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TWO NEW SPECIES OF *LITOMOSOIDES* (NEMATA: ONCHOCERCIDAE) FROM *CTENOMYS OPIMUS* (RODENTIA: CTENOMYIDAE) ON THE ALTIPLANO OF BOLIVIA

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ABSTRACT: Two filarioid nematodes, *Litomosoides andersoni* n. sp. and *Litomosoides ctenomyos* n. sp. (Nemata: Onchocercidae), are described from the mesenteries of the subterranean rodent *Ctenomys opimus* (Rodentia: Hystriognathi) collected on the altiplano of Bolivia. Specimens collected near Rancho Huancaroma (Oruro Dept.) in 1984 and 1986 can be recognized as undescribed by the structures of the spicules and stoma and the shape of the ovjector. This record represents the first time members of the genus *Litomosoides* have been recovered from rodents of the family Ctenomyidae; this also represents the first published report of these nematodes from mammals in Bolivia.

Species of the genus *Ctenomys* de Blainville occur in all major habitat types in the neotropics south of about latitude 16°S in lowland subtropical savanna and about latitude 11°S in the high altitude (>3,500 m) Puna, Altiplano, and Cerrado de Andes (Mares and Ojeda, 1982; Reig, 1986; Contreras et al., 1987). The northern limit of distribution of these subterranean rodents in central lowland Bolivia is about 16°30'S, defined by the termination of the northernmost extent of the Chaco-dry forest and the beginning of lowland subtropical forest and palm-nut savannas (Unzueta, 1975). In lowland Bolivia, ctenomyids occur in friable, well-drained soils (S. L. Gardner, pers. obs.); in the high-altitude region of western Bolivia, these rodents occur in colonies in friable soils throughout their range (S. L. Gardner, pers. obs.). The northern limit of distribution of ctenomyids in high-altitude habitats in the Andes is undefined.

Presently, 39 species of ctenomyids are recognized (Mares and Ojeda, 1982; Wilson and Reeder, 1993); however, in rodents of the genus *Ctenomys*, levels of variation in diploid and fundamental number of chromosomes are extremely high (Cook and Yates, 1994). Thus, a species of *Ctenomys* described and defined without data on chromosomes may actually represent a complex of undetected species, and as many as 60 or more cryptic species may exist in southern South America.

Filarioid nematodes of the genus *Litomosoides* Chandler, 1931, occur in the abdominal and thoracic cavities of mammals of the orders Didelphimorpha, Chiroptera, and Rodentia in the Neotropical and Nearctic regions (Bain et al., 1989). Filarioid nematodes of the genus *Litomosoides* have been reported from hosts in the Palearctic region (Gupta and Trivedi, 1989); however, the specimens of Gupta and Trivedi (1989) appear more similar to filarioid nematodes of the genus *Litomosa* Yorke and Mapleston, 1926.

Scott et al. (1951) detailed the life history of *Litomosoides carinii* Travassos, 1919, from experimental infections. The cotton rat, *Sigmodon hispidus* Say and Ord, was used as the definitive host, and the tropical rat mite, *Bdellonyssus bacoti* (Hirst), was used as the intermediate host. In the arthropod, microfilariae exsheath in the gut, enter the hemocoel, and develop into third-stage juveniles (Anderson, 1992). During the blood meal, the microfilariae are transmitted as infective third-stage juveniles to the definitive host (mammal). Within the circulatory system of the definitive host, third-stage microfilariae

undergo an additional molt to fourth-stage juveniles that later molt into adults in the mesenteries.

Subsequent to the work by Scott et al. (1951), additional life cycle experiments were conducted with *Litomosoides galizae* Bain, Petit, and Diagne, 1989, *Litomosoides petteri* Bain, Petit, and Berteaux, 1980, and *Litomosoides legerae* Bain, Petit, and Berteaux, 1980, using *B. bacoti* as the intermediate host. These experimental infections were used to characterize more completely the details of microfilariae at each stage in the life cycle (Bain et al., 1980, 1989). However, except for the work by Forrester and Kinsella (1973), there have been no experiments on host specificity and identity of the intermediate hosts for those species of *Litomosoides*.

The present paper includes the descriptions of 2 new species of filarioid nematodes of the genus *Litomosoides* sensu Gardner and Schmidt, 1986, found in the mesenteries of rodents of the genus *Ctenomys* (Rodentia: Ctenomyidae) collected in 1984 and 1986 from a single locality on the altiplano of Bolivia.

MATERIALS AND METHODS

Individual nematodes that we determined represent 2 new species of the genus *Litomosoides* were recovered from *Ctenomys opimus* Wagner collected in Bolivia during May through August in the years 1984 and 1986. These collections were part of a larger study to survey the biodiversity of the parasites of mammals of Bolivia. Blood smears were prepared, fixed in 100% methanol, stained with Wright's stain, and examined for the presence of microfilariae. Adult filarioid nematodes were isolated from the abdominal and thoracic regions of freshly killed hosts and were killed in glacial acetic acid. The adult filarioid nematodes were then fixed in 10% formalin or stored in 70% ethanol.

In the laboratory, specimens were cleared over a period of 5–7 days by evaporation of a solution of 70% ethanol, 2% glycerol, and 2% lactic acid. Quantitative measurements were taken using both a calibrated ocular micrometer and a computer-aided image measurement system. Drawings were made with the aid of a drawing tube. Microfilariae were dissected from broken females for detailed drawing and measurement. In the description, n = number of individuals, SD = standard deviation, CV = coefficient of variation, and means are in parentheses.

DESCRIPTION

Litomosoides andersoni n. sp.

(Figs. 1–14)

General: With characters of the genus (sensu Gardner and Schmidt, 1986). Males about ½ length of females. Lateral amphids visible with slightly narrowing cephalic extremity. Reduced lateral alae (Fig. 14). Well-cuticularized stoma wider than long, expanding posteriad to a width greater than the anterior part; posterior ½ of the stoma embedded in the muscular part of esophagus. Nerve ring about ⅓ distance from anterior extremity (Fig. 1); excretory pore at level of nerve ring. Long

FIGURES 1–14. Drawings of *Litomosoides andersoni* n. sp. (scale bar same for Figs. 2–4). 1. Anterior end of female showing positions of the nerve ring and ovijector. 2. Anterior end of female showing detail of the stoma. 3. Anterior end of male showing detail of the stoma. 4. Microfilaria extracted from the uterus. 5. Posterior end of male showing the position of the spicules and papillae. 6. Area rugosa. 7. Right spicule. 8. Cloacal papillae. 9. Left spicule. 10. Tail of female showing phasmid ducts. 11. En face, note lack of any visible structures. 12. Tail of female. 13. Ovijector. 14. Cross section of male at mid-body.

and tapering tail (Fig. 10). Sheath of microfilaria longer than body, with longest part at tail (Fig. 4).

Male: $n = 16$, total length 21–31 (27) mm, SD = 2 mm, CV = 0.09. Maximum body width 119–172 (147), SD = 15, CV = 0.11. Anterior body width 25–43 (37), SD = 4, CV = 0.12. Width of stoma 4–10 (8), SD = 2, CV = 0.24. Length of stoma 3–8 (5), SD = 1, CV = 0.24. Body width at base of esophagus 56–74 (64), SD = 5, CV = 0.07. Length of esophagus 501–764 (661), SD = 77, CV = 0.12. Esophagus width at midpoint 15–37 (23), SD = 5, CV = 0.24. Distance from nerve ring to anterior end 220–531 (362), SD = 71, CV = 0.20. Body width at nerve ring 31–65 (49), SD = 7, CV = 0.14. Length of left spicule 286–654 (556), SD = 125, CV = 0.23.

Description of spicules: Left spicule. Length of calomus 127–316 (211), SD = 45, CV = 0.21; width of manubrium 7–17 (13), SD = 2, CV = 0.18; length of vellum 53–160 (90), SD = 32, CV = 0.36; length of lamina 79–459 (326), SD = 113, CV = 0.35. Lamina and calomus relatively well cuticularized; calomus slightly longer than membranous lamina. Lamina narrows to a thin flagellum, terminating in a very thin small hook (Fig. 9). Right spicule. Length 65–101 (77), SD = 8, CV = 0.10, much shorter than left spicule. From manubrium, calomus relatively long, tapering posteriad with a complex lamina and vellum terminating in a sharp hook (Fig. 7). Spicules similar to those described for the “carinii” group defined by Bain et al. (1989) (see Diagnosis). Length of tail 140–272 (216), SD = 30, CV = 0.14. Body width at cloaca 38–57 (46), SD = 5, CV = 0.10. No post-cloacal papillae; 2 pairs of cloacal papillae (Fig. 8); tail with 4 or 5 coils.

Female: $n = 14$, length 61–81 mm (69), SD = 7 mm, CV = 0.10. Maximum body width 244–367 (296), SD = 32, CV = 0.11. Anterior width of body 30–74 (42), SD = 13, CV = 0.30. Width of body at base of esophagus 71–116 (98), SD = 14, CV = 0.14. Length of stoma 4–7 (5), SD = 1, CV = 0.19. Width of stoma 5–13 (10), SD = 2, CV = 0.23. Esophagus length 632–924 (788), SD = 75, CV = 0.10. Esophagus width 23–35 (29), SD = 3, CV = 0.12. Distance from nerve ring to anterior end 322–693 (450), SD = 135, CV = 0.30. Body width at nerve ring 51–100 (66), SD = 12, CV = 0.18. Distance from vulva to anterior end 863–1,198 (972), SD = 89, CV = 0.09. Body width at vulva 97–157 (125), SD = 16, CV = 0.13. Vulva immediately posterior to esophageal-intestinal junction, ovjector muscular, forming a loop just posterior to vagina (Figs. 1, 13). Body width at anus 58–94 (73), SD = 10, CV = 0.13. Length of tail 201–675 (539), SD = 139, CV = 0.26. Tail with phasmids clearly visible (Fig. 10).

Microfilaria: From specimens dissected from uterus of female nematode, mean measurement lengths including sheath ($n = 10$): length 65, width 5. Sheath of microfilaria longer than body, with longest part of sheath at posterior end (Fig. 4). From specimens measured without sheath in blood smear, mean measurements ($n = 100$): length 37, width 6.

Taxonomic summary

Symbiotype: Holosymbiotype: *Ctenomys opimus*, American Museum of Natural History (AMNH) catalog no. 260839; field collection no. SG#61-84; Museum of Southwestern Biology (MSB), Division of Biological Materials, New Mexico, kryovoucher no. NK11511. Allosymbiotype: *Ctenomys opimus*, AMNH catalog no. 260843; field collection no. SG133-84; MSB Division of Biological Materials, New Mexico, kryovoucher no. NK11583. Collected August 1984.

Type locality: 3.5 km northeast of Rancho Huancaroma, Departamento de Oruro, Bolivia, South America (17°40'S, 67°27'W, elev. 4,000 m).

Specimens deposited: Holotype male (NK11511G): H. W. Manter Laboratory (HWML) 39122. Allotype female (NK11583AA): HWML 39123.

Etymology: Named in honor of Dr. Sydney Anderson, leader of our field expeditions and a pioneering mammologist in Bolivia.

Prevalence: In 1984, 9/22 (40%) of individuals of *C. opimus* examined from the type locality were infected with *L. andersoni*.

Diagnosis

Litosomoides andersoni n. sp. can be distinguished from all other species of *Litosomoides* except *L. thomomydis* Gardner and Schmidt, 1986, and *L. westi* Gardner and Schmidt, 1986, by the structure of the stoma. These 3 species possess a stoma that is broader than long with most of the posterior part being embedded in the esophagus. However,

the stoma of *L. andersoni* is shorter and thicker and possesses a different shape than those of *L. thomomydis* and *L. westi*.

Litosomoides andersoni n. sp. can also be distinguished from *L. thomomydis* by the shape of the spicules; in *L. andersoni*, the right spicule terminates distally in a sharp hook, whereas the lamina of the right spicule of *L. thomomydis* is more rounded and lacks a hook. The spicules resemble those of the “carinii” group as defined by Bain et al. (1989; p. 285) in the following: “Dans le deuxième type, représenté par *L. carinii* et *L. scotti*, le spicule droit est sclérifié jusqu'à son extrémité distale, avec un bourrelet subterminal, bien marqué sur la face dorsale, qui peut délimiter un capuchon terminal (*L. carinii*); le talon est fort. Le spicule gauche a une lame composée d'une partie simple et bien sclérifiée, plus courte que la manche; la partie postérieure entièrement membraneuse n'est bien visible que chez *L. scotti*.”

Litosomoides andersoni can be differentiated from *L. westi* on the shape of the tail; *L. andersoni* lacks any caudal projections, whereas *L. westi* has a tail ending in 3 well-developed points (see Gardner and Schmidt, 1986).

Litosomoides ctenomyos n. sp.

(Figs. 15–28)

General: With characters of the genus (sensu Gardner and Schmidt, 1986). Viewed en face, cephalic extremity lacking visible structures. Cylindrical stoma longer than wide with irregularly thickened walls, about ¼ of stoma embedded in esophagus (Figs. 16, 17). Nerve ring located about ¼ of length of esophagus from anterior end (Fig. 15), excretory pore at level of nerve ring. Reduced lateral alae (Fig. 27). Sheath of microfilariae about the length of the body (Fig. 19).

Male: $n = 6$. Total length 27–31 (28) mm, SD = 1 mm, CV = 0.05. Maximum body width 92–170 (140), SD = 27, CV = 0.19. Body width at anterior end 39–43 (41), SD = 1, CV = 0.03. Stoma width 7–9 (8), SD = 1, CV = 0.11; stoma length 13–18 (15), SD = 2, CV = 0.10. Body width at esophagus base 60–77 (67), SD = 6, CV = 0.09. Esophagus length 511–730 (640), SD = 75, CV = 0.11; esophagus width 24–28 (25), SD = 2, CV = 0.06. Distance of nerve ring to anterior end 205–425 (317), SD = 90, CV = 0.28. Width of body at nerve ring 56–61 (58), SD = 2, CV = 0.04.

Description of spicules: Spicules similar to those described for the “sigmodontis” group by Bain et al. (1989). Right spicule much shorter than left. Manubrium and calomus well cuticularized, much longer than the lamina portion of the spicule. Lamina without vellum, strongly cuticularized. Spicule tapers posteriorly ending in a slender tip (Fig. 28). Right spicule less cuticularized than those usual for the carinii group, blade is lacking a phalange and it tapers with 2 cuticular borders. Length of right spicule 73–91 (81), SD = 7, CV = 0.08. Left spicule long and slender; calomus and lamina portions of almost equal proportions. Vellum relatively well developed, extending from the junction of the calomus and the lamina, disappearing in about the distal ⅓ of the length of the spicule. Distal portion becoming narrow and ending in a rodlike structure with a slightly hooked terminus (Fig. 20). Blade simple and longer than handle, vellum not as well developed as those of the carinii group. Length of left spicule 189–385 (296), SD = 66, CV = 0.22; calomus length 119–131 (125), SD = 5, CV = 0.03; manubrium width 7–14 (12), SD = 3, CV = 0.21; lamina length 143–192 (160), SD = 19, CV = 0.11; vellum length 32–71 (52), SD = 14, CV = 0.26; tail length 151–194 (171), SD = 16, CV = 0.09.

Body width at cloaca 45–51 (48), SD = 2, CV = 0.04. Number of cloacal papillae 6–12 (10), SD = 2, CV = 0.20. Tail rounded with 4–5 coils, 8–9 post-cloacal papillae and 1 pair of cloacal papillae (Figs. 18, 21).

Female: $n = 5$. Maximum body width 264–333 (300), SD = 25, CV = 0.08. Width at anterior end 44–62 (56), SD = 7, CV = 0.13. Body width at esophagus base 98–144 (116), SD = 17, CV = 0.15. Stoma length 17–20 (18), SD = 2, CV = 0.06; stoma width 6–11 (9), SD = 2, CV = 0.22. Length of esophagus 833–872 (853), SD = 17, CV = 0.02. Width of esophagus 27–39 (31), SD = 5, CV = 0.15. Length of nerve ring to anterior 110–598 (416), SD = 186, CV = 0.45. Body width at nerve ring 70–118 (91), SD = 20, CV = 0.22. Vulva posterior to esophagus with a bulbous muscular ovjector (Figs. 15, 23). Distance from vulva to anterior end 1,125–2,170 (1,474), SD = 415, CV = 0.28. Body width at vulva 124–181 (158), SD = 21, CV = 0.14. Tail tapers with visible phasmids (Figs. 24, 26).

Microfilaria: From specimens dissected from uterus of female nem-

FIGURES 15–28. Drawings of *Litomosoides ctenomyos* n. sp. (scale bar same for Figs. 16, 17). 15. Anterior end of female showing positions of the nerve ring and the ovijector. 16. Anterior end of the female showing detail of the stoma. 17. Anterior end of the male showing detail of the stoma. 18. Posterior end of the male showing positions of the spicules and the cloacal and post-cloacal papillae. 19. Microfilaria extracted from uterus. 20. Left spicule. 21. Cloacal and post-cloacal papillae. 22. En face. 23. Ovijector. 24. Tail of female. 25. Area rugosa. 26. Tail of female showing phasmid ducts. 27. Cross section of male at mid-body. 28. Right spicule.

atode, mean measurements ($n = 10$): length 72, width 5. Sheath of microfilaria about length of body (Fig. 19). No microfilaria were found in blood smears.

Taxonomic summary

Symbiotype: Holosymbiotype: *Ctenomys opimus*, MSB Division of Mammals catalog no. 57198; Division of Biological Materials, New Mexico, kryovoucher no. NK14766. Field collection number SG328-86. Collected October 1986.

Type locality: 3.5 km northeast of Rancho Huancaroma, Departamento de Oruro, Bolivia, South America ($17^{\circ}40'S$, $67^{\circ}27'W$, elev. 4,000 m).

Specimens deposited: Holotype male (NK14766B): HWML 39124. Allotype female (NK14766A): HWML 39125.

Etymology: Named after the genus of host, meaning "of *Ctenomys*."

Prevalence: In 1986, 2/8 (25%) of individuals of *C. opimus* examined from the type locality were infected with *L. ctenomyos*.

Diagnosis

Litomosoides ctenomyos n. sp. can be distinguished from *L. carinii*, *L. scotti* Forrester and Kinsella, 1973, *L. silvae* Padilha and de Faria, 1977, *L. guiterasi* (Vigueras, 1934) Sandground, 1934, *L. brasiliensis* Almeida, 1936, *L. molossi* Esslinger, 1973, *L. chandleri* Esslinger, 1973, and *L. petteri* based on the shape of the right spicule as described by Bain et al. (1989) for the "carinii" group. The lamina of the right spicule of *L. ctenomyos* is smooth and tapering, lacking the hooked phalange at the terminus. *Litomosoides ctenomyos* most closely resembles *L. barretti* Muller, 1980, *L. teshi* Esslinger, 1973, *L. esslingeri* Bain, Petit, and Diagne, 1989, *L. sigmodontis* Chandler, 1931, and *L. leonilavazquezae* Caballero and Caballero, 1931, based on stoma and spicule structure. The spicules resemble those of the "sigmodontis" group as defined by Bain et al. (1989; p. 285) in the following: "Dans l'un, représenté par *L. sigmodontis*, *L. galizai* n. sp. et *L. kohnae* n. sp., le spicule droit est peu sclérifié; sa région distale est effilée, soutenue par deux fines baguettes cuticulaires, et se termine par une courte languette membraneuse, en général repliée dorsalement sous le spicule; la tige est souvent peu saillante. Le spicule gauche a une lame constituée d'un axe sclérifié plus long que le manche; la moitié antérieure est bordée par de larges ailes membraneuses, plissées longitudinalement et donc bien visibles même sans dissection.

Litomosoides ctenomyos can be distinguished from *L. barretti* by the shape of the right spicule and the lack of papillae near the tip of the tail; from *L. teshi* in the shape of the stoma and the shape of the tail in the female, and from *L. sigmodontis* in lacking anteriorly directed cephalic structures (papillae) and in the shape of the spicules. *Litomosoides ctenomyos* can be differentiated from *L. leonilavazquezae* by the size of the body of both males and females and the greater number of unpaired post-cloacal papillae.

DISCUSSION

The finding of filarioid nematodes of the genus *Litomosoides* in rodents of the family Ctenomyidae from Bolivia greatly increases the known host range and known geographic distribution of these filarioid nematodes. Rodents of the genus *Ctenomys* exhibit a strongly subterranean lifestyle (Nevo, 1979). Our observations of individuals of *C. opimus* in colonies in at least 3 different geographic localities in Bolivia indicate that these rodents rarely emerge completely from their burrow systems during daylight hours. On several occasions at 1 locality (Bolivia: Cruce Ventilla, $19^{\circ}08'S$, $66^{\circ}07'W$, elev. 3,950), individuals of *C. opimus* were collected from the same burrow systems from which were collected rodents of the genera *Galea* Meyen (Hystricognathi: Caviidae) and *Phyllotis* Waterhouse (Sciurognathi: Muridae). At this locality, no adult helminths were found that were shared by other rodents living syntopically with *C. opimus*. The rodents of the genera *Galea*, *Ctenomys*, and *Phyllotis* represent 2 major phylogenetic lineages: 1 lineage in

the Hystricognathi Tulberg and 1 lineage in the Sigmodontinae Wagner. Only 1 species of helminth (represented by metacercariae of *Taenia talicei* Dollfus, 1960) was found to be shared among species of *Galea*, *Ctenomys*, and *Phyllotis* sharing burrow systems.

It is interesting to note the morphological similarities in the stoma of *L. andersoni*, *L. thomomydis*, and *L. westi*. The latter 2 species occur only in rodents of the family Geomyidae in the central Nearctic region. Geomyoid rodents are a relatively old group, having originated in North America with no evidence of a fossil history outside the Nearctic region (Russell, 1968). Members of the family Geomyidae occur from southern Canada south through suitable habitat across the isthmus of Panama into northern Colombia in South America, whereas ctenomyid rodents have a strictly southern neotropical distribution, having originated from hystricognath ancestors, perhaps as late as the Pliocene (Gardner, 1991). There is no evidence of any possible contact between geomyids and ctenomyids; therefore, the similarity of morphological characters between at least 2 species of their nematodes appears to be a result of morphological convergence. It is also possible that there may have been a host switch from an ancestor derived from the Nearctic region. The questions presented above can probably be answered most readily by performing an historical-phylogenetic analysis including species of both *Litomosoides* and *Litomosa* using data derived from studies of both morphological and molecular characters. This analysis would provide some spatial/temporal frame that would allow an understanding of the diversification of members of these genera of nematodes.

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