoryzomys chacoensis</i> (n = 8)	<i>Holochilus chacarius</i> (n = 2)	<i>Akodon azarae bibianae</i> (n = 1)	<i>Oligoryzomys fornesi</i> (n = 1)
Body length (in mm)	24.25 ± 2.5 (20.56–28) CV = 10.3	23.1; 19.6	23.1	21.94
Width	149 ± 13.2 (128–165) CV = 8.8	123; 120	156	150
Buccal capsule length	17.4 ± 1.2 (16–19) CV = 6.8	18; 19	20	21
Buccal capsule width	7.5 ± 0.7 (6–8) CV = 9.3	7; 9	8	9
Oesophagus	590 ± 111.3 (432–750) CV = 18.8	543; 555	750	525
Nerve-ring	365 ± 121.6 (144–480) CV = 33.3	342; 348	375	?
Tail	232 ± 25.4 (210–280) CV = 10.9	222; 250	240	240
Left spicule	300 ± 40.2 (260–375) CV = 13.4	330; 310	300	340
Spicule handle	134 ± 19.2 (100–160) CV = 14.3	160; 130	140	150
Right spicule	85.5 ± 4.1 (80–90) CV = 4.7	88; 95	90	80
Area rugosa length	1,659 ± 223.7 (1,260–1,880) CV = 13.4	1,620; 1,500	1,350	2,100
Area rugosa from cloaca	745 ± 162.5 (564–1,059) CV = 21.8	630; 675	570	660
				617 ± 83 (560–739) CV = 13.4

Table 2. Measurements of females of *Litomosoides navonae* n. sp. from different host species from Formosa and Chaco provinces.

Measurements	Selvas del Río de Oro, Chaco			
	El Colorado, Formosa	<i>Holochilus chacarius</i> (n = 2) ¹	<i>Akodon azarae bibianae</i> (n = 2) ²	<i>Oligoryzomys fornesi</i> (n = 2) ³
Host species	<i>Oligoryzomys chacoensis</i> (n = 9)	<i>Holochilus chacarius</i> (n = 2) ¹	<i>Akodon azarae bibianae</i> (n = 2) ²	<i>Oligoryzomys fornesi</i> (n = 2) ³
Body length (in mm)	59.30 ± 9.4 (50.6–72.6) CV = 15.8	70.12; 70.62	59.4; 77.055	75.57–72.03
Width	251 ± 30.6 (195–285) CV = 12.1	246; 273; 286	325; 312; 279	276 ± 7 (264–282) CV = 2.5
Buccal capsule length	20.8 ± 1.9 (18–23) CV = 9.1	23; 22; 22; 21	21; 22; 23	21.8 ± 2 (20–25) CV = 9.1
Buccal capsule width	9 ± 1.1 (8–11) CV = 12.2	8; 8; 9; 8	9; 9; 10	8.8 ± 0.4 (8–9) CV = 4.5
Oesophagus	791 ± 113 (580–920) CV = 14.2	645; 800; 735; 1,020	1,000; 610; 840	941 ± 158 (728–1,125) CV = 16.7
Nerve-ring	458 ± 69 (360–560) CV = 15	411; 279	475; 420; 450	416 ± 65 (340–490) CV = 15.6
Vulva	1,817 ± 249 (1,430–2,250) CV = 13.7	1,482; 1,494; 1,560	1,300; 1,950	1,910 ± 259 (1,550–2,136) CV = 13.5
Vulva to oesoph.-int. junction	991 ± 252 (600–1,400) CV = 25.4	832; 689; 535	275; 1,140	1,017 ± 337 (675–1,395) CV = 33.1
Tail	545 ± 100 (375–690) CV = 18.3	405; 520; 390	500; 540	606 ± 169 (399–800) CV = 27.8
				731 ± 149 (504–908) CV = 20.3

¹ Two complete female, 2 anterior extremities and 1 posterior extremity.² Two complete female and 1 anterior extremity.³ Two complete female, 3 anterior extremities and 3 posterior extremities.

Fourth-stage female larva and juvenile female (Figures 37–38).

External walls of buccal capsule irregular, with insipient ring in anterior region; buccal cavity tubular, smooth. Amphids conspicuous. Vagina globular, slightly posterior to oesophago-intestinal junction. Tail attenuated.

Measurements: L4 specimen found in *N. squamipes* (host CP002, Misiones; filarioid deposited CHMLP No. 5398): Length 22.8 mm; width 120; buccal capsule 21 long, 9 wide; oesophagus 870 long; vulva 1,120 from anterior extremity, 200 from oesophago-intestinal junction; tail 325 long.

Measurements: Juvenile adult specimen found in *O. chacoensis* (host UP185, El Colorado, Formosa; filarioid deposited CHMLP No. 5399): Length 25.5 mm; width 180; buccal capsule 21 long, 9 wide; oesophagus muscular, length 900; vulva 1,210 from anterior extremity, 300 from oesophago-intestinal junction; tail 590 long.

Remarks

The buccal capsule of the L4 stage of *L. navonae* n. sp. is relatively longer than that of the adults, and it has narrower walls; the same features were observed in larval *L. sigmodontis* and *L. legerae*, both parasites of rodents (Bain et al., 1980; Maréchal et al., 1996), and also larvae of *L. brasiliensis*, a parasite of bats (Guerrero et al., 2002). The larval stages of these species exhibit long, narrow buccal capsules, which become wider in adults where they adopt the definitive shape, i.e. either developing irregular walls, as in *L. sigmodontis*, *L. legerae* and *L. navonae*, or showing annular enlargements, as in *L. brasiliensis* (see Bain et al., 1980; Maréchal et al., 1996; Guerrero et al., 2002). Moreover, the oesophagus/body-length ratio increases from the L4 stage to the adult in *L. navonae* (female ratio 26.2–28.3 in larvae; mean 88.4 in adults), and also the vulva/body-length ratio (20.3–21 in larvae; mean 47.7 in adults). These differential increases in the ratios make the vulva appear to move backwards from the oesophago-intestinal junction (200–300 μm in larvae; mean 600 μm in adults).

Discussion

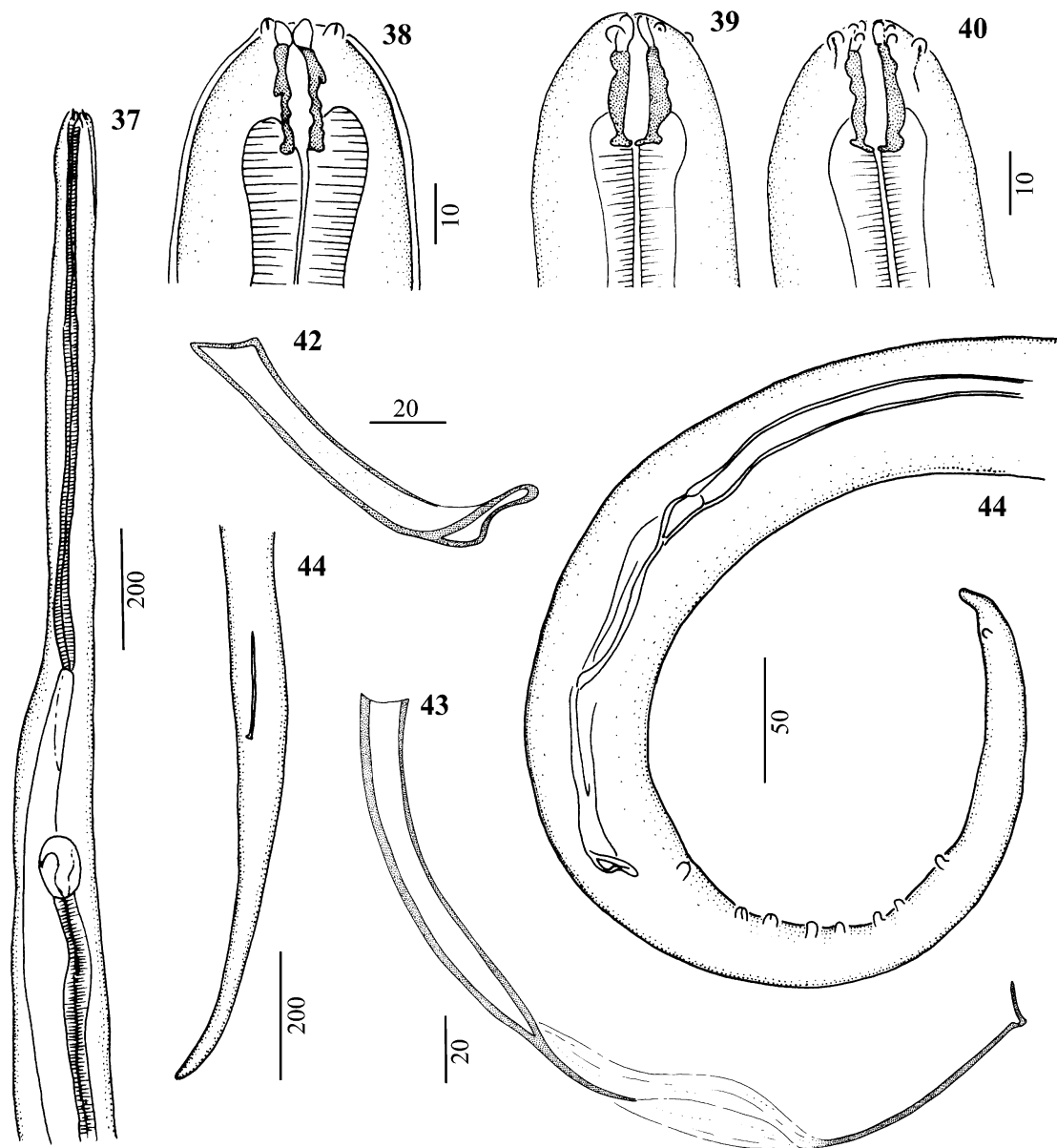
Litomosoides navonae n. sp. is the third species of the genus described from the reserve UNLP Valle

del Arroyo Cuñá Pirú, Misiones, along with *L. odilae* Notarnicola & Navone, 2002, a parasite of *Oligoryzomys nigripes*, and *L. anguyai* Notarnicola, Bain & Navone, 2002 found in *Oxymycterus misionalis*. *Oligoryzomys fornesi*, *O. chacoensis*, *Holochilus chacarius* and *Akodon azarae bibianae* represent new host records for this genus, and Chaco and Formosa are new localities.

The larval stages described here add new information on the ontogenesis of *Litomosoides* parasitic in rodents. The larval stages of *L. navonae* can be recognised by the bottle-shaped buccal cavity, salient amphids and by the shape of the spicules. In addition, during development from larva to adult, the oesophagus tends to reduce its length allometrically in relation to the body, and the vulva tends to move further posterior to the oesophago-intestinal junction. These observations also agree with those of other authors (Bain et al., 1980; Maréchal et al., 1996; Guerrero et al., 2002).

Only three, of almost 10 different species of sigmodontine rodents examined in the reserve, were parasitised by species of *Litomosoides* (see Pardiñas et al., 2003; Cirignoli et al., in press; Notarnicola, 2004, for a taxonomic account of the rodents studied). In the Paranaense Biogeographical Province, *L. navonae* is exclusively a parasite of *Nectomys squamipes*, as are *L. odilae* and *L. anguyai* for their respective hosts. *N. squamipes* was frequently found near the Cuñá Pirú stream, while *O. nigripes* and *O. misionalis* were trapped in 'capueras'. However, in the Chaqueña Biogeographical Province (Selvas del Río de Oro and El Colorado), *L. navonae* parasitised *O. fornesi*, *O. chacoensis*, *H. chacarius* and *A. a. bibianae*, thus not being host-specific in this biome.

Nectomys squamipes was also found parasitised by *L. kohnae* Bain, Petit & Diagne, 1989 in São Paulo, Brazil (Vaz, 1934), but this filarioid is readily differentiable from *L. navonae* by the oesophagus not being divided and the shape of the buccal capsule (Bain et al., 1989). For the same host species, in Floresta Estadual de Itapetiniga (São Paulo) and Município Sumidouro (Rio do Janeiro), two neighbouring localities in Brazil, the presence of *L. carinii* (Travassos, 1919) has been reported (Rodrigues, 1976; Gomes & Vicente, 1984). However, the description and measurements given for *L. carinii* in Rodrigues (1976) do not agree with the re-description of this filarioid in Bain et al. (1989), and Rodrigues' specimens more



Figures 37–44. *Litomosoides navonae* n. sp. Fourth-stage larva (Hosts: 37,38, 41 *Oligoryzomys chacoensis*; 39,40,42–44 *Holochilus chacarius*). 37. Female anterior region. 38. Female head, median view. 39,40. Male head, lateral and median views. 41. Female tail, ventral view. 42. Right spicule, lateral view. 43. Left spicule, lateral view. 44. Male tail, lateral view.

closely resemble *L. kohnae* (cf. Vaz, 1934, and Bain et al., 1989).

Given the large range of *N. squamipes*, which extends between Venezuela and southern Brazil (Ernest, 1986), it should be expected that different species of *Litomosoides* should be found parasitising this rodent in various regions of its distribution. Similarly, *H. chacarius* is parasitised by *L. patersoni* (Mazza, 1928) in Salta (Mazza, 1928), and by

L. navonae in Chaco and Formosa. This host is restricted to Paraguay and northeastern Argentina, inhabiting the Yungas gallery forests, the humid and dry Chaco espinal and the Delta of the Paraná (Massoia, 1976; Cirignoli et al., in press).

The morphologically well differentiated filarial species found in *Nectomys* or *Holochilus* throughout their range could indicate how isolated the populations of these rodent are, and could

therefore be interpreted either as: (a) an early stage in the speciation processes that could be taking place in *Nectomys* and *Holochilus*; or (b) extra support for the capture phenomenon theory for the evolution of *Litomosoides* (see Brant & Gardner, 2000; Guerrero et al., 2002). In order to clarify these alternatives, it is necessary that new areas of southern Brazil and northern Argentina need to be investigated.

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