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REDESCRIPTION OF *ECHINOCOLEUS HYDROCHOERI* (TRAVASSOS, 1916) (NEMATODA: TRICHURIDAE) FROM *HYDROCHOERIS HYDROCHAERIS* LINNAEUS, 1766 (RODENTIA: CAVIIDAE) FROM ARGENTINA

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?1 ABSTRACT: Twenty-eight Capillariinae species have been recorded in rodents; 1 of these species was reported from a caviomorph
?2 rodent, *Hydrochoeris hydrochaeris* (capybara), and placed in the genus *Echinocoleus* by Moravec (1982). However, both original description and subsequent contributions of *Echinocoleus hydrochoeri* are poor and incomplete. In this paper, this species is redescribed, and a new geographical distribution is reported. The redescription is based on morphologic and morphometrical features; intestine ends in a cloaca beside ejaculatory duct, caudal bursa composed of 2 large ventrolateral lobes with a fleshy internal part and a membranous external part (they are not united dorsally with a membrane), 1 pair of caudal papillae, terminal part of cylindrical cirrus ornamented with thin and thick spines (and particular pattern distribution), sclerotized spicule in male, and vulvar appendage in female, and 3 bacillary bands (1 ventral and 2 lateral). Generic and specific analyses were performed to establish new standards for future studies on the systematic position of Capillariinae species. This study presents new morphological information and a new record of a capillariid species from Argentina.

A recent survey on capillariids of murid rodents carried out in Argentina reaffirmed the difficulty of studying this nematode group, e.g., paucity of good morphological characteristics and complex systematics (Robles et al., 2012), despite the tentative classification of Moravec (1982) and its support from many studies (Mas-Coma and Esteban, 1985; Baruš and Sergeeva, 1990; Moravec and Spratt, 1998; Pisanu and Bain, 1999; Spratt, 2006; Robles et al., 2008, 2012; Gibbons, 2010).

The latest analysis (Robles et al., 2012) stressed that the subfamily Capillariinae has only a few representative species in rodents, and they are very diverse. Twenty-eight species of Capillariinae were recorded in rodents, belonging to 9 genera: *Aonchotheca* López-Neyra, 1947; *Baruscapillaria* Moravec, 1982; *Capillaria* Zeder, 1800; *Calodium* Dujardin, 1845; *Echinocoleus* Lopez-Neyra, 1947; *Eucoleus* Dujardin, 1845; *Liniscus* Dujardin, 1845; *Pseudocapillaria* Freitas, 1959; and *Tenoranema* Mas-Coma and Esteban, 1985 (Robles et al., 2012). One of these species was reported from a caviomorph rodent, *Hydrochoeris hydrochaeris* L., 1766, and placed in the genus *Echinocoleus* by Moravec (1982).

Hydrochoeris hydrochaeris (capybara) is the largest living rodent on earth and is one of the most intensely used wildlife species in South America due to the value of its hide and also because it provides an additional source of protein for many local communities (Quintana et al., 1992; Bolkovic et al., 2006). This rodent has been recorded as a host to several helminth species (e.g., Freyre et al., 1979; Salas and Herrera, 2004; Sinkoc et al., 2009). Among these helminths, *Echinocoleus hydrochoeri* (Travassos, 1916) Moravec, 1982 has been found in different studies from Argentina, Brazil, and Venezuela (Mayaudon, 1980; Costa and Catto, 1994; Bonuti et al., 2002; Sinkoc et al., 2004, 2009; Corriale et al., 2011). However, both its original description and subsequent redescriptions are poor and incomplete (e.g., Travassos, 1916; Freitas and Lent, 1936; Lopez Neyra, 1947).

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Specimens of a species of Capillariinae species were recovered during a parasitological survey of capybaras from 2 localities from Corrientes Province, Argentina. The general observed characters matched those of the genus *Echinocoleus* and species *E. hydrochoeri* (Travassos, 1916; Moravec, 1982), respectively. In this paper, this species is redescribed, reviewing its placement in the genus *Echinocoleus*. In addition, a new geographical distribution is reported for this parasite.

MATERIALS AND METHODS

Capybaras belong to the family Caviidae, within the group of native hystricognath rodents of the New World (Woods, 1984; Galliari et al., 1996), and they have a wide distribution in South America (Redford and Eisenberg, 1992). During a study on the biology of capybaras, 94 specimens in total were necropsied: 68 from Estancia Rincón del Socorro, Esteros del Iberá and 26 from the commercial farm "Ayuí," Santo Tomé, Corrientes Province.

The viscera was fixed in 10% formalin, and an aliquot of intestinal and stomach contents was fixed in 5% formalin and examined in the laboratory. Capillariid specimens were collected from the stomach and small intestine, preserved in 70% ethanol, cleared in lactophenol, studied under 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 et al. (1987); Justine (1989a, 1989b, 1990); Justine and Roguin (1990), Pisanu and Bain (1999), Spratt (2006), and Robles et al. (2012). Measurements are given in micrometers, unless otherwise specified and presented as mean followed by the range in parentheses (Table I). ?3

Table II shows all described species of the genus *Echinocoleus* with their main morphological features, measurements, synonyms, references, hosts, infection site, and geographic distribution. Mammal host names are updated (Wilson and Reeder, 2005).

Some specimens were dehydrated in ethanol series (75, 80, 85, 90, 96, and 100%), dried using the critical point method, examined with the aid of scanning electron microscopy (6360 LVLV; JEOL, Tokyo, Japan), and photographed.

Specimens of nematodes were deposited in Colección Helmintológica del Museo de La Plata (MLP), La Plata, Buenos Aires Province, Argentina.

REDESCRIPTION

Echinocoleus hydrochoeri (Travassos, 1916) Moravec, 1982

(Figs. 1–27; Table I)

General: Oral aperture small, terminal and rounded, not surrounded by elevations. Cephalic papillae not observed. A relatively thick stylet

TABLE I. Main morphological features and measurements of *Echinocoleus hydrochoeri*.

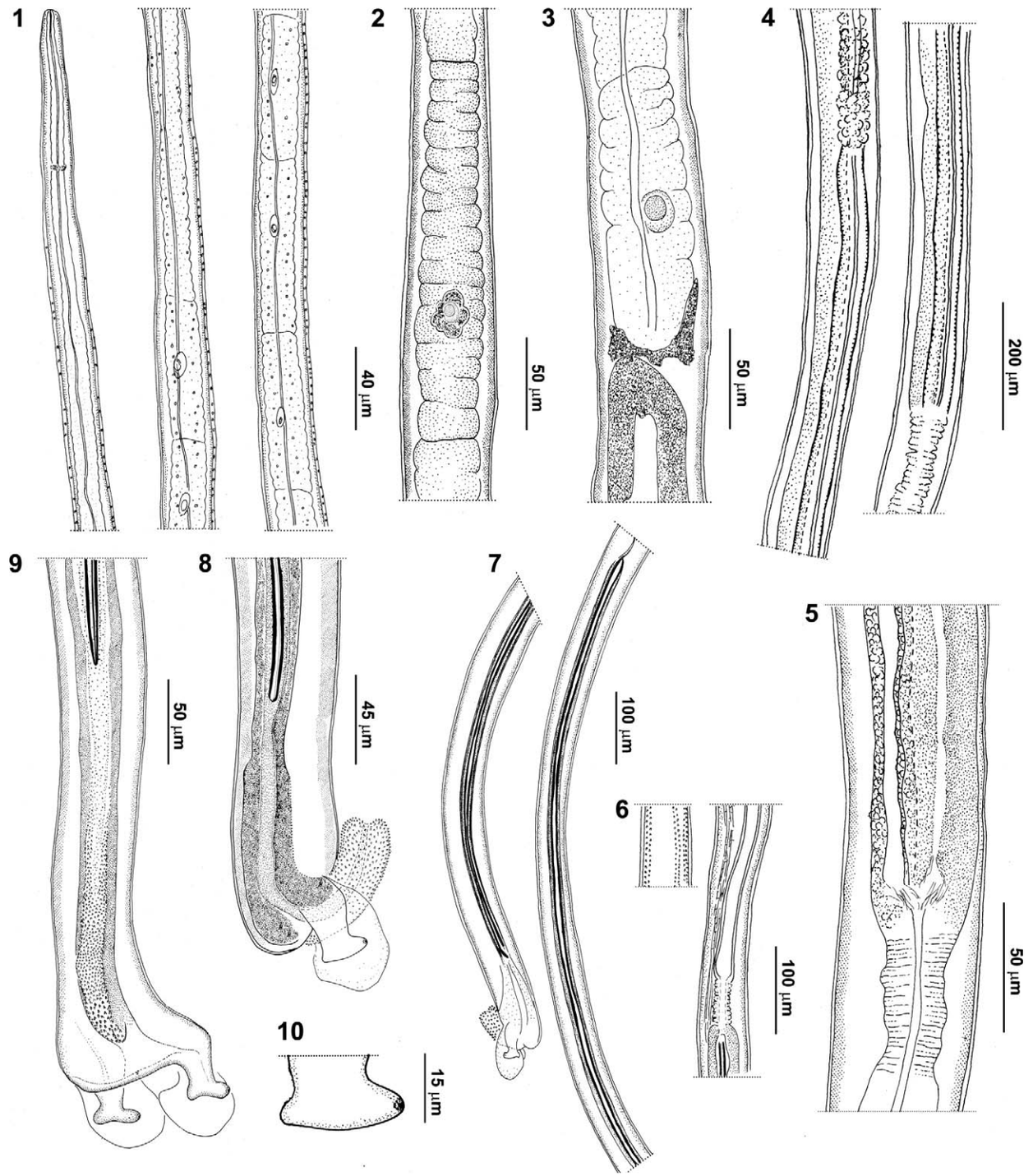
Species	*Capillaria* (*Thominx*) *hydrochaeri* Travassos, 1916	*Capillaria hydrochoeri* Travassos, 1916	*Echinocoleus hydrochoeri* (Travassos, 1916) Moravec, 1982
Synonyms			*Capillaria* (*Thominx*) *hydrochoeri* Travassos, 1916 *Capillaria hydrochoeri*, Travassos, 1927 *Eucoleus hydrochoeri* Lopez-Neyra 1947 *Thominx hydrochoeri* Skrjabin et Schikhobalova, 1954
References	Travassos, 1916	Freitas and Lent, 1936	This study
Type host	*Hydrochaerus capibara* Caviidae: Rodentia: Mammalia	*Hydrochaerus capibara* Caviidae: Rodentia: Mammalia	*Hydrochoeris hydrochaeris** Caviidae: Rodentia: Mammalia
Site of infection	Stomach and small intestine	Stomach and small intestine	Stomach and small intestine
Geographic distribition	Angra dos Reis, Estado do Rio and zoological garden, Rio de Janeiro, Brazil	Brazil	Corrientes, Argentina
Illustration	Not given	Drawing	Drawing, photos
Bacillary bands	Not given	Not given	1 ventral and 2 lateral
Male (N) (mm)			
Body length (mm)	10–20	14	16.67–20.35
Body width	9	32–56	50–60
Nerve ring (dfae)	—		70–85
Muscular esophagus length	—	384	440–650
Glandular esophagus length (mm)	5	6.3	7.0–8.0
Spicular sheath length	Spinous	Spinous	Spinous
Spicular length (mm)	1.35	1.36–1.6	1.33–2.0
Caudal lobes†	Two lobes provided by a strong ray of end bifida	Two cuticular projections membranous, not together.	Two ventrolateral lobes, with a fleshy axial part; each lobe shows a terminal expansion (as a hammer), one larger directed ventrally and another smaller directed dorsally
Membranous bursa†	—	Small membranous bursa	Membranous bursa, with each lobe surrounded with an external wide membranous part subovale
Caudal papillae†	—	Each membrane supported by 1 big papillae (1 pair)	Ventral projection with a terminal conspicuous papilla (1 pair)
Ratio anterior/posterior body length	—	1:1.3	1:1.3
Female (N) (mm)		Gravid and immature	Gravid
Body length (mm)	21–23	25.7–26.4 (15.2)	32.28–41.93
Body width	6	32–80	70–100
Nerve ring	—	128 (122)	70–85
Muscular esophagus length	—	400 (400)	570–650
Glandular esophagus length (mm)	6–7	5.5–6.2 (5.06)	7.41–7.52
Vulva (mm)	—	—	7.65–8.81
Protruding vulva	Present, bell-shaped appendage elevated	Present, bell-shaped appendage elevated	Present, bell-shaped appendage elevated
Distance vulva-esophagus	—	0	40–100
Vagina	—	—	760–940
Egg length	48–55	—	46–50
Egg width	22–23	—	23–30
Ratio anterior/posterior body length	—	1:3 (1:1.7)	1:1.3

* Mentioned as *Hydrochoeris capibara* by Travassos, 1916; Freitas and Lent, 1936.
† Mentioned in original description: Travassos, 1916; "two handles large provided by a strong ray of end bifida." Freitas and Lent, 1936; "two cuticular projections membranous, not together. Each membrane supported by one big papillae."

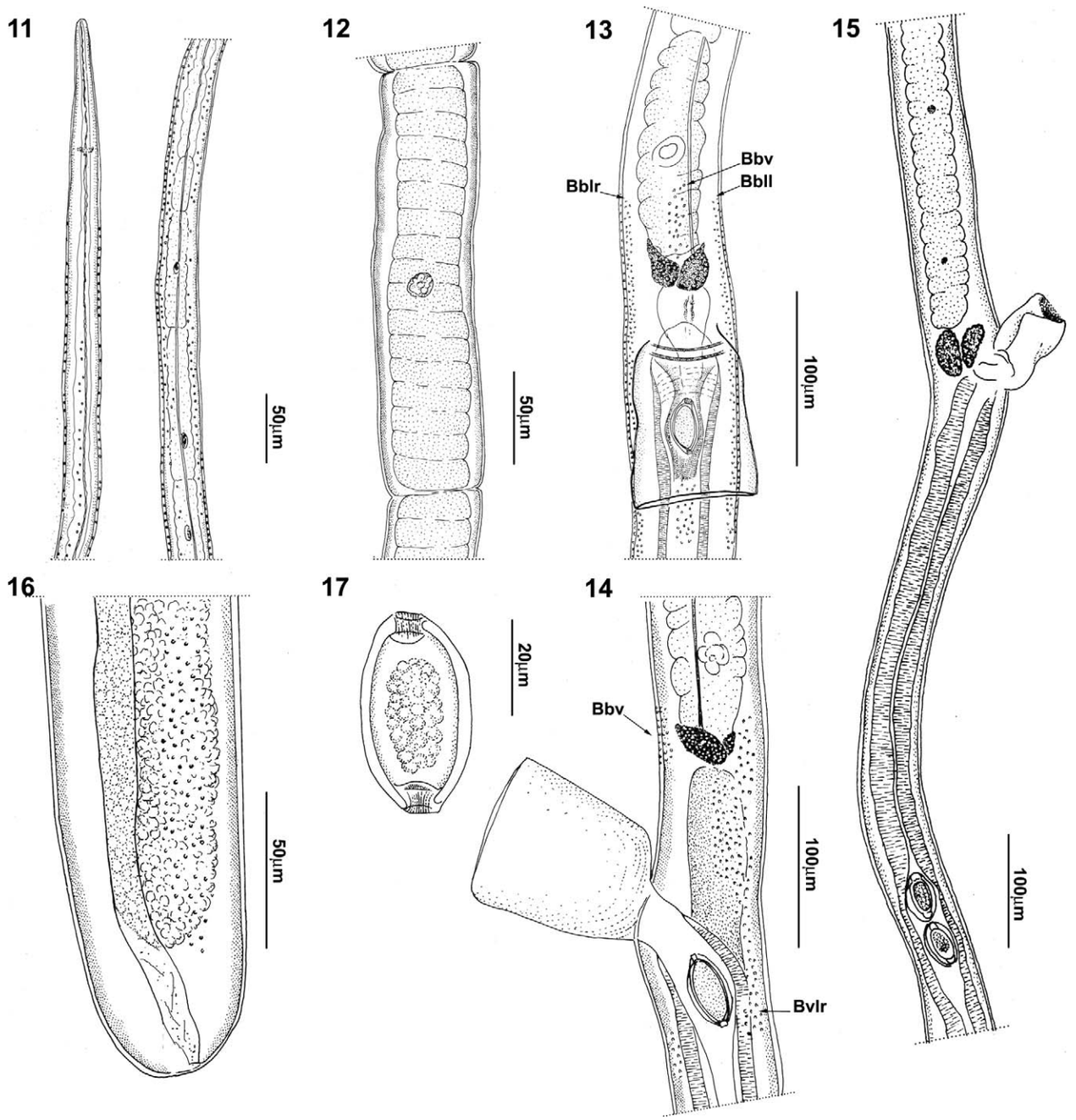
TABLE II. Main morphological features and measurements of *Echinocoleus* species.

Species	*E. cyanopicae* López-Neyra, 1947	*E. auritae* (Travassos, 1914) López-Neyra, 1947	*E. confusus* (Freitas et Almeida, 1935) López-Neyra, 1947	*E. ellisi* (Johnston et Mawson, 1945) Moravec, 1982
Synonyms	*Thominx cyanopicae* Skrjabin et Schikhobalova, 1954	*Capillaria auritae* Travassos, 1914 *Echinocoleus auritae* López-Neyra, 1947 *Thominx auritae* Skrjabin et Schikhobalova, 1954	*Capillaria contorta* Freitas et Almeida, 1934 (*non* Creplin, 1839) *Capillaria confusa* Freitas et Almeida, 1935 *Echinocoleus confusus* López-Neyra, 1947 *Thominx confusa* Skrjabin et Schikhobalova, 1954	*Capillaria ellisi* Johnston et Mawson, 1945 *Thominx* ellisi Skrjabin et Schikhobalova, 1954
References	López-Neyra, 1947; Skrjabin and Schikhobalova, 1954; Skrjabin et al., 1957	Freitas and Lent, 1935; 1936; López-Neyra, 1947; Skrjabin and Schikhobalova, 1954; Skrjabin et al., 1957	Freitas and Lent, 1936; López-Neyra, 1947; Skrjabin and Schikhobalova, 1954; Skrjabin et al., 1957	Skrjabin and Schikhobalova, 1954; Skrjabin et al., 1957; Moravec, 1982
Type host	*Cyanopica cyanus*	*Didelphys aurita*	*Aramides cayanea*	*Cygnus atratus*†
Other hosts	—	*Philander opossum**	—	—
Family: order: class host	Corvidae: Passeriformes: birds	Didelphidae: Didelphiomorphia: Mammalia	Rallidae: Gruiformes: birds	Anatidae: Anseriformes: birds
Site of infection	Small intestine	Small intestine	Esophagus	—
Geographic distribition	Spain	Brazil	Brazil	South Australia
Bacillary bands	One dorsal and 1 ventral	Yes, not described	Yes, not described	Not given
Male (N) (mm)				
Body length (mm)	9.5–12.5	10.2–11.5	5.44–6.06	9.2
Body width	65–80	21–78	50–70	36
Nerve ring	—	64–72	—	—
Muscular esophagus length	75–80	240–320	81–94	—
Glandular esophagus length (mm)	3.64–4.4	5.0–5.5	2.1–2.4	—
Spicular sheath length (mm)	100–120	51–54	0.24	—
Spicular length (mm)	1.18–1.28	1.1	0.27	1.4
Caudal lobes	Two lateral lobes and 2 hemispherical ventrolateral lobes	Two lateral lobes	Two lateral lobes and 2 ventral lobes	Two lateral lobes
Membranous bursa	Bilobed membrane	Bilobed membrane	Rounded membrane	Bilobed membrane
Caudal papillae	Two large dorsolateral and two small postcloacal papillae (2 pairs); and 2 very small and 2 external particularly small papillae (2 pairs)	Ywo dorsolateral papillae (1 pair)	Two large dorsal papillae and 2 small ventral papillae (2 pairs), and 2 very small adcloacal papillae (1 pair)	Papillae not mentioned
Ratio anterior /posterior body length	1:1.6–1:1.84	1:1.07	1:1.5	1: 1.4
Female (N) (mm)				
Body length (mm)	17–18.8	12.9–16.8	6.06	15.9
Body width	80–100	42–114	100	63
Nerve ring	—	86–102	—	
Muscular esophagus length	—	230–290	100	—
Glandular esophagus length (mm)	6.4–7.2	4.9–7	2.5	—
Vulva (mm)	—	—	—	—
Protruding vulva	Absent	Present, slightly elevated	Absent	Present, tubular slightly elevated
Distance vulva-esophagus	0	71–157	27	—
Egg length	60–63	52–62	56	51
Egg width	28–30	20–24	24	37
Ratio anterior/posterior body length	1:1.61–1:1.5	1:1.5	1:1.2	1:1

* Mentioned as *Metachirops opossum* by Freitas and Lent, 1936.
† Mentioned as *Chenopsis* (*cygnus*) *atrata* by Johnston and Mawson, 1945.



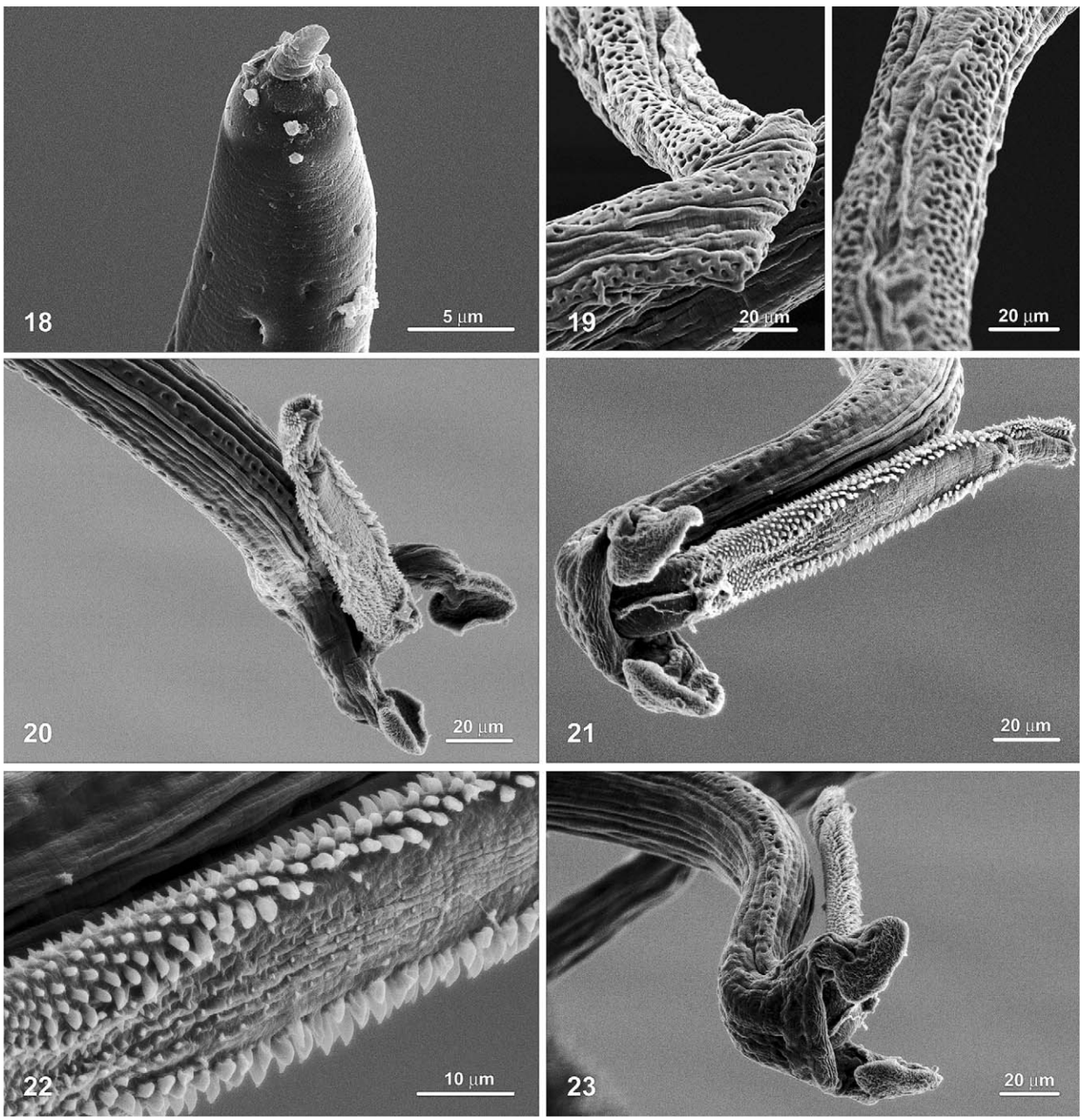
FIGURES 1–10. *Echinocoleus hydrochoeri*. Male. (**1**) Anterior region. (**2**) A stichocyte, at mid-length of esophagus. (**3**) Last stichocyte, esophageal-intestinal junction, pseudo-coelomocyte. (**4**) End of seminal vesicle, ejaculatory duct, intestine and beginning of cloaca. (**5**) Junction of intestine and ejaculatory duct with cloaca. (**6**) Anterior cloaca, entry of spicule in posterior cloaca and retractor muscle of spicule. (**7**) Caudal region, posterior cloaca with complete spicule. (**8**) Caudal region, terminal part of cloaca and extruded cirrus, lateral view (1 ventral papilla on lateral lobe). (**9**) Same part, subdorsal view, no extruded cirrus (other specimen). (**10**) Detail of a lobe with papilla in terminal expansion directed ventrally.



FIGURES 11–17. *Echinocoleus hydrochoeri*. Female. (**11**) Anterior region. (**12**) A stichocyte at mid-length of esophagus. (**13**) Esophageal-intestinal junction with posterior part of last stichocyte, 2 pseudo-ceolomocytes, and vulvar protuberance, ventral view (Bbv, bacillary band ventral; Bbll, bacillary band lateral left; Bblr, bacillary band lateral right). (**14**) Same region in right lateral view, showing a bacillary band. (**15**) Same region in left lateral view, showing the vagina and beginning of uterus (intestine not represented). (**16**) Posterior region, subventral view. (**17**) An egg, near vulva.

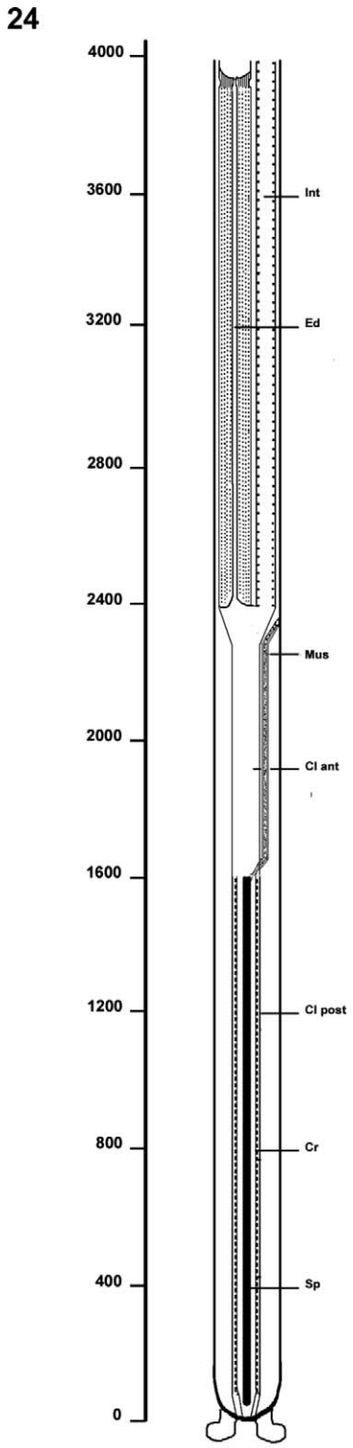
protruded out of middle portion of the mouth of a male (Fig. 18), stylet not observed in females. Stichosome consisting of a single row of stichocytes, elongated stichocytes with granular cytoplasm, large nuclei containing nucleoli; at junction with intestine, 2 pseudo-coelomocytes well developed (Figs. 3, 13). Three conspicuous bacillary bands (Fig. 19), 1 ventral and 2 lateral, extending along body (Figs. 19–21, 25); narrow at their anterior extremity, slightly wider at mid-body and posterior extremity, beginning 80–150 from apex (Figs. 1, 11). The presence of bacillary bands, except in vulvar area of females, does not alter continuity of transverse striations in the dorsal and ventrolateral planes.

Male (6 specimens): Body 18.65 (16.67–20.35) mm long, 55 (50–60) wide at esophagus-intestine level; nerve ring observed with difficulty (70–85); muscular esophagus 508 (440–650) (Fig. 1); entire esophagus 7.58 (6.85–8.42) mm long, stichosome: single row of 37 (30–43) stichocytes; first stichocyte 82 (50–125) long, terminal stichocyte 151 (120–200), other stichocytes 233 (210–260) long (Figs. 2, 3). Posterior length of body 11.07 (9.55–12.5) mm. Intestine joins the ejaculatory duct and forming the



FIGURES 18–23. Scanning electron micrographs of *Echinocoleus hydrochoeri*. Male. (**18**) Anterior end with stylet protruded out of middle portion of the mouth (the white spots are artifacts). (**19**) Bacillary bands: 3 bacillary bands, 1 ventral and 2 lateral, extending along body, view of mid-body, two different views. (**20**) Tail extremity, ventral view, with cirrus and lobes terminally expanded with two projections, ventral and dorsal. (**21**) Tail extremity, dorsal view, with cirrus showing dorsal spines of end portion greater than other, leaving an area without spines. (**22**) Detail of spines of cirrus, dorsal view. (**23**) Tail extremity, dorsolateral view, with bacillary band. Female.

cloaca that is divided into anterior and posterior cloaca (Figs. 4–6). Ejaculatory duct 1.66 (1.14–2.15) mm long. Cloaca 2.33 (2.95–2.62, n = 4) mm long; anterior cloaca 772 (675–925, n = 4) long and posterior cloaca 1.567 (1375–1700) mm long (Fig. 26). Evertible cirrus 20–30 width with terminal part ornamented with thin and thick spines showing apparent plane of distribution; dorsal median area without spines, and first lines of spines (from the area without spines) greater than the rest, especially that those in the anterior portion (Figs. 8, 9, 20–22). Cloaca with thick muscle layer and thin lumen; expanded posterior to entrance of spicule (Fig. 6). Retracting muscle of spicule thinner than cloaca, attached to body wall at level of cloaca apex (Fig. 24). Spicule well sclerotized 1.55 (1.33–2.0) mm (Fig. 7). Posterior extremity provided with caudal bursa composed of 2 large ventrolateral lobes directed posteriorly and slightly ventrally, with a fleshy axial part, more or less rectangular (Fig. 10); and an external wide membranous suboval part (Figs. 8, 9). Each lobe shows a terminal expansion (as a hammer), 1 larger directed ventrally with a conspicuous papilla and another smaller directed dorsally without visible papilla (Figs. 8–10, 20, 21, 23). Dorsal caudal projection and membrane absent, therefore the 2 lobes are not united dorsally (Fig. 23). Cloacal aperture transverse and directed ventrally (Fig. 21). Percentage anterior/total body



length 40.7 (38.5–42.7). Percentage spicule/posterior body length 14.06 (12.24–17.21).

Female (6 specimens): Body 37.58 (32.28–41.93, n = 4) mm long, 85 (70–100) wide at esophagus-intestine level; nerve ring observed with difficulty (70–85); muscular esophagus 618 (570–650) (Fig. 11); entire esophagus 8.2 (7.61–8.72, n = 5) mm long, stichosome: single row of 41 (37–46) stichocytes; first stichocyte 75 (45–105) long, terminal stichocyte 106 (80–135), other stichocytes 208 (160–250) long (Figs. 12, 13). Posterior length of body 28.11 (22.45–33.24) mm. Vulva close to posterior end of esophagus 69 (40–100) (Fig. 15). Vulvar appendage present, with thin cuticle, tubular in lateral view (Figs. 13, 14, 24). Vagina 835 (760–940) long (Fig. 15). Rectum with several bends; anal aperture a wide slit subterminal (Fig. 25). Tail rounded in lateral view (Fig. 16). Eggs long 23–30 × 46–50, symmetric, poles slightly convex (Fig. 17). Percentage anterior/total body length 21.56 (20.72–23.57).

Taxonomic summary

Type host: Hydrochoerus hydrochaeris L., 1766.

Site of infection: Stomach and small intestine.

Type locality: Angra dos Reis, Brazil.

Other localities: Commercial farm Ayuí (28°27′23.92″S, 56°7′34.99″W), Santo Tomé, and Estancia Rincón del Socorro (28°39′30.90″S, 57°26′04.49″W), Esteros del Iberá, Corrientes Province, Argentina.

Voucher specimens: 11 specimens from Ayuí Colección de Helmintología from Museo de La Plata, Argentina (CHMLP) 6595 and 5 specimens from Estancia Rincón del Socorro CHMLP 6594.

?4

Remarks: Six nominal species were included in *Echinocoleus* by Moravec (1982) but 1 species, *E. eurycercus* (Oshmarin and Parukin, 1963) from *Picus canus* (Piciformes) from the ex USSR, was later transferred into *Tridentocapillaria* Baruš and Sergeeva, 1990 (Baruš and Sergeeva, 1990) and was later proposed as a subgenus of *Capillaria* by Okulewicz (1993) (Moravec, 2001). So, *Echinocoleus* includes 3 species parasitic in birds: the type species *E. cyanopicae* López Neyra, 1947 from *Cyanopica cyanus* (Passeriformes) of Spain; *E. confusus* (Freitas and Almeida, 1935) from *Aramides cayanea* (Gruiformes) of Brazil; and *E. ellisi* (Johnston and Mawson, 1945) from *Cygnus atratus* (Anseriformes) of South Australia; and 2 species parasitic in mammals: *E. auritae* (Travassos, 1914) from *Didelphys aurita* (Didelphidae) of Brazil and *E. hydrochoeri* (Travassos, 1916) from *Hydrochoeris hydrochaeris* (Caviidae) of Brazil and Argentina.

These *Echinocoleus* species differ, among other characteristics, in the number of pairs of caudal papillae (1–4), the presence or absence of ventral lobes, and whether the lateral lobes are united or not into a single dorsolateral membrane.

In detail, *E. cyanopicae*, the type species, has a caudal bursa composed of 2 lateral fleshy lobes united dorsally in a single bilobed membrane and 2 hemispherical ventrolateral lobes, 4 pairs of papillae (with unclear position), spicule sclerotized in males, and no vulvar appendage in female (Table II). The original description did not provide more details.

Echinocoleus confusus has a caudal bursa with 4 lobes, 2 lateral and 2 ventral, and a single rounded membrane containing both lateral lobes; 3 pairs of papillae in the males; and no vulvar appendage in the females. The spicule is poorly sclerotized, and the description indicates that the proximal end was not observed clearly (Table II). These characteristics suggest that this species should be removed from this genus.

Echinocoleus ellisi has been described with little detail, and from the characteristics observed in the male, the caudal bursa is a single bilobed membrane containing 2 lateral lobes (no ventral lobes identified) (Table II).

Echinocoleus auritae has a caudal bursa composed of a bilobed membrane containing 2 lateral lobes and a vulvar appendage slightly elevated in the female (Table II).

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FIGURES 24–25. Diagrammatic representation of *Echinocoleus hydrochoeri*. Male. (**24**) Cloacal region and spicule (Int, intestine; Ed, ejaculatory duct; Mus, muscle; Cl ant, anterior cloaca; Cl post, posterior cloaca; Cr, cirrus; Sp, spicule). (**25**) Transverse section at mid-body level showing the bacillary bands.

TABLE III. Comparison of main features of Capillariinae genera from rodents, with terms clarified.

	Cirrus*	Spicule	Membranous caudal bursa†	Caudal lateral alae	Vulvar appendage
Description	Present or not, terminal part ornamented with spines	Present different degree of sclerotization	End location, present different degree of development, support lobes and papillae	Lateral location, present different degree of development, not support any papillae	Different form and degree of development
Aonchotheca	Not ornamented	Sometimes indistinct due to insufficient sclerotization	Present	Present, well developed	Absent or present
Baruscapillaria	Not ornamented	Spicule well sclerotized	Present	Absent	Absent or present
Capillaria	Ornamented	Spicule well sclerotized, sometimes anterior part indistinct	Absent	Absent	Absent or present
Calodium	Not ornamented	Sometimes little sclerotization	Absent	Present, well developed	Absent or present
Echinocoleus	Ornamented	Spicule well sclerotized	Present	Absent	Absent or present
Eucoleus	Ornamented	Moderately sclerotized, sometimes indistinct	Present, rudimentary	Absent	Absent
Liniscus	Not ornamented	Spicule well sclerotized	Present	Absent	Absent or present
Pseudocapillaria	Not ornamented	Spicule well sclerotized	Absent, rudimentary	Absent	
Tenoranema	Not ornamented	Moderately sclerotized	Present	Present, well developed	Present

* The spicular pouch, called often spicular sheath in Trichuridae, was named as cirrus by Rauther (1909). It is a unique occurrence in the Nematoda that lining of the cloaca (cirrus) is itself evertible (Chitwood and Chitwood, 1950).

† Caudal alae are sometimes modified into forms very characteristic of particular groups and may be termed bursae. These alae are generally distributed throughout the Phasmidia and are absent in the Aphasmidia, except in some genera (Chitwood and Chitwood, 1950). So, this term is habitually used among Capillariinae (López Neyra, 1947; Skrjabin et al., 1957; Pisanú and Bain, 1999; Spratt 2006; Robles et al., 2012). Caudal projections are situated within the caudal alae and supported by them.

Echinocoleus hydrochoeri has a caudal bursa composed of 2 large ventrolateral lobes, with a fleshy internal part and a membranous external part; they are not united dorsally with a membrane; 1 pair of papillae; sclerotized spicule in male, and vulvar appendage in female (Table II).

Other characters would be interesting to compare, but the data are incomplete. For example, it is it not clear whether small stylet is always present in the oral aperture. In *E. hydrochoeri*, it was only observed in a mature male. These cephalic structures are very small and difficult to observe under a light microscope; consequently, until now, they were not considered as character of taxonomic significance.

For the cirrus, it is shown here that the distribution pattern of spines may be very complex, mostly in the distal end. In *E. hydrochoeri*, there is a dorsal area without spines or with very small spines on the cirrus. The descriptions of other species did not compare in detail the extension or distribution of spines.

Three bacillary bands (1 ventral and 2 lateral) were observed in *E. hydrochoeri* and 2 bacillary bands (1 ventral and 1 dorsal) in *E. cyanopicae*. Nevertheless, in general, the bacillary bands are a character difficult to compare, because in most cases the presence only is mentioned without describing the number and position.

DISCUSSION

The paucity of distinctive morphological characteristics in capillariids of birds and mammals has resulted in inadequate descriptions and, in turn, continuing taxonomic and nomenclatural difficulties within the entire group. To date, *E. hydrochoeri* has been placed in 4 genera, i.e., *Capillaria* by Travassos (1916); *Eucoleus* by Lopez Neyra (1947); *Thominx* by Skrjabin et al. (1954); and *Echinocoleus* by Moravec (1982).

The generic assignation was the first point that needed to be established. The amended diagnosis of *Echinocoleus* given by Moravec (1982), "caudal lateral alae in male absent; posterior end of male provided with small membranous bursa, often 2 lobes, supported on either side by 1 short, round or more elongate lobular dorsolateral projection, dorsal caudal projection absent, spicule well sclerotized, medium-sized, spicular sheath spiny, vulvar appendage absent or present," agrees with the general characteristics of the capillariines specimens found in capybaras in this survey.

Systematic problems within Capillariinae have increased because of the erroneous interpretation of the morphology of the posterior extremity in males. In addition to the proposal by Moravec (1982), Table III shows the main morphological characters of species of Capillariinae from rodents.

In this paper, generic and specific analyses were performed to establish new standards for futures studies on the systematic position of species of Capillariinae. Consequently, *E. hydrochoeri* was studied in detail, and new relevant information was provided, such as detail of junction between intestine and ejaculatory duct, caudal bursa composed of 2 large ventrolateral lobes with a fleshy internal part and a membranous external part (they are not united dorsally with a membrane), 1 pair of caudal papillae, terminal part of cylindrical cirrus ornamented with thin and thick spines (and particular pattern distribution), sclerotized spicule in male, and vulvar appendage in female, and 3 bacillary bands (1 ventral and 2 lateral). In addition, it was observed that several details on morphological characteristics of the rest of species included in *Echinocoleus* are missing (Table II). Therefore, only a limited comparison with them was achieved, evidencing the need of a more thorough anatomical review in the future.

Among the infection sites recorded for *Echinocoleus* species, esophagus, stomach, and small intestine, only the small intestine was mentioned by Moravec (1982) in his generic diagnosis (Table

II). In addition, the analysis of data from *Echinocoleus* species shows that some features from *E. confusus* do not agree with the diagnosis, such as the unsclerotized spicule and location in the esophagus. Although detailed morphology and genetic studies are needed, these discrepancies suggest that *Echinocoleus confusus* should be removed from this genus and possibly redesignated as *Eucoleus confusus* n. comb.

The morphological evaluation among *Echinocoleus* species showed that *E. hydrochoeri* and the type species *E. cyanopicae* exhibit the widest differences within the genus and that *E. hydrochoeri* and *E. auritae* (both mammal parasites) seem to be the most similar. Although *E. auritae* has a bilobed membrane, the development and position of the 2 lateral lobes, and the number of papillae are similar to *E. hydrochoeri* (Travassos, 1914; Skrjabin et al., 1957; Tables I, II).

Among the Capillariinae, there are several genera with species distributed in different vertebrate classes, i.e., *Aonchoteca*, *Baruscapillaria*, *Capillaria*, and *Eucoleus*, showing a host range incoherent (Chabaud, 1981). The original description of the genus *Echinocoleus* (Lopez Neyra, 1947) included intestinal parasites of all vertebrate classes. Later, Moravec (1982) reformulated the specific composition of this genus, listing only birds and mammals as hosts. Although this morphological review allowed the restriction of the host range of the genus, life cycles and other ecological and evolutionary factors are not well known yet. Consequently, due to lack of sound information, the host and geographical distribution of different *Echinocoleus* species (from birds: Passeriformes in Spain, Gruiformes in Brazil, Anseriformes in Australia and mammals: Didelphiomorphia in Brazil; see Table II) are still insufficiently known.

The redescribed species is the only *Echinocoleus* found in rodents. Currently, about 8% of species of Capillariinae have been recorded in rodents, and all their descriptions provide some degree of detail from the male caudal region, in particular from lobes and papillae, among other generic characteristics. These species (n = 28) have been included in different genera (Table III), but other features have not been described. Among these, i.e. only about 40% of these species' descriptions offer details of the intestine, ejaculatory duct, and cloaca and about 50% of bacillary bands. It is noteworthy that in most of the original descriptions these characters were not described and that relevant data were only presented in subsequent redescriptions. A complete description of genito-cloacal characters and number and distribution of bacillary bands will allow the elucidation of phylogenetic patterns.

This is the only species of capillariid that has been recorded in species of the family Caviidae. The contrast among the 18 species of possible Caviidae hosts and the single Capillariinae species found in them could be related to an insufficient search, or to the particularity of the historical evolution of these rodents or to their restricted geographical distribution. Further studies on capillariids in South America will elucidate patterns of host and geographical distribution.

This survey represents a new record of a species of Capillariinae from Argentina, being the fourth for this country (Freitas and Lent, 1936; Robles et al., 2008, 2012).

In conclusion, the shape of the tail extremity of *E. hydrochoeri* is singular, if compared with that of the type species *E. cyanopicae*. Presently, the species redescribed here is included in *Echinocoleus*, but this placement might not be its definitive place and it may be changed when more species are redescribed including more characters, being available for comparison details as the bacillary bands, genital tract, and cloaca of male.

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