

A new species of *Versteria* (Cestoda: Taeniidae) parasitizing *Galictis cuja* (Carnivora: Mustelidae) from Patagonia, Argentina: Morphological and molecular characterization

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ABSTRACT

Via morphological and molecular analysis, we describe a new species of taeniid from Patagonia (Argentina): *Versteria cuja* n. sp., parasitizing the Lesser grison *Galictis cuja* (Molina) (Carnivora: Mustelidae). This is the first report of a species of *Versteria* in Argentina and for a native mustelid. The new species (the third in the genus *Versteria*) is proposed using an integrative taxonomic approach, based on traditional morphology (distinctive morphological and morphometric diagnostic characters), genetic distances and phylogeny based on molecular data, the distinct geographical distribution, and the different definitive host species. *Versteria cuja* n. sp. mainly differs from *Versteria mustelae* (Gmelin, 1790) (from Europe) in the number of testes (54–85 vs. 83–127 in *V. mustelae*), the rostellum size (39–75 vs. 85–180 µm in *V. mustelae*), the genital atrium size (170–420 vs. 68–91 µm in *V. mustelae*) and in the hooks' shape. It also differs from the African species *Versteria brachyacantha* (Baer and Fain, 1951) by having smaller measurements regarding the main diagnostic characters, i.e. size of scolex, rostellum and suckers, number, size and shape of rostellar hooks, number of testes, and by having smooth cirrus (vs. cirrus covered with hair-like bristles in *V. brachyacantha*). Phylogenetical analysis using cox1 showed our specimens clustering with North American isolates of *Versteria* sp. in a well-supported American clade (mean genetic divergence 0.024), separated from another clade composed of different isolates of *V. mustelae* (0.093). The close relationship between the new species and the North American species, known as “zoonotic” *Versteria* sp., and responsible for fatal infections by metacestodes in free-ranging wildlife (rodents), captive primates and immunosuppressed people, lead us to think that the zoonotic potential of *Versteria cuja* n. sp. should not be discarded.

1. Introduction

The family Taeniidae comprises four genera: *Echinococcus* Rudolphi, 1801, *Hydatigera* Lamarck, 1816, *Taenia* Linnaeus, 1758 and *Versteria* Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto and Ito (2013) (Nakao et al., 2013). The genus *Echinococcus* consists of nine species (Nakao et al., 2007), *Hydatigera* consists of four species, *Taenia* consists of nearly 44 species (Loos-Frank, 2000; Haukisalmi et al., 2011,

2016; Hoberg, 2006; Rossin et al., 2010; Wu et al., 2021), and *Versteria* consists of two nominal species: *Versteria mustelae* (Gmelin, 1790) (type species), and *Versteria brachyacantha* (Baer and Fain, 1951) (Nakao et al., 2013; Lavikainen et al., 2016). Nakao et al. (2013) proposed the genus *Versteria* to accommodate the two species formerly included in *Taenia*: *Taenia mustelae* Gmelin, 1790 and *Taenia brachyacantha* Baer and Fain (1951) (Nakao et al., 2013). Phylogenies inferred from both nuclear and mitochondrial protein-coding genes had demonstrated *T. mustelae*

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as sister to *Echinococcus*, and the species showing a basal position among members of *Taenia* in a phylogeny based on nuclear 18S rRNA (Nakao et al., 2013). A basal position of *T. mustelae* was also shown in a morphological phylogeny by Hoberg et al. (2000). Morphologically, *Versteria* was differentiated from *Taenia* mainly on morphometric characters: miniature rostellar hooks, small sizes of scolex, rostellum and suckers, short strobila and small number of testes (Nakao et al., 2013). The type host of *Versteria mustelae* is *Mustela nivalis* L. (Carnivora: Mustelidae) from Europe [type material of Rudolphi (1819) (= *Taenia tenuicollis*) deposited in the Vienna Museum, according to Freeman (1956)]. Subsequently, the species was reported parasitizing species of *Mustela* L., *Martes* Pinel and *Neogale* Gray Baryshnikov and Abramov (Mustelidae) from Europe, Russia, Japan and North America, and *Bassaricyon gabbii* (Allen) (Procyonidae) from Brazil (Hoberg et al., 1990; Iwaki et al., 1995; Loos-Frank, 2000; Magalhães Pinto et al., 2009; Lee et al., 2016). *Versteria brachyacantha* was described from the mustelid *Poecilogale albinucha* (Gray) in Africa (Baer and Fain, 1951) (type locality Butare, present Republic of Rwanda). This species was included in *Versteria* because it is morphologically very similar to *V. mustelae*, although molecular data are not available (Nakao et al., 2013). Up to now, species of *Versteria* are known to use mustelids and procyonids as definitive hosts and rodents as intermediate hosts (Lavikainen, 2014; Niedringhaus et al., 2021).

Recent studies suggested that in the Nearctic two *Versteria* species are found. One of them is a *Versteria* sp. reported from Wisconsin (host *Mustela erminea* L.) closely related with *V. mustelae*; and the other one is a “zoonotic” lineage of *Versteria* sp. reported from *M. erminea*, *Neogale vison* (Schreber), a captive orangutan, and humans from Colorado, Oregon, Wisconsin (Zoo) and Pennsylvania (Lee et al., 2016; Niedringhaus et al., 2021). None of these North American species are morphologically described, although they are molecularly characterized through cytochrome *c* oxidase subunit 1 gene (*cox1*) (Goldberg et al., 2014; Lee et al., 2016; Lehman et al., 2019b). Additionally, two cases of metacestodes infection in humans by a species of *Versteria* were reported in Atlantic Canada and Pennsylvania, identified through the mitochondrial 12S rRNA gene and 18 rRNA gene, without morphological description (Barkati et al., 2019; Deplazes et al., 2019). The taxonomic uncertainty of this group complicates the understanding of the natural history of the two *Versteria* species occurring in North America given that ancient reports of *V. mustelae* in both definitive and intermediate hosts in this region (Skinker, 1935; Locker, 1955; Freeman, 1956; Verster, 1969) could be any of these species (see Niedringhaus et al., 2021).

In South America, up to now, there was only one report of adult *Versteria*, in which Magalhães Pinto et al. (2009) reported *V. mustelae* parasitizing the Bushy-tailed olingo *B. gabbii* from Brazil. However, the morphological description was based only on one specimen without gravid proglottids, and there was no molecular characterization. In Patagonia Argentina, there are three species of native mustelids, among them the Lesser grison, *Galictis cuja* (Molina) which has a wide distribution range from southern Peru, western Bolivia, eastern and southern Brazil to Paraguay, Uruguay, central and southern Chile and southern Argentina, occupying a wide variety of habitats (Larivière and Jennings, 2009; Chébez et al., 2014). For a summary of the helminths found in the Lesser grison throughout its distribution, see Bagnato et al. (2022).

In this paper we describe a new species of *Versteria*, based on adults from the small intestine of *Galictis cuja* from northwestern Patagonia, Chubut province, Argentina, for which we provide morphological, molecular and phylogenetic data.

2. Materials and methods

2.1. Study area and sample collection

Between December 2018 and December 2019, six specimens (four males and two females) of *Galictis cuja* (Gc), road killed on National Route N° 259, were collected and transported to the laboratory. The

collection sites were between Esquel and Trevelin cities [43° 2.5'S; 71° 27.06'W, (Gc1, Gc2); 42° 58.5'S; 71° 23.8'W (Gc3-Gc5); 42° 59.1'S; 71° 29.29'W (Gc6)], Chubut province, Argentina. Three specimens were necropsied fresh and three kept frozen (at −18 °C) until further examination. Cestodes were collected individually from the small intestine. Most specimens were fixed in 4% formalin/distilled water, and preserved and stored in 70% ethanol; some others were stored directly in absolute ethanol for molecular analysis. Specimens designated for morphological studies were stained with Semichon's acetic carmine, Langeron's carmine or Gömöri's trichrome, dehydrated in a graduated ethanol series, cleared in eugenol and mounted in Canada balsam for examination under Leica DM500 (Leica, Wetzlar, Germany) light microscope. Drawings were made with the aid of a drawing attachment and photographs were taken with a Leica ICC50W camera with software connected to the microscope. The measurements are given in micrometers (µm) as range, followed by mean in parentheses. Type specimens of *Versteria cuja* n. sp. were deposited in the Helminthological Collection of the Museo de La Plata (MLP-He), La Plata, Argentina. Specimens of *Galictis cuja* were deposited in the Mammal Collection of the Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB-M), Esquel, Argentina.

2.2. DNA extraction, amplification and sequencing

Sequences were generated from a mitochondrial DNA region, cytochrome *c* oxidase subunit 1 gene (*cox1*) extracted from three samples of three proglottids each using the Wizard® Genomic DNA Purification Kit (A1120), according to the manufacturer's instructions. The regions of mDNA were amplified by the polymerase chain reaction (PCR) using previously published oligo-nucleotide primers (Bowles et al., 1992; Bowles and McManus, 1993a; 1993b). Their sequences are Forward: 5'-TTTTTTGGGCATCCTGAGGTTTAT-3', Reverse: 5'-TAAAGAAAGAA-CATAATGAAAATG-3'. The PCRs were performed in a final volume of 50 µl containing 4 µl template, 1X Master Mix-PCR Pegasus (EA0401, Biological Products, Argentina), 10 µM of each primer and free-nuclease water. Negative controls for the PCR were always run to control for contamination. The PCR cycle program consisted of an initial denaturation step at 94 °C for 5 min followed by 40 cycles of 45 s at 94 °C, 40 °C, and 72 °C, and a final extension step at 72 °C for 5 min. The sizes of the amplification products were assessed by electrophoresis in 1% (w/v) Tris-borate/EDTA (TBE) agarose gels and ethidium bromide staining. Relevant bands were sent to purifying and sequencing (Macrogen, Korea). The sequences have been deposited in GenBank. Sequences from the same genus and/or family that the species recorded in the present study were taken from GenBank and then compared using BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>).

2.3. Sequence alignments and phylogenetic analysis

Sequences here obtained were compared with 17 *cox1* sequences (including larval and strobilated stages) of *Versteria* occurring in carnivores, herbivores and/or rodents, representing 13 taxa from different geographical regions (Table 1). The concatenated alignments were performed using Multiple Alignment Fast Fourier Transform software (MAFFT software, available at <http://www.ebi.ac.uk/Tools/msa/mafft/>).

Phylogenetic molecular analyses were conducted on the aligned *cox1* sequences and were inferred by both Maximum-Likelihood (ML) method using MEGA11 (Tamura et al., 2021) and by Bayesian Inference (BI) using Mr. Bayes program (v3.2.6, available at http://www.phylogeny.fr/one_task.cgi?task_type=mrbayes, Huelsenbeck and Ronquist, 2001; Dereeper et al., 2008, 2010). The species *Echinococcus multilocularis* Leuckart, 1863 and *Echinococcus ortleppi* López-Neyra and Soler Planas, 1943 were used as outgroups. Regarding ML, to determine the nucleotide substitution model that gave the best fit to our data set, the MEGA11 software which held the JModel test analysis was employed, with model

Table 1

Taeniid taxa included in the phylogenetic analysis with information on: mammalian host, stage, locality, GenBank accession number (partial cytochrome oxidase subunit I, *cox1*, gene sequences), references and abbreviations used on phylogenetic tree. Data on *Versteria cuja* n. sp. in bold.

Taeniid species	Mammalian host	Stage	Locality	GenBank Accession Number	References	Abbreviation on tree
<i>Versteria cuja</i> n. sp.	<i>Galictis cuja</i> (Molina) (Mustelidae) (Gc)	adult	Argentina (Arg)	OL345572	This study	<i>Versteria cuja</i> n. sp._Arg_Gc3
<i>Versteria</i> sp.	<i>Pongo pygmaeus</i> L. (Hominidae) (Pp)	metacestode	USA (ZooWiUS)	KF303340.1	Goldberg et al. (2014)	<i>Versteria</i> sp._ZooWiUS_Pp
<i>Versteria</i> sp.	<i>Mustela erminea</i> L. (Mustelidae) (Me)	adult	USA (WiUS)	KT223035.1	Lee et al. (2016)	<i>Versteria</i> sp._WiUS_Me
<i>Versteria</i> sp.	<i>Mustela erminea</i>	adult	USA (CoUS)	KT223033.1	Lee et al. (2016)	<i>Versteria</i> sp._CoUS_Me
<i>Versteria</i> sp.	<i>Neogale vison</i> (Schreber) (Mustelidae) (Nv)	adult	USA (OrUS)	KT223034.1	Lee et al. (2016)	<i>Versteria</i> sp._OrUS_Nv
<i>Versteria</i> sp.	Human (Hominidae) (Hu)	metacestode	USA (PeUS)	MK681866.1	Lehman et al. (2019)	<i>Versteria</i> sp._PeUS_Hu
<i>V. mustelae</i> (Gmelin, 1790)	<i>Mustela lutreola</i> (L.) (Mustelidae) (Ml)	adult	Spain (Sp)	MH431789.1	Fournier-Chambrillon et al. (2018)	<i>Versteria mustelae</i> _Sp_Ml
<i>V. mustelae</i>	<i>Myodes glareolus</i> Schreber (Cricetidae) (Mg)	metacestode	Finland (Fi)	EU544559.1	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Fi_Mg
<i>V. mustelae</i>	<i>Myodes rufocanus</i> (Sundevall) (Cricetidae) (Mruf)	metacestode	Finland (Fi)	EU544566.1	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Fi_Mruf
<i>V. mustelae</i>	<i>Myodes rutilus</i> (Pallas) (Cricetidae) (Mrut)	metacestode	Finland (Fi)	EU544567.1	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Fi_Mrut
<i>V. mustelae</i>	<i>Myodes rutilus</i>	metacestode	Russia (Ru)	EU544568.1	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Ru_Mrut
<i>V. mustelae</i>	<i>Myodes rufocanus</i>	metacestode	Russia (Ru)	EU544570.1	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Ru_Mruf
<i>V. mustelae</i>	<i>Myopus schisticolor</i> Lilljeborg (Cricetidae) (Ms)	metacestode	Russia (Ru)	EU544571.1	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Ru_Ms
<i>V. mustelae</i>	<i>Mustela nivalis</i> L. (Mustelidae) (Mn)	adult	Japan (Ja)	AB732960.1	Nakao et al. (2013)	<i>Versteria mustelae</i> _Ja_Mn
<i>V. mustelae</i>	<i>Eospalax baileyi</i> (Thomas) (Spalacidae) (Eb)	metacestode	China (Ch)	KC989834.1	Zhao et al. (2014)	<i>Versteria mustelae</i> _Ch_Eb
<i>V. mustelae</i>	<i>Neogale vison</i>	adult	Poland (Po)	MW476516.1	Klockiewicz et al. (2021)	<i>Versteria mustelae</i> _Po_Nv
<i>Echinococcus</i> (outgroups)						
<i>E. multilocularis</i> Leuckart, 1863	<i>Vulpes</i> spp. (Canidae) (Vu)	adult	USA (US)	AB461419	Nakao et al. (2009)	<i>Echinococcus multilocularis</i> _US_Vu
<i>E. ortleppi</i> López-Neyra and Soler Planas, 1943	Cattle (Ca)	hydatid cyst	Argentina	NC_011122	Nakao et al. (2007)	<i>Echinococcus ortleppi</i> _Arg_Ca

selection based on the Akaike information criterion (AIC). Results indicated that the Hasegawa-Kishino-Yano model (HKY) was the most appropriate. The percentage of trees in which the associated taxa clustered together is shown above the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Join and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with superior log likelihood value. A discrete gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.1546)). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site (below the branches). This analysis involved 18 nucleotide sequences, and there were a total of 380 positions in the final dataset.

The estimates of evolutionary divergence between sequences were conducted in MEGA11 (Tamura et al., 2021). The rate variation among sites was modeled with a gamma distribution (shape parameter = 0.5). All ambiguous positions were removed for each sequence pair (pairwise deletion option). A total of 380 positions were used in the final dataset. Pairwise nucleotide sequence divergences were calculated using the p-distance model with a gamma setting of 0.5. Then, we calculated the mean pairwise divergences for both intra- and interspecific variation (Table 3). For the BI, to determine the evolution model that gave the best fit to our dataset the program jModeltest 2.1.1 (Darriba et al., 2012) was employed, with model selection based on the Akaike information criterion (AIC). Results indicated that AC = CG, AT = GT and an unequal base frequency with an estimate of gamma distributed among-site rate variation (HKY + I) was the most appropriate. The number of substitution types was fixed to 2. The 4 by 4 model was used for substitution, while rate variation across sites was fixed to “gamma”. Four Markov

Chain Monte Carlo (MCMC) chains were run for 10,000 generations, sampling every 10 generations, with the first 250 sampled trees discarded as “burn-in”. Finally, a 50% majority rule consensus tree was constructed.

3. Results

3.1. Description of the new species

Taeniidae Ludwig, 1886

Versteria Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto and Ito (2013).

Versteria cuja n. sp. Bagnato, Gilardoni and Digiani.

Adult (Figs. 1–3).

Material studied. Fragments of at least nine adults: nine fragmentary strobili with their scolices, 20 strobilar fragments without scolices (including immature, mature and gravid proglottids) and isolated gravid proglottids.

Description. Strobila short, exact length of gravid specimens unknown, but probably between 80 and 100 mm. Immature and mature proglottids wider than long, gravid proglottids elongate. Scolex 276–345 (309) in length (n=7) by 216–397 (284) wide (n = 9) (Fig. 1A). Rostellum 39–75 (63) in length (n = 6) by 30–89 (66) wide (n = 7), distinctly smaller than suckers (Fig. 1A). Rostellar armature consists of two rows, each one of ca. 24 very small hooks (48 in total). There is no difference between large and small hooks. Hooks 12–17 in length (n = 7) by 6–10 wide (n = 7) (Fig. 2A). These have a short and sharply curved blade, short, straight to sinuous handle, and long stout guard. The handle has a stout bulb at the end; frequently the posterior edge was

Table 2
Comparison of the main morphometrical diagnostic characters of the two nominal species of *Versteria* against *Versteria cuja* n. sp. Measurements in micrometers. **Abbreviations:** DH, definitive host; IH, intermediate host; L, length; LH, large hooks; SH, small hooks; W, width.

Versteria Species	Versteria cuja n. sp.	Versteria mustelae (Gmelin, 1790)									Versteria brachyacantha (Baer and Fain, 1951)	
Locality	Argentina	USA				Germany	France	France	Switzerland	Switzerland, France	Russia	Republic of Rwanda
	This study	Skinker (1935)	Locker (1955)	Freeman (1956)	Verster (1969)	Thienemann (1906)	Joyeux and Baer (1934)	Joyeux and Baer (1936)	Whal (1967)	Verster (1969)	Abuladze (1964)	Baer and Fain (1951)
Scolex	276-345	237-303	-	200-440	-	333-400	300	260-350	300	-	449-477	480
Rostellum	39-75	61-77	-	70-97	-	133	85-90	100-180	91	-	108	126
Suckers	87-151	77-110	-	92-132	-	100-133	120	60-100	130-150	-	167-186	176
N° hooks	48	48	44-48	47-66	-	50-52	52	52	37-43	38	50	54
Hooks size (LH, SH)	12-17	15-16	16-18/ 14-17	14-20	-	16-38/ 13-86	20	20	19-20	18-22	18-21/ 12-15	26-28
N° testes	54-85	90-125	-	-	97-117	114	90-110	110	100-110	83-127	114	100-145
Cirrus-sac L	210-311	193-220	-	-	138-250	150-250	160	175-250	229-274	104-306	352-369	240-280
Cirrus-sac W	130-185	130-154	-	-	90-120	105-113	70-80	40-90	123-146	75-137	158-176	120
Cirrus	unarmed, smooth	-	-	-	-	-	-	-	-	unarmed, smooth	-	armed, hairlike bristles
Genital atrium size	170-420	-	-	-	-	-	-	-	68-91	-	-	-
Uterus	branched (12-28)	10-19	-	10-23	13-18	12-18	12-15	12-14	28	10-23	14-16	saccular/branched (14-17)
IH	Ctenomys sp. (Ctenomyidae), unpublished data	Rodents (various species of Cricetidae, Muridae, Spalacidae) Eulipotyphla (Talpidae)									unknown	
DH	Galictis cuja (Molina) (Mustelidae)	Mustelids [Martes, Neogale, Mustela] Procyonids (Bassaricyon gabbii (Allen))]									Poecilogale albinucha (Gray) (Mustelidae)	

Table 3
Intra- and interspecific pairwise divergence within genus *Versteria* in the complete sequences of mitochondrial *cox1* gene. **Abbreviations:** AH, accidental host; IH, intermediate host; DH, definitive host.

<i>Versteria</i> species	Geographical distribution	Mean intraspecific pairwise distance	Mean interspecific pairwise distance
Intraspecific			
<i>Versteria cuja</i> n. sp. (DH: mustelid)	South America (Argentina)	0.000	
<i>Versteria</i> sp. (AH: primates, human, DH: mustelids)	North America (Wisconsin Zoo, Colorado, Oregon, Pennsylvania)	0.011	
<i>Versteria mustelae</i> (Gmelin, 1790) (IH: rodents, DH: mustelids)			
Between European isolates	Spain, Poland, Finland	0.006	
European vs. Japanese isolates	(Spain, Poland, Finland)-Japan	0.035	
European vs. Chinese isolates	(Spain, Poland, Finland)-China	0.026	
European vs. Siberian isolates	(Spain, Poland, Finland)-Siberia	0.033	
European vs. US isolates	(Spain, Poland, Finland)-Wisconsin	0.029	
European vs. Chinese isolates	(Spain, Poland, Finland)-China	0.026	
Siberian vs. Japanese isolates	Siberia-Japan	0.008	
Siberian vs. US isolates	Siberia-Wisconsin	0.040	
Japanese vs. US isolates	Japan-Wisconsin	0.032	
Siberian vs. Chinese isolates	Siberia-China	0.032	
Japanese vs. Chinese isolates	Japan-China	0.024	
US vs. Chinese isolates	Wisconsin-China	0.022	
Interspecific			
<i>V. cuja</i> n. sp. vs. <i>Versteria</i> sp.			0.024
<i>V. cuja</i> n. sp. vs. <i>V. mustelae</i>			0.093
<i>Versteria</i> sp. vs. <i>V. mustelae</i>			0.096

folded (Fig. 2A–C). Suckers 87–151 (109) in length (n = 26) by 73–126 (106) wide (n = 13) (Fig. 1A). Neck 768–1,958 (1,274) in length (n = 9) by 264–450 (358) maximum width (n = 10) (Fig. 1A). Proglottids apolyptic and craspedote. Immature proglottids 113–733 (458) in length (n = 216) by 476–1,489 (916) wide (pw, proglottid width) (n = 216) (Fig. 3A), length/width ratio 0.2–0.8 (0.5) (n = 216). Mature proglottids 476–2,027 (1,230) in length (n = 171) by 1,117–1,941 (1,535) maximum width (n = 171) (Figs. 1B and 3B), length/width ratio 0.4–1.1 (0.8) (n = 171). Gravid proglottids 1,474–4,347 (3,159) in length (n = 88) by 1,117–1,945 (1,681) maximum width (n = 87) (Fig. 1C), length/width ratio 1.0–2.9 (1.9) (n = 87). Proglottids becoming more elongate posteriorly. Genital pores irregularly alternating (Fig. 3B), protruding, opening from anterior to roughly at middle of proglottid margin. Genital atrium subspherical, well-developed, 170–420 (315) deep (n = 202) (Fig. 1B and C, 3B–D). Longitudinal osmoregulatory canals 48 wide (n = 4); transverse connecting canals narrower, 45 wide (n = 4). Distance between longitudinal canals 477–1,237 (984) (n = 125) in immature proglottids (Figs. 3A), 926–1,273 (1,080) (n = 33) in mature proglottids, and 685–1,290 (1,055) (n = 27) in gravid proglottids. Terminal genital

ducts pass longitudinal osmoregulatory canals ventrally (Fig. 1B). Testes subspherical, relatively few, 54–85 (68) (n = 28) in number, mostly anterior to female organs; 25–54 (46) major diameter (n = 38) by 20–57 (43) minor diameter (n = 38) (Figs. 1B and 3B). Testicular fields confluent anteriorly, and situated between longitudinal osmoregulatory canals, from anterior proglottid margin to anterior margin of ovary, few in postero-poral field 12–36 (18) (n = 23). Relative length of testicular fields (length of the antero-poral field/length of the postero-poral field) 0.9–1.4 (1.1) (n = 26). Cirrus sac elliptical to subspherical, 210–311 (259) transverse diameter (n = 81) (cl, cirrus sac length) by 130–185 (159) longitudinal diameter (n = 81) in mature proglottids (Figs. 1B), 167–330 (261) transverse diameter (n = 22) by 159–200 (176) longitudinal diameter (n = 22) in gravid proglottids, usually overlapping or extending across longitudinal ventral canal (Fig. 1C). Relative length of cirrus sac (cl/pw) 0.13–0.22 (0.17) (n = 100). Cirrus smooth, 417–1,014 (659) in length (n = 12) by 33–54 (42) wide (n = 12) (Figs. 1B and 3C). Deferent duct forming loops inside and outside cirrus sac, surrounded by prostatic cells (Figs. 1B, 3B–C, E). Ovary posteriad, median, bilobed, 327–458 (396) in length (n = 44) by 444–929 (634) total width (ow, ovary width) (n = 44). Poral and aporal lobes subequal in size (Figs. 1B and 3B). Relative ovary width on proglottid width (ow/pw) 0.35–0.44 (0.40) (n = 44). Vitellarium posterior to ovary, transversely elongated, 135–194 (166) in length (n = 49) by 375–691 (544) wide (vw, vitellarium width) (n = 49) (Figs. 1B and 3B). Relative vitellarium with on proglottid width (vw/pw) 0.30–0.42 (0.35) (n = 49). Relative vitellarium width on ovary width (vw/ow) 0.76–1.02 (0.89) (n = 47). Maximum size of seminal receptacle 135–152 (144) in length (n = 10) by 84–117 (100) wide (n = 10) (Figs. 1B and 3F). Ootype and Mehlis’ gland subspherical, 78–191 (129) in length (n = 30) by 41–120 (88) wide (n = 29) (Fig. 1B). Vagina running posterior to cirrus sac and deferent duct, slightly widened and undulating. Vaginal sphincter absent. Vaginal pore posterior to male pore (Figs. 1B, 3B–D). Uterus appearing as median longitudinal stem; gravid uterus with several lateral branches, 12–28 (20) (n = 43) in number, arising regularly, each one with a secondary bifurcation (Fig. 1C). Eggs spherical or subspherical, 25–31 (27) major diameter (n = 67) by 22–29 (25) minor diameter (n = 67), with embryophore or outer shell 1–4 (3) thick (n = 68) (Figs. 1C, 3G–H).

3.2. Taxonomic summary

Type definitive host: *Galictis cuja* (Molina) (Carnivora: Mustelidae).
Type locality: Between Esquel and Trevelin cities (43°2.504’S, 71°27.056’W), National Route N°259, Chubut province, Argentina.

Site of infection: Small intestine.
Prevalence and intensity of infection: Three out of six Lesser grisons infected with 1–13 specimens by host.

Type specimens: Syntypes, MLP-He 7771 (13 fragments, 3 with scolex, neck and immature proglottids, 1 with immature proglottids, 4 mature proglottids and 5 gravid proglottids); vouchers (7 fragments, 2 with mature proglottids, 1 with mature and gravid proglottids and 4 with gravid proglottids), MLP-He 7772.

Host specimens deposited: LIEB-M-1626, LIEB-M-1787 and LIEB-M-1789, skull or skull’s parts and tissues (muscle and liver).

Etymology: The specific epithet refers to the specific epithet in the name of the type definitive host, *Galictis cuja*. **cuja:** latinization of the host’s common name (“cuya”) in Chile and Peru, used in the original description of *Mustela cuja* Molina (see Mouchard, 2019).

GenBank accession numbers: **OL345569**, **OL345573** and **OL345572** (cox1, adults).

ZooBank access number: LSID: urn:lsid:zoobank.org:pub:3A82F343-FDDB-4205-9DE0-171F9A591FD6

3.3. Remarks

According to the diagnosis given by Nakao et al. (2013), *Versteria*

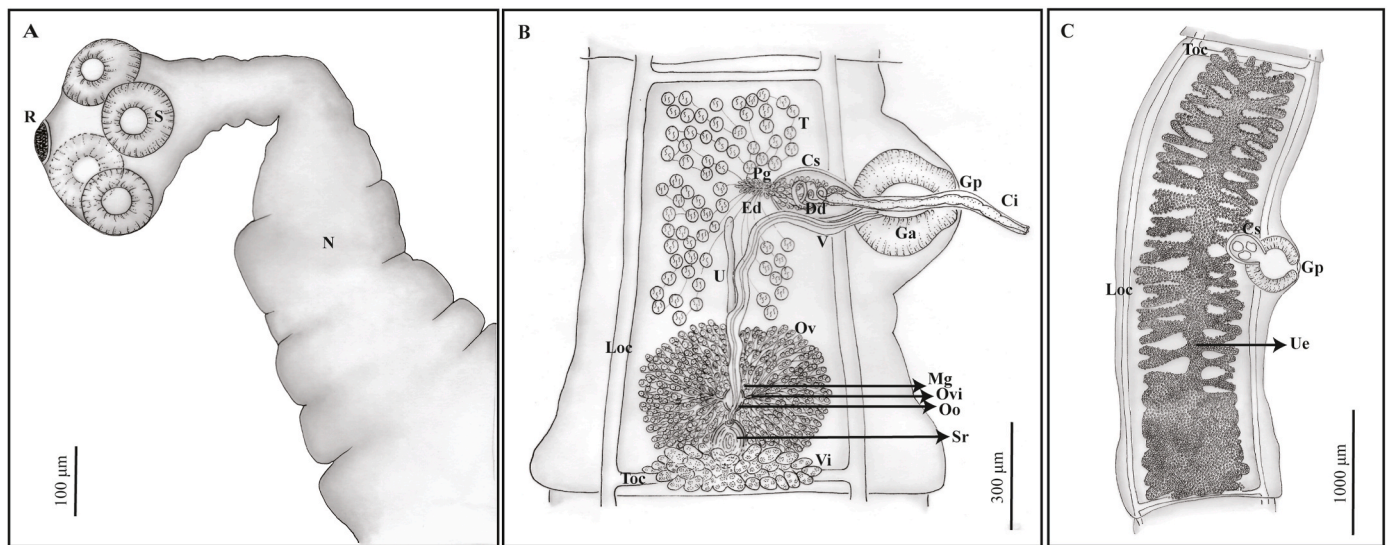


Fig. 1. (A–C). Line drawings of *Versteria cuja* n. sp. (Cestoda: Taeniidae) from the Lesser grison *Galictis cuja* (Molina) from Chubut province, Argentina. (A) Scolex, showing rostellum, suckers, and neck. (B) Mature proglottid. (C) Gravid proglottid. **Abbreviations:** Ci, cirrus; Cs, cirrus sac; Dd, deferent duct; Ed, efferent ducts; Ga, genital atrium; Gp, genital pore; Loc, longitudinal osmoregulatory canals; Mg, Mehlis's gland; N, neck; Oo, ootype; Ov, ovary; Ovi, oviduct; Pg, prostatic gland; R, rostellum; S, suckers; Sr, seminal receptacle; T, testes; Toc, transverse osmoregulatory canals; U, uterus; Ue, uterus with eggs; V, vagina; Vi, vitellarium.

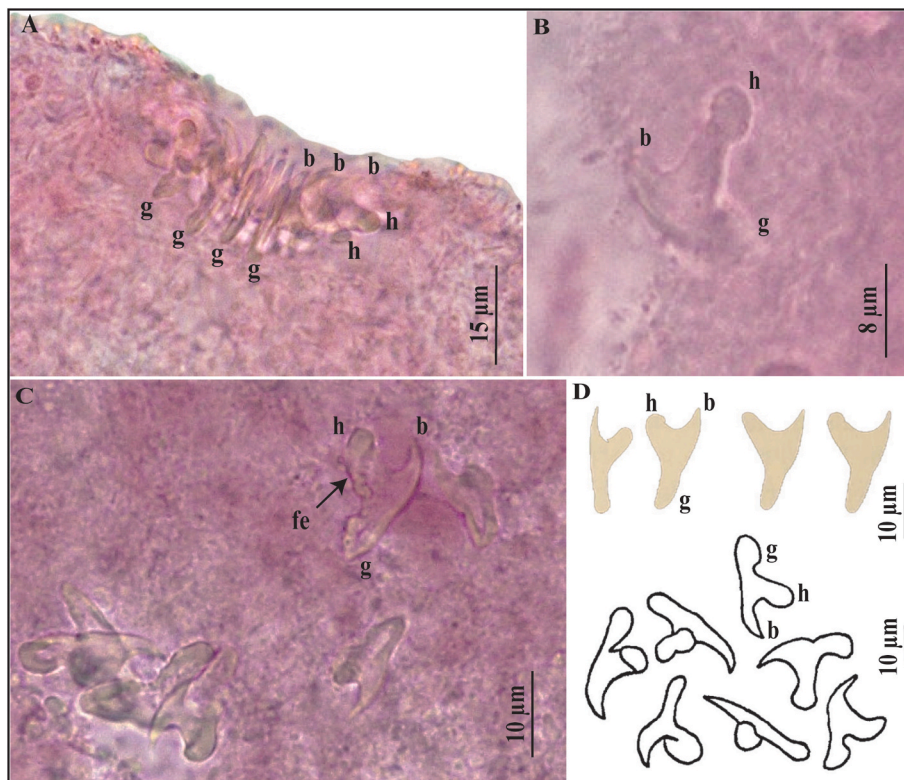


Fig. 2. (A–D). Rostellum and rostellar hooks of *Versteria* spp. (Cestoda: Taeniidae) from different mustelids. (A–C) Microphotographs of rostellum and rostellar hooks of *Versteria cuja* n. sp. from the Lesser grison *Galictis cuja* (Molina) from Chubut province, Argentina. (A) Rostellum and crown of rostellar hooks, lateral view. (B) Isolated rostellar hook. (C) Other isolated rostellar hooks showing one in detail, top right. (D) Rostellar hooks of *Versteria mustelae* (Gmelin, 1790) from *Mustela erminea* L. from Bienne, Switzerland, taken from Wahl (1967) (top row); and rostellar hooks of *Versteria brachyacantha* (Baer and Fain, 1951) from *Poecilogle albinucha* (Gray) from Butare city, Rwanda, taken from Baer and Fain (1951) (lower group). **Abbreviations:** b, blade; fe, folded edge; g, guard; h, handle.

cuja n. sp. belongs to the genus *Versteria* by having a short strobila, immature and mature proglottids wider than long, gravid elongated proglottids; scolex, rostellum and suckers small, rostellum with two rows of very small hooks; genital pores alternating irregularly, opening roughly at the middle of the proglottid margin; terminal genital ducts passing longitudinal osmoregulatory canals ventrally; female glands posterior and median; ovary bilobed; vitellarium posterior to ovary, transversely elongated; vaginal sphincter absent; testes relatively few, mostly anterior to female organs; uterus appearing as median

longitudinal stem; gravid uterus with several lateral branches (Nakao et al., 2013).

Comparing the specimens described herein against the two nominal species of *Versteria*, morphological- and morphometrically the three species do not differ substantially (see Table 2), although there are some differences, as described below will be described below. *Versteria mustelae* was reported repeatedly from Europe, Asia and North America and, since its original description in 1790, there were numerous descriptions made by various authors (Thienemann, 1906; Skinner, 1935; Joyeux and

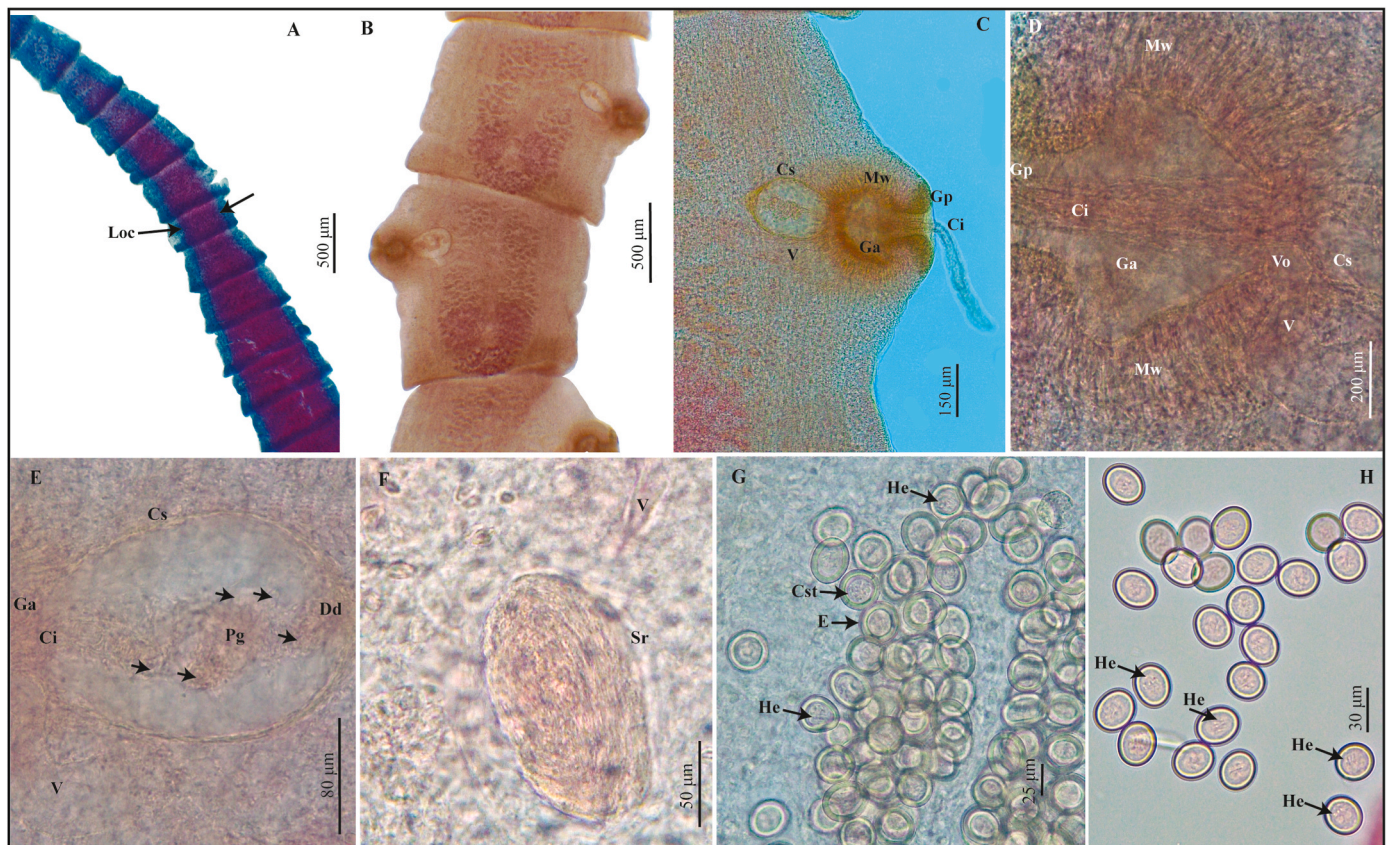


Fig. 3. (A–H). Microphotographs of *Versteria cuja* n. sp. (Cestoda: Taeniidae) from the Lesser grison *Galictis cuja* (Molina) from Chubut province, Argentina. (A) Strobilar fragment with immature proglottids, showing longitudinal osmoregulatory canals (arrows). Gömöri's trichrome. (B) Strobilar fragment with mature proglottids, showing genitalia. Langeron's carmine. (C) Detail of terminal genitalia in mature proglottid. Langeron's carmine. (D) Detail of terminal genital openings into genital atrium. Semichon's acetocarmine. (E) Detail of cirrus sac, showing prostatic gland (arrows indicating prostatic cells) covering the deferent duct. Semichon's acetocarmine. (F) Detail of seminal receptacle. Langeron's carmine. (G) Eggs in different developmental stages. Semichon's acetocarmine. (H) Eggs with mature hexacanth embryo. Semichon's acetocarmine. **Abbreviations:** Ci, cirrus; Cs, cirrus sac; Cst, cell stage; E, embryophore; Ga, genital atrium; Gp, genital pore; He, hexacanth embryo; Loc, longitudinal osmoregulatory canals; Mw, muscular wall of genital atrium; Pg, prostatic gland; Sr, seminal receptacle; V, vagina; Vo, vaginal opening.

Baer, 1934, 1936; Locker, 1955; Freeman, 1956; Abuladze, 1964; Wahl, 1967; Verster, 1969; Magalhães Pinto et al., 2009). However, in the morphometric comparison we only used the measurements of Palearctic specimens of *V. mustelae*, and excluded from *V. mustelae* the measurements of North American specimens (see Table 2). These latter specimens (*Versteria* sp., today) should be compared separately. The size range of *V. mustelae* from Europe and Russia (Siberia) is relatively broad, and the sizes of the new species proposed herein mostly approach or fall within these ranges. However, there are differences between *V. cuja* n. sp. and *V. mustelae* in the number of testes (54–85 vs. 83–127, respectively) (Table 2, Fig. 2A–D), in the rostellum size (39–75 vs. 85–180 µm), in the genital atrium size (170–420 vs. 68–91 µm) and in the hooks' shape. Regarding the hooks' shape, in the rostellar hooks of *V. cuja* n. sp. the angle between blade and handle is more pronounced and the handle is much better differentiated than in those of *V. mustelae*, where the basal part of the handle is markedly expanded (see Fig. 2).

Versteria cuja n. sp. and Nearctic specimens are very similar morphometrically (see Table 2). The ranges of the measurements of the main diagnostic characters (scolex, rostellum, suckers, hooks number and size, cirrus-sac size and uterus) are very similar and partially overlap, except in the number of testes (54–85 vs. 90–125 in Nearctic specimens) (Skinker, 1935; Locker, 1955; Freeman, 1956; Verster, 1969). The rostellar hooks are also similar (Fig. 2A–C), with a short and sharply curved blade, short, straight to sinuous handle, and long stout guard. The hooks of *V. cuja* n. sp. had a length of 12–17 µm vs. 14–20 µm in Nearctic specimens (Fig. 2).

Concerning the African species *V. brachyacantha*, descriptions are much less numerous, i.e. the original description and a further re-description by Verster (1969). *Versteria cuja* n. sp. differs from *V. brachyacantha* by having smaller measurements regarding the main diagnostic characters, i.e. size of scolex, rostellum and suckers, number, size and shape of rostellar hooks, number of testes (Table 2, Fig. 2A–D), and by having a smooth cirrus (vs. covered with hair-like bristles in *V. brachyacantha*) (Baer and Fain, 1951). Regarding the hooks' shape, the angle between blade and handle is more pronounced, and that between handle and guard is less pronounced in the rostellar hooks of *V. cuja* n. sp. than in those of *V. brachyacantha* (see Fig. 2D). Further, the cirrus-sac is wider and rather subspherical in *V. cuja* n. sp. with respect to the other two species (see Table 2).

3.4. Molecular and phylogenetic analysis

The PCR amplification of *cox1*, mtDNA from adult *Versteria cuja* n. sp. gave three products of 373, 377 and 380 bp, respectively, of partial *cox1* sequence. *Versteria cuja* n. sp. sequences coincided in a 97.88% (369/378 bp) (MK6818866.1) with *Versteria* sp. from Pennsylvania (human) and in a 97.85% (364/372 bp) (KT223034.1) with *Versteria* sp. from Oregon (mink). *Cox1* tree topologies resulting from the ML and BI analysis were identical with BI producing higher branch support (Fig. 4). The genus *Versteria* formed a monophyletic group. The isolates obtained in this study appeared on the tree closely related with a group of species from USA: *Versteria* sp. ZooWiUS (Wisconsin) from *Pongo pygmaeus* L.,

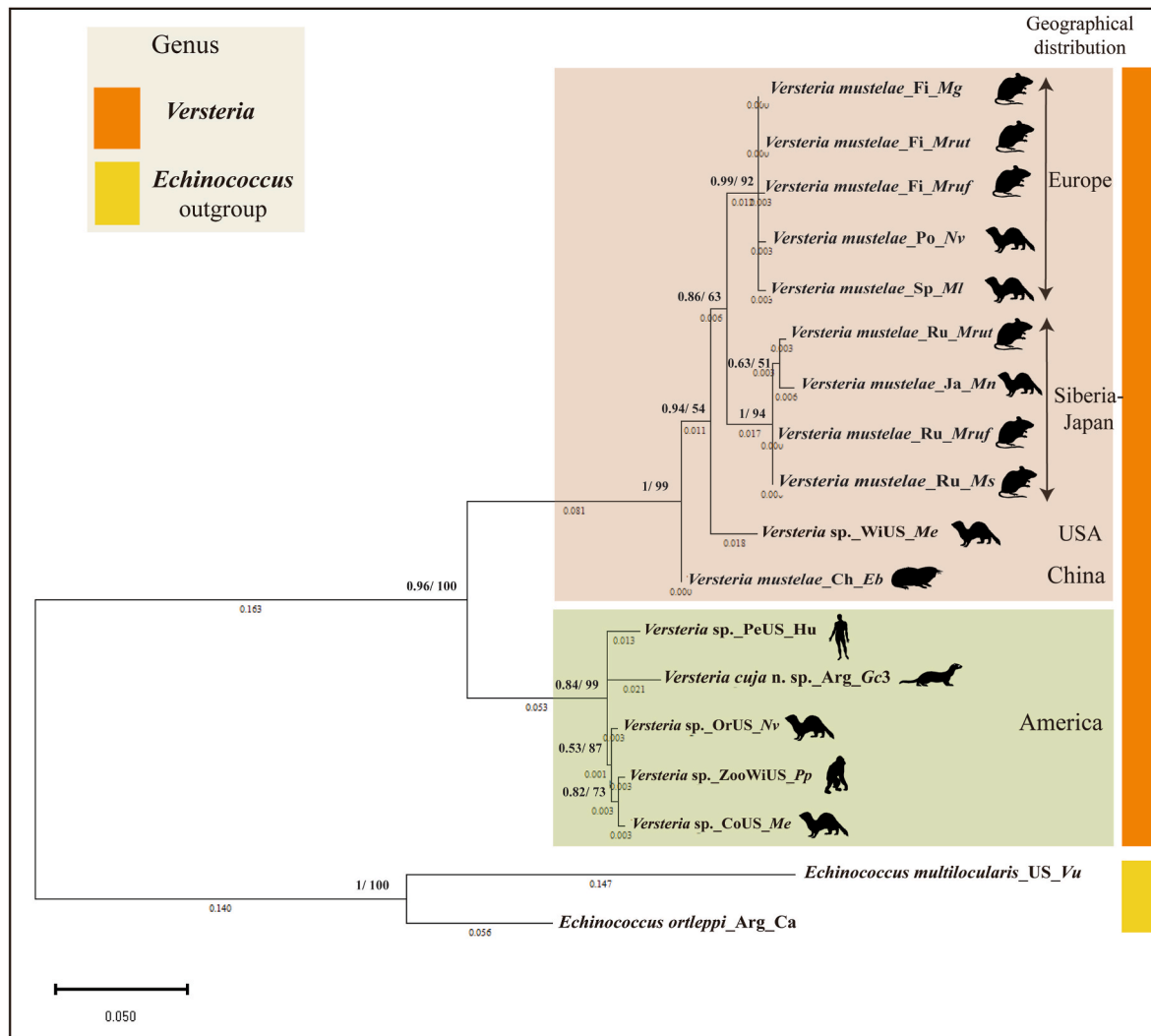


Fig. 4. Phylogenetic relationships of *Versteria cuja* n. sp. (Cestoda: Taeniidae) from the Lesser grison *Galictis cuja* (Molina) from Chubut province, Argentina, and other *Versteria* species, as inferred from mitochondrial cytochrome c oxidase subunit 1 (cox1) gene sequences analyzed using Maximum-Likelihood (ML) and Bayesian Inference (BI) methods. Nodal support is indicated above internodes as BI (posterior probabilities)/ML (bootstrap value); values < 0.70 (BI) and < 50 (ML) are indicated by a dash. The tree is drawn to ML scale, with branch lengths measured in the number of substitutions per site (below the branches).

Versteria sp. CoUS (Colorado) from *Mustela erminea* L., *Versteria* sp. OrUS (Oregon) from *Neogale vison* (Schreber), and *Versteria* sp. PeUS (Pennsylvania) from human, all of them forming a well-supported “American” clade (Table 3, Fig. 4) which is the sister group of another clade mainly composed of *V. mustelae*. This latter large clade is composed in turn of a “European” clade and an “Asian” clade, plus *Versteria* sp. from Wisconsin (USA) and *V. mustelae* from China (Fig. 4). According to the genetic distances (Table 3) obtained in this study, this large clade of *V. mustelae* could represent a species complex, well separated from the “American” clade. The pairwise distances of *V. cuja* n. sp. compared against the North American species were: 0.022 with *Versteria* sp. OrUS, 0.024 with *Versteria* sp. ZooWiUS and *Versteria* sp. CoUS, and 0.026 with *Versteria* sp. PeUS (the “zoonotic” *Versteria* sp.). Whereas the pairwise distance with *Versteria* sp. WiUS from *Mustela erminea* was 0.097, and this latter clustered with *V. mustelae* from Europe and Asia (Table 3, Fig. 4).

3.5. Intra- and interspecific variation between *Versteria* species

Pairwise divergence values of cox1 gene were utilized to numerically evaluate intra- and interspecific variation in *Versteria* species. One isolate of *V. cuja* n. sp. from South America; four isolates of *Versteria* sp. from North America and 11 isolates of *V. mustelae* from the Holarctic

Region (Lehman et al., 2019b) originating from different localities were used for this evaluation. As shown in Table 3, the mean intraspecific divergence values of the complete cox1 sequences between the Holarctic isolates of *V. mustelae* ranged from 0.006 (between European isolates) to 0.040 (between Siberian and US isolates). Mean value between North American isolates of *Versteria* sp. was 0.011. Regarding the mean interspecific divergence values, they were as follows: between *V. cuja* n. sp. and *Versteria* sp. 0.024, between *V. cuja* n. sp. and *V. mustelae* 0.093 and between *Versteria* sp. and *V. mustelae* 0.096 (Table 3).

4. Discussion

The specimens discussed herein belong to the genus *Versteria* within the family Taeniidae and differed molecularly from *V. mustelae* (mean pairwise distance 0.093), integrating a separate clade from the latter. The genus *Versteria* is reported for the first time in Argentina and in a native mustelid. Our specimens clustered (mean genetic divergence, 0.024, Fig. 4) with a group of four North American *Versteria* sp. in a well-supported “American” clade. Of these four species, two (OrUS and CoUS) are strobilate forms which had the mink, respectively, the mink *Neogale vison* from Oregon and the ermine *M. erminea* from Colorado as definitive hosts, respectively (Fig. 4). The other two (ZooWiUS and

PeUS) correspond to metacestodes of *Versteria* sp. which were responsible for a fatal, respectively, for a fatal infection in a captive juvenile Bornean orangutan (born in captivity in the USA) (Goldberg et al., 2014), and for four cases of cysticercosis in immunosuppressed human patients (see Deplazes et al., 2019a; Lehman et al., 2019b).

The relatively low genetic distances between our specimens and the above-mentioned *Versteria* sp. suggest that their conspecificity should not be ruled out. However, it is a challenge to delimit species only on a molecular basis and without the help of the morphology, since there is no description of any of these *Versteria* sp. from USA. In proposing the new species, additionally to the phylogenetic molecular analysis, we also evaluated the distinctive morphological and morphometric characters described above, the Lesser grison *Galictis cuja* as a new definitive host, and the distinct geographical distribution with respect to the nominal species *V. mustelae* and *V. brachyacantha*. Concerning the *V. mustelae* clade, it probably constitutes a species complex, since within this clade the intraspecific variation ranged from 0.006 to 0.040 between the different isolates and different lineages could be differentiated (Europe, Siberia/Japan, US and China) (Table 3, Fig. 4). Regarding the species reported as *V. mustelae* from Brazil (Magalhães Pinto et al., 2009), it probably deserves revision, including further morphological studies based on more specimens (the report was based on a single immature individual), and a molecular characterization.

Recently, Niedringhaus et al. (2021) reported a fatal infection by cysticerci of *Versteria* sp. in a muskrat *Ondatra zibethicus* (L.) in Pennsylvania, USA; remarkably, in the same locality where a case of human cysticercosis was reported (Lehman et al., 2019b). The sequence (cox1) obtained from these cysticerci coincided in a 99% with those of *Versteria* sp. from the mink from Oregon and the ermine from Colorado. Moreover, it was integrated into the clade which also included *Versteria* sp. from the orangutan and from humans (Niedringhaus et al., 2021). Unfortunately, the sequence of *Versteria* sp. from *O. zibethicus* could not be incorporated into our analysis since there is no GenBank accession number in the article by Niedringhaus et al. (2021), and we did not find it in the database. The work by Niedringhaus et al. (2021) points out *O. zibethicus* at least as one of the natural intermediate hosts of this species. Regarding the South American species, cysticerci obtained from the liver of *Ctenomys* sp. (Ctenomyidae) showed sequences of cox1 identical to that of the adult of *Versteria cuja* n. sp. (Bagnato, unpublished data).

Interestingly, though there in the Palearctic, though there are some reports of hyperinfestation by *V. mustelae* in definitive hosts, in the Palearctic (Fournier-Chambrillon et al., 2018), there are no reports of disseminated fatal cases of *V. mustelae* in intermediate hosts, either natural (rodents) or other accidental hosts such as humans or other primates (Niedringhaus et al., 2021).

The identification of the Nearctic taxon reported until now as *Versteria* sp., as well as new data on its life-cycle become critical in view of its potential for zoonotic disease. Indeed, the few cases of metacestodes reported from humans are suggesting a potentially emergent zoonosis caused by accidental ingestion of the eggs of these tapeworms (Deplazes et al., 2019; Lehman et al., 2019b).

The close relationship between the new South American species and the lineage known as “zoonotic” *Versteria* sp., responsible for fatal infections by metacestodes in free-ranging wildlife (rodents), captive primates and immunosuppressed people, lead us to think that the zoonotic potential of *Versteria cuja* n. sp. should not be discarded.

Author contributions

EB conceived and designed research, analyzed host samples, studied and identified the parasites, wrote the manuscript. CG performed the phylogenetic analysis. GMM contributed with supplies and reagents. MCD studied and identified the parasites, supervised the work. All authors read and approved the manuscript.

Note

Nucleotide sequence data reported in this paper are available in the GenBank™ database under the accession numbers: OL345569, OL345573, OL345572 (cox1).

Declaration of competing interest

None.

Acknowledgments

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