



Natural life cycle and molecular characterization of *Taenia talicei* Dollfus, 1960 (Cestoda: Taeniidae) from northwestern Patagonia, Argentina

Estefanía Bagnato^{a,b,*}, Juan José Lauthier^c, Federico Brook^{a,b}, Gabriel Mario Martín^{a,b}, María Celina Digiani^d

^a Centro de Investigación Esquel de Montaña y Estepa Patagónica (CIEMEP), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET)- Universidad Nacional de la Patagonia "San Juan Bosco" (UNPSJB), San Martín 558, (9200), Esquel, Chubut, Argentina

^b Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Facultad de Ciencias Naturales, Sede Esquel, UNPSJB, Ruta Nacional N° 259, 16.4 Km, (9200), Esquel, Chubut, Argentina

^c Instituto de Medicina Traslacional e Ingeniería Biomédica (IMTIB), CONICET-IUHI-HIBA, Potosí 4240, (C1199ACL), Buenos Aires, Argentina

^d División Zoología Invertebrados, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, CONICET-Centro Científico Tecnológico La Plata, Buenos Aires. Paseo del Bosque s/n La Plata, (1900), Buenos Aires, Argentina

ARTICLE INFO

Keywords:

Taenia
Life cycle
Ctenomys
Lycalopex
Cox1
Argentina

ABSTRACT

Through morphological and molecular studies, the natural life cycle of *Taenia talicei* Dollfus, 1960 (Cestoda: Taeniidae) from Argentine Patagonia is elucidated, involving subterranean rodents (Ctenomyidae) as intermediate hosts, and the Andean fox *Lycalopex culpaeus* (Canidae) as definitive host. Metacestodes (mono- and polycephalic fimbriocerci) were found mainly in the peritoneal cavity of *Ctenomys terraplen*, and the strobilate adult in the intestine of *L. culpaeus*. Correspondence between metacestodes and strobilate adults was based primarily on number, size and shape of rostellar hooks: 45–53 hooks alternated in two rows, small hooks 88–180 µm long and large hooks 230–280 µm long, with the characteristic shape described in the two main description of the species, both that of the metacestode (original description) and that of the strobilate adult (obtained experimentally). Further genetic analysis (cox1 gene mtDNA) corroborated the conspecificity between the metacestodes and the strobilate adults found in the Andean fox in the same study area. Genetic analysis also revealed conspecificity of the taxon found in Patagonia with the species registered in GenBank as *T. talicei*, obtained from different intermediate and definitive hosts from Peru and Argentina. *Taenia talicei* was previously reported from Argentina in the form of metacestodes naturally infecting two other species of *Ctenomys*. However, the strobilate adult was only described from the experimental infection of a domestic dog. Hence, this is the first report of the natural life cycle of *T. talicei* and of a species of *Taenia* endemic from South America.

1. Introduction

The genus *Taenia* Linnaeus, 1758 is one of the most studied tapeworms, but its taxonomy, systematics, and species still remain controversial and conflicting (Ganzorig and Gardner, 2024). Species of the genus are not easily identified by morphological means, since many of the characters overlap. This does not so much apply to the few human parasitic species, but rather to those from carnivores, particularly when several species occur in one host species within a given geographical area (Loos-Frank, 2000). Identification of species and separation from the rest is possible using molecular methods, but they must have been

previously correctly described by morphological methods. Verster (1969) published her invaluable revision of *Taenia* and not only set standards on important and less important characters but also decided on the taxonomy and validity of species (Loos-Frank, 2000).

Phylogeny is fundamental as it constrains explanations about history and forms our foundation for recognizing and diagnosing species. In the absence of such a framework taxonomists historically relied on intuitive processes, personal judgment and authority, often embracing a typological view of species that disregarded otherwise unequivocal historical and biological criteria (Hoberg, 2006). During the last ten years, researchers have made several contributions on the phylogeny of these

* Corresponding author. Laboratorio de Investigaciones en Evolución y Biodiversidad (LIEB), Facultad de Ciencias Naturales, Sede Esquel, UNPSJB, Ruta Nacional N° 259, 16.4 Km, (9200), Esquel, Chubut, Argentina.

E-mail addresses: ebagnato@comahue-conicet.gob.ar (E. Bagnato), juanjoselauthier@gmail.com (J.J. Lauthier), brook.federico@gmail.com (F. Brook), gmartin@yahoo.com (G.M. Martín), mdigiani@fcnym.unlp.edu.ar (M.C. Digiani).

<https://doi.org/10.1016/j.ijppaw.2024.101035>

Received 4 November 2024; Received in revised form 23 December 2024; Accepted 23 December 2024

Available online 24 December 2024

2213-2244/© 2024 The Authors. Published by Elsevier Ltd on behalf of Australian Society for Parasitology. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

important parasites (e.g., Hoberg, 2006; Lavikainen et al., 2008, 2016; Haukisalmi et al., 2011; Nakao et al., 2013; Terefe et al., 2014; Lee et al., 2016; Arrabal et al., 2017, 2023; Wu et al., 2021; Bagnato et al., 2022, 2023; Shanebeck et al., 2024). The cestode family Taeniidae actually consists of four valid genera, *Taenia*, *Hydatigera* Lamarck, 1816; *Versteria* Nakao, Lavikainen, Iwaki, Haukisalmi, Konyaev, Oku, Okamoto and Ito (2013) and *Echinococcus* Rudolphi, 1801 Nakao et al., (2013). The genus *Echinococcus* is monophyletic due to a remarkable similarity in morphology, features of development and genetic makeup. By contrast, *Taenia* is a highly diverse group formerly made up of different genera. Recent molecular phylogenetic analyses strongly suggest the paraphyly of *Taenia* (Nakao et al., 2013).

Species of *Taenia* have a life cycle that requires two obligate mammalian hosts, an intermediate herbivore and a definitive terrestrial carnivore. *Taenia* species have worldwide distribution, although endemic species are known from each zoogeographic region (Ganzorig and Gardner, 2024). The cysticercus is the characteristic metacestode of the taeniids (Chervy, 2002), but a small group of *Taenia* species (e.g. *T. selousi* Mettrick, 1962; *T. endotheracicus* (Kirschenblatt, 1948); *T. twitchelli* (Schwartz, 1927) shows metacestodes of the polycephalic type, characterized by scoleces with elongate stalks arising by exogenous budding from a central bladder that later regresses. These polycephalic metacestodes, as well as the fimbriated metacestodes or fimbriocerci (elongate, unsegmented metacestodes with characteristic folds, e.g., *T. martis*, *T. polyacantha*, *T. twitchelli*) are derived with respect to the cysticercus, though their ontogenetic relationships and homology are uncertain (Rausch and Fay, 1988; Hoberg et al., 2000; Chervy, 2002).

In 1954, Voge reported the finding of taeniid metacestodes in the peritoneal cavity of the rodents *Ctenomys peruanus* Sanborn and Pearson (Ctenomyidae), *Phyllotis osilae* Allen and *Chinchillula sahamae* Thomas (Cricetidae) from Peru. She paid special attention to the exogenous proliferation exhibited by these metacestodes, and suggested that such type of asexual, metacestodes multiplication, as observed in all specimens studied, and in three species of rodents, should be interpreted as a normal part of the development of this taeniid. She left pending, however, the specific identification of the metacestodes described, until more was known about the strobilate adults of taeniids in the High Andes (Voge, 1954). A few years later, Dollfus (1960) described *Taenia talicei* Dollfus (1960) based on metacestodes recovered from the peritoneal cavity of *Ctenomys torquatus* Lichtenstein from Uruguay. Twenty-eight years later, in 1988, Rausch and Gardner identified metacestodes ("multi-strobilate larvae") in mesenteries of *Ctenomys opimus* Wagner in Bolivia that they identified as *T. talicei* (Gardner et al., 2021). Five decades passed from the publication of Dollfus (1960) until Rossin et al. (2010), in Argentina, redescribed the species based on metacestodes (cysticerci, fimbriocerci and polycephalic larvae) found in the peritoneal cavity of *Ctenomys australis* (Rusconi) and *Ctenomys talarum* Thomas from Buenos Aires province, and strobilate adults obtained through experimental infection of a domestic dog with some of those metacestodes. Latter was the first description of the strobilate adult of this *Taenia* species (Rossin et al., 2010).

More recent publications on *T. talicei* are lacking. Notwithstanding, there are unpublished sequences (Table 1) attributed to this species available in GenBank [30 nucleotide sequences, of which 13 correspond to the NADH dehydrogenase subunit 1 gene (*nad1*) and 17 to cytochrome *c* oxidase subunit 1 (*cox1*)]. Such sequences are derived from strobilate adults recovered from Andean foxes and domestic dogs (definitive hosts) and from metacestodes recovered from *Lagidium peruanum* Meyen (Chinchillidae), *Phyllotis xanthopygus* (Waterhouse) from Peru and *Ctenomys tuconax* Thomas from Argentina (intermediate hosts).

Ctenomys terraplen Brook, González, Tomasco, Verzi and Martin is an endemic tuco-tuco from open areas within the forest between Esquel and Corcovado in northwestern Chubut province (Argentina), recently described by Brook et al. (2024). The species belongs to the

"magellanicus" species group, the most species-rich and widely distributed lineage in Patagonia. *Ctenomys terraplen* inhabits open areas in Subantarctic or Andean-Patagonian forests, in sandy and clayey soil (Brook et al., 2024). To date, the only known endoparasite for *C. terraplen* is *Versteria cuja* Bagnato, Gilardoni and Digiani, 2022 (Taeniidae), in the form of metacestodes affecting several organs (Bagnato et al., 2022; 2023). In Bagnato et al. (2023) *C. terraplen* was consigned as *Ctenomys* sp. 1 because the species was not named at that moment. Within the framework of the study of Patagonian *Ctenomys* (Brook, in review, PhD Thesis), we had the opportunity to examine several specimens of tuco-tucos of different species from Chubut province, including eleven specimens of *C. terraplen* and one identified as *Ctenomys* aff. *C. terraplen*. Three of the rodents examined harbored, in the peritoneal cavity, mono and polycephalic metacestodes. These metacestodes, however, differed in several aspects (size of the scolex, number, size and shape of hooks, localization in the host) from the metacestodes of *Versteria cuja* from the same host species described in a previous work (Bagnato et al., 2023). In addition, the scoleces of these new metacestodes were morphologically similar to those of some strobilated adults of a taeniid species obtained by the first author from an Andean fox from the same area (unpubl. data). Morphological and molecular analyses were then conducted on these new metacestodes and on the strobilate adults found in the Andean fox, in order to investigate their relationship and that with other taeniid species. Resulting from those investigations, in this paper we shed light on the natural life cycle of *T. talicei* from Argentine Patagonia, provide morphological and molecular characterizations of the parasite stages found in their respective hosts, and assess the position of *T. talicei* in a partial phylogeny including 34 species of taeniids.

2. Materials and methods

2.1. Study area and sample collection

Between December 2018 and June 2019 five dead specimens (three females and two males) of *Lycalopex culpaeus* (Lc) were collected and transported to the laboratory for standard mammalian studies and parasitological examination. Four specimens (Lc1-4) were given to us by a local farmer from the vicinity of Laguna La Zeta (42° 48.9' S; 71° 22.9' W); the fifth one (Lc5) was found road-killed in Los Alerces National Park (42° 58.2' S; 71° 35' W), near Esquel, Chubut province, Argentina. Specimen LIEB-M-1806 (Lc2) was necropsied fresh and the other ones were kept frozen at -18 °C until further examination.

In addition, between January 2018 and April 2022, 12 specimens of tuco-tucos (Rodentia: Ctenomyidae), sampled as part of FB's Doctoral Thesis were examined for parasites. Eleven tuco-tucos were identified as *Ctenomys terraplen* from Laguna Terraplén (42.96°S, 71.49°W), near Los Alerces National Park (LANP), Corcovado (43.54° S, 71.46° W) and areas between these two localities. Another specimen (*Ctenomys* aff. *C. terraplen*) was collected at Laguna El Cronómetro (43.24° S, 71.09° W), Chubut province, Patagonia, Argentina. All captures were made under permits provided by Dirección Fauna y Flora Silvestre from the Ministerio de Agricultura, Ganadería, Industria y Comercio del Chubut [Resolutions N° 098/2018, N° 097/2019 (foxes); 1468/2019, N° 404/2021, N° 103/2023 (tuco-tucos)]. Specimens of *Ctenomys* were caught using Oneida Victor N° 0 traps with rubber covers and euthanized by cervical dislocation (Sikes et al., 2011). Some of the specimens were prospected for parasites fresh, others were frozen at -18 °C until examination and others were placed in 96 % ethanol directly.

All hosts were inspected for endoparasites under a Leica EZ4 stereomicroscope (Leica, Wetzlar, Germany). The gastrointestinal tract was separated into oesophagus, stomach, caecum and intestine. The body cavity, liver, pancreas, spleen, gall bladder, gonads, lungs, heart and kidneys were also examined for parasites.

Table 1

Taeniid taxa included in the phylogenetic analysis with information on mammal host, stage, locality, GenBank accession number [partial cytochrome oxidase subunit I (Cox1) gene sequences], references and code used on phylogenetic tree; records of *Taenia taliceii* Dollfus (1960) are in bold. **Abbreviations:** A, adult; M, metacestodes.

Taeniid species	Mammalian host	Stage	Locality	GenBank Accession Number	References	Code on the tree
<i>Taenia</i> Linnaeus, 1758						
<i>T. taliceii</i> Dollfus (1960)	<i>Ctenomys terraplen</i> (Ctenomyidae) (Ct29.1)	metacestode	Argentina (Arg)	PP738877	This study	<i>Taenia taliceii</i> _Arg_PP738877_Ct29.1
<i>T. taliceii</i> Dollfus (1960)	<i>Ctenomys terraplen</i> (Ctenomyidae) (Ct29.2)	metacestode	Arg	PP738957	This study	<i>Taenia taliceii</i> _Arg_PP738957_Ct29.2
<i>T. taliceii</i> Dollfus (1960)	<i>Ctenomys terraplen</i> (Ctenomyidae) (Ct30)	metacestode	Arg	PP738958	This study	<i>Taenia taliceii</i> _Arg_PP738958_Ct30
<i>T. taliceii</i> Dollfus (1960)	<i>Lycalopex culpaeus</i> (Canidae) (Lc5)	adult	Arg	PP738968	This study	<i>Taenia taliceii</i> _Arg_PP738968_Lc5
<i>Taenia</i> sp.	<i>Lycalopex culpaeus</i> (Canidae) (Lc1)	adult	Peru (Per)	MG385632	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_MG385632_Lc1
<i>T. taliceii</i> Dollfus (1960)	<i>Lycalopex culpaeus</i> (Canidae) (Lc2)	adult	Per	MG385629	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_MG385629_Lc2
<i>T. taliceii</i> Dollfus (1960)	<i>Ctenomys tuconax</i> (Ctenomyidae) (Ctu)	metacestode	Arg	PP050508	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Arg_PP050508_Ctu
<i>T. taliceii</i> Dollfus (1960)	<i>Phyllotis xanthopygus</i> (Cricetidae) (Px1)	metacestode	Per	PP050507	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_PP050507_Px1
<i>T. taliceii</i> Dollfus (1960)	<i>Phyllotis xanthopygus</i> (Cricetidae) (Px2)	metacestode	Per	PP050506	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_PP050506_Px2
<i>T. taliceii</i> Dollfus (1960)	<i>Canis lupus familiaris</i> (Canidae) (Clf1)	adult	Per	PP050501	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_PP050501_Clf1
<i>T. taliceii</i> Dollfus (1960)	<i>Canis lupus familiaris</i> (Canidae) (Clf2)	adult	Per	PP050498	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_PP050498_Clf2
<i>T. taliceii</i> Dollfus (1960)	<i>Lagidium peruanum</i> (Chinchillidae) (Lp)	metacestode	Per	PP050500	Gomez-Puerta et al. (unpublished)	<i>Taenia taliceii</i> _Per_PP050500_Lp
<i>T. arctos</i> Haukisalmi et al. (2011)	<i>Alces alces</i> (Cervidae) (Aa)	metacestode	Finland (Fin)	GU252131	Lavikainen et al. (2010)	<i>Taenia arctos</i> _Fin_GU252131_Aa
<i>T. arctos</i> Haukisalmi, Lavikainen, Laaksonen and Meri, 2012	<i>Ursus arctos horribilis</i> (Ursidae) (Uah)	adult	United States (USA)	KF356387	Catalano et al. (2014)	<i>Taenia arctos</i> _USA_KF356387_Uah
<i>T. asiatica</i> Eom and Rim, 1993	Human (Hu)	adult	Japan (Jap)	LC405943	Yamasaki et al. (2021)	<i>Taenia asiatica</i> _Jap_LC405943_Hu
<i>T. caixuepengi</i> Wu2021	<i>Ochotona curzoniae</i> (Ochotonidae) (Oc)	metacestode	China (Chi)	MT882036	Wu et al. (2021)	<i>Taenia caixuepengi</i> _Chi_MT882036_Oc
<i>T. crassiceps</i> (Zeder, 1800; Rudolphi, 1810)	?	?	Canada (Can)	NC_002547	Le et al. (2000)	<i>Taenia crassiceps</i> _Can_NC_002547
<i>T. crocutae</i> Mettrick and Beverly-Burton, 1961	<i>Crocota crocuta</i> (Hyaenidae) (Cc)	adult	Africa (Afr)	NC_024591	Terefe et al. (2014)	<i>Taenia crocutae</i> _Afr_NC_024591_Cc
<i>T. hydatigena</i> Pallas, 1766	<i>Ovis</i> sp. (Bovidae) (Ov)	metacestode	Chi	NC_012896	Jia et al. (2010)	<i>Taenia hydatigena</i> _Chi_NC_012896_Ov
<i>T. krabbei</i> Moniez, 1879	<i>Vulpes lagopus</i> (Canidae) (Vl)	adult	Norway (Nor)	EU544576	Lavikainen et al. (2008)	<i>Taenia krabbei</i> _Nor_EU544576_Vl
<i>T. laticollis</i> Rudolphi, 1819	?	adult	Fin	AB731727	Nakao et al. (2013)	<i>Taenia laticollis</i> _Fin_AB731727
<i>T. lynciscapreoli</i> Haukisalmi et al. (2016)	<i>Lynx lynx</i> (Felidae) (Ll)	adult	Fin	JX860629	Haukisalmi et al. (2016)	<i>Taenia lynciscapreoli</i> _Fin_JX860629_Ll
<i>T. madoquae</i> (Pellegrini, 1950)	?	adult	Kenya (Ken)	AB731726	Nakao et al. (2013)	<i>Taenia madoquae</i> _Ken_AB731726
<i>T. martis</i> (Zeder, 1803)	?	metacestode	Croatia (Cro)	AB731758	Nakao et al. (2013)	<i>Taenia martis</i> _Cro_AB731758
<i>T. multiceps</i> Leske, 1780	<i>Canis lupus familiaris</i> (Canidae) (Clf)	adult	Chi	NC_012894	Jia et al. (2010)	<i>Taenia multiceps</i> _Chi_NC_012894_Clf
<i>T. omissa</i> Lühe, 1910	<i>Puma concolor</i> (Felidae) (Pc)	adult	Per	KR095314	Gomez-Puerta et al. (2016)	<i>Taenia omissa</i> _Per_KR095314_Pc
<i>T. omissa</i> Lühe, 1910	<i>Puma concolor</i> (Felidae) (Pc)	adult	Arg	OQ921988	Arrabal et al. (2023)	<i>Taenia omissa</i> _Arg_OQ921988_Pc
<i>T. ovis</i> (Cobbold, 1896)	<i>Ovis</i> sp. (Bovidae) (Ov)	metacestode	New Zealand (NZ)	AB731675	Nakao et al. (2013)	<i>Taenia ovis</i> _NZ_AB731675_Ov
<i>T. pisiformis</i> (Bloch, 1780)	<i>Canis lupus familiaris</i> (Canidae) (Clf)	adult	Chi	NC_013844	Jia et al. (2010)	<i>Taenia pisiformis</i> _Chi_NC_013844_Clf
<i>T. polyacantha</i> Leuckart, 1856	<i>Vulpes vulpes</i> (Canidae) (Vv)	adult	Turkey (Tur)	MN067543	Erol et al. (2021)	<i>Taenia polyacantha</i> _Tur_MN067543_Vv
<i>T. regis</i> Baer, 1923	<i>Panthera leo</i> (Felidae) (Pl)	adult	Afr	NC_024589	Terefe et al. (2014)	<i>Taenia regis</i> _Afr_NC_024589_Pl
<i>T. saginata</i> Goeze, 1782	Human (Hu)	adult	Belgium (Bel)	NC_009938	Jeon et al. (2007)	<i>Taenia saginata</i> _Bel_NC_009938_Hu
<i>T. serialis</i> (Gervais, 1847)	?	adult	Australia (Aus)	AB731674	Nakao et al. (2013)	<i>Taenia serialis</i> _Aus_AB731674
<i>T. solium</i> Linnaeus, 1758	<i>Sus scrofa domesticus</i> (Suidae)	metacestode	Ecuador (Ec)	AB066491	Nakao et al. (2002)	<i>Taenia solium</i> _Ec_AB066491_Ssd

(continued on next page)

Table 1 (continued)

Taeniid species	Mammalian host	Stage	Locality	GenBank Accession Number	References	Code on the tree
<i>T. tianguangfui</i> Wu, Li L., Fan, Ni, Ohiolei, Li W. H., Li J. Q., Zhang, Fu, Yan and Jia (2021)	<i>Neodon fuscus</i> (Cricetidae) (Nf)	metacestode	Chi	MT882037	Wu et al. (2021)	<i>Taenia tianguangfui</i> _Chi_MT882037_Nf
<i>T. twitchelli</i> Schwartz, 1924	<i>Gulo gulo</i> (Mustelidae) (Gg)	adult	Rusia (Rus)	EU544598	Lavikainen et al. (2008)	<i>Taenia twitchelli</i> _Rus_EU544598_Gg
<i>Hydatigera</i> Lamarck, 1816						
<i>H. kamiyai</i> Iwaki, 2016	<i>Apodemus flavicollis</i> (Muridae) (Af)	metacestode	Serbia (Ser)	OQ569731	Lavikainen et al. (2016)	<i>Hydatigera kamiyai</i> _Ser_OQ569731_Af
<i>H. krepkogorski</i> Schulz and Landa, 1934	?	metacestode	Chi	AB731762	Nakao et al. (2013)	<i>Hydatigera krepkogorski</i> _Chi_AB731762
<i>H. parva</i> Baer, 1926	?	metacestode	Chi	AB731763	Catalano et al. (2019)	<i>Hydatigera parva</i> _Chi_AB731763
<i>H. taeniformis</i> Batsch, 1786	<i>Mastomys huberti</i> (Muridae) (Mh)	metacestode	Senegal (Sen)	MH036507	Nakao et al. (2013)	<i>Hydatigera taeniformis</i> _Sen_MH036507_Mh
<i>Echinococcus</i> Rudolphi, 1801						
<i>E. multilocularis</i> Leuckart, 1863	<i>Vulpesspp.</i> (Canidae) (Vu)	adult	USA	AB461419	Nakao et al. (2009)	<i>Echinococcus multilocularis</i> _USA_AB461419_Vu
<i>E. oligarthrus</i> (Diesing, 1863)	<i>Puma concolor</i> (Felidae) (Pc)	adult	Arg	KX129804	Arrabal et al. (2017)	<i>Echinococcus oligarthrus</i> _Arg_KX129804_Pc
<i>E. orteppi</i> López-Neyra and Soler Planas, 1943	Cattle (Ca)	hydatid cyst	Arg	NC_011122	Nakao et al. (2007)	<i>Echinococcus orteppi</i> _Arg_NC_011122_Ca
<i>Versteria</i> Nakao, Lavikainen, Iwaki, Haukisalml, Konyaev, Oku, Okamoto and Ito, 2013						
<i>V. cuja</i> Bagnato, Gilardoni and Digiani, 2022	<i>Galictis cuja</i> (Mustelidae) (Gc)	adult	Arg	OL345572	Bagnato et al. (2022)	<i>Versteria cuja</i> _Arg_OL345572_Gc
<i>V. cuja</i> Bagnato, Gilardoni and Digiani, 2022	<i>Ctenomys terraplen</i> (Ctenomyidae) (Ct)	metacestode	Arg	ON980784	Bagnato et al. (2022)	<i>Versteria cuja</i> _Arg_ON980784_Ct
<i>V. mustelae</i> (Gmelin, 1790)	<i>Eospalax baileyi</i> (Spalacidae) (Eb)	metacestode	Chi	KC898934	Zhao et al. (2014)	<i>Versteria mustelae</i> _Chi_KC898934_Eb
<i>V. mustelae</i> (Gmelin, 1790)	<i>Myodes rufocanus</i> (Cricetidae) (Mruf)	metacestode	Rus	EU544570	Lavikainen et al. (2008)	<i>Versteria mustelae</i> _Ru_EU544570_Mruf
<i>V. mustelae</i> (Gmelin, 1790)	<i>Mustela lutreola</i> (Mustelidae) (Ml)	adult	Spain (Spa)	MH431789	Fournier-Chambrillon et al. (2018)	<i>Versteria mustelae</i> _Sp_MH431789_Ml
<i>V. rafei</i> Shanebeck et al. (2024)	<i>Neogale vison</i> (Mustelidae) (Nv)	adult	Can	OR448764	Shanebeck et al. (2024)	<i>Versteria rafei</i> _Can_OR448764_Nv
<i>Versteria</i> sp.	<i>Mustela erminea</i> (Mustelidae) (Me)	adult	USA	KT223035	Lee et al. (2016)	<i>Versteria</i> _sp_USA_KT223035_Me
<i>Versteria</i> sp.	Human (Hominidae) (Hu)	metacestode	USA	MK681866	Lehman et al. (2019)	<i>Versteria</i> _sp_USA_MK681866_Hu
<i>Versteria</i> sp.	<i>Mustela erminea</i> (Mustelidae) (Me)	adult	USA	KT223033	Lee et al. (2016)	<i>Versteria</i> _sp_USA_KT223033_Me
<i>Versteria</i> sp.	<i>Pongo pygmaeus</i> (Primates) (Pp)	metacestode	USA	KF303340	Goldberg et al. (2014)	<i>Versteria</i> _sp_USA_KF303340_Pp

2.2. Parasitological study

Both metacestodes (fimbriocerci) and strobilate adults were mostly fixed in 4 % formalin/distilled water after washing in 0.9 % saline, and preserved and stored in 70 % ethanol. Other specimens were stored directly in absolute ethanol for molecular analysis. Specimens intended for morphological study were stained with Borax 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. To study the rostellum and rostellar hooks in detail, rostellum from several metacestodes and adults were dissected, mounted between slide and coverslip in Hoyer's and Berlese's fluids and allowed to dry.

Photographs were taken with a Leica ICC50W camera with software connected to the microscope. Measurements, unless otherwise stated, are given in micrometres (μm) as mean \pm standard deviation, followed by range in parentheses. Prevalence and mean intensity were calculated following Bush et al. (1997). Mounted vouchers of metacestodes and not well clarified strobilate adult of *T. talicei* were deposited in the Parasitological Collection of the *Laboratorio de Investigaciones en Evolución y Biodiversidad* (LIEB-Pa), Esquel, Chubut province, Argentina. Complete specimens or skulls of *L. culpaeus*, *C. terraplen* and *Ctenomys* aff. *C. terraplen* were deposited in the Mammal Collection of the LIEB (LIEB-M), Esquel, Chubut province, Argentina.

2.3. DNA extraction, amplification and sequencing

DNA extractions were performed on four samples: three *C. terraplen* metacestodes from Corcovado, and one *L. culpaeus* strobilate adult from Los Alerces National Park. For each sample, the Puro PB-L Genomic DNA Purification Kit (Quilmes, Argentina) was used according to the manufacturer's instructions. A mitochondrial DNA region, cytochrome c oxidase subunit 1 gene (cox1) was amplified by polymerase chain reaction (PCR) using previously published oligonucleotide primers (Bowles et al., 1992; Bowles and McManus, 1993a, 1993b). The forward primer sequence was 5'-TTTTTTGGGCATCCTGAGGTTTAT-3', and the reverse primer sequence was 5'-TAAAGAAAGAACATAATGAAATG-3'. 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 nuclease-free water. Negative controls were always included to monitor for contamination. The PCR cycle program consisted of an initial denaturation at 94 °C for 5 min, followed by 40 cycles of 94 °C for 45 s at 40 °C, 90 s at 72 °C, with a final extension at 72 °C for 3 min. Amplification products were visualized by electrophoresis in 1% (w/v) Tris-borate/EDTA (TBE) agarose gels stained with ethidium bromide. Amplicons were submitted for sequencing to Macrogen Inc. (South Korea) using the same primers employed for amplification.

2.4. Sequence alignments and phylogenetic analysis

Sequences obtained from fimbriocerci of *C. terraplen* were aligned and compared with the *cox1* sequences obtained from strobilate adults of the Andean fox using Multalin software (available at <http://www.sacs.ucsf.edu/cgi-bin/multalin.py>).

The sequences obtained were later deposited in GenBank and compared using BLAST (<https://blast.ncbi.nlm.nih.gov/Blast.cgi>) with other 49 *cox1* sequences (including strobilate adults and metacestodes) of *Taenia* species occurring in carnivores, ungulates and rodents, representing 34 taxa from different geographical regions (Table 1). The concatenated alignments were performed using Multiple Alignment Fast Fourier Transform (MAFFT) software (available at <https://www.ebi.ac.uk/jdispatcher/msa/mafft/summary?jobId=mafft-I20240503-145848-0392-17861125-p1m>).

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). 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 selection based on the Akaike information criterion (AIC). Models with the lowest BIC scores (Bayesian Information Criterion) are considered to describe the substitution pattern the best. Non-uniformity of evolutionary rates among sites may be modeled by using a discrete Gamma distribution (+G) with 5 rate categories and by assuming that a certain fraction of sites are evolutionarily invariable (+I). For estimating ML values, a tree topology was automatically computed. The analysis involved 53 nucleotide sequences. Codon positions included were

1st+2nd+3rd + Noncoding. All positions containing gaps and missing data were eliminated. There were a total of 200 positions in the final dataset. Evolutionary analyses were conducted in MEGA7.

The number of substitution types was fixed to 2. For Bayesian Inference (BI) 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.

2.5. Statistical analysis

A 1-way analysis of variance was performed (factor: intermediate host species) using the R software and plyr package (R Core Team, 2024) in R Studio (RStudio Team, 2024) for comparison measurements between metacestodes of *C. terraplen* and *Ctenomys* aff. *C. terraplen* (data used in discussion section, e.g., *p* value).

3. Results

Metacestodes of *Taenia talicei* were found in two individuals of *C. terraplen* (Fig. 1 A, C-D) from Corcovado and in the one identified as *Ctenomys* aff. *C. terraplen* from Laguna El Cronómetro (LEC) (Fig. 1B).

Cyclophyllidea van Beneden in Braun (1900)

Taeniidae Ludwig, 1886

Taenia Linnaeus, 1758

Taenia talicei Dollfus (1960)

3.1. Description of metacestodes

Based on 27 monocephalic and 7 polycephalic metacestodes

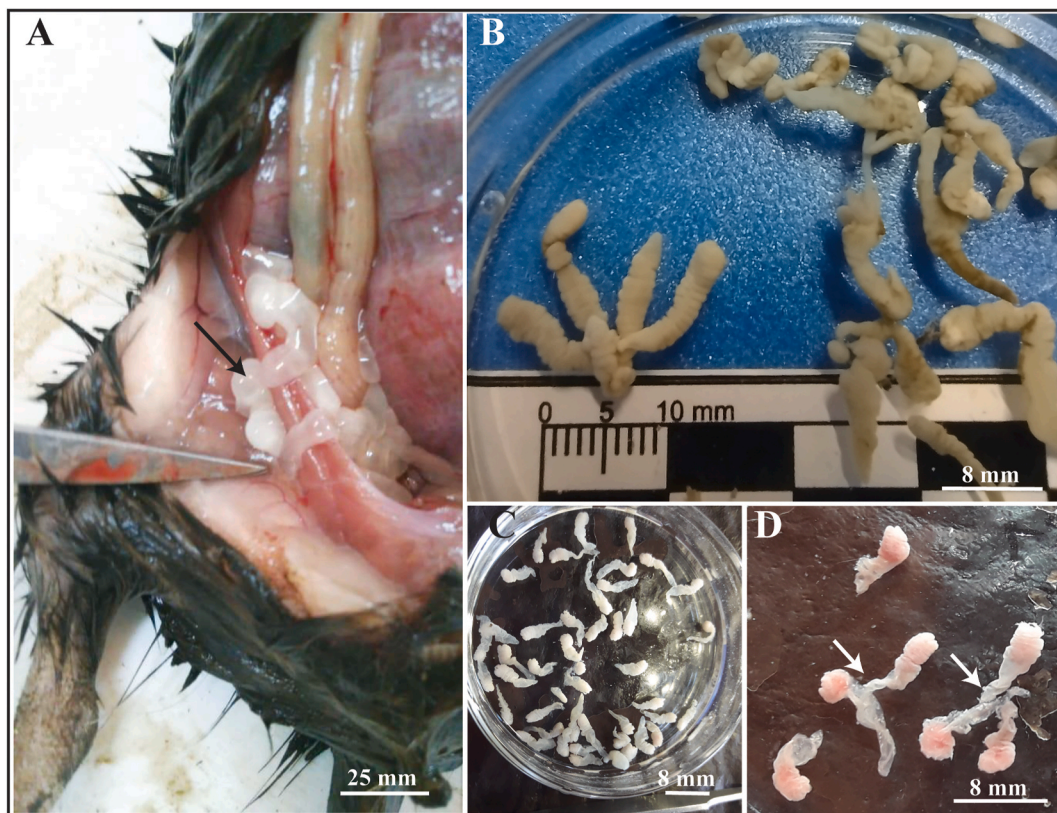


Fig. 1. (A–D). Metacestodes of *Taenia talicei* Dollfus (1960) (Cestoda: Taeniidae) invading peritoneal cavity in *Ctenomys* spp. (Rodentia: Ctenomyidae) from Chubut province, Argentina. (A) Fimbriocerci (arrow) in peritoneal cavity of *C. terraplen* Brook, González, Tomasco, Verzi and Martin from Corcovado. (B) Multiple (polycephalic) fimbriocerci from *C. aff. C. terraplen* from Laguna El Cronómetro. (C) Monocephalic fimbriocerci from *C. terraplen*. (D) Polycephalic fimbriocerci (arrows) from *C. terraplen*. Arrows indicate the common bladder.

(fimbriocerci) (Figs. 1–2, Table 2). Metacestodes elongated, white, with invaginated scoleces (Fig. 1).

Monocephalic metacestodes from Corcovado (Fig. 2A–F): body 8 ± 2.4 (2.4–11.9) mm ($n = 18$) long by 3.1 ± 0.6 (2.4–4) mm ($n = 18$) maximum wide. Suckers diameter 345 ± 105 (280–500) ($n = 4$); rostellum diameter 583 ± 118 (470–800) ($n = 8$); invaginated scolex 2.6 ± 0.8 (0.9–3.7) ($n = 8$) mm long by 1.5 ± 0.4 (1–1.9) ($n = 7$) mm wide.

Monocephalic metacestodes from LEC (Fig. 2G–I): 16 ± 5.8 (11.5–29.4) mm ($n = 8$) long by 3.3 ± 0.5 (2.5–3.9) mm ($n = 8$) maximum wide. Suckers not visible, rostellum diameter 613 ± 134 (420–730) ($n = 4$).

Polycephalic metacestodes from LEC: composed of two to five fimbriocerci arising from a common bladder (Fig. 1B). Whole forms 19.4 ± 6.3 (11–27.8) mm ($n = 7$) long by 7.9 ± 4.5 (3.3–14.9) mm ($n = 7$) maximum wide. Individual fimbriocerci of polycephalic metacestodes: 10.7 ± 1.5 (8.7–12.6) mm ($n = 18$) long by 3 ± 0.2 (2.6–3.2) mm ($n = 18$) maximum wide. Common bladder 1.7 ± 0.3 (1.4–2.4) mm ($n = 8$) long by 1.8 ± 0.5 (1.1–2.8) mm ($n = 8$) maximum wide. Scolex 4.1 mm

($n = 1$) long by 1.4 mm ($n = 1$) maximum wide.

Rostellar hooks fully formed, arranged in two rows, with three typical parts: handle, blade and guard. Number and dimensions of large and small hooks (according to Haukisalmi et al., 2011) of metacestodes from these and from other intermediate hosts (data from literature) are given in Table 2.

3.2. Description of adult scolex and proglottids

Strobilate adults (Fig. 3): white *in vivo*. Strobila >47 mm ($n = 1$) total length. Scolex 870 ± 40 (820–900) ($n = 4$) long by 900 ± 180 (750–1110) ($n = 4$) wide, bearing four rounded muscular suckers 330 ± 64 (270–390) in diameter (Fig. 3 A, C). Rostellum armed, 583 ± 125 (430–690) in diameter, with two rows of hooks. Number and dimensions of large and small hooks (Fig. 3 B, D, E) (according to Haukisalmi et al., 2011) of strobilate adults from this and from other known definitive hosts (data from literature) are given in Table 3.

Partial length of strobilate adults fragment 25 ± 9 (13–34) ($n = 4$)

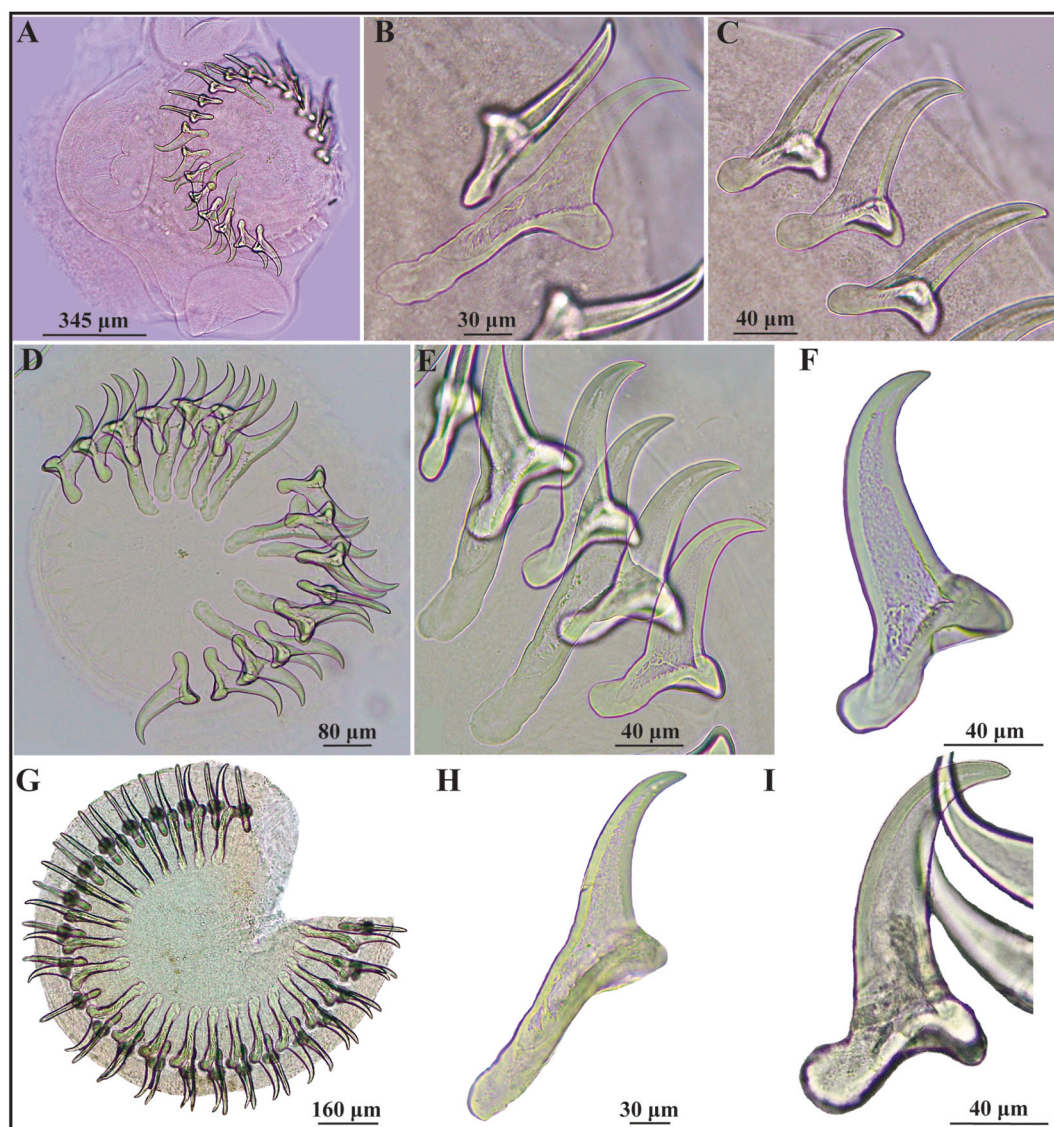


Fig. 2. (A–I). Rostellar hooks of metacestodes of *Taenia talicei* Dollfus (1960) (Cestoda: Taeniidae) in *Ctenomys* spp. (Rodentia: Ctenomyidae) from Chubut province, Argentina. (A–C). Scolex and rostellar hooks of fimbriocerci from *C. terraplen* Brook, González, Tomasco, Verzi and Martin from Corcovado (individual LIEB-M-1735). (A) Scolex showing rostellum with rostellar hooks, and suckers. (B) Large hook. (C) Small hooks. (D–F). Rostellar hooks of fimbriocerci from *C. terraplen* (individual LIEB-M-1736). (D) Rostellum showing alternating hooks, large and small. (E) Large and small hooks. (F) Small hook. Hoyer's mounting fluid. (G–I). Rostellum and rostellar hooks of fimbriocerci from *Ctenomys* aff. *C. terraplen* from Laguna El Cronómetro (individual LIEB-M-1809). (G) Rostellum showing the two crowns of alternating hooks, large and small. (H) Large hook. (I) Small hook. Berlese's mounting fluid.

Table 2

Comparison of morphometrics of metacestodes (single fimbriocerci) of *Taenia taliceii* Dollfus (1960) from intermediate hosts reported from South America (in μm). Abbreviations: n, number of measurements; SD, standard deviation.

Hosts	<i>Ctenomys terraplen</i> Brook, González, Tomasco, Verzi & Martin				<i>Ctenomys</i> aff. <i>C. terraplen</i>				<i>Ctenomys torquatus</i> Lichtenstein				<i>Ctenomys peruanus</i> Sanborn & Pearson				<i>Ctenomys australis</i> (Rusconi)				<i>Ctenomys talarum</i> Thomas				<i>Phyllotis xanthopygus</i> (Waterhouse)			
Reference	Present study				Present study				Dollfus (1960)				Voge (1954)				Rossin et al. (2010)				Rossin et al. (2010)				Gomez-Puerta (2017)			
Locality/ Country	Corcovado, Chubut province, Argentina				Laguna El Cronómetro, Chubut province, Argentina				Montevideo, Uruguay				Puno Department, Peru				Buenos Aires province, Argentina				Buenos Aires province, Argentina				Marangani District, Cusco, Peru			
Characters	N	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range				
LARGE HOOKS																												
Total length (TL)	24	268 \pm 15	230–280	33	263 \pm 13	230–280	2	–	245–247	–	–	–	–	190–220	50	236 \pm 2	230–243	50	243 \pm 3	240–248	14	228 \pm 1	218–237	–	–			
Total width (TW)	24	77 \pm 15	40–94	27	70 \pm 10	50–81	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	77 \pm 0.6	72–82	–	–			
Basal length (BL)	24	159 \pm 17	120–180	27	158 \pm 12	130–170	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	148 \pm 0.9	141–153	–	–			
Apical length (AL)	24	128 \pm 7	110–140	26	125 \pm 5	120–130	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	109 \pm 0.5	106–112	–	–			
Guard length (GL)	24	26 \pm 8	13–44	27	23 \pm 5	13–31	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	22 \pm 0.3	21–25	–	–			
Guard width (GW)	24	34 \pm 6	25–50	27	34 \pm 5	25–43	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	30 \pm 0.3	29–32	–	–			
Blade curvature (BC)	24	22 \pm 25	6–140	26	17 \pm 4	9–25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	17 \pm 0.3	15–18	–	–			
Handle width (HW)	24	29 \pm 4	18–37	27	30 \pm 6	19–38	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	19 \pm 0.5	15–22	–	–			
N° large hooks	3	25 \pm 1	24–26	4	25 \pm 2	23–27	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
SMALL HOOKS																												
Total length (TL)	49	152 \pm 20	88–180	32	159 \pm 11	130–180	2	–	154–160	–	–	–	–	120–140	50	154 \pm 4	150–160	50	161 \pm 3	158–168	14	147 \pm 0.6	144–155	–	–			
Total width (TW)	45	79 \pm 13	50–130	25	72 \pm 13	49–88	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	80 \pm 0.8	75–84	–	–			
Basal length (BL)	45	81 \pm 20	9–100	25	77 \pm 11	56–90	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	77 \pm 0.9	70–81	–	–			
Apical length (AL)	45	120 \pm 8	100–130	25	113 \pm 6	100–130	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	104 \pm 0.4	101–105	–	–			
Guard length (GL)	45	21 \pm 5	13–31	25	20 \pm 4	12–29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	22 \pm 0.4	21–25	–	–			
Blade curvature (BC)	45	16 \pm 4	7–24	24	16 \pm 6	6–25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	20 \pm 0.2	20–22	–	–			
N° small hooks	3	25 \pm 1	24–26	4	24 \pm 2	22–26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
N° total hooks	2	48	48	4	49 \pm 3	45–53	2	–	48–52	–	–	–	–	40–44	10	46 \pm 3	40–50	10	46 \pm 6	40–52	48	–	44–50	–	–			
Body length (mm)	11	7 \pm 2	2–10	–	–	–	2	6	–	–	–	–	–	9–15	10	20 \pm 8	9–35	10	11 \pm 5	5–20	–	9.6	6–12	–	–			
Maximum body width (mm)	12	7 \pm 0.4	3–4	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			
Suckers diameter	4	345 \pm 105	280–500	–	–	–	–	–	–	–	–	–	–	–	10	291 \pm 22	260–320	10	258 \pm 40	200–320	–	315	304–324	–	–			
Rostellum diameter	8	583 \pm 118	470–800	4	613 \pm 134	420–730	–	–	–	–	–	–	–	–	10	424 \pm 47	370–500	10	407 \pm 12	390–420	–	629	612–647	–	–			
Scolex length (+invaginated neck) (mm)	8	2.6 \pm 0.8	0.9–3.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.09	1.08–1.12	–	–			
Scolex width (+invaginated neck) (mm)	7	1.5 \pm 0.4	1–1.9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–			

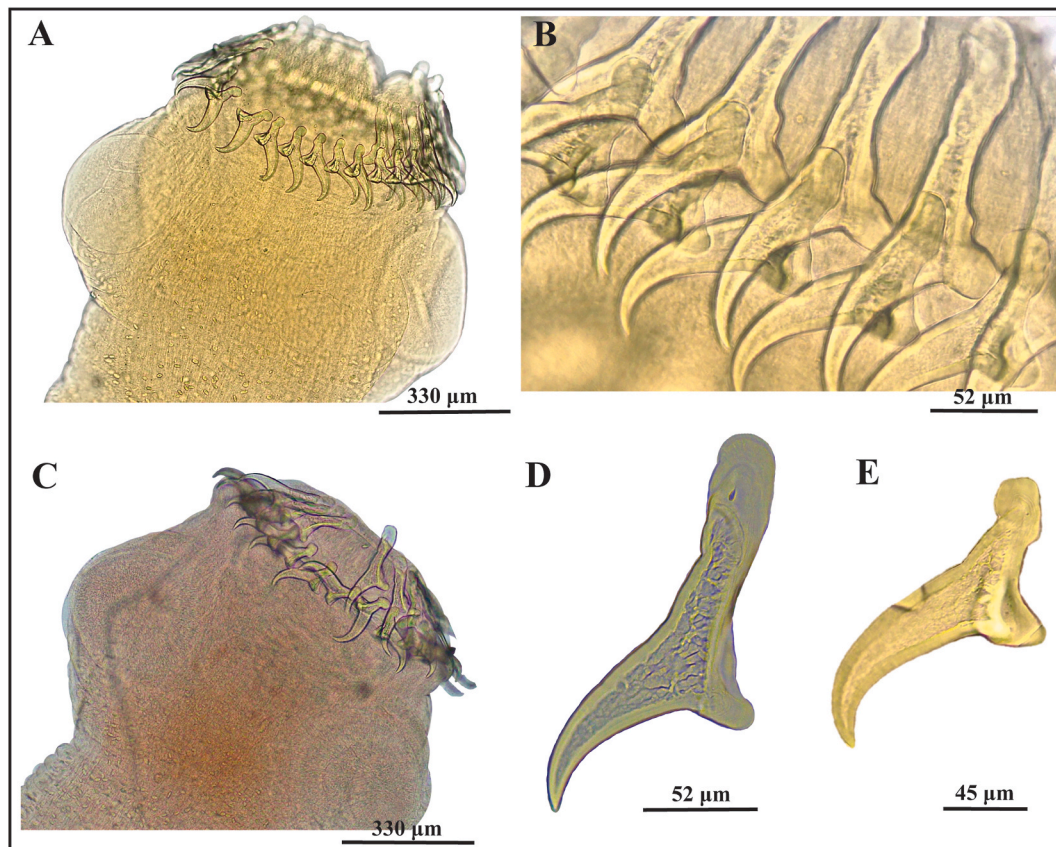


Fig. 3. (A–D). Rostellar hooks of strobilate adults of *Taenia talicei* Dollfus (1960) (Cestoda: Taeniidae) in *Lycalopex culpaeus* (Molina) (Carnivora: Canidae) from Chubut province, Argentina. (A–B). From Laguna La Zeta. (A) Scolex, showing rostellum with hooks, and suckers. (B) Alternating large and small hooks. (C) Small hooks. (D–F) From Los Alerces National Park. (D) Scolex, showing rostellum with hooks, and suckers. (E) Large hook. (F) Small hooks.

mm by 1280 ± 200 (940–1520) ($n = 6$) maximum wide. Proglottids acraspedote. Immature proglottids 430 ± 20 (500–900) ($n = 15$) long by 600 ± 90 (520–700) ($n = 15$) wide; mature proglottids 600 ± 50 (540–630) ($n = 15$) long by 890 ± 210 (690–1110) ($n = 15$) wide and gravid proglottids 830 ± 120 (630–1030) ($n = 35$) long by 1120 ± 250 (700–1380) ($n = 35$) wide. Distance from the lateral margin to the osmoregulatory canals in immature proglottids 110 ($n = 1$), not observed in mature proglottids; in gravid proglottids 100 ± 40 (80–130) ($n = 10$). Distance between osmoregulatory canals in immature proglottids 380 ± 100 (250–460) ($n = 20$), not observed in mature proglottids; in gravid proglottids 830 ± 160 (720–950) ($n = 14$).

The few strobili available were stained with conventional cestode staining methods, but without good results. Differentiation was not attained, precluding the observation of the genitalia or other internal organs and obtaining additional meristic data.

3.2.1. Taxonomic summary

Intermediate hosts: Tuco-tuco del bosque, *Ctenomys terraplen* Brook, González, Tomasco, Verzi and Martin; *Ctenomys* aff. *C. terraplen* (Rodentia: Ctenomyidae).

Definitive host: Andean fox, *Lycalopex culpaeus* (Molina) (Carnivora: Canidae).

Site of infection: in intermediate hosts, peritoneal cavity; in definitive host, small intestine.

Localities: Corcovado (43.54° S, 71.46° W) (metacestodes in *C. terraplen*); Laguna El Cronómetro (43.24° S, 71.09° W) (metacestodes in *Ctenomys* aff. *C. terraplen*); field near Laguna La Zeta (42.81° S, 71.38° W) and Los Alerces National Park (42.97° S, 71.58° W) (strobilate adults in *L. culpaeus*), Chubut province, Argentina.

Prevalence (P) and intensity of infection: In *C. terraplen*: P = 18.2

% (two out of eleven). The two specimens were infected with 34 and 45 monocephalic metacestodes, and two and three polycephalic metacestodes, respectively. *Ctenomys* aff. *C. terraplen*: the only infected specimen harboured 19 metacestodes (12 mono- and seven polycephalic metacestodes). In *Lycalopex culpaeus*: P = 40 % (two out of five Andean foxes infected with two and four strobilate adults, respectively).

Material deposited (vouchers): From *C. terraplen* and *Ctenomys* aff. *C. terraplen*: mono- and polycephalic metacestodes, LIEB-Pa-97. From *L. culpaeus*: strobilate adults, LIEB-Pa-96.

Host specimens deposited: LIEB-M-1735, LIEB-M-1736 (*C. terraplen*), LIEB-M-1809 (*Ctenomys* aff. *C. terraplen*), LIEB-M-1806, LIEB-M-1792 (*L. culpaeus*).

GenBank access numbers: PP738877, PP738957, PP738958 (cox1, fimbriocerci from *C. terraplen*, Corcovado); PP738968 (cox1, strobilate adult from *L. culpaeus*, Los Alerces National Park).

Comments.

The number, size and shape of the large and small hooks observed in our specimens were largely coincident with the data published by Dollfus (1960) and Rossin et al. (2004, 2010) on metacestodes of *T. talicei* from *Ctenomys* spp. Proliferating metacestodes reported by Voge (1954) from Peruvian rodents (including a species of *Ctenomys*), could be conspecific with *T. talicei* according to Rossin et al. (2010). All of these records fall within the range of measurements of the specimens studied herein (Table 2). Additionally, all the previous works indicated the peritoneal cavity as the site of infection in the intermediate hosts. Although Dollfus and Rossin et al. also found metacestodes in the liver, we did not find metacestodes in other organs.

Monocephalic and polycephalic metacestodes were found in the two localities. However, larger, more developed metacestodes and a greater proportion of polycephalic metacestodes were found in *Ctenomys* aff.

Table 3

Comparison of morphometrics of adult scoleces of *Taenia talicei* Dollfus (1960) from definitive hosts reported from South America (in μm). Abbreviations: n, number of measurements; SD, standard deviation.

Hosts	<i>Lycalopex culpaeus</i> (Molina) (natural host)			<i>Canis lupus familiaris</i> Linnaeus, 1758 (experimental host)			<i>L. culpaeus</i> (natural host)			<i>Lycalopex gymnocercus</i> Fischer (natural host)		
Reference	Present study			Rossin et al. (2010)			Ayala-Aguilar et al. (2013)			Sciocchia (2015)		
Locality/Country	Chubut province, Argentina			Buenos Aires province, Argentina			La Paz, Bolivia			Buenos Aires province, Argentina		
Characters	N	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range	n	Mean \pm SD	Range
LARGE HOOKS												
Total length (TL)	5	266 \pm 5	260–270	–	238	232–242	–	210	200–220	7	225	–
Total width (TW)	5	99 \pm 20	75–120	–	–	–	–	–	–	7	63	–
Basal length (BL)	5	172 \pm 11	160–180	–	–	–	–	–	–	–	–	–
Apical length (AL)	5	132 \pm 8	120–140	–	–	–	–	–	–	–	–	–
Guard length (GL)	5	26 \pm 4	20–31	–	–	–	–	–	–	–	–	–
Guard width (GW)	5	35 \pm 7	25–44	–	–	–	–	–	–	–	–	–
Blade curvature (BC)	5	17 \pm 3	13–19	–	–	–	–	–	–	–	–	–
Handle width (HW)	5	35 \pm 4	30–38	–	–	–	–	–	–	–	–	–
N° large hooks	1	24	–	–	–	–	–	–	–	–	–	–
SMALL HOOKS												
Total length (TL)	12	155 \pm 11	130–170	–	168	150–187	–	130	130–150	7	148	–
Total width (TW)	12	88 \pm 14	60–110	–	–	–	–	–	–	7	48	–
Basal length (BL)	12	91 \pm 5	81–96	–	–	–	–	–	–	–	–	–
Apical length (AL)	12	119 \pm 10	100–130	–	–	–	–	–	–	–	–	–
Guard length (GL)	12	22 \pm 7	10–38	–	–	–	–	–	–	–	–	–
Blade curvature (BC)	12	17 \pm 2	12–19	–	–	–	–	–	–	–	–	–
N° small hooks	1	24	–	–	–	–	–	–	–	–	–	–
N° total hooks	1	48	–	46	–	44–50	–	40	36–42	–	–	35–40
Body length (mm)	1	>470	–	–	268	273–391	–	–	5–20	–	–	–
Maximum body width (mm)	–	–	–	–	–	–	–	–	–	–	–	–
Suckers diameter	4	330 \pm 64	270–390	–	273	220–330	–	330	320–350	–	–	–
Rostellum diameter	4	583 \pm 125	430–690	–	168	150–187	–	–	–	–	–	–
Scolex length (mm)	4	0.87 \pm 0.04	0.82–0.9	–	0.63	0.45–0.86	–	0.58	0.57–0.59	–	–	–
Scolex width (mm)	4	0.90 \pm 0.18	0.75–1.11	–	0.1	0.71–1.2	–	1.03	0.82–1.11	–	–	–

C. terraplen from Laguna El Cronómetro (LEC). Moreover, we found significant differences ($p = 4.2e-05^{***}$) in the body size between the metacestodes from Corcovado and those from LEC. Such differences in the body size of the whole metacestodes may be attributed to the age of the infection. Indeed, the tuco-tucos from Corcovado presented smaller and probably not fully developed metacestodes, with few polycephalic metacestodes and little budding per vesicle, unlike the infection of the tuco-tuco from LEC where the metacestodes were much larger, and polycephalic metacestodes were more abundant, there was higher number of budding per vesicle and each fimbriocercus was much larger (twice as large) than the forms from Corcovado (Fig. 1B, D). This confirms what was observed by Voge (1954), who attributed differences in size among metacestodes from different hosts, as well as the relative size of the common vesicle and the proportion of multiple and simple fimbriocerci, to the age of the infection. According to Voge (1954), in recent infections simple cysticerci predominate whereas in older infections additional metacestodes proliferate from the bladder and multiple metacestodes increase in number. In these presumably fully grown metacestodes, the common bladder was usually much smaller or entirely absent, being replaced in some forms by a hardened tissue. Similarly, Rossin et al. (2010) registered monocephalic fimbriocerci in *C. australis*, which were twice as large as those found in *C. talarum* in the same study area and, in turn, all were larger than the measurements reported by Dollfus (1960). Rossin et al. (2010) also found cysticerci co-occurring with fimbriocerci and polycephalic metacestodes, what was interpreted as polymorphism in larval development of this species. Therefore, metacestodes of *T. talicei* seem to have a relatively wide range of hosts and morphometric variability, the latter not depending on the host species but on the age of the infection and the degree of development in which the metacestodes are found. This means that we should rely mainly on the shape, size and number of hooks rather than the measurements of the whole metacestode to help determine this taeniid species.

In regard to the strobilate adult, our identification was based mainly on the morphology and measurements of the rostellum, suckers and hooks, using the description by Rossin et al. (2010). Indeed, shape and measurements of hooks from strobilate adults were very similar to those recorded by Rossin et al. (2010) (from the experimental infection of a domestic dog in Argentina), but also to those found by Ayala-Aguilar et al. (2013) (as *Taenia* sp.) from a naturally infected Andean fox in Bolivia (Table 3, Figs. 1–4 in Rossin et al., 2010, Figs. 1–2 in Ayala-Aguilar et al., 2013).

3.3. Molecular and phylogenetic analysis

Based on morphological evidence we performed molecular analyses of fimbriocerci from *C. terraplen* and a strobilate adult from *L. culpaeus*. PCR amplification of *cox1*, mtDNA from fimbriocerci in the peritoneal cavity of *C. terraplen* produced six products of 371, 378, 282, 382, 380 and 373 bp, respectively. Amplification from the intestinal worm in the Andean fox produced two products, both of 375 bp. All these sequences showed 100 % similarity.

Regarding the phylogenetic tree, as outgroup we selected a species within the genus *Versteria* instead of a more distantly related species. This decision was based on prior observations indicating that the use of highly divergent outgroups resulted in excessive divergence, causing the collapse of the group of interest and hindering the resolution of phylogenetic relationships among the species. This approach preserved the phylogenetic structure within the group and allowed for a more robust interpretation of the results. Results indicated that the Hasegawa-Kishino-Yano model (HKY) (G + I) was the most appropriate. The percentage of trees in which the associated taxa clustered together is shown under the branches. Initial tree(s) for the heuristic search were obtained automatically by applying Neighbor-Joining and BioNJ algorithms to a matrix of pairwise distances estimated using the Maximum Composite Likelihood (MCL) approach, and then selecting the topology with

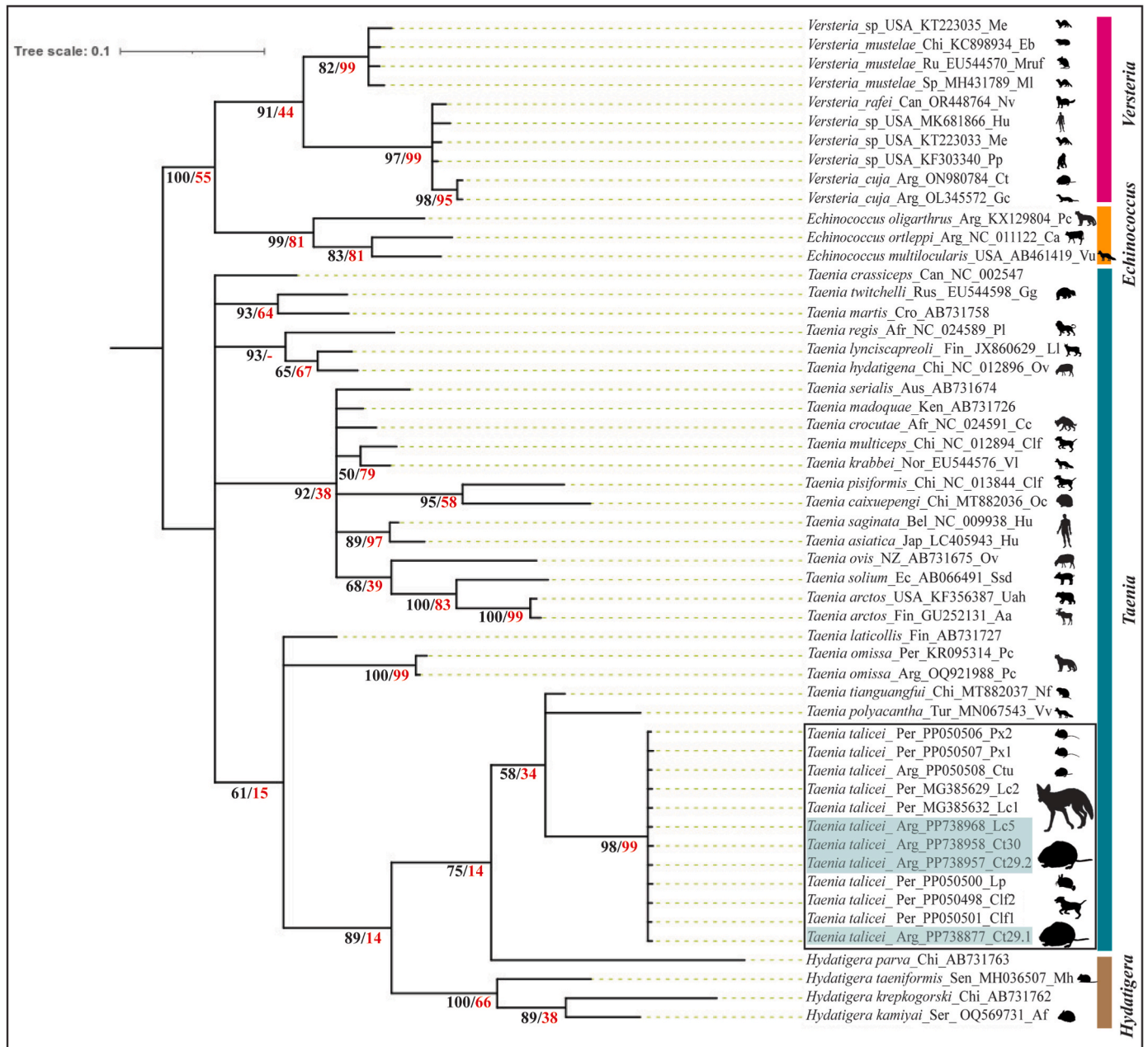


Fig. 4. Phylogenetic relationships of *Taenia talicei* Dollfus (1960) (Cestoda: Taeniidae) from the tuco-tuco *Ctenomys terraplen* Brook, González, Tomasco, Verzi and Martin (Arg.Ct29-30) and the Andean fox *Lycalopex culpaeus* (Molina) (Arg.Lc) from Chubut province, Argentina, with other Taeniidae genera, 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 under the internodes as BI (posterior probabilities, black)/ML (bootstrap value, red); 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). The subclade of *T. talicei* is indicated in the black rectangle and the sequences of the present study are highlighted in light blue; its hosts are indicated to be larger than the rest.

superior log likelihood value. A discrete gamma distribution was used to model evolutionary rate differences among sites (5 categories (+G, parameter = 0.15)). The tree is drawn to scale, with branch lengths measured in the number of substitutions per site (under the branches). This analysis involved 53 nucleotide sequences and there was a total of 200 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). Pairwise nucleotide sequence divergences were calculated using the Tamura-Nei model with a gamma setting of 0.5.

Then, we calculated the mean pairwise divergences for both intra- and interspecific variation. 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 + G + I) was the most appropriate.

Cox1 tree topologies resulting from the ML and BI analysis were identical, with BI producing higher branch support (Fig. 4). The genus *Taenia* formed a paraphyletic group. The isolates obtained in this study appeared in the phylogenetic tree closely related to a group of species from Peru and Argentina, composed of *Taenia* sp. from *L. culpaeus*

(MG385632.1, 99.73 % similarity, Peru); *T. talicei* from *L. culpaeus* (MG385629.2, 99.73 % similarity, Peru) and from *C. l. familiaris* (PP050501.1, PP050498.1, 100 % similarity, Peru); *T. talicei* from *Ctenomys tuconax* (Argentina), *Phyllotis xanthopygus* (Peru), and *Lagidium peruanum* (Peru), with genetic distances of 0.00 (Table 4). The clade composed of *T. talicei* formed the closely related group and had the lowest genetic distance (0.09) (Table 4), with *Taenia tianguangfui* Fan et al. (2014). The highest genetic distance was observed with *Taenia pisiformis* (Bloch, 1780) Gmelin, 1790 (0.26) (Table 4).

4. Discussion

Our analyses confirmed not only that the metacestodes from *Ctenomys* spp. and the Andean fox are the same (100 % similarity between

cox1 sequences), but they also belong to the species *T. talicei*, with genetic distances of 0.00 between the sequences deposited in GenBank and ours (Table 4). We can thus confirm the presence of *T. talicei* in north-western Patagonia, Argentina, with a life-cycle involving the subterranean rodents of the genus *Ctenomys* (i.e., *C. terraplen* and *Ctenomys* aff. *C. terraplen*) as intermediate hosts, and the Andean fox *L. culpaeus* as definitive host.

Taenia talicei shares with *T. polyacantha* Leuckart, 1856 the type of larva (fimbriocercus), rodents as intermediate hosts and canids as definitive hosts. However, its distribution is in the northern hemisphere (Abuladze, 1964; Verster, 1969; Rausch and Fay, 1988). On the other hand, the very low genetic distance with *T. tianguangfui* is also remarkable, this species was described from a metacestode (cysticercus) in a rodent, *Neodon fuscus* (Buchner), but the strobilate adult or its

Table 4

Intra- and interspecific pairwise divergence within genus *Taenia* in the complete sequences of mitochondrial cox1 gene. The new data are in bold.

<i>Taenia</i> species	Geographical distribution	Intraspecific pairwise distance	Interspecific pairwise distance
Intraspecific			
<i>Taenia talicei</i> _Arg_PP738877_Ct29.1	Patagonia Argentina	0.00	
<i>Taenia talicei</i> _Arg_PP738957_Ct29.2	Patagonia Argentina	0.00	
<i>Taenia talicei</i> _Arg_PP738958_Ct30	Patagonia Argentina	0.00	
<i>Taenia talicei</i> _Arg_PP738968_Lc5	Patagonia Argentina	0.00	
<i>Taenia talicei</i> _Per_MG385632_Lc1	Peru	0.00	
<i>Taenia talicei</i> _Per_MG385629_Lc2	Peru	0.00	
<i>Taenia talicei</i> _Arg_PP050508_Ctu	North-western Argentina	0.00	
<i>Taenia talicei</i> _Per_PP050507_Px1	Peru	0.00	
<i>Taenia talicei</i> _Per_PP050506_Px2	Peru	0.00	
<i>Taenia talicei</i> _Per_PP050501_Clf1	Peru	0.00	
<i>Taenia talicei</i> _Per_PP050498_Clf2	Peru	0.00	
<i>Taenia talicei</i> _Per_PP050500_Lp	Peru	0.00	
Interspecific			
<i>T. talicei</i> vs.	China		0.09
<i>Taenia tianguangfui</i> _Chi_MT882037_Nf			
<i>Taenia polyacantha</i> _Tur_MN067543_Vv	Türkiye		0.11
<i>Taenia hydatigena</i> _Chi_NC_012896_Ov	China		0.14
<i>Taenia crassiceps</i> _Can_NC_002547	Canada		0.16
<i>Taenia laticollis</i> _Fin_AB731727	Finland		0.16
<i>Taenia regis</i> _Afr_NC_024589_Pl	Africa		0.16
<i>Taenia twitchelli</i> _Ru_EU544598_Gg	Russia		0.16
<i>Taenia lynciscapreoli</i> _Fin_JX860629_Ll	Finland		0.16
<i>Versteria mustelae</i> _Chi_EU544570_Mruf	China		0.16
<i>Taenia crocutae</i> _Afr_NC_024591_Cc	Africa		0.17
<i>Taenia serialis</i> _Aus_AB731674	Australia		0.17
<i>Versteria mustelae</i> _Ru_EU544570_Mruf	Russia		0.17
<i>Versteria</i> _sp_USA_KF303340_Pp	USA		0.17
<i>Versteria rafei</i> _Can_OR448764_Nv	Canada		0.17
<i>Taenia martis</i> _Cro_AB731758	Croatia		0.18
<i>Versteria mustelae</i> _Sp_MH431789_Ml	Spain		0.18
<i>Versteria</i> _sp_USA_KT223035_Me	USA		0.18
<i>Versteria</i> _sp_USA_KT223033_Me	USA		0.18
<i>Versteria</i> _sp_USA_MK681866_Hu	USA		0.18
<i>Versteria cuja</i> _Arg_OL345572_Gc	Argentina		0.18
<i>Versteria cuja</i> _Arg_ON980784_Ct	Argentina		0.18
<i>Taenia madoquae</i> _Ken_AB731726	Kenya		0.19
<i>Taenia multiceps</i> _Chi_NC_012894_Clf	China		0.19
<i>Taenia saginata</i> _Bel_NC_009938_Hu	Belgium		0.19
<i>Hydatigera parva</i> _Sen_MH036507_Mh	Senegal		0.19
<i>Taenia asiatica</i> _Jap_LC405943_Hu	Japan		0.20
<i>Taenia krabbei</i> _Nor_JX507239_Vl	Norway		0.20
<i>Echinococcus orteppi</i> _Arg_NC_011122_Ca	Argentina		0.20
<i>Taenia arctos</i> _Fin_KF356387_Uah	Finland		0.21
<i>Taenia caixuepengi</i> _Chi_MT882036_Oc	China		0.21
<i>Taenia omissa</i> _Arg_OQ921988_Pc	Argentina		0.21
<i>Taenia omissa</i> _Per_KR095314_Pc	Peru		0.21
<i>Taenia ovis</i> _NZ_AB731675_Ov	New Zealand		0.21
<i>Hydatigera krepkogorski</i> _Chi_AB731762	China		0.21
<i>Hydatigera taeniformis</i> _Bel_AB745096	Belgium		0.21
<i>Echinococcus multilocularis</i> _USA_AB461419_Vu	USA		0.21
<i>Taenia arctos</i> _Fin_GU252131_Aa	Finland		0.22
<i>Hydatigera kamiyai</i> _Ser_OQ569731_Af	Serbia		0.22
<i>Echinococcus oligarthrus</i> _Arg_KX129804_Pc	Argentina		0.22
<i>Taenia solium</i> _Ecu_AB066491_Ssd	Ecuador		0.24
<i>Taenia pisiformis</i> _Chi_NC_013844_Clf	China		0.26

definitive host are still unknown. In addition, the distribution is very distant (China) (Fan et al., 2014; Wu et al., 2021). It can also be observed in the phylogeny that the *T. talicei* group together with *T. tianguangfui*, *T. polyacantha* and the *Hydatigera* species have a recent appearance with respect to evolutionary time.

Taenia talicei is the first described species of *Taenia* that can be considered endemic from South America (Rossin et al., 2010) and, up to now, records of the species are far more frequent from its intermediate hosts than from definitive ones. The former are mainly small rodents, preferably of the genus *Ctenomys* that inhabit Argentina, Bolivia and Uruguay (*C. australis*, *C. talarum*, *C. tuconax*, *C. terraplen*, *C. aff. C. terraplen*, *C. opimus*, *C. torquatus*), whereas in Peru this taeniid was found not only in tuco-tucos (*C. peruanus*) but also in other rodents, including larger ones such as the northern viscacha *Lagidium peruanum* (available data in GenBank, see Table 1). The metacestodes found in *Phyllotis xanthopygus* from Peru by Gomez-Puerta (2017) could reasonably be attributed to this species, based on morphology, hosts, site of infection, and geographic location. Therefore, we can not rule out that other rodent species are involved in the cycle in this study area (i.e., Patagonia). However, other species of cricetid rodents (belonging to genera *Abrothrix*, *Geoxus*, *Irenomys*) from the area where we collected *T. talicei* have been examined, but with negative results.

Until now, there was no published information on the natural definitive hosts of *T. talicei*. In Argentina, Rossin et al. (2004) obtained the strobilate adult through the experimental infection of a domestic dog with metacestodes from naturally infected *C. talarum* and *C. australis*. Rossin et al. (2010) speculated that the natural definitive hosts could be wild carnivores inhabiting the area where metacestodes were collected (south-eastern Buenos Aires province), such as the Geoffroy's cat *Leopardus geoffroyi* d'Orbigny and Gervais, or the Pampas fox *Lycalopex gymnocercus* Fischer, both known to prey on *C. talarum* and *C. australis*. Some years later Scioscia (2015, PhD Thesis) found strobilate adult cestodes that were identified as *Taenia* sp. in Pampas foxes from the southern departments of Villarino, Patagones and Tandil (Buenos Aires province). A prevalence of 25 % (n = 80) and mean intensity of 4.9 was found. Scioscia (2015) inferred that the species in question could be *T. talicei* according to the number, size and morphology of the rostellar hooks, but in the absence of mature proglottids in good condition the identity of the species could not be confirmed. The measurements of rostellar hooks provided by Scioscia (2015) are quite close to the mean values of the species (Table 3) and, looking at the photographs presented in her work, it is possible to infer that it is indeed *T. talicei*.

Thus, the few available evidence indicates that the natural definitive hosts of this taeniid species in South America would be canids: the Andean fox *L. culpaeus*, at least in localities from the Andean region and the South American Transition zone (sensu Morrone et al., 2022). Uncertainties or possible erroneous identifications of *Taenia* in both *L. culpaeus* and *L. gymnocercus* (Ayala-Aguilar et al., 2013; Oyarzún-Ruiz et al., 2020; Gomez-Puerta et al., unpublished data), and the Pampas fox *L. gymnocercus* in the Chacoan subregion and Andean region (Scioscia, 2015) should be mentioned. Regarding the Andean fox, it is distributed from Colombia through the Andes Mountains to the southern tip of South America, where it reaches the Atlantic coast towards the east (Chébez et al., 2014). It is an opportunistic predator whose diet fluctuates throughout the year according to the availability of resources, including small mammals -mainly rodents, among them *Ctenomys*-, lagomorphs, ungulates, birds, reptiles, arthropods and carrion (Pia et al., 2003; Zapata et al., 2005, 2007; Walker et al., 2007; Chébez et al., 2014). The heterogeneous distribution of the different rodent species that serve as prey for the Andean fox throughout its distribution might explain the presence of the parasite in such a number of intermediate hosts in Argentina, Bolivia and Peru.

Among more than 30 species of endoparasites reported from the Andean fox throughout its distribution (Fugassa, 2020), the lack of previous reports of *T. talicei* is rather striking. There are, however, reports of strobilate adults of other members of *Taenia* that were attributed

to non-endemic species such as *T. hydatigena* Pallas, 1766 and *T. multiceps* Leske, 1780 (Moro, 1998; Oyarzún-Ruiz et al., 2020) or remained without specific identification (*Taenia* sp.) (Ayala-Aguilar et al., 2013). The finding of Moro (1998) was not accompanied by illustrations that make inferences about the identity of the species involved. Instead, the findings of Ayala-Aguilar et al. (2013) and Oyarzún-Ruiz et al. (2020) included photographs and, based on the morphology, host, and geographic localization it is likely that such findings correspond actually to *T. talicei*. Unfortunately, such reports did not include genetic data that we could use in our analyses.

Thus, the few available evidence indicates that the natural definitive hosts of this taeniid species in South America would be canids. It is confirmed for the Andean fox *L. culpaeus*, at least in localities from the Andean region and the South American Transition zone (sensu Morrone et al., 2022) (this work, Gomez-Puerta et al., unpublished data). And we should also mention the uncertain, unconfirmed records or possible erroneous identifications (discussed above) in both *L. culpaeus* (Ayala-Aguilar et al., 2013; Oyarzún-Ruiz et al., 2020), and *L. gymnocercus* in the Andean region (Oyarzún-Ruiz et al., 2020) and Chacoan subregion (Scioscia, 2015). There are no evidence, so far, that *T. talicei* would be present in felids.

Regarding whether *T. talicei* is a potentially zoonotic species, Rossin et al. (2010) pointed out that since the species can develop in domestic dogs, and *Ctenomys* species can be found in urban or semi-urban environments, the possibility exists of establishing synanthropic cycles that include the dog as definitive host, making it relevant as a route of human exposure. However, to date there is no confirmation that the species affects humans.

This study is the first report of the natural life cycle of an endemic species of *Taenia* from South America. It integrates molecular and ecological aspects of the interaction between a fox, a subterranean rodent and a parasitic tapeworm. Future studies could show this tapeworm to be more widespread geographically, probably infecting more species, both intermediate and definitive.

CRediT authorship contribution statement

Estefanía Bagnato: Writing – review & editing, Writing – original draft, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Juan José Lauthier:** Writing – review & editing, Software, Methodology, Formal analysis. **Federico Brook:** Writing – review & editing, Resources, Methodology, Data curation. **Gabriel Mario Martín:** Writing – review & editing, Resources, Methodology. **María Celina Digiani:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Data curation, Conceptualization.

Funding

This work was supported by the Agencia Nacional de Promoción de la Investigación, el Desarrollo Tecnológico y la Innovación, Argentina (E.B., PICT N°, 2019-00569), (M.C.D., PICT N°, 2019-03535).

Declarations of interest

none.

Acknowledgements

The authors specially thank Turcato family, Ricardo (estate owner), M. Dromaz, I. Powell and family, J. Cignetti and G. Bauer for help in the field. Darío Balcazar, Marina Ibáñez Shimabukuro and Micaela Ricuzzi (Centro de Estudios Parasitológicos y de Vectores-CEPAVE-CCT-CONICET La Plata, Buenos Aires) for molecular analyses (extraction, purification and amplification of ADN). The authors are grateful to the

anonymous reviewers who helped to improve the paper. To the Dirección Fauna y Flora Silvestre from Ministerio de Agricultura, Ganadería, Industria y Comercio del Chubut for collecting permissions. GMM thanks E. Watkins and M. Simeon for economic support.

References

- Abuladze, K.I., 1964. Principles of Cestodology, vol. IV. Akademii Nauk USSR, Moscow, Russia.
- Arrabal, J.P., Arce, L.F., Macchiaroli, N., Kamenetzky, L., 2023. Ecological and molecular associations between Neotropical wild felids and *Taenia* (Cestoda: Taeniidae) in the Atlantic forest: a new report for *Taenia omissa*. *Parasitol. Res.* 122, 2999–3012.
- Arrabal, J.P., Avila, H.G., Rivero, M.R., Camicia, F., Salas, M.M., Costa, S.A., Nocera, C.G., Rosenzvit, M.C., Kamenetzky, L., 2017. *Echinococcus oligarthrus* in the subtropical region of Argentina: first integration of morphological and molecular analyses determines two distinct populations. *Vet. Parasitol.* 240, 60–67. <https://doi.org/10.1016/j.vetpar.2017.03.019>.
- Ayala-Aguilar, G., Nallar, R., Alandia-Robles, E., Alandia-Robles, R., Mollericon, J.L., Ayala-Crespo, G., 2013. Parasitos intestinales del zorro andino (*Lycalopex culpaeus*, Canidae) en el Valle Acero Marka de los Yungas (La Paz, Bolivia). *Ecol. en Bol. 48*, 104–108.
- Bagnato, E., Acuña, F., Brook, F., Martin, G.M., Barbeito, C.G., Digiani, M.C., 2023. Natural life cycle of *Versteria cuja* (Taeniidae) in Argentina and histopathology of metacystodiasis in intermediate hosts. *Parasitology* 150, 488–497. <https://doi.org/10.1017/S0031182023000215>.
- Bagnato, E., Gilardoni, C., Martin, G.M., Digiani, M.C., 2022. A new species of *Versteria* (Cestoda: Taeniidae) parasitizing *Galictis cuja* (Carnivora: Mustelidae) from Patagonia, Argentina: morphological and molecular characterization. *Int. J. Parasitol. Parasites Wildl.* 19, 68–77. <https://doi.org/10.1016/j.ijppaw.2022.07.007>.
- Bowles, J., Blair, D., McManus, D.P., 1992. Genetic variants within the genus *Echinococcus* identified by mitochondrial DNA sequencing. *Mol. Biochem. Parasitol.* 54, 165–174. [https://doi.org/10.1016/0166-6851\(92\)90109-W](https://doi.org/10.1016/0166-6851(92)90109-W).
- Bowles, J., McManus, D.P., 1993a. Molecular variation in *Echinococcus*. *Acta Trop.* 53, 291–305. [https://doi.org/10.1016/0001-706X\(93\)90035-A](https://doi.org/10.1016/0001-706X(93)90035-A).
- Bowles, J., McManus, D.P., 1993b. Rapid discrimination of *Echinococcus* species and strains using a polymerase chain reaction-based RFLP method. *Mol. Biochem. Parasitol.* 57, 231–239. [https://doi.org/10.1016/0166-6851\(93\)90199-8](https://doi.org/10.1016/0166-6851(93)90199-8).
- Brook, F., González, B., Tomasco, I.H., Verzi, D.H., Martin, G.M., 2024. Within the forest: a new species of *Ctenomys* (Rodentia: Ctenomyidae) from northwestern Patagonia. *J. Mammal.* 20, 1–18. <https://doi.org/10.1093/jmammal/gyae101>.
- Bush, A.O., Lafferty, K.D., Lotz, J.M., Shostak, A.W., 1997. Parasitology Meets Ecology on Its Own Terms: Margolis et al. Revisited. *J. Parasitol.* 83, 575. <https://doi.org/10.2307/3284227>.
- Catalano, S., Lejeune, M., Verocai, G.G., Duignan, P.J., 2014. First report of *Taenia arctos* (Cestoda: Taeniidae) from grizzly (*Ursus arctos horribilis*) and black bears (*Ursus americanus*) in North America. *Parasitol. Int.* 63, 389–391. <https://doi.org/10.1016/j.parint.2013.12.012>.
- Catalano, S., Bâ, K., Diouf, N.D., Léger, E., Verocai, G.G., Webster, J.P., 2019. Rodents of Senegal and their role as intermediate hosts of *Hydatigera* spp. (Cestoda: Taeniidae). *Parasitology* 146, 299–304. <https://doi.org/10.1017/S0031182018001427>.
- Chévez, J.C., Pardiñas, U., Teta, P., 2014. *Mamíferos Terrestres. Patagonia sur de Argentina y Chile*. Vázquez Mazzini Editores. Buenos Aires.
- Chervy, L., 2002. The terminology of larval cestodes or metacystodes. *Syst. Parasitol.* 52, 1–33. <https://doi.org/10.1023/A:1015086301717>.
- Darriba, D., Taboada, G.L., Doallo, R., Posada, D., 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nat. Methods* 9, 772. <https://doi.org/10.1038/nmeth.2109>, 772.
- Dereeper, A., Audic, S., Claverie, J.-M., Blanc, G., 2010. BLAST-EXPLORER helps you building datasets for phylogenetic analysis. *BMC Evol. Biol.* 10, 1–6. <https://doi.org/10.1186/1471-2148-10-8>.
- Dereeper, A., Guignon, V., Blanc, G., Audic, S., Buffet, S., Chevenet, F., Dufayard, J.-F., Guindon, S., Lefort, V., Lescot, M., Claverie, J.-M., Gascuel, O., 2008. Phylogeny.fr: robust phylogenetic analysis for the non-specialist. *Nucleic Acids Res.* 36, W465–W469. <https://doi.org/10.1093/nar/gkn180>.
- Dollfus, R., 1960. Cystique d'un nouveau *Taenia*, de la cavité péritonéale d'un *Ctenomys* (Rodentia) del Uruguay. *Arch. la Soc. Biol. Montevideo* 25, 47–51.
- Erol, U., Sarimehmetoglu, O., Utuk, A.E., 2021. Intestinal system helminths of red foxes and molecular characterization *Taeniid* cestodes. *Parasitol. Res.* 120, 2847–2854.
- Fan, Y.L., Lou, Z.Z., Li, L., Yan, H.B., Han, X.M., Li, J.Q., Liu, C.N., Yang, Y.R., McManus, D.P., Jia, W.Z., 2014. Preliminary study on taxonomic status of cysticerci from *Microtus fuscus* in Qinghai-Tibet Plateau of China. *Chinese Vet. Sci./Zhongguo Shouyi Kexue* 44, 789–793.
- Fournier-Chambrillon, C., Torres, J., Miquel, J., André, A., Michaux, J., Lemberger, K., Carrera, G.G., Fournier, P., 2018. Severe parasitism by *Versteria mustelae* (Gmelin, 1790) in the critically endangered European mink *Mustela lutreola* (Linnaeus, 1761) in Spain. *Parasitol. Res.* 117, 3347–3350. <https://doi.org/10.1007/s00436-018-6043-z>.
- Fugassa, M.H., 2020. Updated checklist of helminths found in terrestrial mammals of Argentine Patagonia. *J. Helminthol.* 94, 1–56. <https://doi.org/10.1017/S0022149X20000462>.
- Ganzorig, S., Gardner, S.L., 2024. Eucestoda. In: Gardner, S.L., Gardner, S.A. (Eds.), *Concepts in Animal Parasitology*. Zea Books, Lincoln, Nebraska, United States, pp. 251–261. <https://doi.org/10.32873/unl.dc.ciap18>.
- Gardner, S.L., Botero-Cañola, S., Aliaga-Rossel, E., Dursahinhan, A.T., Salazar-Bravo, J., 2021. Conservation status and natural history of *Ctenomys*, tuco-tucos in Bolivia. *Therya* 12, 15–36. <https://doi.org/10.12933/therya-21-1035>.
- Goldberg, T.L., Gendron-Fitzpatrick, A., Deering, K.M., Wallace, R.S., Clyde, V.L., Lauck, M., Rosen, G.E., Bennett, A.J., Greiner, E.C., O'Connor, D.H., 2014. Fatal metacystode infection in orangutan caused by unknown *Versteria* species. *Emerg. Infect. Dis.* 20, 109–113. <https://doi.org/10.3201/eid2001.131191>.
- Gomez-Puerta, L.A., 2017. Hallazgo de fimbriocercos de *Taenia* sp. (Cestoda: Taeniidae) en el ratón orejón de ancas amarillas (*Phyllotis xanthopygus*). *Rev. Peru. Biol.* 24, 319–322. <https://doi.org/10.15381/rpb.v24i3.13909>.
- Gomez-Puerta, L.A., Alarcon, V., Pacheco, J., Franco, F., Lopez-Urbina, M.T., Gonzalez, A.E., 2016. Molecular and morphological evidence of *Taenia omissa* in pumas (*Puma concolor*) in the Peruvian Highlands. *Brazilian J. Vet. Parasitol. Jaboticabal* 25, 368–373.
- Haukisalmi, V., Lavikainen, A., Laaksonen, S., Meri, S., 2011. *Taenia arctos* n. sp. (Cestoda: Cyclophyllidae: Taeniidae) from its definitive (brown bear *Ursus arctos* Linnaeus) and intermediate (moose/elk *Alces* spp.) hosts. *Syst. Parasitol.* 80, 217–230. <https://doi.org/10.1007/s11230-011-9324-9>.
- Haukisalmi, V., Konyaev, S., Lavikainen, A., Isomursu, M., Nakao, M., 2016. Description and life-cycle of *Taenia lynciscapreoli* sp. n. (Cestoda, Cyclophyllidae). *ZooKeys* 584, 1–23.
- Hoberg, E.P., Jones, A., Rausch, R.L., Eom, K.S., Gardner, S.L., 2000. A phylogenetic hypothesis for species of the genus *Taenia* (Eucestoda: Taeniidae). *J. Parasitol.* 86, 89–98. [https://doi.org/10.1645/0022-3395\(2000\)086\[0089:APHFSO\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2000)086[0089:APHFSO]2.0.CO;2).
- Hoberg, E.P., 2006. Phylogeny of *Taenia*: species definitions and origins of human parasites. *Parasitol. Int.* 55, 23–30. <https://doi.org/10.1016/j.parint.2005.11.049>.
- Huelsbeck, J.P., Ronquist, F., 2001. MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17, 754–755. <https://doi.org/10.1093/bioinformatics/17.8.754>.
- Jeon, H.-K., Kim, K.-H., Eom, K.S., 2007. Complete sequence of the mitochondrial genome of *Taenia saginata*: comparison with *T. solium* and *T. asiatica*. *Parasitol. Int.* 56, 243–246. <https://doi.org/10.1016/j.parint.2007.04.001>.
- Jia, W.-Z., Yan, H.-B., Guo, A.-J., Zhu, X.-Q., Wang, Y.-C., Shi, W.-G., Chen, H.-T., Zhan, F., Zhang, S.-H., Fu, B.-Q., Littlewood, D.T.J., Cai, X.-P., 2010. Complete mitochondrial genomes of *Taenia multiceps*, *T. hydatigena* and *T. pisiformis*: additional molecular markers for a tapeworm genus of human and animal health significance. *BMC Genom.* 11, 447. <https://doi.org/10.1186/1471-2164-11-447>.
- Lavikainen, A., Haukisalmi, V., Lehtinen, M.J., Henttonen, H., 2008. A phylogeny of members of the family Taeniidae based on the mitochondrial *cox1* and *nad1* gene data. *Parasitology* 135, 1457–1467. <https://doi.org/10.1017/S003118200800499X>.
- Lavikainen, A., Haukisalmi, V., Lehtinen, M.J., Laaksonen, S., Holmström, S., Isomursu, M., Oksanen, A., Meri, S., 2010. Mitochondrial DNA data reveal cryptic species within *Taenia krabbei*. *Parasitol. Int.* 59, 290–293. <https://doi.org/10.1016/j.parint.2010.03.003>.
- Lavikainen, A., Iwaki, T., Haukisalmi, V., Konyaev, S.V., Casiraghi, M., Dokuchaev, N.E., Galimberti, A., Halajian, A., Henttonen, H., Ichikawa-Seki, M., Itagaki, T., Krivopalov, A.V., Meri, S., Morand, S., Näreaho, A., Olsson, G.E., Ribas, A., Terefe, Y., Nakao, M., 2016. Reappraisal of *Hydatigera taeniaeformis* (Batsch, 1786) (Cestoda: Taeniidae) *sensu lato* with description of *Hydatigera kamiyai* n. sp. *Int. J. Parasitol.* 46, 361–374. <https://doi.org/10.1016/j.ijpara.2016.01.009>.
- Le, T.H., Blair, D., Agatsuma, T., Humair, P.F., Campbell, N.J.H., Iwagami, M., Littlewood, D.T.J., Peacock, B., Johnston, D.A., Bartley, J., Rollinson, D., Herniou, E.A., Zarlenga, D.S., McManus, D.P., 2000. Phylogenies inferred from mitochondrial gene orders - a cautionary tale from the parasitic flatworms. *Mol. Biol. Evol.* 17, 1123–1125. <https://doi.org/10.1093/oxfordjournals.molbev.a026393>.
- Lee, L.M., Wallace, R.S., Clyde, V.L., Gendron-Fitzpatrick, A., Sibley, S.D., Stuchin, M., Lauck, M., O'Connor, D.H., Nakao, M., Lavikainen, A., Hoberg, E.P., Goldberg, T.L., 2016. Definitive hosts of *Versteria* tapeworms (Cestoda: Taeniidae) causing Fatal infection in North America. *Emerg. Infect. Dis.* 22, 707–710. <https://doi.org/10.3201/eid2204.151446>.
- Lehman, B., Leal, S.M., Procop, G.W., O'Connell, E., Shaik, J., Nash, T.E., Nutman, T.B., Jones, S., Braunthal, S., Shah, S.N., Cruise, M.W., Mukhopadhyay, S., Banzon, J., 2019. Disseminated metacystode *Versteria* species infection in Woman, Pennsylvania, USA. *Emerg. Infect. Dis.* 25, 1429–1431. <https://doi.org/10.3201/eid2507.190223>.
- Loos-Frank, B., 2000. An up-date of Verster's (1969) 'Taxonomic revision of the genus *Taenia* Linnaeus' (Cestoda) in table format. *Syst. Parasitol.* 45, 155–184. <https://doi.org/10.1023/A:1006219625792>.
- Moro, P.L., 1998. Intestinal parasites of the grey fox (*Pseudalopex culpaeus*) in the central Peruvian Andes. *J. Helminthol.* 72, 87–89. <https://doi.org/10.1017/S0022149X00001048>.
- Morrone, J.J., Escalante, T., Rodríguez-Tapia, G., Carmona, A., Arana, M., Mercado-Gómez, J.D., 2022. Biogeographic regionalization of the Neotropical region: new map and shapefile. *An. Acad. Bras. Cienc.* 94, 1–5. <https://doi.org/10.1590/0001-3765202222011167>.
- Nakao, M., Lavikainen, A., Iwaki, T., Haukisalmi, V., Konyaev, S., Oku, Y., Okamoto, M., Ito, A., 2013. Molecular phylogeny of the genus *Taenia* (Cestoda: Taeniidae): Proposals for the resurrection of *Hydatigera* Lamarck, 1816 and the creation of a new genus *Versteria*. *Int. J. Parasitol.* 43, 427–437. <https://doi.org/10.1016/j.ijpara.2012.11.014>.
- Nakao, M., McManus, D.P., Schantz, P.M., Craig, P.S., Ito, A., 2007. A molecular phylogeny of the genus *Echinococcus* inferred from complete mitochondrial genomes. *Parasitology* 134, 713–722. <https://doi.org/10.1017/S0031182006001934>.
- Nakao, M., Okamoto, M., Sako, Y., Yamasaki, H., Nakaya, K., Ito, A., 2002. A phylogenetic hypothesis for the distribution of two genotypes of the pig tapeworm

- Taenia solium* worldwide. *Parasitology* 124, 657–662. <https://doi.org/10.1017/S0031182002001725>.
- Nakao, M., Xiao, N., Okamoto, M., Yanagida, T., Sako, Y., Ito, A., 2009. Geographic pattern of genetic variation in the fox tapeworm *Echinococcus multilocularis*. *Parasitol. Int.* 58, 384–389. <https://doi.org/10.1016/j.parint.2009.07.010>.
- Oyarzún-Ruiz, P., Di Cataldo, S., Cevidanes, A., Millán, J., González-Acuña, D., 2020. Endoparasitic fauna of two South American foxes in Chile: *Lycalopex culpaeus* and *Lycalopex griseus*. *Rev. Bras. Parasitol. Veterinária* 29, 1–15. <https://doi.org/10.1590/s1984-29612020055>.
- Pia, M.V., López, M.S., Novaro, A.J., 2003. Effects of livestock on the feeding ecology of endemic culpeo foxes (*Pseudalopex culpaeus smithersi*) in central Argentina. *Rev. Chil. Hist. Nat.* 76, 313–321. <https://doi.org/10.4067/S0716-078X2003000200015>.
- R Core Team, 2024. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Rausch, R.L., Fay, F.H., 1988. Postoncospherical development and cycle of *Taenia polyacantha* Leuckart, 1856 (Cestoda: Taeniidae). First part. *Ann. Parasitol. Hum. comparée* 63, 263–277. <https://doi.org/10.1051/parasite/1988634263>.
- Rossin, A., Malizia, A.I., Denegri, G.M., 2004. The role of the subterranean rodent *Ctenomys talarum* (Rodentia: Octodontidae) in the life cycle of *Taenia taeniaeformis* (Cestoda: Taeniidae) in urban environments. *Vet. Parasitol.* 122, 27–33. <https://doi.org/10.1016/j.vetpar.2004.03.001>.
- Rossin, M.A., Timi, J.T., Hoberg, E.P., 2010. An endemic *Taenia* from South America: validation of *T. talicei* Dollfus, 1960 (Cestoda: Taeniidae) with characterization of metacestodes and adults. *Zootaxa* 2636, 49. <https://doi.org/10.11646/zootaxa.2636.1.4>.
- RStudio Team, 2024. RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. <http://www.rstudio.com/>.
- Scioscia, N.P., 2015. Parásitos del zorro gris, *Lycalopex gymnocercus* de la provincia de Buenos Aires. Universidad Nacional de Mar del Plata (PhD Thesis).
- Shanebeck, K.M., Bennett, J., Green, S.J., Lagrue, C., Presswell, B., 2024. A new species of *Versteria* (Cestoda: Taeniidae) parasitizing *Neogale vison* and *Lontra canadensis* (Carnivora: Mustelidae) from Western Canada. *J. Helminthol.* 98, e4. <https://doi.org/10.1017/S0022149X23000895>.
- Sikes, R.S., Gannon, W.L., Mammalogists, A.C., of, U.C., of, the A.S., 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *J. Mammal.* 92, 235–253. <https://doi.org/10.1644/10-MAMM-F-355.1>.
- Tamura, K., Stecher, G., Kumar, S., 2021. MEGA11: molecular evolutionary genetics analysis Version 11. *Mol. Biol. Evol.* 38, 3022–3027. <https://doi.org/10.1093/molbev/msab120>.
- Terefe, Y., Hailemariam, Z., Menkir, S., Nakao, M., Lavikainen, A., Haukisalmi, V., Iwaki, T., Okamoto, M., Ito, A., 2014. Phylogenetic characterisation of *Taenia* tapeworms in spotted hyenas and reconsideration of the “Out of Africa” hypothesis of *Taenia* in humans. *Int. J. Parasitol.* 44, 533–541. <https://doi.org/10.1016/j.ijpara.2014.03.013>.
- Verster, A., 1969. A taxonomic revision of the Genus *Taenia* Linnaeus, 1758 s. str. *Onderstepoort J. Vet. Res.* 36, 3–58.
- Voge, M., 1954. Exogenous proliferation in a larval taeniid (Cestoda: Cyclophyllidae) obtained from the body cavity of Peruvian rodents. *J. Parasitol.* 40, 411. <https://doi.org/10.2307/3273887>.
- Walker, R.S., Novaro, A.J., Perovic, P., Palacios, R., Donadio, E., Lucherini, M., Pia, M., Lopez, M.S., 2007. Diets of three species of Andean carnivores in high-altitude deserts of Argentina. *J. Mammal.* 88, 519–525.
- Wu, Y.-D., Li, L., Fan, Y.-L., Ni, X.-W., Ohiolei, J.A., Li, W.-H., Li, J.-Q., Zhang, N.-Z., Fu, B.-Q., Yan, H.-B., Jia, W.-Z., 2021. Genetic evolution and Implications of the mitochondrial genomes of two newly identified *Taenia* spp. in rodents from Qinghai-Tibet plateau. *Front. Microbiol.* 12, 1–10. <https://doi.org/10.3389/fmicb.2021.647119>.
- Yamasaki, H., Morishima, Y., Sugiyama, H., Okamoto, M., 2021. Current situation of human *Taenia asiatica* taeniosis in Japan. *Parasitol. Int.*, 102340 <https://doi.org/10.1016/j.parint.2021.102340>.
- Zapata, S.C., Travaini, A., Delibes, M., Martínez-Peck, R., 2005. Food habits and resource partitioning between grey and culpeo foxes in southeastern Argentine Patagonia. *Stud. Neotrop. Fauna Environ.* 40, 97–103. <https://doi.org/10.1080/01650520500129836>.
- Zapata, S.C., Travaini, A., Ferreras, P., Delibes, M., 2007. Analysis of trophic structure of two carnivore assemblages by means of guild identification. *Eur. J. Wildl. Res.* 53, 276–286. <https://doi.org/10.1007/s10344-007-0095-1>.
- Zhao, F., Ma, J.-Y., Cai, H.-X., Su, J.-P., Hou, Z.-B., Zhang, T.-Z., Lin, G.-H., 2014. Molecular identification of *Taenia mustelae* cysts in subterranean rodent plateau zokors (*Eospalax baileyi*). *Zool. Res.* 35, 313–318. <https://doi.org/10.13918/j.issn.2095-8137.2014.313>.
- Brook, F. (in review). Ecomorfología y distribución del género *Ctenomys* (Rodentia: Ctenomyidae) en el noroeste de Chubut. Universidad Nacional de la Patagonia “San Juan Bosco”, Sede Esquel (PhD Thesis).