J. Parasitol., 98(3), 2012, pp. 000–000

DESCRIPTION OF A NEW CAPILLARIINAE (NEMATODA: TRICHURIDAE) FROM *SCAPTEROMYS AQUATICUS* (CRICETIDAE: SIGMODONTINAE) FROM BUENOS AIRES, ARGENTINA

María del Rosario Robles, Odile Bain, and Graciela Teresa Navone

Centro de Estudios Parasitológicos y de Vectores CEPAVE (CCT- CONICET- La Plata) (UNLP), Calle 2 # 584, La Plata (1900), Buenos Aires, Argentina. *e-mail: rosario@cepave.edu.ar*

ABSTRACT: A new species of *Capillaria* is described on the basis of specimens recovered from the intestine of the swamp rat *Scapteromys aquaticus* (Cricetidae: Sigmodontinae) from Argentina. *Capillaria alainchabaudi* n. sp. and a peculiar species from Australian marsupials are the only 2 species of *Capillaria* sensu stricto parasitic in mammals. A comparison with the Australian species and with the 18 species of this genus described from other vertebrates from the Western Hemisphere is given. The separation of the new species is based on morphologic and morphometrical features, such as intestine ending in cloaca beside ejaculatory duct, 2 lateral nonmembranous caudal lobes, 2 pairs of caudal non-pedunculated papillae, terminal part of cylindrical cirrus ornamented with thin and thick spines, spicule with apex not well sclerotized in the males, a conspicuous vulvar appendage in the females, and 2 bacillary bands. A survey of the literature revealed that the species of Capillariinae from rodents belong to 9 genera, and the total number of species is low compared to the high diversity and abundance of the hosts, particularly if the modern Muroidea are considered.

The Capillariinae Railliet, 1915, represents a large group of trichinelloid nematodes, including about 350 taxa, which parasitize diverse body organs of all classes of vertebrates (Skrjabin et al., 1957; Anderson and Bain, 1982, 2009; Baker, 1987). The classification of the capillariids is one of the most complex and unsatisfactory among nematode parasites due to the paucity of good morphological characteristics (Spratt, 2006). Different systematic proposals based on several morphological criteria have been given over time (e.g., Travassos, 1915; López-Neyra, 1947; Skjrabin et al., 1954, 1957) until Moravec (1982) subsequently proposed a classification system in which he redefined 12 genera, resurrected 2 genera, created 2 new genera and 5 subgenera, and provided a list of species in each genus. He considered the following morphological characters to be the most significant: caudal alae, bursa, lobular projections, spicule, and cirrus (spicular sheath) in the male, and presence or absence of a vulvar appendage, egg shape, and ornamentation in the female.

Although Moravec (1982) proposed this system only as a foundation for further study, it has been supported by cladistic and phylogenetic analyses (Baruš and Libosvársky, 1984; Lomakin and Romashov, 1987), supplemented by some authors (Mas-Coma and Esteban, 1985; Baruš and Sergeeva, 1990; Moravec and Spratt, 1998; Moravec, 2001) and used by many others (Pisanú and Bain, 1999; Anderson, 2000; Spratt, 2006; Robles et al., 2008). Since 1982, several new genera and subgenera have been proposed, some synonymized (see Gibbons, 2010), and, at present, 23 generic and 11 subgeneric taxa are recognized in the Capillariinae (Moravec, 2001; Gibbons, 2010).

Capillariids from mammals remain poorly studied compared to those from cold-blooded vertebrates (Moravec, 1982, 2000, 2001). The taxonomy of mammalian capillariids is still difficult, although descriptions and revisions have been provided by several authors (Freitas and Lent, 1936; Read, 1949; Butterworth and Beverly-Burton, 1980; Bain and Wertheim, 1981; Moravec, 1982; Justine et al., 1987; Justine, 1989a, 1989b, 1990; Pisanú and Bain, 1999; Moravec, 2000). Rodentia represent the most diverse order of mammals in the world (Wilson and Reeder, 2005). However, only 27 capillariine species have been recorded, 4 of which were reported from sigmodontinae rodents (Cricetidae-Muroidea), i.e., *Calodium hepaticum* (Bancroft, 1893), *Eucoleus gastricus* (Baylis, 1926), and *Aonchotheca forresteri* (Kinsella et Pence, 1987) from North America, and *Liniscus diazae* Robles, Carballo, and Navone, 2008 from South America (Freitas and Lent, 1936; López-Neyra, 1947; Read, 1949; Rausch and Rausch, 1973; Moravec, 1982, 2000; Kinsella and Pence, 1987; Robles et al., 2008).

In the present study, we describe specimens recovered in Buenos Aires, Argentina, from the swamp rat *Scapteromys aquaticus* Thomas, 1920. This sigmodontine cricetid rodent is distributed through part of the Río de la Plata basin and some adjacent areas in east-central Argentina and eastern Paraguay (D'Elía and Pardiñas, 2004, 2008; Pardiñas et al., 2008). Seven species of nematodes have already been found in this host, among them a trichurid, but no capillariine (Sutton et al., 1980; Suriano and Navone, 1994; Digiani et al., 2003; Navone et al., 2009).

MATERIAL AND METHODS

During a study on the biology and systematics of rodents, 38 specimens trapped from Los Talas (34°56′S, 57°44′W, Partido de Berisso), Buenos Aires, Argentina, were necropsied.

The viscera were fixed in 10% formalin and examined in the laboratory. Capillariid specimens were collected from the small intestine, preserved in 70% ethanol, cleared in lactophenol, studied using a compound microscope, and illustrated using a camera lucida.

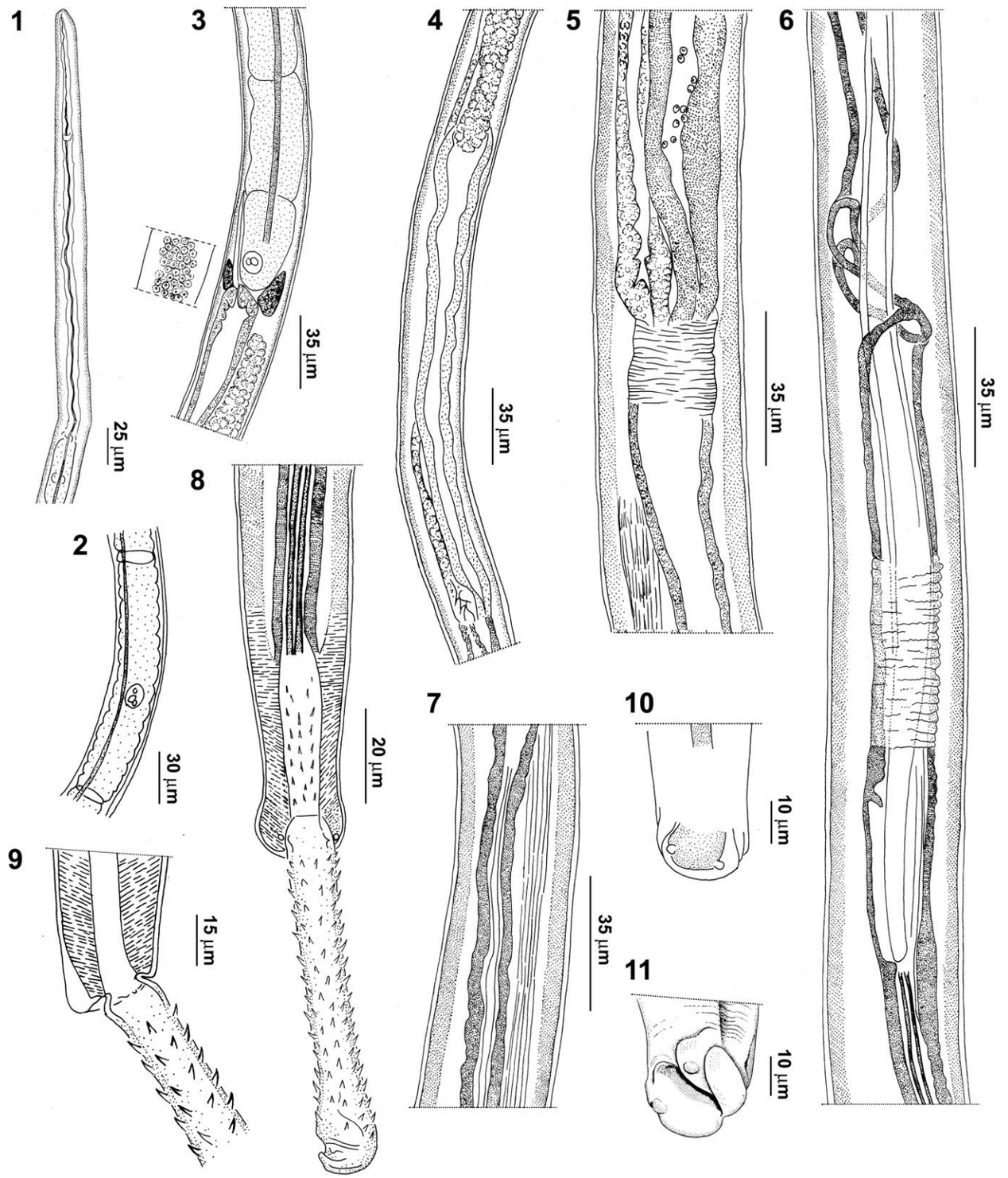
Morphological analysis was performed according to the method proposed by Bain and Wertheim (1981) and followed by Justine in a series of communications (Justine et al., 1987; Justine, 1989a, 1989b, 1990; Justine and Roguin, 1990), Pisanú and Bain (1999), and Spratt (2006). In this method, great attention is given to the posterior internal anatomy of the male, i.e., the end of intestine (which may be in the cloaca or in the ejaculatory duct), seminal vesicle, ejaculatory duct, cloaca, and level of entrance of spicule into the cloaca. Anterior and posterior cloacae are the part anterior or posterior to the entrance of the spicule, respectively (Spratt, 2006). The cuticular lining of the cloaca is called a cirrus by Rauther (1909) instead of a spicular sheath, because it is also present in the anterior part of the cloaca and because this structure is capable of being inserted with the spicule into the vagina during copulation and undoubtedly serves as a true penis (Chitwood and Chitwood, 1950). Measurements of the holotype male and the allotype female are given, followed by the range of the paratypes in parentheses. All measurements are in micrometers unless otherwise stated.

Some specimens were dehydrated in ethanol series (75%, 80%, 85%, 90%, 96%, 100%), dried using the critical point method, examined with

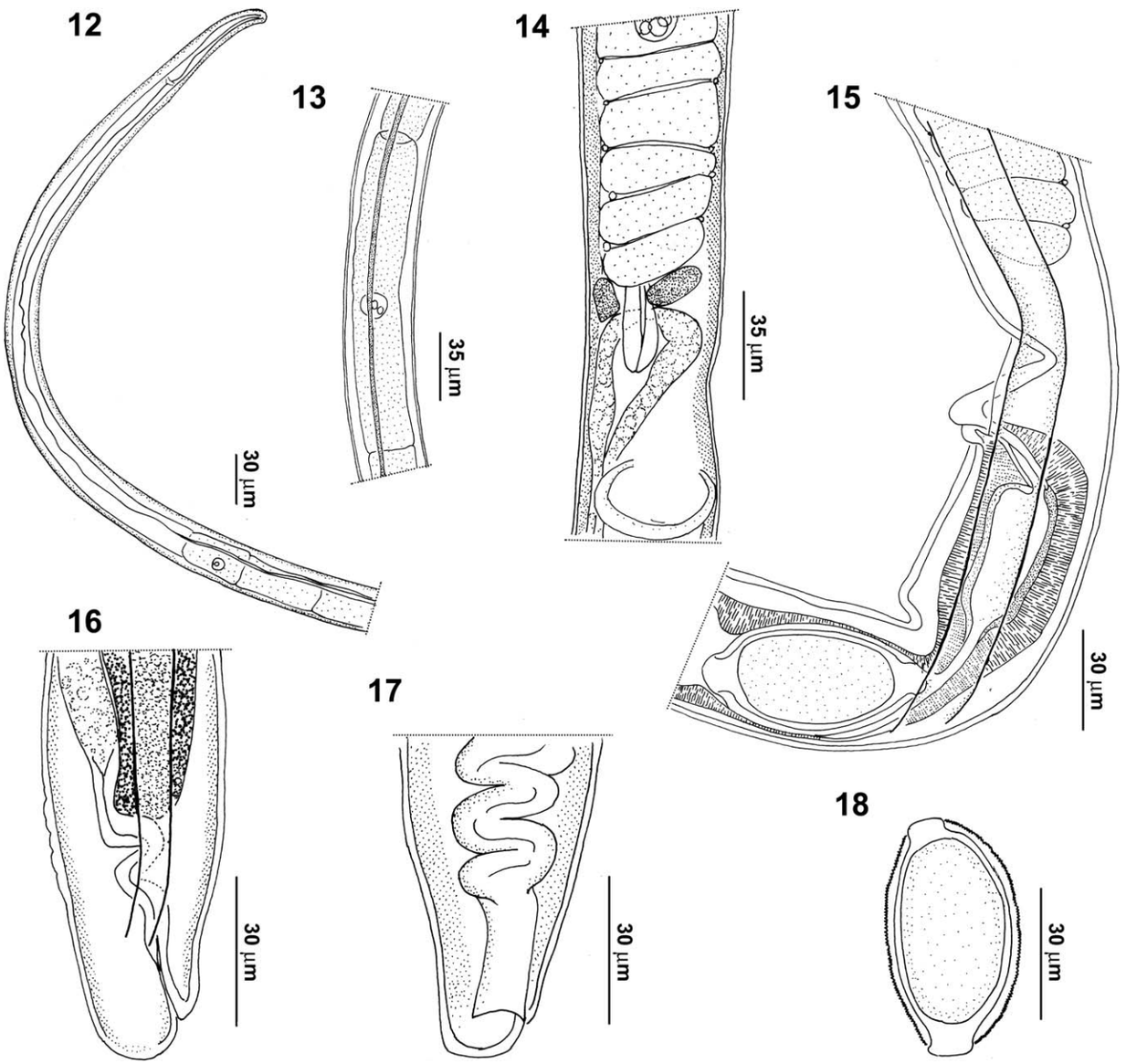
Received 27 September 2011; revised 2 December 2011; accepted 22 December 2011.

* Muséum National d'Histoire Naturelle, UMR 7205 CNRS, CP 52, 61 rue Buffon, 75231 Paris cedex 05, France.

DOI: 10.1645/GE-2991.1



FIGURES 1–11. *Capillaria alainchabaudi* n. sp. Male. (**1**) Anterior region before the first stichocytes. (**2**) A stichocyte, at midlength of esophagus. (**3**) Last stichocyte, esophageal-intestinal junction, pseudocoelomocyte, anterior bend of testis, lateral view (bacillary band drawn at level of esophagus). (**4**) End of seminal vesicle, ejaculatory duct, intestine, and beginning of cloaca. (**5**) Junction of intestine and ejaculatory duct with cloaca (1,650 from tail extremity). (**6**) Entry of spicule in cloaca. (**7**) Cloaca and retractor muscle of spicule (1,050 from tail extremity). (**8**) Caudal region, terminal part of cloaca and extruded cirrus, ventral view (2 ventral papillae on lateral cushions). (**9**) Same orientation, optical sagittal view of cloaca and cirrus. (**10**) Tail extremity, lateral superficial view of a cushion with a ventral and a dorsal papilla (bacillary band drawn in upper part). (**11**) Distal extremity, ventrolateral superficial view of 2 cushions with ventral papillae.



FIGURES 12–18. *Capillaria alainchabaudi* n. sp. Female. (**12**) Anterior region before the first stichocytes. (**13**) A stichocyte at midlength of esophagus. (**14**) Esophageal-intestinal junction with posterior part of last stichocyte, 2 pseudocoelomocytes and vulvar protuberance, ventral view. (**15**) Same region in left lateral view, showing a bacillary band, the vagina, and beginning of uterus (intestine not represented). (**16**) Posterior region, right lateral view, with bacillary band, sinuous rectum, ovary bend. (**17**) Same region, subventral view. (**18**) An egg, near vulva.

the aid of a scanning electron microscope (Jeol 6360 LVLV, Tokyo, Japan), and photographed.

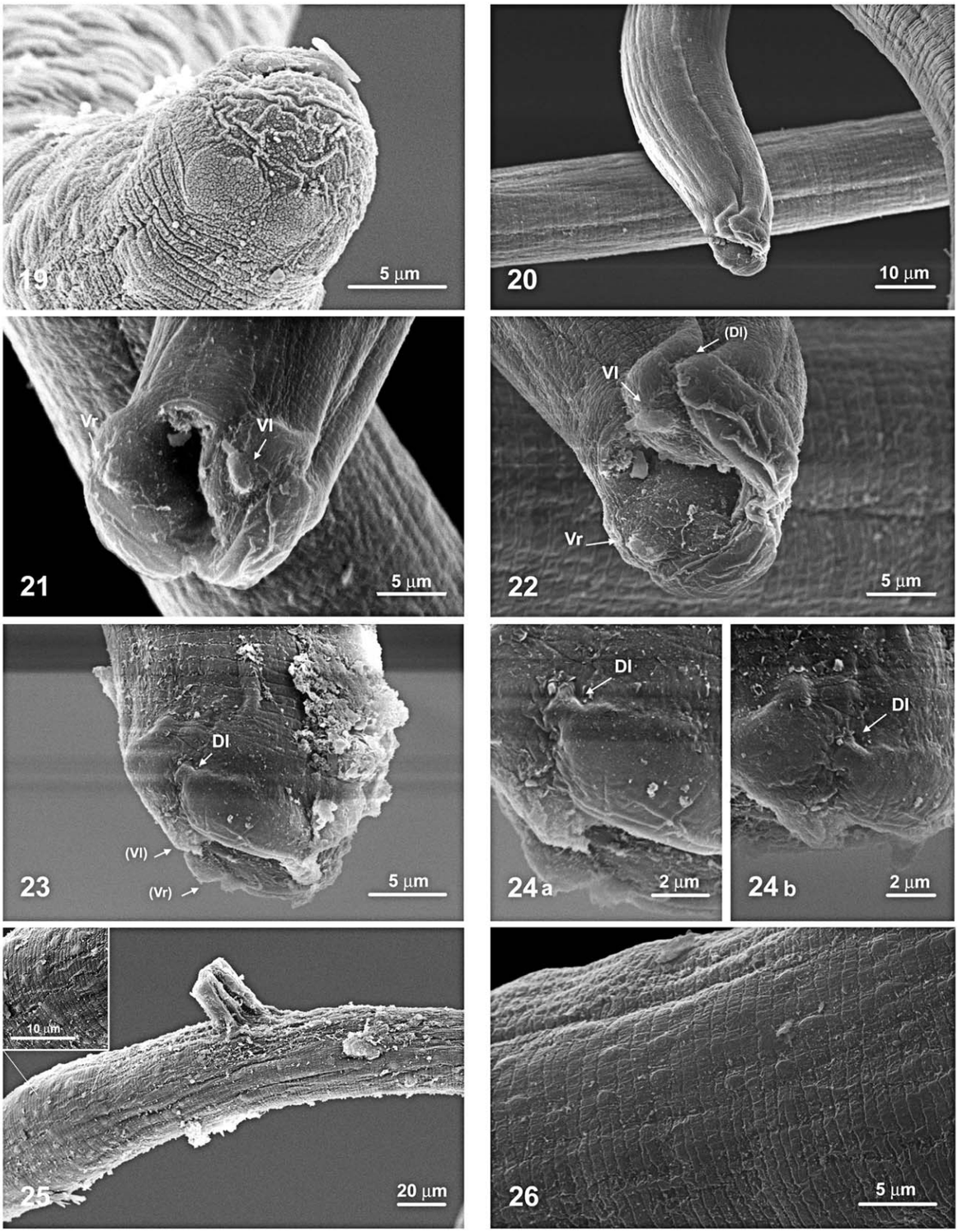
Specimens of nematodes were deposited in the Helminthological Collection of the Museo de La Plata (MLP), La Plata, Buenos Aires, and the Muséum National d'Histoire Naturelle, Paris (MNHN), and hosts were deposited in the Mastozoological Collections of Museo de La Plata (MLP) La Plata, Buenos Aires, Argentina.

DESCRIPTION

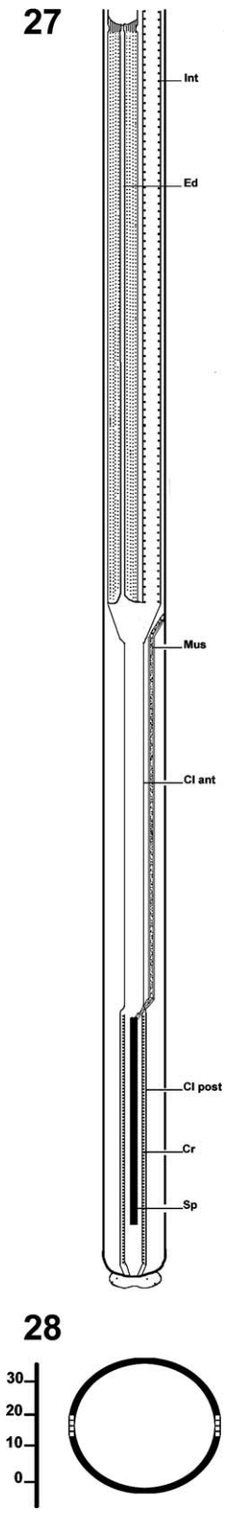
Capillaria alainchabaudi n. sp.
(Figs. 1–28)

General: Oral aperture terminal, slit-like oriented dorsoventrally, with 2 relatively large and flat papillae on each side (Fig. 19). Stichosome with single row of stichocytes; except at extremities, elongated stichocytes with granular cytoplasm, large nuclei containing several nucleoli, and 12–17 transverse muscle fibers per stichocyte. At junction with intestine, 2 pseudo-coelomocytes not well observed. Two identical lateral bacillary bands extending along body, narrow at their extremity, widest at midbody (Fig. 28). Bacillary glands conspicuous; pores opened, or not opened. Presence of bacillary bands does not alter continuity of transverse striations in lateral plane (Fig. 26).

Male: Body 8.7 (6.7–8.7) mm long, 25 (20–35) wide at esophagus-intestine level; nerve ring observed with difficulty (70–85). Muscular esophagus 460 (210–400) (Fig. 1); entire esophagus 2.9 (2.76, 3.1, 3.3; n = 3) mm. Single row of 21–28 stichocytes; first stichocyte 30–32 long, 3 terminal stichocytes 55 to 50 long, other stichocytes 130–150 long (Figs. 2, 3). Intestine normally developed, ending in cloaca beside ejaculatory duct (Figs. 4, 5; scheme Fig. 27). Ejaculatory duct 520 (470, 500; n = 2) long. Cloaca 1,650 (1,500; n = 1) long. Anterior cloaca 1,050 long and 10 wide with thick muscle layer and thin lumen. Expanded posterior to entrance of



FIGURES 19–26. Scanning electron micrographs of *Capillaria alainchabaudi.* Male. (**19**) Anterior end with 2 lateral visible papillae. (**20**) Tail extremity, ventrolateral view of 2 cushions. (**21**) Tail extremity, ventral view of 2 cushions with a ventral papilla (Vl = ventral left, Vr = ventral right). (**22**) Tail extremity, left ventrolateral view of 2 cushions with ventral papillae and with the position of dorsal papilla indicated (Dl = dorsal left). (**23**) Tail extremity, lateral left view of a cushion with dorsal left papillae, and with the position of ventral left and ventral right papillae indicated. (**24a**) Detail of dorsal left papilla in lateral view, plane more ventral. (**24b**) Detail of dorsal left papilla in lateral view, plane more terminal. Female. (**25**) Vulvar region, tubular appendage in lateral view, showing a bacillary band. (**26**) Lateral bacillary bands and details of bacillary glands and transverse striations.



FIGURES 27, 28. Diagrammatic representation of *Capillaria alaincha-baudi.* Male. (**27**) Cloacal region and spicule (Int = intestine, Ed = ejaculatory duct, Mus = muscle, Cl ant = anterior cloaca, Cl post = posterior cloaca, Cr = cirrus, Sp = spicule). (**28**) Transverse section at midbody level showing the bacillary bands.

spicule. Posterior cloaca with terminal portion transparent, widened, then attenuated, 150 long. Cirrus (internal cuticular lining) not transversally pleated, but forming a few longitudinal crests; terminal part ornamented with thin and thick spines directed backward with no apparent plane of distribution; spines distant from each other, particularly at posterior end (Figs. 8, 9). Retracting muscle of spicule as wide as cloaca, attached to body wall at level of cloaca apex (Fig. 7). Spicule apex not identified; both spicule and muscle with similar aspect and width (Figs. 6, 7). Posterior extremity rounded and expanded. Cloacal aperture transverse and flattened laterally, oblique and directed posteriorly, edged with 2 lateral nonmembranous and short lobes, each resembling a cushion in ventral view, an earlobe in lateral view, extending from latero-anterior to latero-posterior aspects. Dorsally, no dorsal membrane linking lobes, but body cuticle thickened (Figs. 10, 11, 20–24). Each lobe with ventral non-pedunculated papilla, posterior to anterior lip of cloacal aperture (Figs. 10, 11, 21, 22); dorsal non-pedunculated papilla also observed in latero-dorsal plane at base of anterior of earlobe (Figs. 10, 22–24). 5

Female: Body 7.8 mm long (7.21–8.03), 40 wide (25–50); nerve ring at 79–85 from anterior extremity; muscular esophagus 375 (310–400) (Fig. 12); entire esophagus 3.36 (2.82–3.77) mm. Single row of 24–32 stichocytes; first stichocyte 28–31 long, 3 terminal stichocytes 125–110 long, other stichocytes 170–250 long (Fig. 13). Vulva close to posterior end of esophagus (Figs. 14, 15), 3,400 from apex. Body constricted anterior to vulva; no membranous vulvar appendage, but conspicuous protuberance, rounded in ventral view, acute or tubular in lateral view, with thickened cuticle and bearing subapical vulva aperture (Figs. 15, 25). Vagina short, with thick musculature; narrow vagina vera 28 long, enlarged vagina uterina 37 long. Posterior end of body slightly constricted laterally and ventrally at level of end of intestine; rectum with several bends and 52 (47–60) long. Anal aperture wide (Fig. 17). Tail 8 (5–8) long, extremity rounded in lateral view, slightly squared in ventral view (Figs. 16, 17). Eggs long 30 × 60 symmetric or not, depending on orientation; egg shell corrugated; poles slightly convex (Fig. 18). 6

Taxonomic summary

Type host: Scapteromys aquaticus Thomas, 1920, male, MLP 08.IV.97.7, others hosts MLP 08.IV.97.8, MLP 08.IV.97.9.

Site of infection: Small intestine.

Type locality: Los Talas (34°56′S, 57°44′W, Partido de Berisso), Buenos Aires, Argentina.

Type specimens: Male holotype 152 YU, female allotype 152 YU (MNHN Paris collection), paratypes (5 females and 1 male) (MLP 6450).

Prevalence and mean intensity: Five of 38 (13%) hosts infected, 3.5 mean intensity and 8.0 in the type host specimen.

Etymology: Dedicated to Dr. Alain Chabaud, a renowned French parasitologist, whose work has inspired other parasitologists around the world.

Remarks

In capillariids, generic identification is the first main point to establish. We used Moravec (1982) and other sources (listed in Moravec, 2001; Gibbons, 2010). We restrict the taxonomic discussion to the 11 genera that include species in mammals.

Several genera are easily excluded based on the characters of the male caudal region, i.e., *Aonchotheca* López-Neyra, 1947, *Calodium* Dujardin, 1845, *Pterothominx* Freitas, 1959, *Tenoranema* Mas-Coma and Esteban, 1985, which have lateral alae; *Baruscapillaria* Moravec, 1982, *Echinocoleus* López -Neyra, 1947, *Liniscus* Dujardin, 1845, and *Pearsonema* Freitas et Mendoça, 1960, which have a membranous caudal bursa; and *Eucoleus* Dujardin, 1845, which is distinctly attenuated at the extremity. Among the 2 last genera, *Pseudocapillaria* has a nonspiny cirrus (contrary to our specimens), and *Capillaria* Zeder, 1800, has a spiny cirrus. The diagnosis of *Capillaria* given by Moravec (1982), ''caudal lateral alae in male absent; posterior end of male rounded, provided with 2 lateral, dorsolateral or ventrolateral lobes; membranous bursa absent; 2 minute pre-anal sessile papillae often present; spicular sheath spiny; vulvar appendage absent or present; intestinal parasites of fishes, amphibians, reptiles, birds, and mammals,'' agrees with the characteristics of the new species, which are tentatively assigned to *Capillaria*, although their spicules are not well sclerotized and the 2 papillae are not precloacal. 7

TABLE I. Update of species from genus (subgenus) *Capillaria* s.s. (subgeneric attributions are absent in those cases where no assignation has been found in the literature).

Genus/subgenus	Species	Authority	Class/order of host	Type host	Other hosts refs.	Site†	Geographic distribution (realm)
Capillaria	*alainchabaudi* n. sp.	This paper	Mammal, Rodentia	*Scapteromys aquaticus*		Intest.	Argentina (Neotropic)
Capillaria (Capillaria)	*anatis*	(Schrank, 1790) Travassos, 1915	Bird, Anseriforms	*Anas boschas*	Skrjabin et al. (1957)	Cecum, intest.	Argentina (Neotropic), Europe?
Capillaria	*aramidesi*	Freitas and Almeida, 1933	Bird, Gruiforms	*Aramides cayanea*		Cecum	Brazil (Neotropic)
Capillaria	*brasiliana*	Freitas, 1933	Bird, Pelecaniforms	*Nycticorax nycticorax*		Intest.	Brazil (Neotropic)
Capillaria (Neocapillaria)	*carioca*	Freitas and Lent, 1935	Actinopterygii, Tetraodontiforms	*Sphaeroides testudineus*		Intest.	Brazil (Neotropic)
Capillaria (Capillaroides)	*catenata**	Cleave et Mueller, 1932	Actinopterygii, Perciforms	*Eupomotis gibbosus*	Skrjabin et al. (1957) Moravec (2001)	Intest.	USA (Nearctic)
Capillaria	*collaris*	Linstow, 1873	Bird, Galliforms	*Gallus gallus*	Skrjabin et al. (1957)	Cecum, intest.	Neotropic, Nearctic, other realms
Capillaria (Neocapillaria)	*cooperi*	Johnston and Mawson, 1945	Actinopterygii, Perciforms	*Callionymus calauropomus*	Skrjabin et al. (1957) Moravec (2001)	–	South Australia (Australasia)
Capillaria (Hepatocapillaria)	*cichlasomae*	Moravec, Scholz, and Mendoza-Franco, 1995	Actinopterygii, Perciforms	*Cichlasoma urophthamulus*		Liver	México (Nearctic)
Capillaria (Hepatocapillaria)	*cyprinodonticola*	Huffman and Bullock, 1973	Actinopterygii, Cyprinodontiforms	*Cyprinodon variegatus*		Liver	USA (Nearctic)
Capillaria (Procapillaria)	*gracilis (= kabatai)*	(Bellingham, 1844) Travassos, 1915	Actinopterygii, Gadiforms	*Merlucius merlucius (= vulgaris)*	Skrjabin et al. (1957) Moravec (2001)	Intest.	Europe (Palearctic)
Capillaria (Neocapillaria)	*hakofugu*	Araki and Machida, 1991	Actinopterygii, Tetraodontiforms	*Ostracion immaculatus*		Rect.	Japan (Palearctic)
Capillaria	*hirundinis**	(Rudolphi, 1819) Travassos, 1915	Bird, Passeriforms	*Hirudo rustica*	Skrjabin et al. (1957)	Intest.	Europe (Palearctic)
Capillaria	*indica*	Subramanian, 1969	Actinopterygii, Perciforms	*Channa gachua*		Intest.	India (Indo-Malayan)
Capillaria (Tridentocapillaria)	*javanensis*	Wakelin, Schmidt, et Kuntz, 1971	Bird, Piciforms	*Dinopium javanense*	Wakelin et al. (1971)	Intest.	Taiwan (Palearctic)
Capillaria	*longistriata*	Walton, 1923	Bird, Piciforms	*Colaptes auratus luteus*		Intest.	USA (Nearctic)
Capillaria	*madnesi*	Wakelin, Schmidt, et Kuntz, 1970	Bird, Passeriforms	*Corvus macrorhynchos*		Stom., intest.	Taiwan (Palearctic)
Capillaria	*manica*	(Dujardin, 1845) Travassos, 1915	Bird, Passeriforms	*Fringilla coelebs*		Intest.	France (Palearctic)
Capillaria (Procapillaria)	*margolisi*	Moravec and Mc Donald, 1981	Actinopterygii, Scorpaeniforms	*Scorpaenichthys marmoratus*		Cecum	British Columbia (Nearctic)
Capillaria (Procapillaria)	*navonae*	Timi, Rossin, and Lanfranchi, 2006	Actinopterygii, Anguilliforms	*Conger orbignianus*		Intest.	Argentina (Neotropic)
Capillaria	*nyrocinarum**	Madsen, 1945	Bird, Anseriforms	*Nyroca marila*	Skrjabin et al. (1957)	Cecum	Denmark (Palearctic)
Capillaria	*ornamentata*	Spratt, 2006	Mammal, Dasyuromorphia	*Antechinus agilis*	Spratt (2006)	Nasal sinus‡	Australia (Australasia)
Capillaria (Tridentocapillaria)	*parusi*	Wakelin, Schmidt, and Kuntz, 1970	Bird, Passeriforms	*Parus monticolus*	Wakelin, et al. (1970)	Intest.	Taiwan (Palearctic)
Capillaria	*patzcuarensis*	Osorio-Sarabia, Perez Ponce de Leon, and Salgado-Maldonado, 1986	Actinopterygii, Atheriniforms	*Chirostoma estor*	Moravec (2001)	Intest.	México (Nearctic)

(Table I continued)

The Journal of Parasitology para-98-03-14.3d 15/3/12 17:38:19 7 Cust # GE-2991

Table I. Continued.

Genus/subgenus	Species	Authority	Class/order of host	Type host	Other hosts refs.	Site†	Geographic distribution (realm)
Capillaria	*phasianina**	Kotlan, 1940	Bird, Galliforms	*Phasianus colchicus*	Skrjabin et al. (1957)	Cecum	Denmark ex USSR (Palearctic)
Capillaria (Neocapillaria)	*pterophylli*	Heinze, 1933	Actinopterygii, Perciforms	*Pterophyllum eimekei (=scalare)*		Intest.	South and North America Europe (Neotropic Holarctic)
Capillaria	*recondita*	Freitas and Lent, 1942	Amphibia, Anura	*Crossodactylus gaudichaudii*		Intest.	Brazil (Neotropic)
Capillaria	*recurvirostrae*	Mawson, 1968	Bird, Charadriiforms	*Recurvirostra novaehollandiae*		Intest.	South Australia (Australasia)
Capillaria	*rigidula*	(Dujardin, 1845) Travassos, 1915	Bird, Passeriforms	*Accetor modularis*		Intest.	France (Palearctic)
Capillaria (Procapillaria)	*schmidti*	Arya, 1985	Chondrichthyes, Rajiforms	*Raja radiata*		Intest.	Southern India (Indo-Malayan)
Capillaria	*skrjabini*	(Lubinova, 1947) Moravec, 1982	Bird, Anseriforms	*Cygnus olor*		Cecum	ex USSR (Palearctic)
Capillaria	*spinulosa*	(Linstow, 1890) Travassos, 1915	Bird, Anseriforms	*Nyroca ferina*		Cecum	Germany Denmark ex USSR (Palearctic)
Capillaria	*tenuissima*	(Rudolphi, 1809) Yamaguti, 1941	Bird, Strigiforms	*Strix uralensis*		Intest.	Japan (Palearctic)
Capillaria	*totani*	(Linstow, 1875) Skrjabin and Schikhoblova, 1954	Bird, Charadriiforms	*Totanus hypoleucos*	Skrjabin et al. (1957)	Intest.	Germany (Palearctic)
Capillaria (Tridentocapillaria)	*tridens*	(Dujardin, 1845) Travassos, 1915	Bird, Passeriforms	*Luscinia luscinia*	Skrjabin et al. (1957), Wakelin et al. (1970)	Intest.	France USA, Cuba (Palearctic, Neotropic)
Capillaria	*uruguayensis*	Calzada, 1937	Bird, Galliforms	*Gallus gallus*		Cecum, intest.	Uruguay (Neotropic)
Capillaria	*vazi*	Freitas, 1933	Bird, Galliforms	*Odontophorus capueira*		–	Brazil (Neotropic)
Capillaria	*venusta*	Freitas and Mendoça, 1958	Bird, Piciforms	*Petroglossus a. aracari*	Freitas and Mendoça (1958) Pinto et al. (1996)	–	Brazil (Neotropic)
Capillaria (Neocapillaria)	*wickinsi*	Ogden, 1965	Actinopterygii/ Pleuronectiforms	*Pleuronectes platessa*		Intest., rect.	Southern North Sea (Palearctic)

* Accurate data on the host type are not available to the authors; the species list was chosen from a list of hosts.
† Site = site of infection; intest = intestine; rect = rectum; stom = stomach.
‡ Proximal.

TABLE II. Main morphological features and measurements of 19 *Capillaria* species from America.

Species	*Capillaria (Capillaria) anatis*	*Capillaria aramidesi*	*Capillaria brasiliana*	*Capillaria (Neocapillaria) carioca*	*Capillaria (Capillaroides) catenata*	*Capillaria collaris*
References	Freitas and Almeida (1935); Lopez-Neyra (1947); Skrjabin et al. (1957)	Freitas and Almeida (1933); Skrjabin et al. (1957)	Freitas (1933); Lopez-Neyra (1947); Skrjabin et al. (1957)	Freitas and Lent (1935); Lopez-Neyra (1947); Skrjabin et al. (1957)	Cleave and Mueller (1932); Skrjabin et al. (1957)	Skrjabin et al. (1957)
Drawing*	Male-female	No	No	Male	Male	Male-female
Bacillary bands	–	–	–	–	–	Slight
Male						
Total length (mm)	7–16.1	6.1	3.7	4.29	8–14	8.9–17.7
Body width	50–70	42	40	40	–	52–63
Stichocytes number	–	–	–	–	–	–
Musc. esoph. length	–	–	–	–	–	–
Total esoph. length (mm)	–	2.3–3.6	–	2.24	–	5.07
Spines of cirrus	Yes	Yes	Yes	Yes	Yes	Yes
Caudal lobes	Two broad	–	–	–	–	Two cuticular
Caudal papillae	–	Large, directed ventrally	One pair, hardly distinguishable	One pair, round dorsolateral	One dorsal pair	–
Spicular length	1,220–1,860	560	530	432	248	1550
Ratio ant/post or percentage ant/total body length	–	6:11† (37.7–59%)‡	5:8†	1:0.9† (52.21%)‡	–	2.3–5† (28.6–56.9%)‡
Female				Unknown		
Total length (mm)	8.4–24.8	4.2	4.9	–	10–15	9.5–20.9
Body width	60–80	32	50	–	55	70
Stichocytes number	–	–	–	–	–	–
Musc. esoph. length	–	–	–	–	–	–
Total esoph. length (mm)	–	–	–	–	–	4.5–5.75
Distance vulva-esoph.	–	42	13	–	0	–
Protruding vulva	Elongated edges	No	No	–	–	Slightly protruding
Egg length	49–65	–	43	–	55	66
Egg width	27–32	–	24	–	27–31	30
Ratio ant/post or percentage ant/total body length	–	5:8†	1:2†	–	–	1:1.4–1:1.6† (27.5–47.4%)‡

* Drawing provided from authors underlined.
† Relation and percentage obtained from studies cited in references.
‡ Approximate percentage obtained from the present study considering the data originally published and placed in the table (total esoph. length/total length).

At present, *Capillaria* is divided into 6 subgenera, i.e., *Capillaria* Zeder, 1800, *Procapillaria* Moravec, 1987, *Neocapillaria* Moravec, 1987, *Capillaroides* Moravec, 1987, *Hepatococapillaria* Moravec, 1987, and *Tridentocapillaria* Barus and Sergeeva, 1990, with only the first parasitic in mammals (Table I). The single *Capillaria* s.s. specimen known from mammals was given no subgeneric assignment (Spratt, 2006). The new species is compared to this species and to the 18 American species of *Capillaria*.

Capillaria ornamentata Spratt, 2006, a parasite of Australian marsupials (*Antechinus* spp.), has many unique characters that differentiate it from *Capillaria chabaudi*, i.e., body extremely long, cuticle ornamented with rugosities, 4 bacillary bands, spicule end broad with 6 rounded points, and a vagina with distal spines (Spratt, 2006).

Among the *Capillaria* s.s. species (Table II), *C. alainchabaudi* n. sp. can be separated from *Capillaria (Capillaria) anatis* (Schrank, 1790), *Capillaria aramidesi* Freitas and Almeida, 1933, *Capillaria brasiliana* Freitas, 1933, and *Capillaria longistriata* Walton, 1923 (from birds); and *Capillaria (Hepatocapillaria) cichlasomae* Moravec, Scholz, et Mendoza-Franco, 1995, *Capillaria (Hepatocapillaria) cyprinodonticola* Huffman et Bullock, 1973, *Capillaria (Procapillaria) navonae* Timi, Rossin, and Lanfranchi, 2006, and *Capillaria patzcuarensis* Osorio-Sarabia, Perez Ponce de Leon, et Salgado-Maldonado, 1986 (from fishes) by the presence of a conspicuous vulvar appendage in females; from *Capillaria recondita* Freitas et Lent, 1942 (from an amphibian) by the presence of an anterior lip of the vulva markedly elevated in females and 2 lobes provided with a narrow cuticle margin (papillae not observed) in males; from *Capillaria collaris* Linstow 1873, *Capillaria (Procapillaria) margolisi* Moravec et Mc Donald, 1981, *Capillaria pterophylli* Heinze, 1933, *Capillaria tridens* (Dujardin, 1845), *Capillaria uruguayensis* Calzada,

TABLE II. Extended.

Capillaria (Hepatocapillaria) cichlasomae	*Capillaria (Hepatocapillaria) cyprinodonticola*	*Capillaria longistriata*	*Capillaria (Procapillaria) margolisi*	*Capillaria (Procapillaria) navonae*	*Capillaria patzcuarensis*
Moravec (2001)	Moravec (2001)	Walton (1923); Lopez-Neyra (1947); Skrjabin et al. (1957)	Moravec and McDonald (1981)	Timi et al. (2006)	Moravec (2001)
Male-female Indistinct	Male-female Indistinct	No Lateral	Male–female Not observed	Male–female Lateral	Female Well visible
1.83	1.29–1.36	20	13.57	8.88–14.45	2.28–2.4
30–50	42–63	40–50	74	50–80	30–45
–	–	–	58	35–46	26–31
138	129–141	–	350	250–410	220–260
0.98	0. 68–0.70	6	9.3	5.6–7.76	1.32–1.51
Yes	Yes	Transversally striated	Yes	Yes	Yes
–	–	Small lateral wings	Sublateral, on each side	Two ventrolateral with cuticular margins	Without lobes
One pair subventral postanal, small inconspicuous	One pair, small slightly outlined dorsolateral	One pair ventrally bent, and a papilla before the cloaca	One large pair and a small pair of sessile ventral near to anus	One large pair posterior to cloaca	–
68–85	99–102	1,500	200	210–0.260	318–320
54%†	50–52%†	1:2.33† (30%)‡	71%†	50.61–70.92%†	–
4.54	4.62–4.92	20–20.5	18.58–21.76	19.28–27.25	4.10–4.68
50–60	109	60–70	93–112	70–110	48–54
38	35	–			26–32
195	159–174	–	360–380	290–430	260–300
2.0	1.50–1.55	–	9.11–10.28 (total)	7.22–11.18	1.39–1.53
0	36–75	–	–	60–240	26
No	No	No	Slightly elevated	No	No
53–60	60–66	45	62–69	65–78	72–81
23–28	36–42	15	25–28	27–34	30–33
44%†	30–34%†	1:1.3–1:1.4†	46–54%†	36.61–51.20%†	–

1937, *Capillaria vazi* Freitas, 1933, and *Capillaria venusta* Freitas et Mendoça, 1958 (from birds) by esophagus and total body lengths (see Table II), and from *Capillaria carioca* Freitas et Lent, 1935 (from birds) and *Capillaria (Capillaroides) catenata* Cleave et Mueller, 1932 (from fish) by having 2 pairs of caudal papillae. Table II lists the main morphological features and measurements (generally ranges of paratypes) of these 19 species (Travassos, 1915; Walton, 1923; van Cleave and Mueller, 1932; Freitas, 1933, 1935; Freitas and Almeida, 1933, 1935; Freitas and Lent, 1935, 1942; Calzada, 1937; López-Neyra, 1947; Skrjabin et al., 1957; Freitas and Mendoça, 1958; Freitas et al., 1959; Moravec and McDonald, 1981; Moravec, 1982, 2001; Baruš and Sergeeva, 1990; Timi et al., 2006).

Capillaria chandleri Read, 1949, and *Capillaria michiganensis* Read, 1949, parasites of American rodents *Spermophilus franklini* and *Ondatra zibethicus*, respectively, were originally described as *Capillaria* sensu lato. Their generic assignment according to the classification of Moravec (1982) is difficult since the males are unknown (Read, 1949). However, the females of these species can be differentiated from *C. alainchabaudi* n. sp. by a number of morphometrical features, including their much shorter length.

DISCUSSION

Capillaria sensu Moravec included a list of 33 species in 1982, which were mainly parasites of birds (22) and fishes (9) and, more rarely, of reptiles and amphibians (1 species in each group); none was parasitic in mammals. During the last 30 yr, only 5 new species have been described from *Capillaria* (Table I). Two were transferred to this genus, *Capillaria* (*Hepatocapillaria*) *cyprinodonticola* and *Capillaria* (*Neocapillaria*) *cooperi* (Johnston

TABLE II. Extended.

Capillaria pterophylli	*Capillaria recondita*	*Capillaria tridens*	*Capillaria uruguayensis*	*Capillaria vazi*	*Capillaria venusta*	*Capillaria alainchabaudi n. sp.*
Lopez–Neyra (1947); Skrjabin et al. (1957)	Freitas and Lent (1942); Skrjabin et al. (1957)	Lopez–Neyra (1947); Skrjabin et al. (1957); Baruš and Sergeeva (1990)	Calzada (1937); Skrjabin et al. (1957)	Freitas (1933); Skrjabin et al. (1957)	Freitas and Mendoça (1958); Freitas et al. (1959)	This paper
Male–female	Male–female	Male–female	Male	Female	Male–female	Male–female
–	Indistinct	Four bands	–	–	–	Two bands
8.3	3.73–4.99	12.99–15.48	10.6–12	15.5	14.69–18.86	6.7–8.7
40–50	57	15–18	–	–	66–86	
40–45	–	–	–	–	–	21–28
–	258		–	–	435–548	210–400
4.7	2.64	5.81–6.3	5.5	–	6.64–7.97	2.76–3.3
No	No	Yes	Transverse striation	Yes	Yes	Yes
Two small convexities	Two lateral with narrow cuticular margin	Three lobes, with a membranous bursa	Two short, round, joined by narrow, hardly visible membrane	Rudimentary bursa in the shape of triangular protrusions	–	Two lateral non membranous lobes
–	Not observed	–	–	–	–	Two pairs: one ventral and one dorsal
180	140–150	1,100–1,630	1,100	1,070	1,410–1,780	150 (incomplete)
1:0.75† (56.6%)‡	–	1:1.3† (40.7–44.9%)‡	1:2.5,1:0927,1:1.2† (45.8–51.8%)‡	1:2†	1.41–1.78† (42.2–45.2%)‡	1:1.61–1:2.13† (36–53%)
18–19	6.03–7.43	18.5–29.2	15.–18	24.4	18.26–26.03	7.21–8.03
60–70	55–60	90–114	–	–	113–131	
–	–	–	–	–		24–32
–	195–252	–	–	–	505–609	310–400
12.4	2.68–3.11	6.28–7.27	6	–	6.47–9.55	2.82–3.77
–	0	–	40–50	32	60–160	40–50
Yes	Anterior lip elevated	–	Slightly protruding	Yes	Slightly protruding	Conspicuous protruberance
50	–	57–70	50	59	59–63	60
20	–	27–37	28	22	25–39	30
1:2† (62.2–68.8%)‡	–	–	1:3–1:1.5† (33.3–40%)‡	5:16†	1:1.65–1:2.5† (35.43–36.7%)‡	1: 1.76–1:2.03† (43–50%)

et Mawson, 1945) (Moravec, 1987), and 2 transferred to other genera, *Amphibiocapillaria serpentina* (Harwood, 1932) and *Piscicapillaria orectolobi* (Johnson et Mawson, 1951) (Moravec, 1986, 1987), bringing the total number of known species to 38.

Remarkably, mammals are still almost absent in the host range of *Capillaria*, with only 1 species, *C. ornamentata*, in an Australian marsupial, and the new species described here in a South American rodent sigmodontine. Perhaps future morphological and genetic studies will clarify the relationships between these species and those from other host groups attributed presently to *Capillaria*.

Eleven genera of Capillariinae are present in mammals, of which 9 are from rodents. The 28 species parasitic in rodents are from *Aonchotheca*, *Baruscapillaria*, *Capillaria*, *Calodium*, *Echinocoleus*, *Eucoleus*, *Liniscus*, *Pseudocapillaria*, and *Tenoranema*. The same generic diversity and paucity of species are noted in North and South American rodents, with a total of only 12 species (López-Neyra, 1947; Read, 1949; Moravec, 1982; Mas-Coma and Esteban, 1985; Kinsella and Pence, 1987; Pisanú and Bain, 1999; Spratt, 2006; Robles et al., 2008). The distribution of species and genera around the world shows no recognizable geographic pattern. The ancient rodents (Caviidae, Gliridae, and Sciuridae) are rather well represented in the host distribution compared to the modern Muroidea, despite the latter group being the most commonly examined for parasites (Table III).

In addition, despite the large number of potential rodent hosts, only about 5.5% of Caviidae, 3.6% of Gliridae, 1.5% of

TABLE III. Species of Capillariinae from rodents.

Genus	Species	Authority, other refs	Order/family host	Type host	Site*	Geographic distribution (realm)
Aonchoteca	*annulosa*	(Dujardin, 1845) López-Neyra, 1947	Myomorpha Muridae	*Rattus norvegicus*	Intest.	Europe ex USSR(Palearctic)
Aonchoteca	*forresteri*	(Kinsella and Pence, 1987) Pisanú and Bain, 1999	Myomorpha Cricetidae	*Oryzomys palustris*	Stom.	USA (Nearctic)
Aonchoteca	*myoxinitelae*	(Diesing, 1851) Moravec, 1982	Sciuromorpha Gliridae	*Eliomys quecinus*	Intest.	Europe (Palearctic)
Aonchoteca	*murissylvatici*	(Diesing, 1851) Moravec, 1982	Myomorpha Muridae	*Apodemus sylvaticus*	Intest.	Europe, ex USSR, USA (Palearctic, Nearctic)
Aonchoteca	*legerae*	(Justine, Ferte and Bain, 1987) Pisanú and Bain, 1999	Sciuromorpha Gliridae	*Eliomys quecinus*	Intest.	Europe (Palearctic)
Aonchoteca	*praeputialis*	(Obendorf, 1979) Spratt, 2006	Myomorpha Muridae	*Rattus fuscipes*	Duct of preputial glands	Australia (Australasia)
Aonchoteca	*ransomia*	(Barker et Noyes, 1915) Moravec, 1982	Myomorpha Cricetidae	*Ondatra zibethica*	Intest.	USA (Nearctic)
Aonchoteca	*tamiasstriatae*	(Read, 1949) Moravec, 1982	Sciuromorpha Sciuridae	*Tamias striatus*	Intest.	USA (Nearctic)
Aonchoteca	*wioletti*	(Rukhlyadeva, 1959) Moravec, 1982	Myomorpha Cricetidae	*Arvicola terrestris*†	Stom.	Russia (Palearctic)
Baruscapillaria	*conspecta*	Spratt, 2006	Myomorpha Muridae	*Rattus fuscipes*	Intest.	Australia (Australasia)
Baruscapillaria	*multicellularis*	(Yamaguti, 1941) Moravec, 1982	Myomorpha Muridae	*Rattus norvegicus*	Intest.	Japan (Palearctic)
Baruscapillaria	*prashadi*	(Maplestone et Bhaduri, 1942) Moravec, 1982	Myomorpha Muridae	*Rattus norvegicus*	–	India (Indo-Malayan)
Baruscapillaria	*traverae*	(Ash, 1962) Moravec, 1982	Myomorpha Muridae	*Rattus norvegicus*	Intest.	Hawaii
Calodium	*hepaticum*	(Bancroft, 1893) Moravec, 1982	Myomorpha Cricetidae	*Sigmodon hispidus*	Liver	USA (Nearctic, other realms)
Capillaria	*alainchabaudi* n. sp.	This paper	Myomorpha Cricetidae	*Scapteromys aquaticus*	Intest.	Argentina (Neotropic)
Capillaria s.l.	*chandleri*	Read, 1949	Sciuromorpha Sciuridae	*Citellus franklini*	Intest.	USA (Nearctic)
Capillaria s.l.	*michiganensis*	Read, 1949	Myomorpha Cricetidae	*Ondatra zibethicus*	Intest.	USA (Nearctic)
Echinocoleus	*hidrochoeri*	(Travassos, 1916) Moravec, 1982	Hystricomorpha Caviidae	*Hydrochoerus hydrochaeris*	Stom., intest	USA (Nearctic)
Eucoleus	*bacillatus*	(Eberth, 1863) Lopez-Neyra, 1947	Myomorpha Muridae	*Rattus norvegicus*	Esoph.	Probably Europe (Palearctic)
Eucoleus	*baskakowi*	Schulz, 1929	Sciuromorpha Sciuridae	*Spermophilus musicus*	Trachea, esoph.	Russia (Palearctic)
Eucoleus	*gastricus*	(Baylis, 1926) Lopez-Neyra, 1947	Myomorpha Muridae	*Rattus norvegicus*	Stom., esoph.	Europe ex USSR, Japan South America (Palearctic, Neotropic)
Eucoleus	*lemmi*	(Retzius, 1841) Skrjabin, Shikhobalova, et Orlov, 1957	Myomorpha Cricetidae	*Arvicola terrestris*	Gastric mucosa	Sweden, ex USSR (Palearctic)
Eucoleus	*medjerdae*	(Bernard, 1964) Moravec, 1982	Myomorpha Muridae	*Mus musculus*	–	–
Eucoleus	*plumosus*	Spratt, 2006	Myomorpha Muridae	*Rattus fuscipes*	Intest.	Australia (Australasia)
Liniscus	*papillosus*	(Polonio, 1860) Moravec, 1982	Myomorpha Muridae	*Rattus norvegicus*	Urinary bladder	Europe (Palearctic)
Liniscus	*diazae*	Robles, Carballo, and Navone, 2008	Myomorpha Cricetidae	*Oxymycterus rufus*	Urinary bladder	Argentina (Neotropic)
Pseudocapillaria	*americana*	(Read, 1949) Moravec, 1982	Sciuromorpha Sciuridae	*Glaucomys volans volans*	Intest.	USA (Nearctic)
Tenoranema	*alcoveri*	Mas-Coma and Esteban, 1985	Sciuromorpha Gliridae	*Eliomys quecinus*	Intest.	Spain (Palearctic)

* Site = site of infection; intest = intestine; rect = rectum; stom = stomach.
†

The Journal of Parasitology para-98-03-14.3d 15/3/12 17:38:22 11 Cust # GE-2991

Sciuridae, 0.9% of Cricetidae, and 0.5% of Muridae species have been recorded as hosts for capillariids. Moreover, 5 capillariid species have been described from sigmodontine rodents, which represent 1.4% of the species identified as hosts. Of these, 2 have been recorded from Argentina (Robles et al., 2008). The contrast between the large number of possible rodent hosts and the small number of capillariids may be due to either an insufficient search, or a particularity in the historical evolution of these nematodes.

However, the anatomical site of infection also must be considered in the phylogeny of mammalian capillariids. For example, species of *Liniscus* are only found in the urinary bladder, species of *Calodium* are only found in the liver, and species of *Eucoleus* are typically found in the esophagus and stomach. Most of the species in *Capillaria* s.s. are found in the small and large intestines and the cecum. Genetic studies are needed to confirm whether morphology and site specificity of these genera parallel the evolution of the subfamily.

The present paper constitutes the second record of a *Capillaria* species from mammals, the first record of the genus from sigmodontine rodents, and the second record of a capillariid species from Argentina.

ACKNOWLEDGMENTS

We thank Marcela Lareschi for her cooperation in the host collections, Ulyses Pardiñas for the identification of the hosts, Mike Kinsella for the critical reading of the manuscript and for the revision into English, María Cristina Estivariz for her assistance with the drawings, and Patricia Sarmiento for the SEM photographs. This study was funded by Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Agencia Nacional de Promoción Científica y Tecnológica (PICT 33019- Director GN; PICT 1634-Director MRR). G.N. and M.R.R. are members of CONICET.

LITERATURE CITED

Anderson, R. C. 2000. Nematode parasites of vertebrates. Their development and transmission, 2nd ed. CAB International, Wallingford, U.K., 650 p.

———, and O. Bain. 2009. Spirurida. Diplotriaenoidea, Aproctoidea and Filarioidea. *In* Keys to the nematode parasites of vertebrates, R.C. Anderson, A.G. Chabaud, and S. Willmott (eds.). CAB International, Wallingford, U.K., p. 391–448.

Bain, O., and G. Wertheim. 1981. Helminthes d'Oiseaux et de Mammifères d'Israël. IX. Compléments morphologiques sur quelques *Capillaria* (Nematoda, Trichinelloidea). Bulletin du Muséum National d'Histoire Naturelle, Section A, **3:** 1061–1075.

Baker, M. R. 1987. Synopsis of the nematode parasitic in amphibians and reptiles. Occasional papers in biology 11. Memorial University of Newfoundland, St. Johns, Newfoundland, Canada, 325 p.

Baruš, V., and J. Libosvársky. 1984. On phenetic and cladistic relations among genera of family Capillariidae. Folia Parasitologica **31:** 227–240.

———, and T. P. Sergeeva. 1990. A new genus of capillariids from birds, *Tridentocapillaria* gen. n. (Nematoda: Capillariidae). Folia Parasitologica **37:** 67–75.

Butterworth, E. W., and M. Beverly-Burton. 1980. The taxonomy of *Capillaria* spp. (Nematoda: Trichuroidea) in carnivorous mammals from Ontario, Canada. Systematic Parasitology **1:** 211–236.

Calzada, V. 1937. Nuevos nematodes. Dos nuevas especies del genero *Capillaria* Zeder, *Capillaria montevidensis* and *Capillaria uruguayensis*. Parasitos de *Gallus* dom.- L. Anales de Facultad de Veternaria, Montevideo **3:** 73–79.

Chitwood, B. G., and M. B. Chitwood. 1950. An introduction to nematology. University Park Press, Baltimore, Maryland, 213 p.

D'elía, G., and U. F. J. Pardiñas. 2004. Systematics of Argentinean, Paraguayan, and Uruguayan swamp rats of the genus *Scapteromys* (Rodentia, Cricetidae, Sigmodontinae). Journal of Mammalogy **85:** 897–910.

———, and ———. 2008. *Scapteromys aquaticus*. *In* IUCN 2011. IUCN Red List of Threatened Species, version 2011.1. Available at: www.iucnredlist.org. Accessed.

Digiani, M. C., C. A. Sutton, and M. C. Durette-Desset. 2003. A new genus of Nippostrongylinae (Nemadoda: Heligmonellidae) from the water rat *Scapteromys aquaticus* (Sigmodontinae) in Argentina. Journal of Parasitology **89:** 124–132.

Freitas, J. F. 1933. Sur deux nouvelles especes du genre "*Capillaria*" Zeder 1800. Comptes Rendus de la Societe de Biologie, Paris **114:** 962–964.

———. 1935. Nota previa sobre duas novas especies do genero "*Capillaria*" (Nematoda) o referencia a novoa hospedadores de helminthos connocidos. Revista de Medecina y Cirugia do Brasil **43:** 301–303.

———, and L. Almeida. 1933. Novo nematodeo do ave do Brasil: *Capillaria aramidesi* n. sp. Archivos da Escola Superior de Agricultura e Medicina Veterinaria, Rio de Janeiro **20:** 169–170.

———, and ———. 1935. Capillariinae parasitas do esophago e papo de aves. Memórias do Instituto Oswaldo Cruz **30:** 123–156.

———, and H. Lent. 1935. Capillariinae de animaes de sangre frio (Nematoda: Trichuroidea). Memórias do Instituto Oswaldo Cruz **30:** 241–284.

———, and ———. 1936. Estudo sobre os Capillarinae parasitos de mammiferos. Memórias do Instituto Oswaldo Cruz **3:** 123–156.

———, and ———. 1942. Primeira especie de *Capillaria* parasite de batraquio sul-Americano (Nematodo: Trichuroidea). Revista Brasileira de Biologia **2:** 325–330.

———, and J. M. Mendoça. 1958. Nova *Capillaria* parasita de araçari (Nematodo, Trichuroidea). Atas Sociedade de Biologia do Rio de Janeiro **2:** 39–40.

———, ———, and J. P. Guimaraes. 1959. Sobre algunas especies do genero *Capillaria* Zeder, 1800 parasitas de Aves (Nematoda, Trichuroidea). Memórias do Instituto Oswaldo Cruz **57:** 17–32.

Gibbons, L. M. 2010. Keys to the nematode parasites of vertebrates. Supplementary volume. CAB International, Wallingford, U.K., 416 p.

Justine, J. L. 1989a. Une nouvelle espèce de *Capillaria* (Nematoda, Capillariinae) parasite de chauve-souris (Mammalia, Chiroptera) du Gabon. Bulletin de Museum National d'Histoire Naturelle, Paris, 4th sér., **2:** 333–347.

———. 1989b. Quatre nouvelles espèces de *Capillaria* (Nematoda, Capillariinae) parasites de Chiroptères du Gabon. Bulletin de Museum National d'Histoire Naturelle, Paris, 4th sér. **3:** 535–561.

———. 1990. *Capillaria dessetae* n. sp. (Nematoda, Capillariinae) parasite de Lagomorphe au Népal; intérêt de l'appareil reproducteur mâle interne pour la taxonomie des Capillariinae. Systematic Parasitology **17:** 125–132.

———, H. Ferte, and O. Bain. 1987. Trois *Capillaria* (Nematoda) de l'intestin du lérot en France. Rapports avec un *Capillaria* de l'estomac du sanglier. Bulletin du Museum National d'Histoire Naturelle, section A **9:** 579–604.

———, and L. Roguin. 1990. *Capillaria murissylvatici* (Nematoda, Capillariinae), parasite d'un Rongeur du Baluchistan Iranien. Bulletin du Muséum National d'Histoire Naturelle, section A **12:** 19–33.

Kinsella, J. M., and D. B. Pence. 1987. Description of *Capillaria forresteri* sp. n. (Nematoda: Trichuridae) from the rice rat *Oryzomys palustris* in Florida, with notes on its ecology and seasonal variation. Canadian Journal of Zoology **65:** 1294–1297.

Lomakin, V. V., and B. V. Romashov. 1987. Morphological-taxonomical analysis and phylogenetic relationships of nematodes of the family Capillariidae Railliet, 1915. Trudy Gelan **35:** 87–94.

López-Neyra, C. R. 1947. Los Capillariinae. Memorias de la Real Academia de Ciencias Exactas, Físicas y Naturales, Serie de Ciencias Naturales **12:** 1–248.

Mas-Coma, S., and J. G. Esteban. 1985. *Tenoranema alcoveri* g. n., sp. n. (Trichuridae: Capillariinae), a nematode parasitizing *Eliomys quercinus* (Rodentia: Gliridae). Folia Parasitologica (Praha) **32:** 35–42.

Moravec, F. 1982. Proposal of a new systematic arrangement of nematodes of the family Capillaridae. Folia Parasitologica **29:** 119–132.

———. 1986. Review of capillariids nematodes (Capillariinae) parasitic in amphibians and reptiles. Part 2. Genus *Amphibiocapillaria*. Vestnik Ceskoslovenske Spolecnosti Zoologicke **50:** 217–230.

———. 1987. Revision of capillariid nematodes (subfamily Capillariinae) parasitic in fishes. Studies CSAV No. 3 Academia, Prague, Czech Republic, 141 p.

———. 2000. Review of capillariid and trichomoidid nematodes from mammals in the Czech Republic and the Slovak Republic. Acta Societas Zoologicae Bohemicae **64:** 271–304.

———. 2001. Trichinelloid nematodes parasitic in cold-blooded vertebrates. Academia, Prague, Czech Republic, 429 p.

———, and T. E. McDonald. 1981. *Capillaria margolisi* sp. nov. (Nematoda: Capillariidae) from a marine fish, *Scorpaenichthys marmoratus* (Ayres), from the west coast of Canada. Canadian Journal of Zoology **59:** 88–91.

———, J. Prokopič, and V. Shlikas. 1987. The biology of nematodes of the family Capillaridae Neveu-Lemaire, 1936. Folia Parasitologica **34:** 39–56.

———, and D. M. Spratt. 1998. *Crocodylocapillaria longiovata* n. gen., n. sp. (Nematoda: Capillariidae) from the stomach of crocodiles in Australia and New Guinea. Journal of Parasitology **84:** 426–430.

Navone, G. T., J. Notarnicola, S. Nava, M. R. Robles, C. Galliari, and M. Lareschi. 2009. Arthropod and helminth assemblage in sigmodontine rodents from Rio de la Plata's wetlands, Argentina. Mastozoología Neotropical **16:** 121–133.

Pardiñas, U. F. J., G. D'elía, and P. Teta. 2008. Una introducción a los mayores sigmodontinos vivientes: Revisión de *Kunsia* Hershkovitz, 1966 y descripción de un nuevo género (Rodentia: Cricetidae). Arquivos do Museu Nacional, Río de Janeiro **66:** 509–594.

Pisanú, B., and O. Bain. 1999. *Aonchotheca musimon* n. sp. (Nematoda: Capillariinae) from the mouflon *Ovis musimon* in the sub-Antartic Kerguelen archipelago, with comments on the relationships with *A. bilobata* (Bhalerao, 1933) Moravec, 1982 and other species of the genus. Systematic Parasitology **43:** 17–27.

Rausch, R. L., and V. R. Rausch. 1973. *Capillaria maseri* sp. n. (Nematoda) from insectivores (Soricidae and Talpidae) in Oregon. Proceedings of the Helminthological Society of Washington **40:** 107–112.

Rauther, M. 1909. Morphologie und Verwandtschaftsbezie-hungen der Nematode. Ergebnisse und Fortschritte der Zoologie **1:** 491–590.

Read, C. P. 1949. Studies on North American helminths of the genus *Capillaria* Zeder, 1800 (Nematoda): I. Capillarids from mammals. Journal of Parasitology **35:** 223–229.

Robles, M. R., M. C. Carballo, and G. T. Navone. 2008. A new species of *Liniscus* (Nematoda: Trichuridae) from *Oxymycterus rufus* and *Akodon azarae* (Cricetidae: Sigmodontinae) in Buenos Aires Province, Argentina. Journal of Parasitology **94:** 909–917.

Skrjabin K. I, N. P. Shikhobalova, and I. V. Orlov. 1957. Trichocephalids and capillariids of animals and man and the diseases caused by them. Osnovy nematodologii 6. Izd. AN SSSR, Moscow, Russia, 597 p.

———, ———, A. A. Sobolev, A. A. Paramonov, and V. E. Sudarikov. 1954. Camallanata, Rhabditata, Tylenchata, Trichocephalata, Dioctophymata and the list of parasitic nematodes according to their hosts. *In* Key to parasitic nematodes IV, K. Skrjabin (ed.). Publishing House of the USSR Academy Science, Moscow, Russia, 927 p.

Spratt, D. M. 2006. Description of capillariid nematodes (Trichinelloidea: Capillariidae) parasitic in Australian marsupials and rodents. Zootaxa **1348:** 1–82.

Suriano, D. M., and G. T. Navone. 1994. Three new species of the genus *Trichuris* Roederer, 1761 (Nematoda-Trichuridae) from caviomorph and cricetid rodents in Argentina. Research and Reviews in Parasitology **54:** 39–46.

Sutton, C. A., A. Chabaud, and M. C. Durette-Desset. 1980. Contribución al conocimiento de la fauna parasitologica argentina VI. Sobre un nuevo Lauroiinae (Nematoda, Ascaridida). Bulletin du Museum National d'Histoire Naturelle, Paris, 4th ser., section 2A, **1:** 81–85.

Timi, J. T., M. A. Rossin, and A. L. Lanfranchi. 2006. A new species of *Capillaria* (Nematoda: Capillariidae) parasitizing *Conger orbignianus* (Pisces: Congridae) from Argentina. Journal of Parasitology **92:** 628–630.

Travassos, L. 1915. Contribuicoes para o conhecimento da fauna helmintolojica brasileira. Sobre as especies brasileiras do genero *Capillaria* Zeder, 1800. Memórias do Instituto Oswaldo Cruz **7:** 146–172.

van Cleave, H. V., and J. F. Mueller. 1932. Parasites of the Oneida Lake fishes. Part I. Descriptions of new genera and new species. Roosevelt Wild Life Annals **4:** 1–71.

Walton, A. C. 1923. Some new and little known nematodes. Journal of Parasitology **10:** 59–70.

Wilson, D. E., and D. M. Reeder. 2005. Mammal species of the world: A taxonomic and geographic reference, 3rd ed. The Johns Hopkins University Press, Baltimore, Maryland, 2,142 p.