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Sección Especial

LOS MAMÍFEROS COMO HOSPEDADORES DE PARÁSITOS

Artículo

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NATIVE AND EXOTIC SMALL MAMMALS AS HOSTS OF *Hydatigera taeniaeformis* SENSU STRICTO LARVAE ON PIG FARMS OF CENTRAL ARGENTINA: A STUDY OF PREVALENCE AND PHYLOGENETIC RELATIONSHIPS

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ABSTRACT. Small mammals, including those inhabiting human-modified habitats, transmit zoonotic diseases such as cysticercosis. This disease is caused by *Cysticercus fasciolaris*, the larval form of species within the *Hydatigera taeniaeformis* s.l. group. While the life cycle of these flatworms is well understood, certain aspects of their phylogeny remain unknown. Studies in Europe, Asia, and Africa suggest that the species *Hydatigera taeniaeformis* s.s. exclusively infects small mammals of the family Muridae. However, no studies have been conducted in the Americas until now. In this study, small mammals were captured on 18 pig farms in the province of Buenos Aires throughout a year. Necropsies of captured individuals were performed, and the presence of cysts was recorded. The prevalence of cysticercosis was analyzed for the entire assemblage, with species as the explanatory variables. Species-specific prevalence was also modeled, considering season and type of farm as the explanatory variables. Cysts were collected from *Akodon azarae*, *Oligoryzomys flavescens*, *Rattus novergicus*, and *Rattus rattus* identified through molecular techniques, comparing their DNA sequences with those stored in GenBank for phylogenetic hypothesis. A total of 460 small mammals were analyzed, including the introduced species *R. novergicus*, *R. rattus*, and *M. musculus* and the native species *A. azarae*, *O. flavescens*, *Oxymycterus rufus*, *Didelphis albiventris*, and *Lutreolina crassicaudata*. The prevalence of cysticercosis was similar between species, and it showed a seasonal association in *R. norvegicus* and *A. azarae*. Phylogenetic analysis confirmed the presence of *Hydatigera taeniaeformis* s.s. in cricetids, suggesting a recent spillover event associated with European colonization in the Americas.

RESUMEN. PEQUEÑOS MAMÍFEROS NATIVOS Y EXÓTICOS COMO HOSPEDADORES DE LARVAS DE *Hydatigera taeniaeformis* SENSU STRICTO EN GRANJAS PORCINAS DEL CENTRO DE ARGENTINA: ESTUDIO DE SU PREVALENCIA Y RELACIONES FILOGENÉTICAS. Los pequeños

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mamíferos, incluidos aquellos que habitan en hábitats modificados por la especie humana, transmiten enfermedades zoonóticas como la cisticercosis. Esta enfermedad es causada por *Cysticercus fasciolaris*, la forma larvaria de especies pertenecientes al complejo *Hydatigera taeniaeformis* s.l. Aunque se conoce bien el ciclo biológico de estos platelmintos, algunos aspectos de su filogenia aún son desconocidos. Algunos estudios realizados en Europa, Asia y África sugieren que la especie *Hydatigera taeniaeformis* s.s. infecta exclusivamente a pequeños mamíferos de la familia Muridae. Sin embargo, hasta ahora no se habían realizado estudios en el Continente Americano. En este estudio se capturaron pequeños mamíferos en 18 granjas porcinas de la provincia de Buenos Aires a lo largo de un año. Se realizaron necropsias de los individuos capturados y se registró la presencia de cisticercos. Se calculó y modeló la prevalencia de cisticercosis para todo el ensamble, con las especies como variables explicativas. También se modeló la prevalencia especie-específica, considerando la estación y el tipo de granja como variables explicativas. Se colectaron cisticercos de *Akodon azarae*, *Oligoryzomys flavescens*, *Rattus novergicus* y *Rattus rattus* para su análisis filogenético, y se identificaron mediante técnicas moleculares, que compararon sus secuencias de ADN con las almacenadas en *GenBank*. Se analizó un total de 460 pequeños mamíferos, incluidas las especies introducidas *R. novergicus*, *R. rattus* y *M. musculus* y las especies autóctonas *A. azarae*, *O. flavescens*, *Oxymycterus rufus*, *Didelphis albiventris* y *Lutreolina crassicaudata*. La prevalencia de cisticercosis fue similar entre especies y mostró una asociación estacional en *R. norvegicus* y *A. azarae*. El análisis filogenético confirmó la presencia de *Hydatigera taeniaeformis* s.s. en cricétidos, lo que sugiere un evento de *spillover* reciente asociado a la colonización europea de las Américas.

Palabras clave: Ecology, infection, livestock, parasitology, rodents, tapeworms.
Key words: Ecología, ganado, infección, parasitología, roedores, tenias.

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INTRODUCTION

Some small mammals are involved in the transmission of many different diseases, whether of viral, bacterial, protozoan, or helminthic origin (Gegúndez & Lledó 2005; Luis et al. 2013; Morand et al. 2015), representing a health risk to both wild and domestic animals and humans (Meerburg et al. 2009; Backhans & Fellström 2012).

Infestation by small mammals is common in human-modified habitats, such as poultry, dairy, and pig farms, due to management practices and the availability of resources such as food, shelter, and water (Gómez Villafañe et al. 2001; Gómez Villafañe & Busch 2007; Lovera et al. 2015, 2019; Montes De Oca et al. 2020). On these farms, both exotic and native rodents, as well as opossum species, have been found carrying several pathogens such as viruses, bacteria, protozoa, ectoparasites, and helminths (Webster & Macdonald 1995; Daniels et al. 2003; Kijlstra et al. 2008; Perez Carusi et al. 2009; Backhans & Fellström 2012; Lovera et al. 2017; Alonso et al. 2020).

Particularly, rodents are hosts of many helminth parasites and are mentioned as main pathogen reservoirs in human-modified habitats, including zoonotic helminth species (Hancke et al. 2011; Himsworth et al. 2013; Morand et al. 2015; Fitte et al. 2017; Hancke & Suárez 2017), such as flatworms implicated in cysticercosis (Hancke et al. 2011; Martínez et al. 2013; Fitte et al. 2017; Hancke & Suárez 2017, 2018). Cysticercosis is a disease caused by different species of parasitic flatworms, as they belong to the *Hydatigera taeniaeformis* sensu lato (Batsch 1786). The cestode uses felids and carnivores as definitive hosts, while the metacestode form (larval forms also named *Cysticercus fasciolaris*, cyst form, or *Strobilocercus fasciolaris*, when it shows strobilization) can be found parasitizing mainly rodents, which act as intermediate hosts (Abuladze 1970; Hoberg 2002; Lavikainen et al. 2016). Species belonging to this species group are implicated in human infection, with reported cases in Argentina, Japan, and Sri Lanka (Sterba & Barus 1976; Ekanayake et al. 1999).

The life cycle of *Hydatigera taeniaeformis* s.l. is well known, but aspects of its biology remain unsolved. One of the main issues concerns the phylogenetic relationships between the species of the genus *Hydatigera* and their relationship with their intermediate hosts. Lavikainen et al. (2016) have proposed the existence of three clades of parasitic flatworms included among the haplotypes of *Hydatigera taeniaeformis* s.l. studied: *H. taeniaeformis* s.s. (clade A), *H. kamiyai* (clade B), and *Hydatigera* sp. (clade C). In turn, the authors state that infection by *H. taeniaeformis* s.s. is restricted to members of the family Muridae, while *H. kamiyai* is found in both Muridae and Cricetidae. Only specimens from Europe, Africa, and Asia have been considered in that study. In the Americas, only Mello et al. (2018) reported *H. taeniaeformis* s.s. in a *Guerlinguetus ingrami* (Rodentia: Sciuridae) in Brazil; so, the reported cases of flatworms in small mammals on this continent, whether introduced or native, are very poor. Furthermore, although cysts of *H. taeniaeformis* have been reported in *Rattus norvegicus, R. rattus, Akodon azarae,* and *Oligoryzomys flavescens* (Miño et al. 2013; Fitte et al. 2017; Hancke & Suárez 2017), they were only studied by molecular analysis in *R. norvegicus* (Martínez et al. 2013).

The aims of this work are (1) to report the prevalence of cysts of *H. taeniaeformis* s.l. on native and exotic wild small mammals on pig farms in central Argentina; (2) to provide the first molecular analysis of the infection of cysts of *H. taeniaeformis* s.l. on native and exotic small mammals in Argentina; and (3) to describe the phylogenetic relationships between local *H. taeniaeformis* s.l. species.

MATERIALS AND METHODS

Study area

This study took place on 18 pig farms located in the counties of Exaltación de la Cruz, Las Heras, Marcos Paz, and San Andrés de Giles, in the northeast of the province of Buenos Aires (**Fig.** 1). This area belongs to the Rolling Pampas complex of the Pampas Ecoregion, characterized by a temperate climate with a mean annual precipitation of 1 014 mm and a mean annual temperature of 17.4 °C (Portela et al. 2009; Morello et al. 2012; Pérez et al. 2015). The landscape is dominated by crop fields and rangelands, with scattered towns and cities, and farms, mainly poultry, pigs, dairy, and feedlots (Fraschina et al. 2014). Seven extensive and 11 intensive pig farms were sampled. Intensive and extensive pig farms in the study area mainly refer to the number of animals and the organization of their production. On intensive pig farms, the number of pigs was 2 550 ± 1 565 (EE), and there is a sequential organization of the production in indoor pens with limited movement and strict control of feeding and growth. On the extensive pig farms, 250 ± 288 pigs were raised in indoor or outdoor pens, and a more relaxed control of growth and feeding was found (Montes De Oca et al. 2020).

Trapping survey

Live trapping of small mammals was conducted from spring 2014 to winter 2016. Each pig farm was sampled seasonally for one year. Small mammals were captured using cage-live traps (15 x 16 x 31 cm), baited with a mix of meat and carrot, and Sherman traps (8 x 9 x 23 cm), baited with a mix of peanut butter, bovine fat, and rolled oat. Both types of traps were placed together along transects and distributed in different environments within the farms (e.g., vegetated areas, food storage sheds, pig sheds, drainage channels, etc.). In each trapping session, the location of the traps was the same. Traps were active for three consecutive nights and were checked daily during the mornings. All captured individuals were sexed, weighed, measured, and identified to species level. For a full description of the assemblage of small mammals on these studied farms, please see Montes De Oca et al. (2020).

Extraction and conservation of cyst samples

Individuals captured were humanly sacrificed after a deep anaesthesia made with an intramuscular injection of ketamine-acepromazine. Rodents were sacrificed by cervical dislocation and opossums by an injection of euthanasic (pentobarbital sodium/phenytoin). The captured animals were handled in accordance with the National Animal Protection Law 14 346 and its amendments, as well as the Ethics Committee of the National Council for Scientific and Technical Research (CONICET 2005) and the Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education (Sikes 2016). The experimental procedure was approved by the Institutional Commission for the Care and Use of Laboratory Animals, Facultad de Ciencias Exactas y Naturales (experimental project n°125/2019, CICUAL-FCEN). A necropsy was conducted on each captured individual. Parasitic larval capsules of metacestodes (cysticerci) of *C. fasciolaris* were searched on the surface of the liver, and their presence or absence was recorded (**Fig.** 2 photo). Cysticerci samples belonging to one *Rattus rattus* [host identification code (ID): MP1308, S. A. de Giles], one *Akodon azarae* (ID: MP 1330, S. A. de Giles), and one *Oligoryzomys flavescens* (ID: MP1380, Las Heras) were preserved in ethanol at 96% for morphological and molecular confirmation.

Parasitological index

The prevalence of infection was calculated for each small mammal species, as well as the prevalence for each season and type of pig farm (intensive or extensive), using a Bayesian approach (Speybroeck et al. 2013). To perform the Bayesian estimation, a prior uniform probability distribution of the sensibility (SE = 1) and specificity (SP = 1) was used due to the lack of information. The prior probability of the dispersion parameter of Beta distribution was set to improve the prevalence estimation, assuming the range of the dispersion parameter (φ) as double the prevalence's standard deviation for the different species (Wan et al. 2014), based on previous studies (*Rattus norvegicus*, Hancke et al. 2011; Lovera et al. 2017; Hancke & Suárez 2018; *Rattus rattus*, Fitte et al. 2017, *Mus musculus*, Fitte et al. 2017; Hancke & Suárez 2018; *Akodon azarae*, Miño et al. 2013; Lovera et al. 2017; *Oligoryzomys flavescens*, Hancke & Suárez 2018). The mean of the maximum and minimum values of the known standard deviation of native species was used for *Didelphis albiventris*, *Lutreolina crassicaudata*, and *Oxymycterus ruffus*. The 95% credibility interval was informed for each

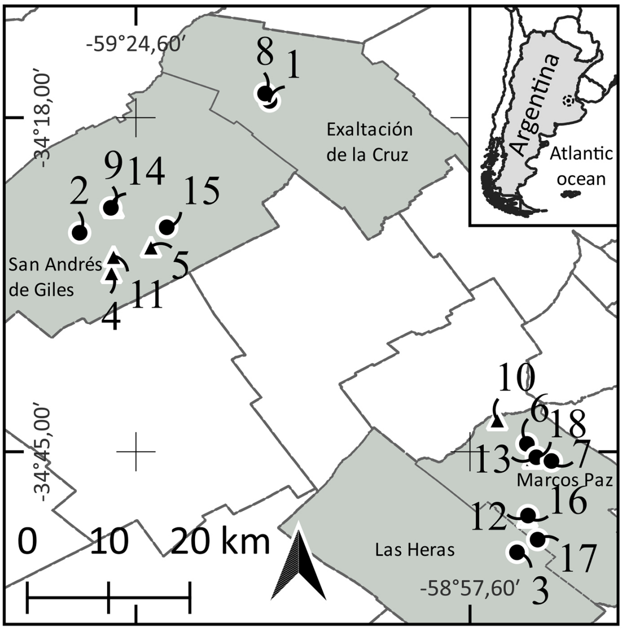

Fig. 1. Distribution of sampled pig farms (1-18) located in the counties of Exaltación de la Cruz, Las Heras, Marcos Paz, and San Andrés de Giles, province of Buenos Aires, Argentina, between spring 2014 to winter 2016. Triangle: intensive pig farms. Circle: extensive pig farms.

case. Prevalences were estimated using JAGS (Plummer 2003), through the package prevalence (Devleesschauwer 2022) in the R software (R Core Team 2020). Moreover, a Generalized Linear Model using a Bayesian approach was used to assess the influence of the small mammal species on the overall prevalence (Inchausti 2023), with a Bernoulli family and a logit link function. The small mammal species with at least one individual infected were used as the explanatory variable. To use informative priors, a prior sensibility test was performed. To assess the convergence of the Markov Chain Monte Carlo (MCMC) performed, three chains with 3 000 iterations were run, with a post-warmup draw of 2 000 and a thin of three. Furthermore, a Hierarchical Model was run to assess the effect of the seasons and the type of pig farm on the species-specific prevalence of those species with at least one capture in each of the four seasons, using the season and the type of pig farm as the explanatory variables and the farm as a random factor. The prior sensibility test and convergence assessment were made as in the Generalized Linear Model. These models were performed using the package *brms* (Bürkner 2021) and plotted using the package *bayesplot* (Gabry et al. 2019) in R (R Core Team 2020) and R Studio (R Studio Team 2019) software. Also, the expected occurrence of the infection of cysts of *H. taeniaeformis* s.l. on the studied farms was evaluated according to the mean small mammal trap success threshold value reported by Lovera et al. (2017).

Morphological and molecular identification of cysts

For identification, a parasite specimen was chosen from a host species for which no records were available. Morphological examination was conducted by observing the parasite structures with a Nikon loupe, model SMZ800, at 4X.

The molecular characterization was conducted through amplification and sequence for two ADN regions: a fragment of the mitochondrial subunit cytochrome oxidase I (COI) and the ribosomal region 28S. Genomic DNA was extracted from samples using Kit DNAeasy Tissue (Qiagen, USA) following the protocol of the manufacturer.

Amplification of the fragment COI was achieved by the forward COI1 5'-TTTTTTGGGCATCCTGAGGTTTAT-3' and reverse COI2 5'-AAAGAAAGAACATAATGAAAATG-3' primers (Bowles et al. 1992) with the following PCR conditions: initial denaturation at 95 °C for 5 min followed by 40 cycles of denaturation (94 °C for 1 min), annealing (50 °C for 1 min) and extension (72 °C for 1 min) and a final extension step at 72 °C for 10 min. Amplification of the region 28S was performed using forward JB10 5'-GATIACCCGCTGAACTTAAGCATAT-3' and reverse JB9 5'-GCTOCATTCACAAACACCCCGACTC-3' primers with the following PCR conditions: an initial denaturation at 95 °C for 5 min followed by 35 cycles of denaturation (94 °C for 30 s), anneling (59 °C for 30 s), and extension (72 °C for 1 min), and a final extension step at 72 °C for 10 min. Each amplicon expected size was corroborated and visualized on agarose gel at 1%. The fragments were purified with ExoI-FastAP enzymes (ThermoFisher Scientific). Finally,

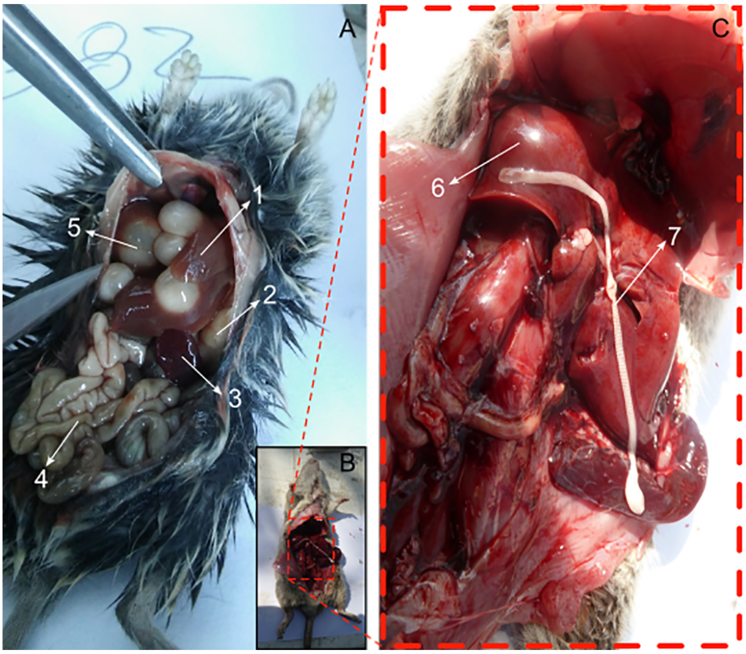

Fig. 2. A. Cysticerci of *Hydatigera taeniaeformis* s.s. in an individual of *Akodon azarae*; 1: outer liver surface, 2: stomach, 3: spleen, 4: small intestine, 5: Cysticercus. **B.** General view of a parasitized *Rattus norvegicus*. **C.** Strobilocercus deployed by hand over the liver surface, 6: inflamed infected liver, 7: metacestode deployed manually by the researcher (strobilocercus). Individuals were captured in the county of Marcos Paz, province of Buenos Aires, Argentina, between spring 2014 and winter 2016.

PCR products were sequenced in an ABI 3500xl DNA analyzer (Applied Biosystem, Unidad de Secuenciación INTA, Castelar, Buenos Aires, Argentina).

Molecular analyses

A total of 26 COI sequence fragments and 13 of 28 S sequence fragments from previously published isolates from other host-geographical regions and other species from the genus *Hydatigera*, *Taenia*, and *Echinococcus* were obtained from the Genebank database to observe the genetic distances (Tables S3 and S4). The haplotypes described by Lavikainen et al. (2016) were included among the COI sequences to analyze the genetic distances with the sequences of this study and to classify them in the previously proposed molecular clades A (*H. taeniaeformis* s.s), B (*H. kamiyai*) and C (*Hydatigera* sp.). COI sequences of cysts of *H. taeniaeformis* s.l. from *Rattus norvegicus* (Martínez et al. 2013) were also included. All sequences were aligned using CustalW from the program Bioedit. The substitution model was selected by an Akaike Information Criterion (AIC) through the program JModelTest2 (Darriba et al. 2012) resulting in the GTR + G model for COI and the HKY + I model for 28S.

A Bayesian inference (BI) method was used through the Beast v 1.8.4 (Drummond et al. 2012) program to evaluate the phylogenetic relationships with a starting tree randomly generated under a coalescent constant size model as tree prior, a relaxed clock model of uncorrelated lognormal distribution for both regions (Drummond et al. 2006), and using the substitution models identified previously. Chain length was set to 50 million generations for the MCMC simulations, and sampling trees were taken every 5 000 generations. Log files were analyzed in Tracer v.1.5.0 (Rambaut & Drummond 2009), and the effective sample sizes (> 200) were used to evaluate MCMC convergence within chains. TreeAnnotator 1.8.4 package from the BEAST program was used to summarize the output trees with a burn-in parameter setting of 1 000. Trees were visualized with the FigTree 1.3 program (Rambaut 2014).

RESULTS

A total of 475 small mammals were captured, of which 460 were analyzed, with a trapping effort of 2 360 cage live traps-night and 2 463 Sherman traps-night. Small mammals captured belonged to eight species: three to the introduced muridae *Rattus norvegicus* (n: 278), *Rattus rattus* (n: 15), and *Mus musculus* (n: 68); three to the native sigmodontinae, *Akodon azarae* (n: 51), *Oligoryzomus flavescens* (n: 2) and *Oxymycterus rufus* (n: 6); and two to the native didelphidae *Didelphis albiventris* (n: 32) and *Lutreolina crassicaudata* (n: 8). For a full description of the assemblage of small mammals in these pig farms, see Montes De Oca et al. (2020).

Cysticerci infection

In the pig farms studied, all three species of Muridae were infected by cysts of *H. taeniaformis* s.l., two species of

Table 1

Prevalence of *H. taeniformis* larvae in the captured species on pig farms located in the counties of Exaltación de la Cruz, Las Heras, Marcos Paz, and San Andrés de Giles, province of Buenos Aires, Argentina, between spring 2014 and winter 2016. n: total number of individuals examined. P: prevalence in percentage (95% credibility interval). The number of farms with any infected individuals is given in parenthesis in the species column. *Rn: Rattus norvegicus, Rr: Rattus rattus, Mm: Mus musculus, Aa: Akodon azarae, Of: Oligoryzomys flavescens, Lc: Lutreolina crassicaudata, Da: Didelphis albiventris, Or: Oxymycterus rufus.*

Species	Overall		Season								Type of pig farm			
			Summer		Fall		Winter		Spring		Intensive		Extensive	
	n	P	n	P	n	P	n	P	n	P	n	P	n	P
Rn(12/18)	278	13.0 (9.3-17.1)	70	6.0 (1.7-12.5)	54	22.4 (12.4-34.3)	57	13.0 (9.4-17.2)	97	17.7 (10.9-26.0)	114	15.0 (9.2-22.2)	165	12.2 (7.7-17.6)
Rr(1/18)	15	6.6 (0.2-22.7)	7	14.1 (0.4-44.7)	3	0,00	3	0,00	2	0,00	9	0,00	6	16.3 (0.5-51.1)
Mm(3/18)	68	4.5 (1.0-10.4)	28	7.3 (1.0-19.1)	14	0,00	10	0,00	16	6.5 (0.2-22.0)	29	3.6 (0.1-12.4)	39	5.3 (0.7-14.4)
Aa(3/18)	51	9.7 (3.3-18.9)	2	0,00	20	10.8 (1.8-26.7)	16	0,00	13	23.9 (6.1-48.7)	32	9.9 (2.3-22.1)	19	11.4 (1.8-28.6)
Of(1/18)	2	44.5 (2.3-94.6)	0	-	0	-	2	44.5 (2.3-94.6)	0	-	0	-	2	44.5 (2.3-94.6)
Lc(1/18)	8	12.4 (0.4-40.6)	3	0,00	1	100.00*	0	-	4	0,00	8	12.4 (0.4-40.6)	0	-
Da(1/18)	32	0,00	22	0,00	7	0,00	3	0,00	-	0,00	7	0,00	25	0,00
Or(0/18)	6	0,00	0	-	4	0,00	2	0,00	0	-	1	0,00	5	0,00

*Is not possible to calculate the credibility interval due to the low number of individuals.

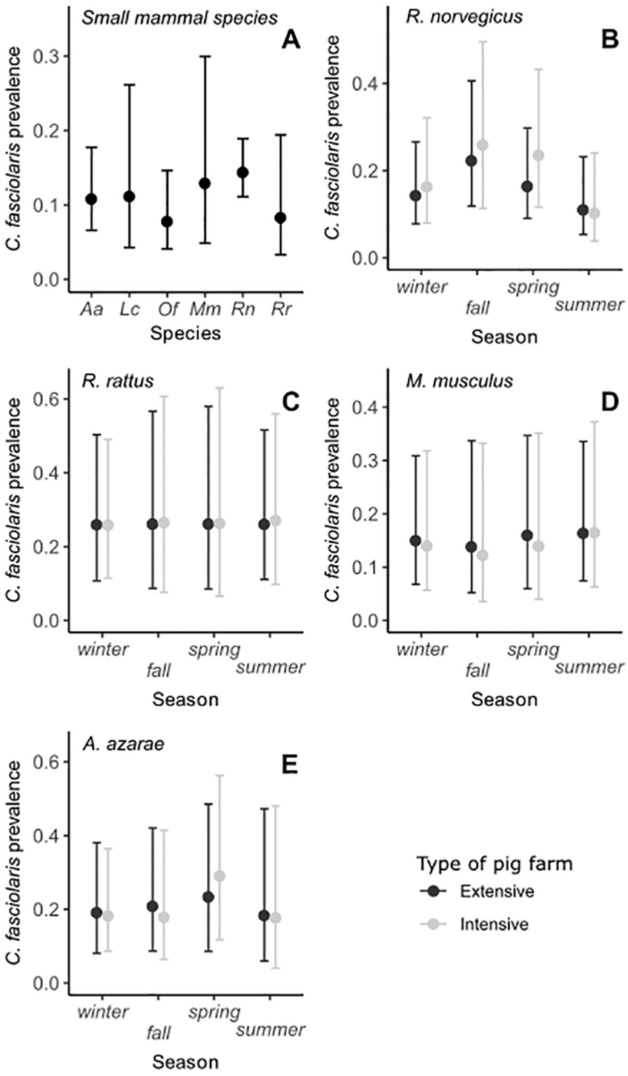

Fig. 3. Prevalence values of (A) Bayesian GLM for the overall prevalence, as a function of small mammal species in the assemblage; hierarchical models for (B) prevalence of *R. rattus*; (C) prevalence of *R. norvegicus*; (D) prevalences of *M. musculus* and (E) *A. azarae*, as function of the seasons and the type of pig farms. Samplings of small mammals were carried out between spring 2014 and winter 2016 in the counties of Exaltación de la Cruz, Las Heras, Marcos Paz, and San Andrés de Giles, province of Buenos Aires, Argentina.

Sigmodontinae, and a single didelphid (**Table** 1). Cysticerci infection was observed in small mammals in 15 of the 18 farms studied. Moreover, farms showed co-occurrence of infected native and exotic small mammals except for one farm, where only one native species (two individuals of *A. azarae*) showed Cysricerci infection (Table S1). All infected small mammal species showed similar prevalence values, with the mean value slightly higher in *R. norvegicus* than in the rest of the species (**Fig**. 3A). *Rattus norvegicus* showed Cysticerci infection in both extensive and intensive pig farms, along all seasons (**Table** 1) and on most farms (Table S1). Also, it showed a higher prevalence during the fall in both farm types (**Fig**. 3B). In turn, infected *R. rattus* were observed only in an extensive pig farm in the summer (Table S1). However, the model showed no association between the prevalence and the season or the type of farm (**Fig**. 3C). Infected *M. musculus* were observed in three of both extensive and intensive pig farms during the summer and spring (**Table** 1), but as for *R. rattus*, the model showed no association between the prevalence and the season or the type of farm (**Fig**. 3D). The native *A. azarae* carrying cyst of *H. taeniaeformis* s.l. was captured in both extensive

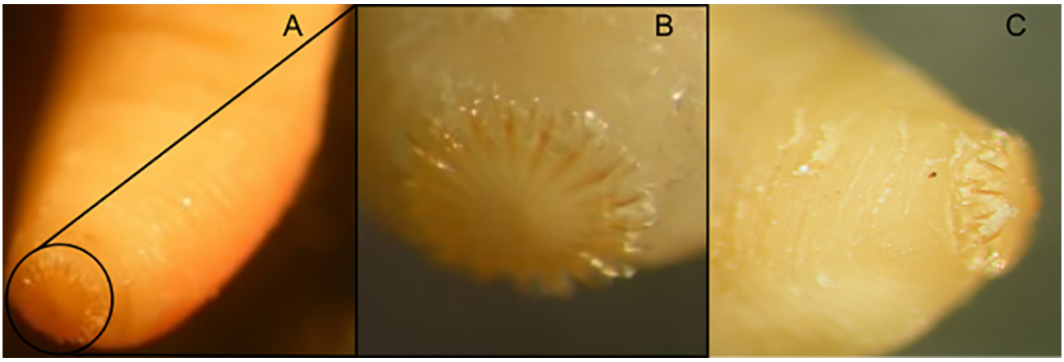

Fig. 4. A. General view of the double row of hooks in the rostellum. **B.** Front detail of the double row of hooks in the rostellum. **C.** Side detail of the double row of hooks in the rostellum. This parasite was obtained from an individual of *Akodon azarae* captured in San Andres de Giles, province of Buenos Aires, Argentina, between spring 2014 and winter 2016.

and intensive pig farms during the fall and spring (**Table** 1), and according to the model, the mean prevalence was slightly higher in intensive pig farms during the spring (**Fig**. 3E). Two infected individuals of *O. flavescens* were captured in an extensive pig farm during the winter. The opossum *L. crassicaudata* was found infected only in an intensive pig farm during the fall. The natives *D. albiventris* and *O. rufus* did not show evidence of Cysticerci infection (**Table** 1). According to the threshold level proposed by Lovera et al. (2017), while 16/18 farms were expected to be infected, the effective values were 15/18 farms infected, showing an overall accuracy of 94.4% (Table S2).

Morphological identification

Morphological identification of the helminths examined from a *Rattus rattus* (ID: MP1308) and an *Akodon azarae* (ID: MP1330) showed typical characteristics of strobilocercus metacestode (family Taeniidae): the body measured 5.5 cm and less than 2 cm in length, respectively, each one possessed a large scolex 0.9 mm and 0.3 mm long and 1.1 mm wide; four prominent lateral suckers; a rostellum armed with a double row of 32 hooks; and the segmented strobilocercus terminated with a bladder (**Figs**. 4A and 4B). Infertile cysts with the inner and outer membrane but without strobilation were observed in *O. flavescens* (ID: MP1380).

Molecular identification and phylogenetics analysis

The length of partial COI and 28S sequences determined from the worms identified from the three host individuals from three different species [*Rattus rattus* (ID: MP1308), *Akodon azarae* (ID: MP1330) and *Oligoryzomys flavescens* (ID: MP1380)] were 400 bp and 270 bp, respectively, and were deposited in the GenBank database with the following accession numbers: OQ785353, OQ785637, and OQ785706 for COI sequences and OQ786864-OQ786866 for the 28S ribosomal region.

From the search with blast tools, samples MP1308, MP1330, and MP1380 showed a similarity of 100% to *Hydatigera taeniaeformis* s.s. in all three cases for both amplified regions. Phylogeny according to BI based on COI and 28S fragments confirmed that they were clustered together with species of the *Hydatigera* genus (**Fig**. 5 and **Fig**. 6) and as the sister group of species from the *Taenia* genus. From the analysis of new and previously published partial COI sequences, the three major clades within the genus *Hydatigera* were recovered: *H. taeniaeformis* s.s. (Clade A), *H. kamiyai* (Clade B), and *Hydatigera* sp. (Clade C). In particular, *H. taeniaeformis* s.s. presented two subclades, one of which is composed of haplotypes present mainly in Asia, while the other one contains diverse haplotypes from not only Asia but also from Europe, South Africa, Oceania, and even one haplotype from North America. The three isolates analyzed in this study and the one from *R. norvegicus* from our study area (Martínez et al. 2013, GenBank accession number: OQ786791) were grouped together with this latter subclade and shared the same sequence with haplotype A12 from Spain.

DISCUSSION

This study reports the first phylogenetic analysis of *H. taeniformis* s.s. in Argentina in both native and invasive commensal small mammals and the first evidence of infection of this tapeworm in the native didelphid *Lutreolina crassicaudata*. The only record available from the Americas until now was published by Mello et al. (2018), analyzing the phylogeny of cysticerci present in a squirrel of Brazil.

Rodents and production systems, whether crop or livestock farming, have a long history of co-existence, marked mainly by damage to production and the risk of disease transmission to humans and livestock (Zinsser 1935; Singleton et al. 1999; Stenseth et al. 2003). European colonists rapidly introduced livestock and their production form to the Americas, mainly cattle and pigs, used as a primary source of food for the conquerors and, later, as a food resource for the general population (Del Río Moreno 1996; Ginja et al. 2019). These breeding systems favor the occurrence of invasive commensal rodents (e.g., *R. norvegicus*, *R. rattus*, and *M. musculus*), due to the generation of favorable microhabitats with high availability of food and shelter (Gómez Villafañe et al. 2003; Gómez Villafañe & Busch 2007; Fraschina et al. 2012; Lovera et al. 2015, 2019; Montes De Oca et al. 2020). In turn, as these types of farms settle in near-native grasslands, native rodent species (e.g., *A.*

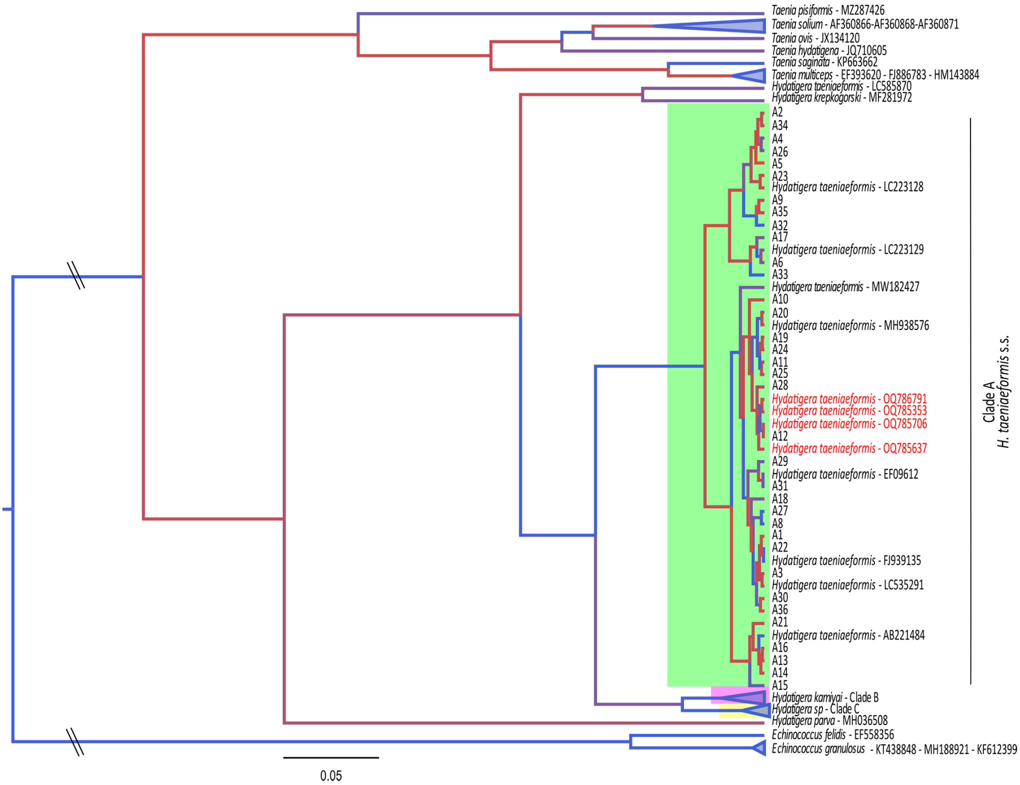

Fig. 5. Bayesian phylogenetic tree out using COI gene fragment of *H. taeniaeformis.* The colors of the branches indicate the posterior probabilities of each node, where values ≥ 0.7 are shown in blue, and those < 0.1 are shown in dark red, with the intermediated values indicated in a range of colour between them. The sequence obtained from the GeneBank database is identified with the accession number. Sequences of the haplotypes from clades A (light green), B (pink), and C (yellow) described by Lavikainen et al. (2016) are listed with their respective host species and the country of collection in Table S3. Clades B, C, and species groups were collapsed. The scale bar represents the number of substitutions per site. The individuals from which the sequences were extracted were captured in the localities of San Andres de Giles, Las Heras, and Marcos Paz, province of Buenos Aires, Argentina, between spring 2014 and winter 2016 (in red).

azarae, *O. flavescens*, etc.) frequently occur. Consequently, it is common for farmers to use rodent control methods, such as the use of domestic cats (*Felis silvestris catus*) (Montes De Oca et al. 2020), among others. This would allow the cycle of *H. taeniformis* s.s. to be completed, using both invasive and native rodent species as intermediate hosts, increasing the risk factor of transmission to another domestic animal or, inclusively, to humans (Meerburg et al. 2006).

In relation to the prevalence of *H. taeniformis* s.s. larvae in the small mammal assemblage on extensive and intensive pig farms, our results are in accordance with those described by Lovera et al. (2017) for dairy and pig farms, when the prevalence was related to *R. norvegicus* or the total small mammal abundances. *Rattus norvegicus* is the dominant species in these farms and appears to play a key role in the transmission of this pathogen, among others, to small mammals. Additionally, all the infected species showed similar levels of prevalence. Therefore, the development of control and monitoring strategies for this helminth should involve both native species and commensal murids. Moreover, according to the species-specific models, our results showed that the season influenced the prevalence level in *R. norvegicus* and *A. azarae*, but not in *R. rattus* and *M. musculus* cases. In this regard, some studies point out that host population abundances could play an important role in increasing the prevalence of this helminth in the rodent population (Duque et al. 2012), while others relate the seasonality to climatic conditions such as humidity or temperature (Theis & Schwab 1992). Our study is not clear on this point, since the increase in prevalence in summer and fall could be related to the seasonal changes in population abundance of *R. norvegicus* and *A. azarae*, or it could be indicating more favorable climatic conditions for the development of the infection. Future studies are needed to clarify the relationships found.

Our molecular analysis showed that the helminth cyst present in *R. rattus* and *R. norvegicus* (sequenced by Martínez et al. 2013) in our study area belongs to the *H. taeniaeformis* s.s. species. Moreover, two cricetid species, *A. azarae* and *O. flavescens* were also found infected with

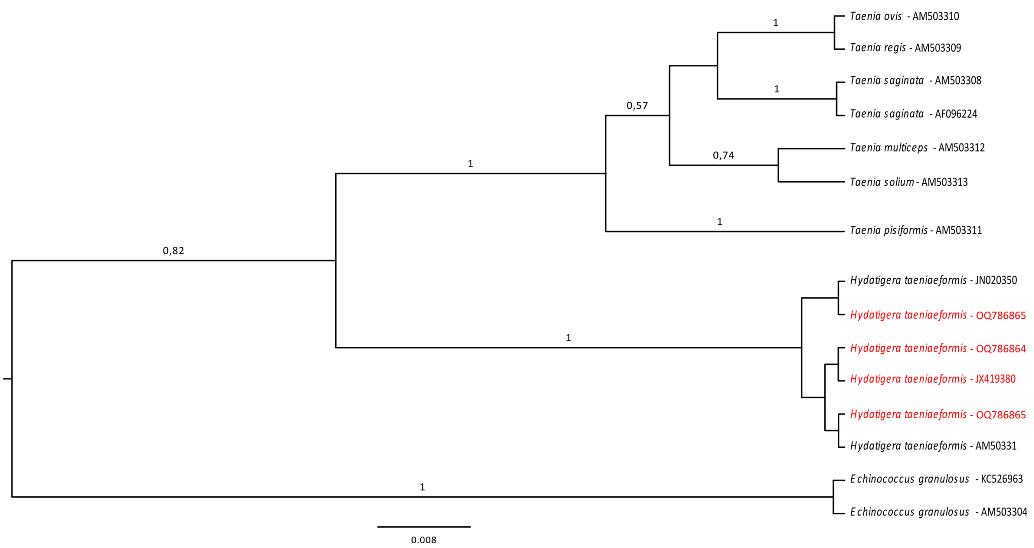

Fig. 6. Bayesian phylogenetic tree out using 28S gene fragment of *H. taeniaeformis*. Numbers above the branches indicate posterior probabilities. The sequence obtained from the GeneBank database is identified with the accession number. Sequences of the haplotypes are listed with their respective host species and the country of collection in Table S4. The individuals from which the sequences were extracted were captured in the localities of San Andres de Giles, Las Heras, and Marcos Paz, province of Buenos Aires, Argentina, between spring 2014 and winter 2016 (in red).

them, even though Lavikainen et al. (2016) suggested that the infection for this species is restricted to murid species. This could be related to the fact that these authors did not include cricetid samples from America.

Considering the above, this finding may be related to the relatively recent history of the colonization of the Americas. It is possible that the maritime transport of slaves, resources, and troops between European metropolises and their colonies in Latin America was a driving factor in the colonization of the "New World" by synanthropic species, including *R. norvegicus* (Hulme 2009; Puckett et al. 2016), in addition to livestock and domestic animals (i.e., cows, horses, dogs, and cats), around 250 years ago (Jumar 2002; Ruiz-García & Alvarez 2008). Along with the stowaway host, its parasites may have arrived, such as *H. taeniformis* s.s. Unlike African, Asian, and European Cricetid species, which would have a longer co-evolutionary history with parasitic species of *H. taeniformis* s.l., native rodents would act as naive hosts, being susceptible to infection (Lymbery et al. 2014). Future studies using molecular techniques such as molecular clocks (Kimura 1968) are needed to accurately elucidate the recent history of dispersal of this parasite and may help to understand the spillover event found here.

Finally, we would like to mention that the lack of sequences of *H. taeniformis* s.l. from domestic hosts compared to wild fauna is striking. Only a few sequences from domestic cats are available (Lavikainen et al. 2008, 2016; Liu et al. 2011; Galimberti et al. 2012; Jia et al. 2012), and none of them belong to the Americas. This limits the understanding of the parasitological relationships (i.e., the ecology of its transmission) between domestic animals and the wild fauna. Moreover, to understand in depth the parasitology of *H. taeniformis* s.l. and given the existence of typically infective variants of cricetids (*H. kamiyai*, Lavikainen et al. 2016), it is necessary to extend this type of study to natural areas.

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ONLINE SUPPLEMENTARY MATERIAL

Table S1 - **Table** S2 - **Table** S3 - **Table** S4