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PUDICINAE (NEMATODA: HELIGMONELLIDAE) PARASITIC IN ENDEMIC CHILEAN RODENTS (CAVIOMORPHA: OCTODONTIDAE AND ABROCOMIDAE): DESCRIPTION OF A NEW SPECIES AND EMENDED DESCRIPTION OF PUDICA DEGUSI (BABERO AND CATTAN) N. COMB.

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Corresponding Author:	María Celina Digiani, Ph.D. Museo de La Plata Paris, FRANCE
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	Museo de La Plata
Corresponding Author's Secondary Institution:	
First Author:	María Celina Digiani, Ph.D.
First Author Secondary Information:	
Order of Authors:	María Celina Digiani, Ph.D.
	Carlos Landaeta-Aqueveque, PhD
	Paula Carolina Serrano
	Juliana Notarnicola, PhD
Order of Authors Secondary Information:	
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PUDICINAE (NEMATODA: HELIGMONELLIDAE) PARASITIC IN ENDEMIC CHILEAN RODENTS (CAVIOMORPHA: OCTODONTIDAE AND ABROCOMIDAE): DESCRIPTION OF A NEW SPECIES AND EMENDED DESCRIPTION OF *PUDICA DEGUSI* (BABERO AND CATTAN) N. COMB.

María Celina Digiani*†, Carlos Landaeta-Aqueveque‡, Paula Carolina Serrano†, and Juliana Notarnicola§

*Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

Correspondence should be sent to María Celina Digiani at:

mdigiani@fcnym.unlp.edu.ar

Abstract: We report the finding of 2 species of *Pudica* (Nematoda: Heligmonellidae: Pudicinae) in 2 rodents endemic to Chile, the Common Degu *Octodon degus* (Octodontidae) and the Bennett's Chinchilla Rat *Abrocoma bennettii* (Abrocomidae). *Pudica degusi* (Babero and Cattan, 1975) n. comb., originally described as a species of *Longistriata* (Heligmosomidae), was found in the Common Degu; through the study of its synlophe, the species is reassigned to the Heligmonellidae: Pudicinae and the genus *Pudica*, and is revalidated through comparison with the remaining species of the genus. *Pudica cattani* n. sp. is described from both *O. degus* and *A. bennettii*. It is characterized by its large body size, bursal pattern of type 1-3-1 on right lobe, 1-3-1 tending to 1-4 on left lobe, synlophe with 11 ridges including a careen, dorsal ray of the bursa dividing proximally and bursal rays 9 and 10 relatively short. *Pudica degusi* n. comb. and *Pudica cattani* n. sp. were found in the same host species but not as coparasitic in the same individuals. The Common Degu is confirmed as the sole and primary host of *Pudica degusi* n. comb. It is unlikely that it is the primary host for *Pudica cattani* n. sp., whose host affinities are less clear, mainly due to the scarcity of data. *Pudica cattani* n. sp. is

the first helminth reported from the Bennett's Chinchilla Rat. Both findings enlarge the host range of the Pudicinae to the families Octodontidae and Abrocomidae, i.e., 9 out of the 11 extant families of caviomorphs, thereby establishing the presence of this nematode subfamily as typical parasites of the Neotropical Hystricognathi.

The mammalian genus *Octodon* Bennett (Caviomorpha, Octodontidae) comprises 4 species known as "degus": *Octodon degus* (Molina), *Octodon lunatus* Osgood, *Octodon pacificus* Hutterer, and *Octodon bridgesii* Waterhouse. The first 3 species mentioned are endemic to Chile, occurring between approximately 28°S and 38°S (Yáñez and Muñoz-Pedreros, 2009), and *O. bridgesii* is distributed primarily in Chile but also extends to Argentina, in the Neuquén Province (Díaz et al., 2015). The Common Degu, *O. degus* is the most common species of the genus. Reports on helminths from this species account for 7 species of nematodes and 2 species of cestodes (see Table I).

On the other hand, the genus *Abrocoma* Waterhouse, also endemic to South America, is currently composed of 8 species. Two of these: *Abrocoma cinerea* Thomas and *Abrocoma bennettii* Waterhouse are present in Chile. The other 6 are restricted to the vicinities of their type localities, 1 in Bolivia and 5 in Argentina. The Ashy Chinchilla Rat *A. cinerea* is distributed throughout the high Andes (above 3,700 m), from Arequipa in southern Peru to northeastern Chile in the Regions of Antofagasta and Tarapacá. Whereas the Bennett's Chinchilla Rat *A. bennettii* is endemic to Chile, being restricted to the western Andean slopes from the regions of Antofagasta in the north to O'Higgins in the south, and from sea level to 4,000 m (Patton and Emmons, 2015). Up to now, no helminths have been described from *A. bennettii*.

During a study conducted to assess the factors involved in the sharing of parasites between native and exotic hosts in Central Chile (Landaeta-Aqueveque, 2013), we

found in 2 *O. degus* few specimens of a nematode identified as *Longistriata degusi* Babero and Cattan (1975) (Heligmosomidae), a species originally described from this same host, but whose synlophe remained unknown. In this paper we study and describe the synlophe in the specimens collected, and rectify the assignment of the species at the genus and family level, transferring it to the genus *Pudica* (Heligmonellidae: Pudicinae). In addition, we found specimens of another bursate nematode in another specimen of *O. degus* and in 1 *A. bennettii*. These nematodes were found to belong to a new species of *Pudica*, which is also described and illustrated.

MATERIALS AND METHODS

Thirty-one degus were captured along 5 localities between the Coquimbo and Metropolitana Regions in Chile as follows: Las Chinchillas national reserve 31°30'31.76"S, 71° 6'21.93"W (11 individuals), Putaendo 32°37'1.98"S, 70°41'5.24"W (4 individuals), Pudahuel 33°26'56.63"S, 70°50'5.78"W (6 individuals), Calera de Tango 33°40'0.90"S, 70°48'1.63"W (2 individuals), and Talagante 33°41'1.21"S; 70°49'40.30"W (8 individuals). These localities encompassed agricultural areas (Putaendo) and both protected (Las Chinchillas N. R.) and non-protected wild areas (Pudahuel, Calera de Tango and Talagante), all at altitudes lower than 1,100 meters above sea level (masl). Five Bennett's chinchilla rats were captured in 3 of the mentioned localities between the Valparaíso and the Metropolitana Regions: Putaendo (2 individuals), Calera de Tango (2 individuals) and Talagante (1 individual). Rodents were caught with live traps and killed with an isoflurane overdose. Gastrointestinal tracts were examined for the presence of helminths. Nematodes were recovered from the intestine, fixed and stored in 70% ethanol and studied in temporary mounts in Amman's lactophenol under a Leica DM 2500 microscope provided with a drawing attachment (Leica, Wetzler, Germany). The synlophe was studied following Durette-

Desset (1985) and the nomenclature referring to the axis of orientation follows Durette-Desset and Digiani (2005). Ridges, including careen, are numbered from left to right, from 1 to *n* for dorsal ridges and from 1' to *n'* for ventral ridges. Ridges are considered as right-dorsal or left-ventral with respect to the axis of orientation. The nomenclature used for the study of the caudal bursa follows Durette-Desset and Digiani (2012). The nomenclature for parasites above the family group follows Durette-Desset and Chabaud (1993). Measurements are in micrometres, except otherwise stated. SpL/BL and UtL/BL mean the proportion of the spicule length to the body length and of the uterus length to the body length, respectively. Type and voucher specimens of parasites were deposited in the Invertebrate Zoology Collection of the Museo Nacional de Historia Natural de Chile, Santiago, Chile (MNHNCL), and in the Helminthological Collection of the Museo de La Plata, La Plata, Argentina (MLP-He). The nomenclature of the hosts at species level follows Díaz et al. (2015) and Patton and Emmons (2015). Voucher specimens of hosts are deposited in the Vertebrate Zoology Collection of the MNHNCL.

DESCRIPTION

***Pudica degusi* (Babero and Cattan, 1975) n. comb.**

(=*Longistriata degusi* Babero and Cattan, 1975)

(Figs. 1-3)

Synlophe (on 1 male and 1 incomplete female): The poor condition of the specimens prevented us from making sections at other body levels than at mid-body (Figs. 1, 2). The unique female specimen lacked its posterior extremity and was rather shrunken, as evidenced in the transverse section (Fig. 2). Cuticle bearing longitudinal, uninterrupted ridges appearing posterior to cephalic vesicle in both sexes, disappearing just anterior to caudal bursa in male. In both sexes, at mid-body, 11 ridges: careen plus

5 dorsal and 4 ventral. Presence of well developed careen made up of 2 large ridges of similar size (male), or with the ventral ridge slightly larger (female). All ridges well developed (large to medium-sized). Largest ridges are those forming careen (1 and 1'), then ridges 5 and 6. Gradient in ridge size present dorsally starting from ridge 5 to the left (ridges 5-4-3). Double axis of orientation of the ridges, right axis inclined at 55° and left axis at 70° to sagittal axis in male. Inclination not calculated in female due to the deformation of the body section.

Male (n = 2): 3.80 and 3.60 mm long; 70 and 70 wide at mid-body. Cephalic vesicle 50 and 45 long; 25 and 28 wide. Nerve ring observed in specimen #2 at 125 from apex. Excretory pore and deirids not observed. Esophagus 245 and 255 long.

Caudal bursa subsymmetrical, with pattern of type 1-4 in both lobes (Fig. 3). Rays 2 shorter than rays 3 and curved inwards, rays 4 and 5 diverging at about half of their length. Rays 6 longer than rays 3, reaching distal bursal margin. Left ray 3 arising at same level as ray 6, right ray 3 arising slightly more distally.

Dorsal lobe medium-sized. Rays 8 thin, arising from base of dorsal ray, parallel throughout their length to common trunk, then to rays 6, not reaching level of extremities of these latter. Dorsal ray dividing at base into 2 branches, each one divided at about distal third into 2 long and parallel sub-branches, rays 9 (external) and rays 10 (internal) (Fig. 3). Genital cone conical, moderately developed, 40 long and 30 wide at base in specimen #1, papillae 7 and 0 not observed. Spicules subequal, alate, 500 and 480 long, ending in sharp tip. Spicular alae visible. SpL/BL 13.2 and 13.3%.

Female (on 1 incomplete specimen): Anterior fragment 3.55 mm long and 70 wide at about mid-body, broken before uterus. Cephalic vesicle 45 long and 20 wide. Nerve ring at 125 from apex. Excretory pore and deirids not observed. Esophagus 265 long.

Taxonomic summary

Host: Octodon degus (Molina, 1782) (Rodentia, Octodontidae).

Localities: Talagante (33°41'1.21"S; 70°49'40.30"W) 650 masl, Pudahuel (33°26'56.63"S, 70°50'5.78"W) 500 masl, Región Metropolitana, Chile.

Site: Small intestine.

Prevalence and intensity of infection: P = 6.45% (2 out of 31 hosts examined). Mean Intensity (MI) = 5 (9 and 1 specimens, respectively, in the hosts from Talagante and Pudahuel.

Material deposited: 1 male, 1 female MNHNCL NEM-15014.

Remarks

The morphological and morphometrical characters of these specimens correspond well with the species accurately described by Babero and Cattan (1975) as *Longistriata degusi*. Despite the scarcity of the material obtained herein, we were able to complete the original description based on the fully extended caudal bursa in the male and by providing details of the synlophe at the mid-body in both sexes. The lack of the female posterior extremity avoided providing an accurate description of the ovejector and other morphometrical data such as the uterus length, UtL/BL and egg number, not included in the original description.

The presence of a cephalic vesicle and a synlophe with an axis of orientation that is not bilaterally symmetrical, places these specimens into the superfamily Heligmosomoidea, as redefined by Durette-Desset (1983) and Durette-Desset and Chabaud (1993). Two out of the 6 families of Heligmosomoidea are well represented in South American Hystricognathi rodents (or Caviomorpha): the Viannaiidae and the Heligmonellidae, this latter with 2 subfamilies, the Heligmonellinae and the Pudicinae. The specimens described herein cannot not be assigned to the Viannaiidae, whose representatives in caviomorphs are characterized by synlophes without a careen and

having small, subequal ridges, mostly separated into 2 well distinct groups, dorsal and ventral (Durette-Desset, 1983; Beveridge et al., 2013). Neither can they be assigned to the Heligmonellidae: Heligmonellinae, which are characterized by synlophes lacking a careen and having the left ridge and the right ridge (the single ridges situated just opposite the lateral cords) distinct and larger than the other ridges (Beveridge et al., 2013). The presence of a well-developed careen in our specimens, together with having between 8 and 12 ridges, the absence of gubernaculum, and spicules with conspicuous alae, allow them to be easily assigned to the subfamily Pudicinae of the Heligmonellidae. Among these, the presence only of continuous (uninterrupted) ridges, both ridges of the careen with similar development and larger than the other ridges, and the rays 9 and 10 being of similar length allow us to assign the species to the genus *Pudica* Travassos and Darriba, 1929 (Durette-Desset and Justine, 1991; Beveridge et al. 2013; Durette-Desset et al., in press). The genus *Pudica* is currently comprised of 12 species, all parasitic in caviomorph rodents of the families Echimyidae (8 species), Dasyproctidae (2 species), Caviidae and Ctenomyidae (1 species each) (Durette-Desset et al., in press).

Pudica degusi n. comb. differs from the majority of the species in the genus mainly by its bursal characters, i.e., by having rays 2 and 3 well separated. This character distinguishes it clearly from all the species having rays 2 and 3 V-shaped or even joined to different degrees, such as *Pudica pudica* (Travassos, 1921) (type species), *Pudica alpha* (Travassos, 1918), *Pudica gamma* (Travassos, 1918), *Pudica maldonadoi* (Artigas and Pacheco, 1933) and *Pudica nematodiriformis* (Travassos, 1918) (see Travassos, 1937). It also differs from the group of species having rays 2 and 3 slightly distant but distinctly grouped and separated from the other rays, such as *Pudica pujoli* Durette-Desset, 1990, *Pudica tenua* Durette-Desset, 1970 and *Pudica*

ctenomydis Rossin, Timi and Malizia, 2006 (Durette-Desset, 1970, 1990; Rossin et al., 2006).

Pudica degusi n. comb. is also distinguished from *Pudica cercomysi* (Durette-Desset and Tchéprakoff, 1969), and from *Pudica evandroi* (Travassos, 1937) by the lateral bursal pattern. These 2 latter species show bursal patterns of type 1-3-1 but also other remarkable differences: *P. evandroi* shows both lateral trunks of rays 3-5 and the trunk of the dorsal ray strongly thickened, whereas *P. cercomysi* shows the rays 4-6 very long and thin (Travassos, 1937; Durette-Desset and Tchéprakoff, 1969). *Pudica degusi* n. comb also differs from *Pudica ginsburgi* Durette-Desset, Deharo, Santiváñez-Galarza and Chabaud, 2001 by having the same pattern in both lobes and by the proximal division of the dorsal ray, instead of *P. ginsburgi* which shows a pattern of type 1-4 on the right lobe and 1-3-1 on the left lobe, plus a distal division of the dorsal ray (Durette-Desset et al., 2001).

The bursal pattern of type 1-4 on both lobes is a character shared only with *Pudica gonosoma* Cassone and Durette-Desset, 1991, parasitic in *Dasyprocta azarae* Lichtenstein (Dasyproctidae) from southern Paraguay. However, *P. degusi* n. comb is readily distinguishable from *P. gonosoma* by the absence of a post vulvar expansion in the female, the proximal division of the dorsal ray, the rays 2, 3, 6 and 8 thick and the rays 9 and 10 long. Whereas *P. gonosoma* is characterized by having a post vulvar expansion in the female, the dorsal ray divided distally, rays 2, 3, 6 and 8 thin, rays 8 short and sinuous and rays 9 and 10 minute, as well as a synlophe with only 8 ridges (2 forming careen, 3 dorsal, 3 ventral) (Cassone and Durette-Desset, 1991).

The synlophe was only described in 9 species of *Pudica*. It is characterized by having 8-12 ridges (including the careen) of variable size, and frequently by the presence of ventral comaretes, i.e., large ridges derived from the fusion of two or more

contiguous ridges. *Pudica degusi* n. comb. and *Pudica tenua* share the same number of 11 ridges in the synlophe. But *Pudica degusi* n. comb. is characterized by having all the ridges well developed, in contrast with *P. tenua* which has 2-3 ventral large comaretes, with the remaining dorsal and ventral ridges being much smaller than those forming the careen (Durette-Desset, 1970). *Pudica tenua* had been differentiated as well by its bursal characters (consigned above) and by its tiny body size, being the smallest species in the genus (males 1.25 mm, females 1.8 mm.).

***Pudica cattani* n. sp.**

(Figs. 4-21)

General: Large nematodes, mostly loosely and irregularly coiled, or uncoiled. Deirids situated close to the esophago-intestinal junction in males, always anterior to it in females. Excretory pore always distal to deirids, at same level or posterior to the esophago-intestinal junction in females, always posterior to it in males (Fig. 4a-c).

Head: Cephalic vesicle present. In apical view, oral opening shamrock shaped, surrounded by thick ring. Two amphids, 4 externo-labial and 4 cephalic papillae visible (Fig. 5).

Synlophe (studied in 2 males and 2 females): In both sexes cuticle bearing longitudinal, uninterrupted ridges appearing posterior to cephalic vesicle, disappearing just anterior to caudal bursa in males and at ovejector level in females. In both sexes, from the level of distal esophagus to the posterior third of body length: 11 ridges (careen plus 5 dorsal and 4 ventral). Presence of a well-developed careen, made up of 2 large ridges similar in size, or with the ventral one slightly larger (see Figs. 9, 11). At esophageal level, all ridges well developed: ridges of careen large, remaining ridges medium-sized (Figs. 6, 7). At mid-body and within posterior third of body length: ridge 2’ markedly smaller than the other ridges (Figs. 8, 9). Gradients in ridge size absent at

mid-body. Upper part of right-ventral quadrant free of ridges. Double axis of orientation of the ridges, right axis inclined at 60-65° to sagittal axis, left axis subfrontal. Within posterior third of body length, in both sexes, ridges smaller but always in same number and with same orientation than at mid-body (Figs. 10, 11). From the level of the spicules to the posterior end in males, and from the ovejector level in females, ridges decreasing progressively in size, especially on the right, although ridge number not decreasing (Figs. 12-15).

Males (holotype followed by range and mean of 20 paratypes): 8.60 (6.40-10.65; 8.58) mm long and 170 (70-170; 129) wide at mid-body. Cephalic vesicle 85 (70-100; 84) long and 50 (25-55; 46) wide. Nerve ring, excretory pore and deirids situated at 240 (220-280; 241) (n = 17), 460 (325-580; 484) (n = 16) and 380 (280-480; 402) (n = 17) from apex, respectively. Esophagus 450 (310-460; 427) long (n = 18).

Caudal bursa subsymmetrical, with pattern of type 1-3-1 on right lobe and 1-3-1 tending to 1-4 on left lobe. Right ray 6 diverging from common trunk at same level as right ray 2, considerably proximal to origin of ray 3. Left ray 6 diverging from common trunk just distally to origin of left ray 2 and proximally to that of ray 3. Rays 2 and 3 similar in length, well separated, both directed forward and reaching bursal margin. Rays 4 and 5 diverging at about distal third of their length. Rays 6 similar in length to rays 2 and 3, reaching posterior bursal margin. Dorsal lobe moderately developed. Rays 8 stout, arising from base of dorsal ray, contiguous and parallel throughout their length to common trunk and then to rays 6, not reaching bursal margin. Dorsal ray dividing at about proximal third of its length into 2 robust branches, each one divided distally into 2 short, parallel sub-branches, rays 9 (external) and rays 10 (internal) (Fig. 16). Genital cone rather cylindrical, 30 (30-40; 32) long and 40 (30-50; 37) wide at base (n = 5), ventral lip shorter than dorsal one (Fig. 17). Papillae 7 and 0 not observed. Spicules

subequal, alate, 1,000 (925-1,080; 1,003) long, ending in blunt tips. Spicular alae conspicuous (Figs. 18, 19). SpL/BL 11.6% (9.4-14.5; 11.8%).

Females (allotype followed by range and mean of 21 paratypes): 16.50 (13.70-21.00; 16.60) mm long and 130 (110-180; 145) wide at mid-body. Cephalic vesicle 85 (75-110; 93) long and 45 (40-60; 53) wide. Nerve ring, excretory pore and deirids situated at 260 (215-290; 262) (n = 16), 510 (455-640; 546) (n = 14) and 420 (380-495; 451) (n = 13) from apex, respectively. Esophagus 475 (440-535; 490) long. Reproductive tract monodelphic. Vulva situated at 145 (110-162; 144) from caudal extremity. Vagina vera 45 (15-50; 31) long, vestibule 240 (210-320; 268), sphincter 40 (35-50; 45) long and 45 (40-60; 48) wide, infundibulum 200 (120-345; 202) (n = 17) (Fig. 20). Uterus 2.71 (1.45-3.90; 2.85) mm long, containing 70 (30-100; 61) eggs (n = 14), 95-125 long and 35-50 wide. UtL/BL 16.4% (8.9-21.7; 17.3%). Posterior extremity abruptly tapering behind vulva. In several specimens, presence of a wide cuticular fold just posterior to vulva, partly surrounding the posterior end and leaving the tail free (Fig. 21a). Tail 40 (40-90; 56) long.

Material from *Abrocoma bennettii*

Male: It was represented by a posterior extremity, identified as *Pudica cattani* n. sp. by the morphology of the caudal bursa, spicules and synlophe.

Measurements of 3 females (2 complete specimens + 1 posterior extremity): 16.40 and 18.50 mm long. Cephalic vesicle 90 and 90 long; 55 and 45 wide. Nerve ring and excretory pore not observed, deirids observed in specimen #2 at 405 from apex. Esophagus 530 long in specimen #1.

Posterior part of body (n = 3): Vulva at 160-180 from caudal extremity. Vagina vera 15-20 long, vestibule 260-275 long, sphincter 50 long and 42-50 wide, infundibulum 140-180 long. Uterus 3.35-3.85 mm long, containing 74-89 eggs, 85-105

long and 30-43 wide. UtL/BL 20.8-22.9%. Tail 40-50 long.

Taxonomic summary

Type-host: Octodon degus (Molina) (Rodentia, Octodontidae).

Type-locality: Pudahuel (33°26'56.63"S, 70°50'5.78"W), 500 masl., Región Metropolitana, Chile.

Site: Small intestine.

Prevalence and intensity of infection: 1 out of 31 hosts examined was parasitized by 125 specimens.

Type material: Holotype, male, MNHNCL NEM-15007; allotype, female, MNHNCL NEM-15008. Paratypes: 7 males, MNHNCL NEM-15009; 7 females, MNHNCL NEM-15010; 18 males, MNHNCL NEM-15011; 18 females, MNHNCL NEM-15012; 17 males and 20 females, MLP-He 7396.

Other material studied: 1 male, 3 females parasitic in *Abrocoma bennettii* Waterhouse (Rodentia, Abrocomidae) from Calera de Tango (33°40'0.90"S, 70°48'1.63"W), 810 masl., Región Metropolitana, Chile. Site: Small intestine. MNHNCL NEM-15013.

Etymology: In honor of Prof. Dr. Pedro Cattan, prominent Chilean parasitologist and pioneer on ecological studies on the helminths of Chilean rodents, in recognition of his vast work.

Remarks

The specimens studied herein are assignable to the genus *Pudica* (Heligmonellidae, Pudicinae) for the same reasons used in the generic assignment of *Pudica degusi* n. comb., i.e., characters of the synlophe, spicules and caudal bursa (see above).

Pudica cattani n. sp. is distinguished from *P. pudica*, *P. alpha*, *P. gamma*, *P. maldonadoi*, *P. nematodiriformis*, *P. pujoli*, *P. tenua* and *P. ctenomydis* by its bursal

characters, with rays 2 and 3 well separated and a basic lateral pattern of type 1-3-1, instead of one of type 2-2-1 or 2-3 t 2-2-1 (Travassos, 1937; Durette-Desset, 1970, 1990; Rossin et al., 2006).

Pudica evandroi and *P. cercomysi* have lateral patterns of type 1-3-1 on their bursal lobes, similarly to *Pudica cattani* n. sp. However, the 3 species differ in the shape of the bursal rays: *P. evandroi* is characterized by the strong thickening of the lateral trunks of rays 3-5 and the trunk of the dorsal ray (Travassos, 1937), while *P. cercomysi* shows a well developed dorsal lobe and rays 4-6 long, thin and straight (Durette-Desset and Tchéprakoff, 1969). All these characters contrast markedly with *Pudica cattani* n. sp., which has the lateral and dorsal rays robust but not hypertrophied, rays 4 curved anteriad, rays 6 curved posteriad and the dorsal lobe moderately developed.

The new species is also distinguishable from *P. gonosoma* and *P. ginsburgi* mainly by bursal characters. *Pudica gonosoma* has a pattern of type 1-4 on both lobes (vs. 1-3-1 and 1-3-1 tending to 1-4 in *Pudica cattani* n. sp.), rays 8 short and the dorsal ray divided distally (vs. rays 8 long and dorsal ray divided at proximal third); in addition, the females show a remarkable post vulvar expansion (Cassone and Durette-Desset, 1991), absent in the new species. *Pudica ginsburgi* shows a pattern of type 1-4 on the right lobe and 1-3-1 on the left lobe, dorsal ray dividing within its distal half (vs. at proximal third in *Pudica cattani* n. sp), rays 4 and 5 apposed throughout their length (vs. diverging at their distal third) and a marked asymmetry in the length of rays 6 and 8 on each lobe (Durette-Desset et al., 2001), not observed in our specimens.

Finally, the new species is also differentiated from *Pudica degusi* n. comb., described from the same host species, by having the dorsal ray divided more distally (vs. at its base in *P. degusi* n. comb.), pattern of type 1-3-1 on the right lobe and 1-3-1

tending to 1-4 on the left lobe (vs. 1-4 on both lobes), rays 2 and 3 parallel and similar in length (vs. rays 2 shorter and curved inwards) and rays 9 and 10 relatively shorter.

Up to now, the characteristics of the synlophe are known in 10 species of *Pudica*, including *Pudica degusi* n. comb., described herein. *Pudica cattani* n. sp. shares with *Pudica degusi* n. comb. and with *P. tenua* a synlophe of 11 ridges. However, the synlophe in the new species is characterized by having all ridges (except ridge 2') well developed, in contrast with *P. tenua* which has 2-3 ventral comaretes and the remaining dorsal and ventral ridges much smaller than those forming the careen. Moreover, *P. tenua* is remarkably different by its bursal characters (consigned above) and by its tiny body size (see Durette-Desset, 1970), being the smallest species in the genus. Finally, the synlophe of the new species differs from that of *Pudica degusi* n. comb. by having at mid-body ridge 6 equal in size or larger than ridge 5 (vs. 5 >6 in *P. degusi*) and ridge 2' markedly smaller than the remaining ridges (vs. comparable in size to the remaining ridges in *P. degusi*).

The differences between these specimens and the known species of *Pudica* allow us to consider these specimens as a new species, for which the name *Pudica cattani* n. sp. is proposed. It is interesting to note that the body size in species of *Pudica* ranges from 1.25 to 7.0 mm in males and 1.8 to 15.0 mm in females (Durette-Desset et al., in press). The size of the specimens studied here exceeds these ranges (males 8.7 mm, females 16.2 mm, in average), making *Pudica cattani* n. sp. the largest species in the genus.

DISCUSSION

Pudica degusi n. comb. was originally described by Babero and Cattan (1975) as *Longistriata degusi* and the original description did not include transverse sections through the synlophe. The authors were apparently unaware of the redefinition of the

genus *Longistriata* Schulz, 1926, its species composition and host's spectrum given shortly before by Durette-Desset (1971). Indeed, the present definition of *Longistriata* places the genus in the Heligmosomidae and its component species are strictly parasites of Holarctic Soricidae (Durette-Desset, 1971, 1983).

Several years later, Durette-Desset and Justine (1991) performed a cladistic analysis of the Pudicinae, in which they recovered the subfamily as monophyletic and obtained 2 suprageneric groups but did not give them a rank. These authors recognized the possible relationship of *Longistriata degusi* with the Pudicinae in view of some characters of its caudal bursa and its host being a caviomorph rodent. Since the synlophe of *L. degusi* was unknown at that time, Durette-Desset and Justine (1991) did not include this species in their analysis, but anticipated that the character of the bursal rays 9 as long as the rays 10 suggested a proximity to their suprageneric group 2, in which *Pudica* was included.

The description of the synlophe provided herein, in combination with other characters known from the original description, allow us to reassign the species to the subfamily Pudicinae and the genus *Pudica*, confirming the initial assumption of Durette-Desset and Justine (1991). The species is as well validated through the differential diagnosis against the known species of *Pudica*.

Most species in the Pudicinae (43 out of 47) are known only from their type host. But it is also true that certain host species may harbor up to 4 species of Pudicinae in the same individual host. This phenomenon of coparasitism is particularly frequent among the Echimyidae and the Dasyproctidae (spiny rats and agoutis) (Durette-Desset et al., in press).

In this study we found *Pudica degusi* n. comb. and *Pudica cattani* n. sp. in the same host species, however they were not coparasitic in the same individuals.

There seems to be little doubt that *Pudica degusi* n. comb. has strict host specificity: it has not been found in hosts other than *O. degus* and has been reported repeatedly in every survey conducted on this host (Babero and Cattan, 1975; Cattan et al., 1976; Cattan and George-Nascimento, 1978; Landaeta-Aqueveque, 2013).

Pudica cattani n. sp., instead, shows less clear host-parasite relationships. It is reported herein from *Octodon degus* and *Abrocoma bennettii* from 2 different localities, distant each other ca. 84 km. Since up to now these are the only records of the species, it is difficult to assess which one is the primary host. In *O. degus*, it was found in 1 out of 31 hosts examined (P = 3.22%). But it is to be noted that previous surveys on *O. degus* showed consistently an intestinal helminth community composed of the same set of species: *Pudica degusi* n. comb., *Trichuris bradleyi* Babero, Cattan and Cabello, 1975, *Heteroxynema chiliensis* Quentin, 1975, and *Helminthoxys gigantea* (Quentin, Courtin and Fontecilla, 1975) (see Table I). Reports of other helminths have been occasional, involving host-parasite associations that are evidently accidental. It seems then unlikely that *O. degus* is the primary host of *Pudica cattani* n. sp. In *A. bennettii,* it has been found in 1 out of 5 hosts examined, but clearly the number of hosts examined is too low to be representative. Moreover, any inference on the frequency of this association is still hampered by the fact that there are virtually no helminthological surveys conducted on this host (Table I).

The present findings enlarge the host range of the Pudicinae to the families Octodontidae and Abrocomidae, i.e., to 9 out of the 11 extant families of caviomorph rodents, and therefore also to the entire clade of the Octodontoidea [Abrocomidae + (Octodontidae + Ctenomyidae) + (Capromyidae +Echimyidae)] (see Upham and Patterson, 2015). At present, the Pudicinae parasitize 3 out of the 4 recognized clades of living caviomorphs: Erethizontoidea, Cavioidea and Octodontoidea, suggesting that the

association of pudicines with caviomorphs should have preceded the divergence and differentiation of these main lineages.

Available parasitological data in caviomorphs are still fragmentary, particularly among octodontoids. These latter represent 75% of the living species of caviomorphs (Upham and Patterson, 2015), ca. 190 species, of which barely 20 have been investigated for endoparasites. Among the Octodontidae and Abrocomidae, studies are particularly scarce and there is considerable disproportion between ectoparasitological and endoparasitological surveys. For instance, *O. degus* has been reported as host of ca. 20 species of fleas, lice and ticks (González-Acuña and Guglielmone, 2005; González-Acuña et al., 2005; Beaucournu et al., 2014), in contrast with the 9 species of helminths reported (Table I). The parasite record for the other species of degus is even scarcer: the Bridges' Degu *O. bridgesii* and the Coastal Degu *O. lunatus* harbor 3 species of fleas each (Beaucournu et al., 2014) and, regarding endoparasites, 2 of the nematodes mentioned for the Common Degu in Chile were also reported in *O. bridgesii* from Neuquén, Argentina (Table I). Not surprisingly, there is no parasitological information for the Mocha Degu, *O. pacificus*, a species described in 1959 and lacking subsequent records until its recent rediscovery in 2016 (Vianna et al., 2017).

Similarly, the Chilean species of *Abrocoma* were reported harboring 17 species of ectoparasites, mainly fleas and lice (González-Acuña and Guglielmone, 2005; González Acuña et al., 2005; Beaucournu et al., 2014). In contrast, the record of helminths is much poorer, with only 1 species of Oxyurida (Nematoda) described from *Abrocoma cinerea* in Bolivia (Table I).

This study enlarges the diversity of the Heligmosomoidea parasitizing caviomorphs while reinforcing the need for further parasitological studies in this group;

this will allow a fuller understanding of the diversity of nematodes of caviomorphs and the relationships with their hosts.

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Figures 1-3. *Pudica degusi* (Babero and Cattan) n. comb. from *Octodon degus*. (**1, 2**) Synlophe in transverse sections at mid-body (1) Male, (2) Female. (**3**) Male, bursa, ventral view. Abbreviations: (L) left, (V) ventral. All sections oriented as in Fig. 1.

Figures 4-11. *Pudica cattani* n. sp. from *Octodon degus.* (**4**) Anterior extremity, showing variable position of deirids (D) and excretory pore (EP) respect to the esophago-intestinal junction. (a) male, D anterior, EP posterior. (b) female, D anterior, EP at same level. (c) male, D and EP posterior. (**5**) Female, head, apical view. (**6-11**) Synlophe in transverse sections of the body. (6, 7) At level of esophago-intestinal junction. (6) Male. (7) Female. (8, 9) At mid-body. (8) Male. (9) Female. (10-11) At distal third of body length (BL). (10) Male, 72% of BL. (11) Female, 84% of BL (proximal uterus).

Figures 12-19. *Pudica cattani* n. sp. from *Octodon degus.* (**12-15**) Synlophe in transverse sections of the body. (12, 13) Male, 600 and 400 μm, respectively, from bursa. (14, 15) Female, at distal uterus and at infundibulum (800 μm and 400 μm from posterior end, respectively). (**16-19**) Male. (16) Caudal bursa, ventral view. (17) Detail of genital cone, ventral view. (18) Posterior extremity showing bursa and spicules *in situ,* ventral view. (19) Tip of spicules. Abbreviations: (L) left, (V) ventral, (d.l.) dorsal lip, (sp.) spicules, (v.l.) ventral lip. All sections oriented as in Fig. 14.

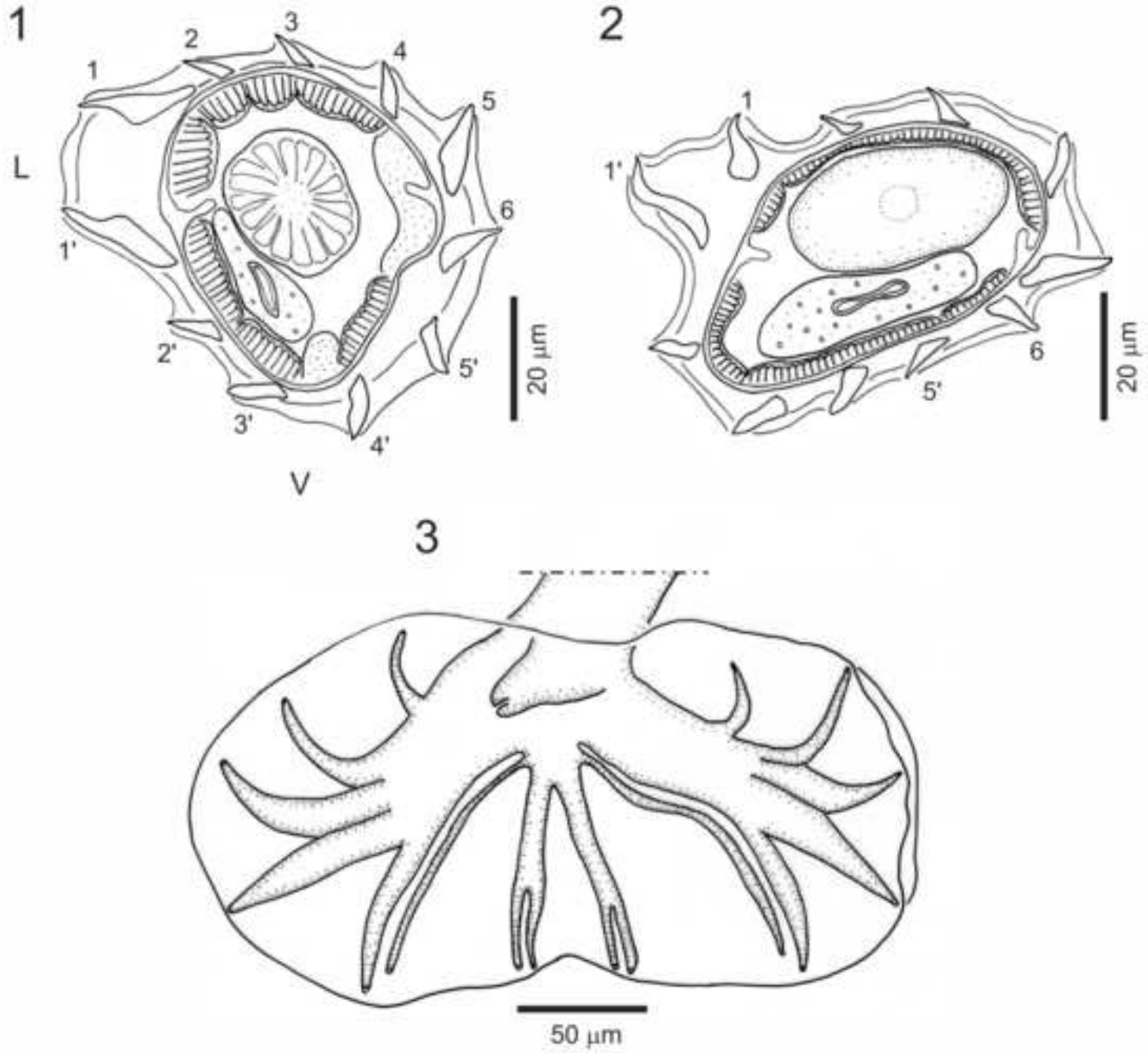
Figures 20-21. *Pudica cattani* n. sp. from *Octodon degus.* Female. (**20**) Posterior extremity showing ovejector and distal uterus, left lateral view. (**21**) Posterior ends showing presence (a) or absence (b) of cuticular fold, left lateral views.

†División Zoología Invertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, (1900) La Plata, Argentina.

‡Departamento de Patología y Medicina Preventiva, Facultad de Ciencias Veterinarias, Universidad de Concepción, Vicente Méndez 595, Chillán, Chile.

§Instituto de Biología Subtropical (IBS), Consejo Nacional de Investigaciones Científicas y Técnicas, CONICET- CCT Nordeste, Universidad Nacional de Misiones (UNaM), Bertoni 85, CP3370 Puerto Iguazú, Misiones, Argentina.

Figure



Figure

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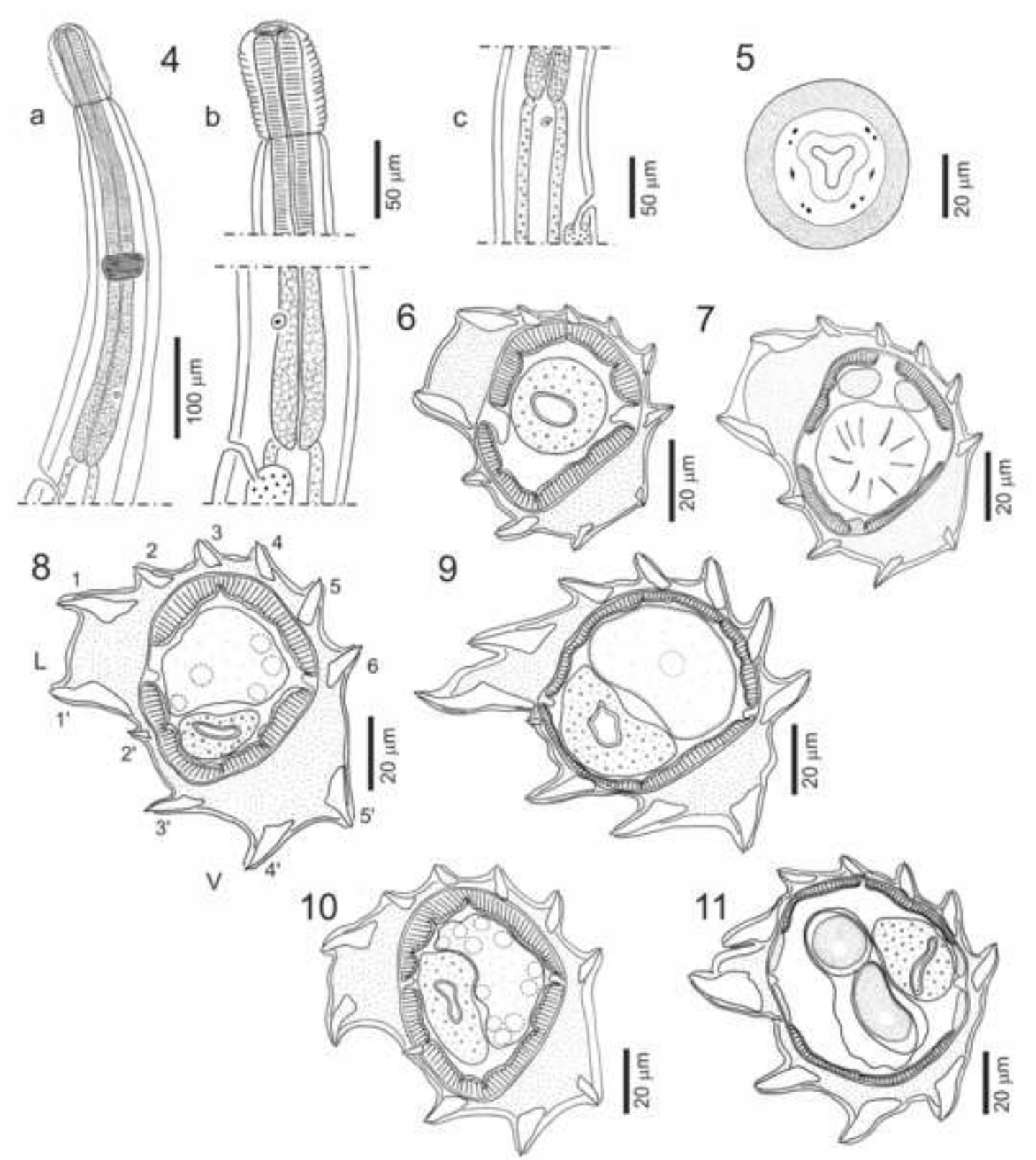

Figure

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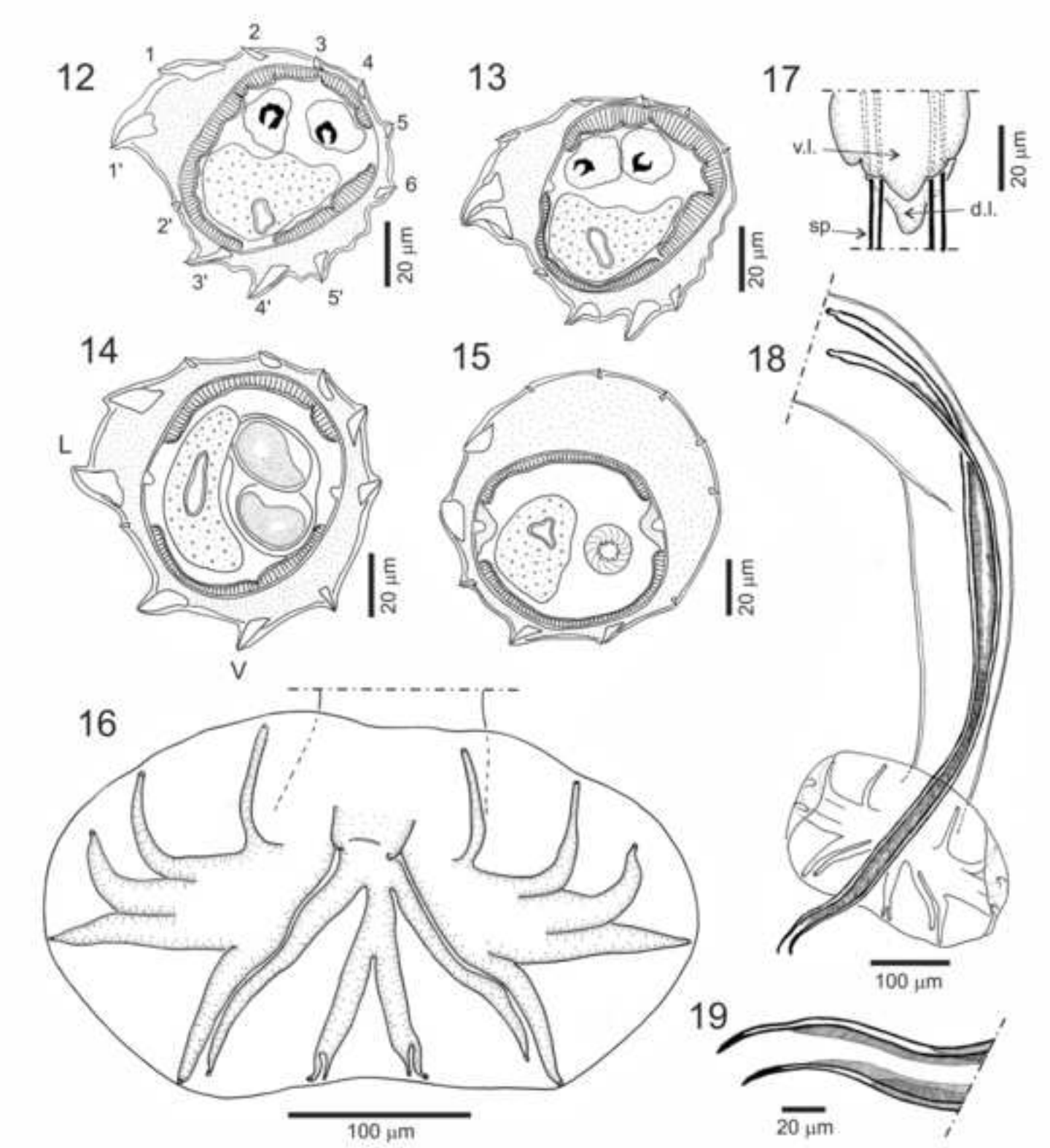

Figure

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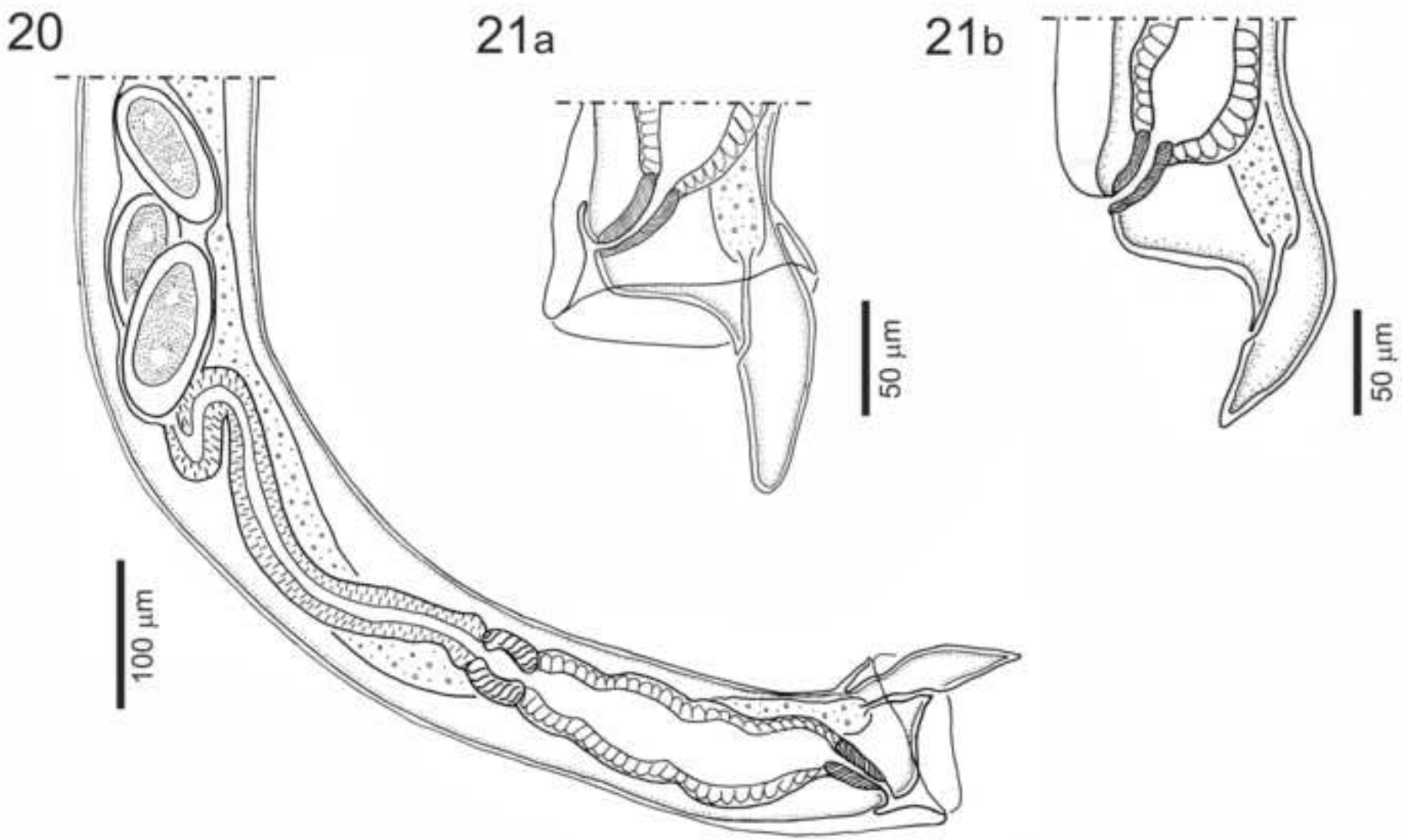

Table I. Helminths described from species of *Octodon* and *Abrocoma*. Abbreviations: **A**: Argentina, **B**: Bolivia, **C**: Chile.

Species	Family	Host (Country)	Reference(s)
Cestoda			
Andrya octodonensis (Babero and Cattan, 1975) (=*Aprostatandrya octodonensis* Babero and Cattan, 1975)	Anoplocephalidae	*Octodon degus* **(C)**	Babero and Cattan (1975)
Echinococcus granulosus (Batsch, 1786)	Taeniidae	*Octodon degus* **(C)**	Tagle (1955)
Echinococcus sp.	Taeniidae	*Octodon degus* **(C)**	Álvarez (1961)
Nematoda			
Trichuris bradleyi Babero, Cattan and Cabello, 1975	Trichuridae	*Octodon degus* **(C)**	Babero et al. (1975); Cattan et al. (1976); Cattan and George-Nascimento (1978); Landaeta-Aqueveque (2013)
Physaloptera sp.	Physalopteridae	*Octodon degus* **(C)**	Babero and Cattan (1975)
Heteroxynema chiliensis Quentin, 1975	Oxyuridae	*Octodon degus* **(C)**	Quentin (1975); Babero and Cattan (1975) ; Cattan et al. (1976); Cattan and George-Nascimento (1978); Landaeta-Aqueveque (2013)
Helminthoxys gigantea (Quentin, Courtin and Fontecilla, 1975) (= *Octodonthoxys gigantea* Quentin, Courtin and Fontecilla, 1975)	Oxyuridae	*Octodon degus* **(C)**	Quentin et al. (1975); Babero and Cattan (1975); Cattan et al. (1976); Cattan and George-Nascimento (1978); Landaeta-Aqueveque (2013)
		Octodon bridgesii **(A)**	Sutton and Hugot (1993)

Helminthoxys abrocomae Hugot and Gardner, 2000	Oxyuridae	*Abrocoma cinerea* (**B)**	Hugot and Gardner (2000)
Graphidioides taglei Babero and Cattan, 1975	Trichostrongylidae	*Octodon degus* **(C)**	Babero and Cattan (1975); Landaeta-Aqueveque (2013)
		Octodon bridgesii (**A)**	Sutton and Durette-Desset (1995)
"Longistriata eta" Travassos, 1937*	Heligmonellidae?	*Octodon degus* **(C)**	Tagle (1955)
Pudica degusi (Babero and Cattan) n. comb. (=*Longistriata degusi* Babero and Cattan, 1975)	Heligmonellidae: Pudicinae	*Octodon degus* **(C)**	Babero and Cattan (1975); Cattan et al. (1976); Cattan and George-Nascimento (1978); **present work**
Pudica cattani n. sp.	Heligmonellidae: Pudicinae	*Octodon degus* **(C)**	**Present work**
		Abrocoma bennettii **(C)**	**Present work**

* Record needing revision. Probably a misidentification of *Pudica degusi* n. comb. *Longistriata eta* was described from a sigmodontine rodent in Brazil and was transferred to *Stilestrongylus* (Heligmonellidae: Nippostrongylinae) by Durette-Desset (1971) when *Longistriata* was redefined.