

Research Paper

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Trichurid nematodes from South American Camelid: an approach to native assemblages through the parasitology of archaeological sites

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Abstract

To gain insights into the trichurid diversity in pre-Hispanic remains of South American camelids (SACs), as well as into modern SAC populations, a bibliographic search was carried out to find parasitological studies. Results showed that a total of 17 studies were performed at archaeological and paleontological sites, in which a total of 213 samples were examined. The sample set was used as the unit of analysis, and 83% of 52 pre-Hispanic sample sets were positive for parasites. Parasitological studies confirmed the pre-Hispanic presence of diverse trichurids: two *Trichuris* species and capillariid eggs with morphological differences that allowed them to be assigned to three different species. Currently, the richness of the native trichurid assemblages in SACs has been extended by the inclusion of two species (*Trichuris* sp. 2 and Capillariinae gen. sp. 1). Modern *T. tenuis* Chandler, 1930, considered SAC-specific, would have invaded SAC populations during the European colonization. The estimate of regional and temporal trichurid prevalence and paleoecological information allowed us to propose a possible origin for some of them. Although the present analysis is exploratory, it should stimulate future studies about the biogeographic history of SAC helminths, provide relevant information to improve descriptions of the Holocene ecology, and identify threatened helminths.

Introduction

The oldest remains of camelids have been found in North America in sediments dating back to about 45 million years ago (Ma) (Webb 1974). Fossil and mitochondrial records (16 and 25 Ma, respectively) suggest that the radiation of camelids during the Miocene led to two divergent phylogenetic lines: the Camelini Tribe Gray, 1821 and the Lamini Tribe Webb, 1965 (Honey *et al.* 1998; Cui *et al.* 2007). Extinct members of the latter colonized South America after the formation of the Isthmus of Panama, 3.5 Ma. During the Pleistocene–Holocene transition (*ca* 10,000–12,000 years before present (BP)), extinct species of this tribe such as *Hemiauchenia* Gervais and Ameghino, 1880 and *Lama gracilis* Gervais and Ameghino, 1881, lost representativeness in the zooarchaeological record, whereas modern ones, such as the guanaco (*Lama guanicoe* Müller, 1776) and the vicuña (*Vicugna vicugna* Molina, 1782), became the only camelids recovered.

South American Camelids (SACs) have represented a key resource for human settlements, from the Central Andes to the Tierra del Fuego archipelago. Although there is no consensus on the phylogenetic history of domestic SAC species such as the llama (*Lama glama* Linnaeus, 1758) and the alpaca (*Lama pacos* Linnaeus, 1758) (Fan *et al.* 2020; Diaz-Maroto *et al.* 2021; among others), their emergence from the wild species mentioned above would have occurred from the Central Andes (Wheeler 1995) up to its southern limit, the Argentine Puna, around 7,000 years BP (Yacobaccio 2021). In the archaeological sites of Peru and the Puna, the evidence of a gradual process of intensification in the use of camelids culminates in the archaeological records of corrals dating back to *ca* 4,500 BP (Yacobaccio 2021). Since the European colonization, wild SACs have been subjected to increasing stresses from human activity. In Patagonia, the invasion of exotic species since the beginning of the 20th century had a particular impact on wild SACs, along with the rapid establishment of extensive sheep farming (Martinic 1976). Currently, the greatest threats to the Patagonian guanaco continue to be their competition with sheep, their hunting, and the fencing of their territories (Baldi *et al.* 2010), whereas in other regions, wild vicuñas and other guanacos populations suffer similar threats (Baldi *et al.* 2016; Arzamendia *et al.* 2019; Carmanchahi *et al.* 2019). Likewise, domestic SACs have also suffered the effects of the European colonization, and studies have estimated that their genetic variability has been reduced by 80% during the first 100 years since the colonization (Wheeler 1995).

Biological invasions and their effects on native communities are widely documented (Vitousek *et al.* 1996; Simberloff *et al.* 2013). Importantly, the invasion of free-living animals can also lead to the simultaneous invasion of their parasites, as well as to an increase in the prevalence of indigenous parasites for which they are potential hosts (Torchin *et al.* 2003; Kelly *et al.* 2009). For example, parasitological studies performed in guanacos during the last 40 years have shown a parasite richness made up of numerous helminths typical of domestic mammals (revised in Fugassa 2020). Thus, it is difficult to discern whether some of the species that currently parasitize SACs have a native or a foreign origin. At present, the gastrointestinal parasite richness of SACs is dominated by nematode species (Leguía & Casas 1999). Strongylids (Subclass Secernentea von Linstow, 1905) are the most studied clade, probably both for their richness within SAC assemblages and for their health implications, whereas the taxonomic and ecological knowledge of enoplids (Subclass Adenophorea Linstow, 1905) that parasitize SACs remains scarce. The species of the Order Enoplida Filipjev, 1929 are grouped into two suborders, Dyoctophimina Chitwood, 1933 and Trichinellina, Hodda 2007, and only representatives of the latter have been reported in SACs (Superfamily Trichinelloidea Ward, 1907). Specifically, species of the Subfamilies Trichurinae Ransom, 1911 and Capillariinae Railliet, 1915, two of the three subfamilies recognized for the Family Trichuridae Ransom, 1911, have been reported in SACs. The former are soil-transmitted helminths that do not require intermediate hosts and whose eggs must mature in the environment before being ingested and hatching in the large intestine of a mammal (Anderson 2000), whereas the latter parasitize various organs of species of all classes of vertebrates and, specifically in SACs, have been found in the small intestine (Leguía & Casas 1999). Capillariid species are widely distributed throughout the world and are one of the most complex groups for their taxonomic and systematic analysis (Moravec *et al.* 1987).

The objective of this study was to analyze the richness and composition of helminths, specifically referring to trichurid species in SACs from a historical perspective. This approach can expose patterns that help to identify the mechanisms or events that determine them.

Materials and Methods

In order to establish the known diversity of trichurid nematodes in pre-Hispanic remains of SACs, as well as to identify their distribution patterns, a bibliographic search was carried out to find parasitological studies on paleontological and archaeological remains of SACs. A bibliographic search was also carried out in Google Scholar and Google to estimate the diversity of trichurids that parasitize modern SAC populations. For this, the descriptors 'trichuris' and the combinations with the common and scientific names of the four SAC species were used, both in Spanish and English; the same procedure was followed for capillariids, using 'capillariid' and 'capillaria' as descriptors.

In addition, a review of the morphometric information of the eggs of the *Trichuris* species found in archaeological and modern material from SACs was carried out to compare their dimensions. Likewise, eggs obtained from female *Trichuris tenuis* Chandler, 1930 isolated from llamas from the Argentine provinces of Jujuy and Tucumán (30 eggs in each case) were also used. To differentiate the eggs from the capillariids found in modern and archaeological material, the shape of the egg and the ornamentation of

the eggshell were also considered because they are features of complementary taxonomic value (Moravec 2001). Specifically, for the eggs of the morphotype called Capillariinae gen. sp. 1, due to its similarity with the eggs of *Calodium hepaticum* Bancroft, 1893, the measures were compared with *C. hepaticum* eggs obtained from the liver of rats. Because homoscedasticity was rejected for each dependent variable using Levene's test, one-way ANOSIM was applied. In all cases, the significance level $p < 0.05$ and the free statistical package Past 4.09 (Hammer *et al.* 2001) were used.

In parasite ecology, some definitions (summarized in Bush *et al.* 1997) must be adapted to the nature of the sample used (Watve & Sukumar 1995). In the present study, parasite richness was defined as the number of taxa observed in each sampling unit, referring mostly to the intestinal infracommunity. Regarding prevalence, unlike the traditional definition (Bush *et al.* 1997), we used the fecal prevalence to indicate the percentage of sampling units in which parasite taxa were detected. The information on the prevalence of trichurids in pre-Hispanic SACs was arranged in temporal periods: Late Holocene (up to 3,000 years BP), Middle Holocene (3,001–6,000 years BP), Early Holocene (6,001–9,000 years BP), and Pleistocene-Holocene transition (9,001–12,000 years BP). Dates were calibrated with Calib 8.2 (2 sigma) for the Southern Hemisphere (Hogg *et al.* 2020) and using the probabilistic median. For publications in which only the dates calibrated with two sigma were reported, for each case, an arithmetical mean was estimated for the chart. The information on the prevalence was also arranged according to geographic origin of the samples: Patagonia and Central Andes.

Precautions regarding the zoological identification of coprolites were taken: samples associated with dates contemporary to the European colonization were included in the review but were excluded from the analysis of pre-Hispanic SAC parasitic assemblages because they could include invasive parasites from exotic species and even feces from introduced artiodactyls, such as goats and sheep. Considering that *Eimeria macusaniensis* Guerrero, Hernandez, Bazalar, and Alva, 1971 is a SAC-specific coccidian and that the nematode *Lamanema chavezii* Becklund, 1963 and the capillariid species Capillariinae gen. sp. 2 were frequently reported in publications on pre-Hispanic SAC parasites, the presence of *E. macusaniensis* or both nematodes mentioned was considered a complementary indicator for the identification of SAC coprolites.

Results and Discussion

Trichuris genus in SACs

The bibliographic search resulted in finding 17 publications related to parasites found in archaeological remains of SACs. These included one study on ectoparasites (Fugassa *et al.* 2017), one study on *E. macusaniensis* (Fugassa *et al.* 2008a), and four unpublished studies (Fugassa 2006; Bayer 2008; Taglioretti 2008; Taglioretti 2015). These 17 studies examined a total of 213 samples consisting mostly of individual coprolites and, on fewer occasions, series of coprolites or pools of them; only two of the samples consisted of enterolites extracted from camelid mummified remains (Leguía *et al.* 1995; Le Bailly *et al.* 2019). About 112 of these samples contained parasites that, due to their specificity, could be assigned to SACs and that came from archaeological levels associated with pre-Hispanic periods.

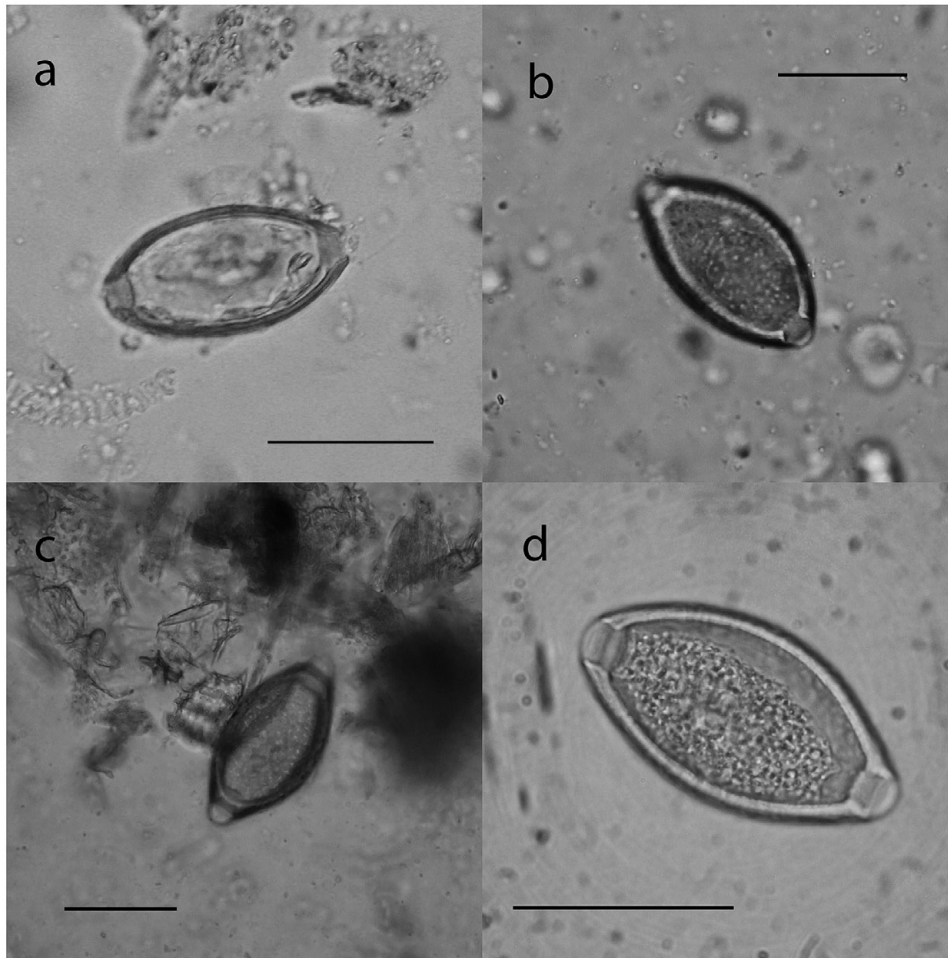


Figure 1. *Trichuris* eggs found in pre-Hispanic and modern SACs. *Trichuris* sp. egg with smooth eggshell in camelid coprolite (a), and *Trichuris* sp. 2 egg with hole eggshell in guanacos coprolite (b), in feces of modern vicuñas (Salta, Argentina) (c), and in *T. tenuis* female recovered of a llama (Jujuy, Argentina) (d). Scale bar = 40 μ m.

However, since some publications did not specify the sample size (number of coprolites per sample), the sample set, defined as a sample belonging to a certain archaeological level and micro-sector, was used as the unit of analysis. A total of 52 sample sets were analyzed for pre-Hispanic SACs, 83% of which were positive for parasites. The genus *Trichuris* was present in SAC remains from all eight South American archaeological sites examined (Figure 1a) and in 28.8% of the 52 pre-Hispanic SAC sample sets (Table 1). In Patagonia, records of the genus *Trichuris* in SACs dated back to ca 11,000 cal. years BP, so its hosts could include extinct SAC species, such as *L. gracilis* and *Hemiauchenia*.

The genus *Trichuris* was reported in all SAC species and in all regions studied, although only 26 species-specific records were found and obtained from necropsies (Table 2). Six species were identified in SACs, although it has recently been suggested that *Trichuris globulosa* von Linstow, 1901 would represent a lineage of *Trichuris ovis* Abildgaard, 1795 (Callejon *et al.* 2015). Only three of these species were identified in South American populations of SACs and only two (*T. ovis* and *T. tenuis*) were reported in all SAC species. All *Trichuris* species parasitize domestic ruminants, although *T. tenuis* is considered specific to SACs (Cafrune *et al.* 1999). In SACs, *T. tenuis* was first

described in captive llamas in the USA (Rickard & Bishop 1991a) and then subsequently reported in vicuñas and llamas from northwestern Argentina (Cafrune *et al.* 1999) and guanacos from Argentine Patagonia (Beldomenico *et al.* 2003). However, this species was originally described in captive individuals of dromedaries in the USA (Chandler 1930) and later reported in sheep from Iran (Mirzayans 1974) and dromedaries from Australia (Beveridge & Green 1981). Regarding *T. tenuis* eggs, the analysis of the distribution of the length of the major axis of eggs obtained from females, as well as of those provided by various authors or recovered from archaeological sites, showed a wide range within some species and an overlapping of measurements among species (Figure 2). This may be due to various factors, such as the change in size that occurs as eggs mature (Yevstafieva *et al.* 2021), and indicates that this feature is not reliable for the zoological identification of eggs and that a robust statistical comparison is not possible.

Eggs whose size, shape, color, and polar plugs corresponded to those of *Trichuris* spp. (Table 3), although they presented an eggshell covered by numerous ellipsoids to circular holes typical of capillariid species, were found in seven SAC archaeological samples (Figure 1b). Although this feature could be product of taphonomic effects, until now, this type of egg has only been

Table 1. Parasitological reports of *Trichuris* sp. in archaeological remains from SACs; (?) Zoological origin not confirmed, (+) Arithmetic mean of two calibrated dates, (*) Revised identity in this work, (**) Mean, (WD) Without data

Archaeological site	Host	Number inventarie	Calibrated years before present**	Reference
ADG, Santa Cruz, Argentina	<i>L. guanicoe?</i>	561	5,597–3,648	In this work (Layer V–VII)
		532	<765	Taglioretti 2015; Taglioretti et al. 2017
	<i>L. guanicoe</i>	573	765–1,359	Taglioretti 2015; Taglioretti et al. 2017
		541	5,597	Taglioretti 2015; Taglioretti et al. 2017
		575	1,359–1,066	In this work (Layer IV–IV)
Arroyo Feo, Santa Cruz, Argentina	<i>L. guanicoe?</i>	1/3	6,799	In this work (Layer IX)
CCP7, Santa Cruz, Argentina	<i>L. guanicoe</i>	9	9,240	Fugassa 2006
	<i>Hemiauchenia/Lama</i> spp.	39*	11,028	Fugassa 2006
CCP5, Santa Cruz, Argentina	<i>L. guanicoe?</i>	50*	7,402	Bayer 2008
Los Viscos, Catamarca, Argentina	SAC?	788	>1,000	Pettrigh et al. 2021
El Yaral, Moquegua, Peru	<i>L. glama</i> and <i>L. pacos</i>	WD	868–1,123	Leguía et al. 1995
Huancaquito, Trujillo, Peru	Domestic SAC	Ca05,ca11, CcaC16, ca25,Cca50, ca62, ca65	525+	Le Bailly et al. 2019
Punta de Peña 4, Catamarca, Argentina	SAC	5, 10	1,394+	Tietze et al. 2021
	SAC?	4, 6	1,394+	Tietze et al. 2021
		16	1119+	Tietze et al. (2021)
		42, 46	2575 - 3212+	Tietze et al. (2021)

found in SACs. Le Bailly *et al.* (2019) also identified this feature and rejected the taphonomic hypothesis due to the regular pattern of this ornamentation in the eggs. These eggs (*Trichuris* sp. 2) had a wide geographic distribution, although with few reports (13.5% of the pre-Hispanic SAC sample sets) and at low densities. Therefore, because the features that characterize these eggs are unclear, they may be underestimated within both archaeological and modern samples. For example, Tietze *et al.* (2021) and Ruiz Hurtado (2016), in coprolites and modern feces respectively, reported *Trichuris* sp. whose images showed eggs with an irregular eggshell. Similar eggs have also been identified in wild vicuñas (Figure 1c), Argentine llamas, and Chilean guanacos (Fugassa pers. obs. 2017). The analysis of the eggshell surface of eggs obtained from *T. tenuis* females exhibited the ornamentation described for *Trichuris* sp. 2 (Figure 1d). No other *Trichuris* species with eggs with these traits have been reported. Members of the Subfamily Trichurinae are described as having a smooth eggshell, a criterion often used to differentiate them from eggs of the Subfamily Capillariinae (Traversa *et al.* 2011), although this may not be a universal trait for the genus *Trichuris*.

As mentioned, Lamini camelids colonized South America about 3 Ma (Wheeler 1995) and their prolonged isolation from Camelini species may also have led to divergence of their parasites. The atypical ornamentation of the eggs observed in *T. tenuis* females and in archaeological remains (*Trichuris* sp. 2) suggests that they correspond to the same species, although the initial reports of *T. tenuis* in various species of Old World modern artiodactyls refute the biogeographic history suggested. Helminth eggs such as *Toxocara* cf. *canis* and *Eucoleus*

cf. *aerophila* have been found in pre-Hispanic Patagonian fox coprolites (Fugassa *et al.* 2022) in the same way as they are currently recovered from various Old World wild canids. A detailed analysis of the genome of the modern and pre-Hispanic populations would probably clarify whether both populations belong to the same species, after so much time of isolation. The eggs of *Trichuris* sp. 2 and those of modern *T. tenuis* probably represent vicariant populations, where modern *T. tenuis* would have entered South America along with the invasion of domestic hosts during the European colonization, whereas one or more native species could have become extinct or remain undetected, in wild relicts or as sibling species (*sensu* Nadler & de León 2011).

Subfamily Capillariinae in SACs

In archaeological deposits, 63.5% of the pre-Hispanic SAC sample sets were positive for capillariid species. Eggs with marked morphological differences were identified, allowing them to be assigned to three different species (Table 4). Capillariinae gen. sp. 1 eggs (Figure 3a) were similar to those of *C. hepaticum* (Figure 3b). These eggs were also found in the human-occupied soil of the CCP7 cave with other parasites that indicated high SAC fecal contamination (Amalfitano *et al.* 2019). Capillariinae gen. sp. 1 has also been found in coprolites from predators with evidence of SAC consumption in Patagonia (Fugassa *et al.* 2006, 2009) and also in rodents and pellets from raptor birds (Fugassa *et al.* 2007; Beltrame *et al.* 2011; Fugassa 2014). The statistical analysis of the dimensions of 843 eggs of this morphotype and of those recovered from coprolites of diverse zoological origin in

Table 2. Parasitological reports of *Trichuris* Roederer, 1761 species in modern SACs

Parasite	Host	Locality	Reference
<i>Trichuris tenuis</i> Chandler, 1930	<i>Lama glama</i>	Jujuy, Argentina	Cafrune <i>et al.</i> 1999; Cafrune <i>et al.</i> 2001
		Oregon, EEUU	Rickard and Bishop 1991a, 1991b
		United Kingdom	De Welchman <i>et al.</i> 2008
	<i>Vicugna vicugna</i>	Jujuy, Argentina	Cafrune <i>et al.</i> 1999
	<i>Lama guanicoe</i>	Chubut, Argentina	Beldomenico <i>et al.</i> 2003
	<i>Lama pacos</i>	Junin, Peru	Casas <i>et al.</i> 2005
		Australia	Rashid <i>et al.</i> 2019
Cotopaxi, Ecuador		Panchi Lema 2021	
<i>Trichuris discolor</i> von Linstow, 1906	<i>Lama glama</i>	Oregon and Washington, EEUU	Rickard and Bishop 1991b
<i>Trichuris ovis</i> Abildgaard, 1795	<i>Lama guanicoe</i>	Patagonia, Argentina	Larrieu <i>et al.</i> 1982
		Puno, Peru	Hilari 1983 in Quispe García 2011
		Cusco, Peru	Hurtado <i>et al.</i> 1985 in Quispe García 2011
	<i>Vicugna vicugna</i>	Puno, Peru	Guerrero 1960 in Quispe García 2011
		Ayacucho, Peru	Choque 1981 in Quispe García 2011
		Junin, Peru	Gonzales-Mugaburu and Parra 1956
		Peru	Martínez and Torres 1983 in Quispe García 2011
	<i>Lama glama</i>	Cajamarca, Peru	Ortiz 2013
		Puno, Peru	Mamani 1983 in Quispe García 2011
		Arequipa, Peru	Valencia 1985 in Quispe García 2011
		Chile	Alcaíno <i>et al.</i> 1991 in Alcaíno and Gorman 1999
		Region I, Chile	Burgos González 1991
	<i>Lama pacos</i>	Puno, Peru	Mamani 1989 in Quispe García 2011
Cajamarca, Peru		Ortiz 2013	
<i>T. skrjabini</i> Baskakov 1924	<i>Lama glama</i>	Oregon and Washington, EEUU	Rickard and Bishop 1991b
<i>Trichuris globulosa</i> von Linstow, 1901	<i>Vicugna vicugna</i>	Puno, Peru	Beltran 1991 in Quispe García 2011
<i>Trichuris lama</i> Ezzat, 1945	<i>Lama glama</i>	Giza, Egipto	Ezzat 1945

Patagonia showed no statistically significant differences between them, so the authors assumed that it was a single species with a wide range of hosts (Taglioretti *et al.* 2014). Although Capillariinae gen. sp. 1 eggs have been previously assigned to *C. hepaticum*, the scatterplot of the egg measurements observed for Capillariinae gen. sp. 1 and *C. hepaticum* eggs obtained from rats (Figure 4), as well as the multivariate analysis one-way ANOSIM, indicated a statistical difference between both groups of eggs ($p = 0.0001$). This, together with the life cycle of *C. hepaticum* (Moravec 1987), suggests that Capillariinae gen. sp. 1 and *C. hepaticum* are different species. As mentioned, in the archaeological sites examined, Capillariinae gen. sp. 1 was found in a wide range of hosts, in high prevalence in pre-Hispanic Patagonian SACs until about 12,000 years ago (Taglioretti 2015) and even in megafauna coprolites from the late Pleistocene (Ruíz Oyarzún *et al.* 2021). Camelids probably obtained this nematode from other mammals in the region because, until now, it has not been found in camelids from the pre-Hispanic Central Andes. The prevalence of Capillariinae gen. sp. 1 found in pre-Hispanic remains of SACs from Patagonia contrasts with the current

prevalence, where only similar eggs were detected in captive SACs in Chile (Ruíz-Oyarzún *et al.* 2017) and in llamas from the province of Salta, Argentina (Fugassa pers. obs. 2017). These two reports of eggs similar to those of Capillariinae gen. sp. 1 demand further studies that can inform whether the species is present in pre-Hispanic SACs or is another species recently acquired from European cattle, such as *Aonchotheca bovis* Schnyder, 1906.

Eggs assigned to Capillariinae gen. sp. 2 showed a more variable size than those of Capillariinae gen. sp. 1, as well as more curved, thin, yellowish-brown eggs with a coarse eggshell (Figure 3c). This species was found in pre-Hispanic archaeological remains in Patagonia as well as in the Central Andes and with a maximum age of about ca. 9,600 years. The eggs of Capillariinae gen. sp. 2 were assigned to different capillariids: *Eucoleus* sp. (Taglioretti *et al.* 2017; Amalfitano *et al.* 2019), *Capillaria* sp. (Leguia *et al.* 1995), and a species of the Subfamily Trichosomoidinae Hall, 1916 (Le Bailly *et al.* 2019). However, because capillariid species within the same genus do not have any uniformity in egg morphology, their assignment to the genus

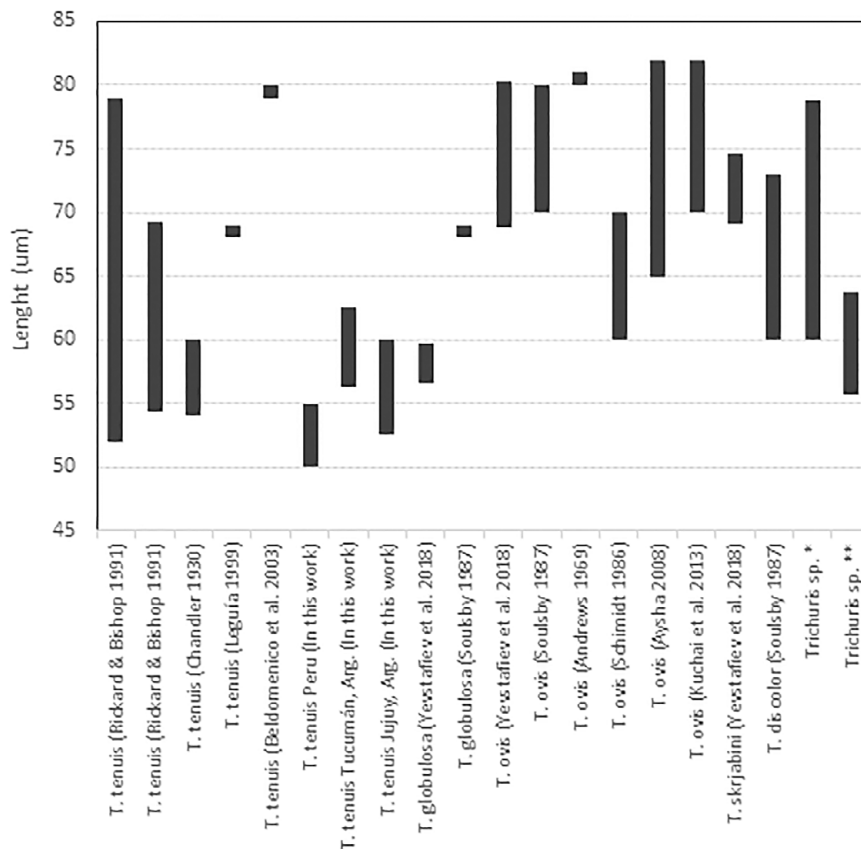


Figure 2. Barplot of the length of *Trichuris* spp. eggs reported in modern and ancient SACs; (*) Pre-Hispanic Patagonian samples, (**) Pre-Hispanic Central Andes samples.

Table 3. Ornamented eggs attributable to *Trichuris* sp. 2 in pre-Hispanic Southern American camelids (SACs); (*) Revised information here, (**) Mean value, (+) Arithmetic mean of two calibrated dates

Host	Archaeological site	Sample	Calibrated years before present**	Reference
Domestic SAC	Huancaquito, Trujillo, Peru	Ca05	525+	Le Bailly <i>et al.</i> 2019
SAC	Los Viscos, Catamarca, Argentina	779	946–962	Petrigli <i>et al.</i> 2021*
		783	597–989	In this work
<i>L. guanicoe</i>	CCP7, Santa Cruz, Argentina	466	4,748	Amalfitano <i>et al.</i> 2017
		436	4,399	Amalfitano <i>et al.</i> 2017
		354	6,142–ca. 3,480	(level III, sector 2) Taglioretti 2015*
		418	3,704–3,675	Amalfitano <i>et al.</i> 2017; Amalfitano 2016

Eucoleus is arbitrary. The absence of an advanced embryonic stage does not allow assigning the species to a member of the subfamily Trichosomoidinae either (Anderson 2000). Although coprolites from various mammalian species in Patagonia were examined, Capillariinae gen. sp. 2 has been found to be exclusively present in SAC coprolites and puma coprolites with evidence of predation on camelids (Fugassa *et al.* 2009). Although all reports of capillariids in modern SACs could not be identified to species, eggs similar to these have been identified in images from parasitological examinations of domestic SACs (Ballweber 2009; Cebra 2014; Hyuga & Matsumoto 2016) – even diagnosed as *Trichuris* sp. (Kutzler 2018), in wild guanacos from Mendoza,

Argentina (Moreno *et al.* 2015), in vicuñas from Bolivia and Peru (Ruiz Hurtado 2016; Pacheco *et al.* 2021), and in wild vicuñas from Catamarca, Argentina (Fugassa pers. obs. 2017). Therefore, it can be postulated that Capillariinae gen. sp. 2 is a helminth with a very specific parasitic relationship with Lamini camelids and that its oldest records date back to at least the late Pleistocene.

Capillariinae gen. sp. 3 eggs (Figure 3d) were only identified in pre-Hispanic camelid coprolites from the CCP7 site in Patagonia, Argentina (Table 4). This morphotype has no visual record in publications about ancient SAC and, although a similar image was identified in a coproparasitological examination of alpacas in

Table 4. Parasitological reports of the Subfamily Capillariinae Railliet, 1915 in SACs archaeological remains; (*) Revised information here, (**) Mean value, (***) Historic sample (Petrigh *et al.* 2019), (+) Arithmetic mean of two calibrated dates, (WD) Without data

Parasite	Locality	Host	Number inventarie	Calibrated years before present**	Reference		
Capillariinae gen. sp.1	ADG, Santa Cruz, Argentina	<i>L. guanicoe?</i>	537	<765	Taglioretti 2015; Taglioretti <i>et al.</i> 2017		
			566	3659	In this work		
			569	3,648–2,902	Taglioretti 2015; Taglioretti <i>et al.</i> 2017		
			574***	765	In this work		
		<i>L. guanicoe</i>	556	7,534–6,327	Taglioretti 2015		
			573	765–1,359	Taglioretti 2015; Taglioretti <i>et al.</i> 2017		
			541	5,597	Taglioretti 2015; Taglioretti <i>et al.</i> 2017		
			CCP7, Santa Cruz, Argentina		<i>L. guanicoe</i>	418	3,704–3,675
	465		6,142–ca. 3,480	(level II, sector 2) Taglioretti 2015*; Taglioretti <i>et al.</i> 2015			
	514	5,802	Amalfitano 2016				
	330	6,064	Amalfitano 2016				
	29	4,303	Taglioretti 2008; Taglioretti <i>et al.</i> 2015				
	354	6,142–ca. 3,480	(level III, sector 2) Taglioretti 2015*				
	436	4,399	Amalfitano <i>et al.</i> 2017				
	12	6,373	Taglioretti 2008; Taglioretti <i>et al.</i> 2015				
	38	3,236–6,991	Taglioretti 2008; Taglioretti <i>et al.</i> 2015				
	383	6,991	Amalfitano 2016				
	11	8,737–9,240	Fugassa 2006; Fugassa 2007; Taglioretti <i>et al.</i> 2015				
	385b	9,320	In this work				
	270	7,846	Taglioretti 2015				
	32	9,649	Taglioretti 2008; Taglioretti <i>et al.</i> 2015				
	530	9,954	Amalfitano 2016				
	30*	9,954	Fugassa 2006				
<i>Hemiauchenia/ Lama spp.</i>	16	10,939–10,208	Fugassa 2006; Taglioretti 2008; Taglioretti <i>et al.</i> 2015				
	439	11,028	Amalfitano 2016				
	39*	11,028	Fugassa 2006				
	245	12,148	Taglioretti 2015				
CCP5, Santa Cruz, Argentina	<i>L. guanicoe</i>	42	7,402	Bayer 2008			
		44*	7,402	Bayer 2008			
		45	7,402	Bayer 2008			
		49	7,402	Bayer 2008			
		24*	7,402	Fugassa 2006; Bayer 2008			
		452	7,402	Taglioretti 2015			
		47	7,402	Bayer 2008			
	<i>L. guanicoe?</i>	50*	7,402	Fugassa 2006; Bayer 2008			

(Continued)

Table 4. (Continued)

Parasite	Locality	Host	Number inventaried	Calibrated years before present**	Reference
	Mylodón Norte I, Santa Cruz, Argentina	<i>L. guanicoe?</i>	749	<1,854	Fugassa and Petrih 2019
	Cueva del Milodón, Chile	<i>Myiodon darwinii</i>	WD	11,256–15,015	Ruiz Oyarzún <i>et al.</i> 2021
Capillariinae gen. sp.2	Arroyo Feo, Santa Cruz, Argentina	<i>L. guanicoe?</i>	3/3	6,799	In this work (Layer IX)
		<i>L. guanicoe?</i>	8/1	6,314	In this work
	ADG, Santa Cruz, Argentina	<i>L. guanicoe</i>	573	765 – 1,359	Taglioretti 2015; Taglioretti <i>et al.</i> 2017
			541	5,597	Taglioretti 2015; Taglioretti <i>et al.</i> 2017
	CMN1, Santa Cruz, Argentina	<i>L. guanicoe</i>	749	<1854	Fugassa & Petrih (2019)
	CCP5, Santa Cruz, Argentina	<i>L. guanicoe</i>	393	2,828	Taglioretti 2015
			47	7,402	Bayer 2008
			<i>L. guanicoe?</i>	50*	7,402
	CCP7, Santa Cruz, Argentina	<i>L. guanicoe</i>	436	4,399	Amalfitano <i>et al.</i> 2017
			29	4,303	Taglioretti 2008; Taglioretti <i>et al.</i> 2015
			354	6,142–ca. 3,480	(level III, sector 2) Taglioretti 2015*
			12	6,373	Taglioretti 2008; Taglioretti <i>et al.</i> 2015
		38	3,236–6,991	Taglioretti 2008; Taglioretti <i>et al.</i> 2015	
		11	8,737–9,240	Taglioretti <i>et al.</i> 2015; González Olivera pers. comm. 2013	
		9	9,240	Fugassa 2006	
32		9,649	Taglioretti 2008; Taglioretti <i>et al.</i> 2015		
Huanchaquito, Trujillo, Peru	Domestic SAC	Ca05	525+	Le Bailly <i>et al.</i> 2019	
El Yaral, Moquegua, Peru	<i>L. glama</i> y <i>L. pacos</i>	WD	868–1,123	Leguía <i>et al.</i> 1995	
Capillariinae gen. sp.3	CCP7, Santa Cruz, Argentina	<i>L. guanicoe</i>	436	4,399	In this work

Japan (Hyuga & Matsumoto 2016), it is insufficient to discuss its identity and its origin. These eggs are similar to others found in rodents in the region, so these cannot be ruled out as sources and, due to their low frequency, it cannot be ruled out that they represent post-depositional contamination from the soil.

Unlike reports of the genus *Trichuris* that parasitize SACs, reports of capillariids in modern camelid species could not be identified to species (Table 5), and there is no information on the identity of the species that parasitize them. Although the morphology of capillariid eggs may present features specific to each species (Moravec 2001), as mentioned, these features are not necessarily shared among species of the same genus. Likewise, a relationship between the structure of the eggshell and the location within the host has been suggested (Romashov 1985), although it has been recently questioned (Borba *et al.* 2021). Therefore, based on both quantitative and qualitative features, the usefulness of capillariid eggs for coproparasitological diagnosis is limited to reporting the operational taxonomic

units (OTUs) – probably species – present and represents only an auxiliary trait for species identification.

Trichurid prevalence in pre-Hispanic SACs

The prevalence of SAC trichurids in Patagonia was two-fold higher than that in the Central Andes (Figure 5). The analysis of the prevalence of each Subfamily showed that it was higher for the Subfamily Trichurinae in the Central Andes. The difference between regions was clearer for the prevalence of the Subfamily Capillariinae, which, in Patagonia, reached 100%. Capillariinae gen. sp. 1 is the species responsible for this contrast.

The prevalence of the genus *Trichuris*, considered as the sum of the prevalence of *Trichuris* sp. and the prevalence of *Trichuris* sp. 2, in the archaeological sites from Patagonia and Central Andes was almost 33.4% lower than that of capillariids (42.3% and 63.5%, respectively). A large part of the pre-Hispanic

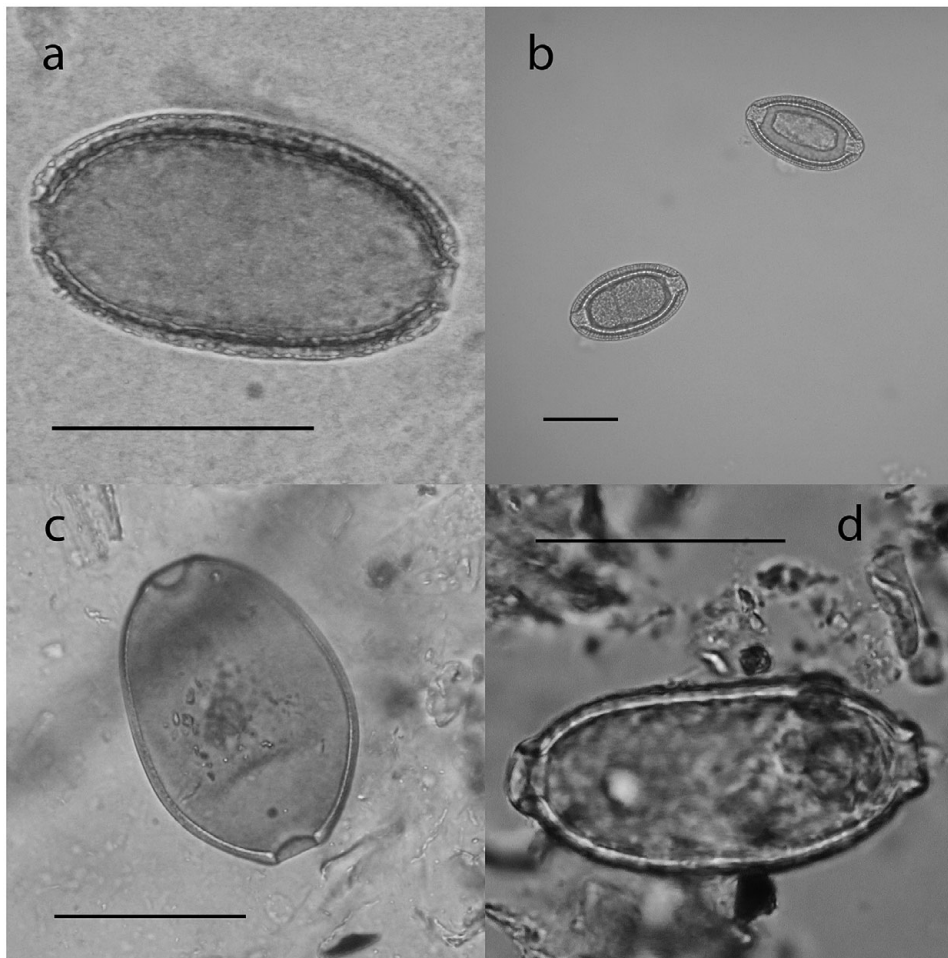


Figure 3. Diversity of Capillariidae eggs reported in pre-Hispanic and modern SACs. (a) Capillariidae gen. sp. 1 in camelid coprolites (CCP7, Santa Cruz, Argentina), (b) *Calodium hepaticum* eggs recovered from rat liver, (c) Capillariidae gen. sp. 2 in camelid coprolites (CCP7, Santa Cruz, Argentina), (d) Capillariidae gen. sp. 3 in coprolite of guanacos (Sample 436, CCP7, Santa Cruz, Argentina). Scale Bar = 40 μm .

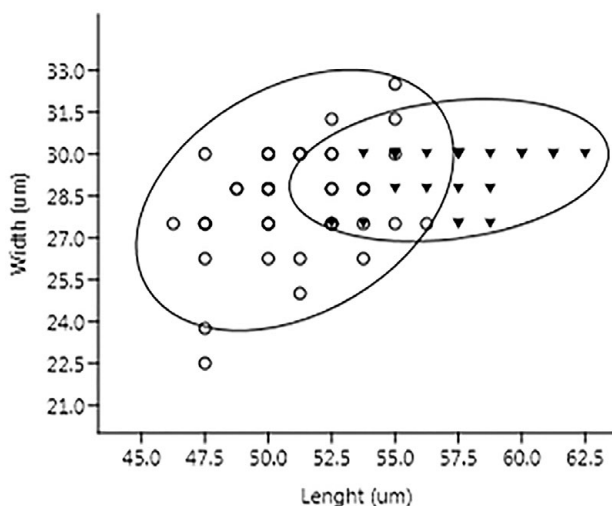


Figure 4. Scatterplot of the Capillariidae gen. sp. 1 eggs in SAC coprolites from CCP7 archaeological site, Patagonia (O), and *Calodium hepaticum* eggs recovered from liver rats (▲). Note: 95% ellipses.

prevalence of capillariids, particularly in Patagonia, was due to Capillariidae gen. sp. 1. This contrasts with the uncertain presence of Capillariidae gen. sp. 1 in modern SACs. The absence of detailed descriptions in reports of trichurids in modern SACs prevents their specific identification. It is possible that Capillariidae gen. sp. 1 has become extinct or remains in wild relicts, according with the trend in its prevalence from the late Pleistocene to the late Holocene (Figure 6a). This hypothesis and the possible responsible ecological processes will require more information.

The analysis of these prevalences for the pre-Hispanic temporal blocks was only possible for Patagonia because the sample from the Central Andes corresponds to the late Holocene. The viability and embryonic development of eggs depend on various environmental factors. *Trichuris trichiura* eggs, for example, have low resistance to moderate humidity conditions and temperatures below 0 °C (Nolf 1932). Other species of the genus show similar features (Yevstafieva *et al.* 2021). This could explain the low prevalence observed for *Trichuris* spp. in the early temporal blocks of Patagonia (Figure 6b). Regarding the highest prevalence of both capillariids -mainly Capillariidae gen. sp. 1 (Figure 6a)- it is

Table 5. Capillarid reports in modern SACs; (WD) Without data

Parasite	Host	Locality	Reference
<i>Capillaria</i> sp.	<i>Lama glama</i>	Chaco, Argentina	Rodríguez Camon et al. 2012
		Jujuy, Argentina	Marin et al. 2009
		Valdivia, Chile	Ruiz-Oyarzún et al. 2017
		Potosí, Peru	Flores and Torres 2003 in Mamani Fernández 2012
		Region I, Chile	Migueles and Gallos 1986 and Barraza 1998 in San Martin da Ordenes 2011
		Jujuy, Argentina	Cafrune et al. 2006b in Aguirre and Cafrune 2007
		Cusco, Peru	Mamani Fernández 2012
		Arequipa, Peru	Mora et al. 2012
		Oregon, EEUU	Cebra and Stang 2008
		Cotabambas, Peru	Barcena and Niño de Gusmán 2012
		Oregon and Washington, EEUU	Rickard and Bishop 1991b
<i>Lama pacos</i>		Altiplano, Chile	Rojas et al. 1993
		New Zealand	Bisset and Vlassoff 1991 in McKenna 1997
		Oregon, EEUU	Cebra and Stang 2008
		Kanto Region, Japan	Hyuga and Matsumoto 2016
		Valdivia, Chile	Leiva 1997
		Indiana, EEUU	Johnson 2010
		Cajamarca, Peru	Ortiz 2013
		La Paz, Bolivia	Beltrán Saavedra et al. 2014
		Puno, Peru	Contreras et al. 2014
		Metropolitan Region, Chile	Salas 1985, Gorman et al. 1986 in San Martin da Ordenes 2011
		Puno, Peru	Mamani 1989 in Quispe García 2011
		Cusco, Peru	Mamani Fernández 2012
		Cusco, Peru	Perez et al. 2014
		Puno, Peru	Quina Quina 2015
		Pasco, Peru	Masson et al. 2016
		Arequipa, Tacna	Torres Huacani 2017
		Pichincha, Ecuador	Salazar Robayo 2015; Salazar et al. 2014
		Cotopaxi, Ecuador	Condor Tapia 2015
Cotopaxi, Ecuador	Regalado Valdivieso 2015		
Arequipa, Peru	Mora et al. 2012		
Valdivia, Chile	Valenzuela et al. 1998		
<i>Lama guanicoe</i>	-	-	Ver Fugassa 2020
<i>Vicugna vicugna</i>		Salta, Argentina	Cafrune et al. 2004
		Catamarca and Jujuy, Argentina	Cafrune et al. 2018
		Jujuy, Argentina	Romero et al. 2018
		La Paz, Bolivia	Ruiz Hurtado 2016
		Catamarca, Argentina	Cardoso 2019
		Cusco, Peru	Pacheco et al. 2021
		La Paz, Bolivia	Beltran 1991 in Quispe García 2011
		La Paz, Bolivia	Beltrán Saavedra et al. 2011
		Cajamarca, Peru	Ortiz 2013
		Tacna, Peru	Quispe García 2011

(Continued)

Table 5. (Continued)

Parasite	Host	Locality	Reference
		Cajamarca, Peru	Curay Cabanillas 2018; Curay Cabanillas <i>et al.</i> 2022
		Cusco, Peru	Mamani Fernández 2012
		Arequipa, Peru	Mora <i>et al.</i> 2012
		Tarija, Bolivia	Martela Mamani 2016
		La Paz, Bolivia	Condori <i>et al.</i> 2012
	SAC	Suiza	Hertzberg and Kohler 2006
		WD	Leguía <i>et al.</i> 1995
<i>Capillaria bovis</i>	<i>Lama pacos</i>	WD	Cited in Mamani Fernández 2012
<i>Aonchoteca</i> sp.	<i>L. glama</i> y <i>L. pacos</i>	WD	Cebra 2014

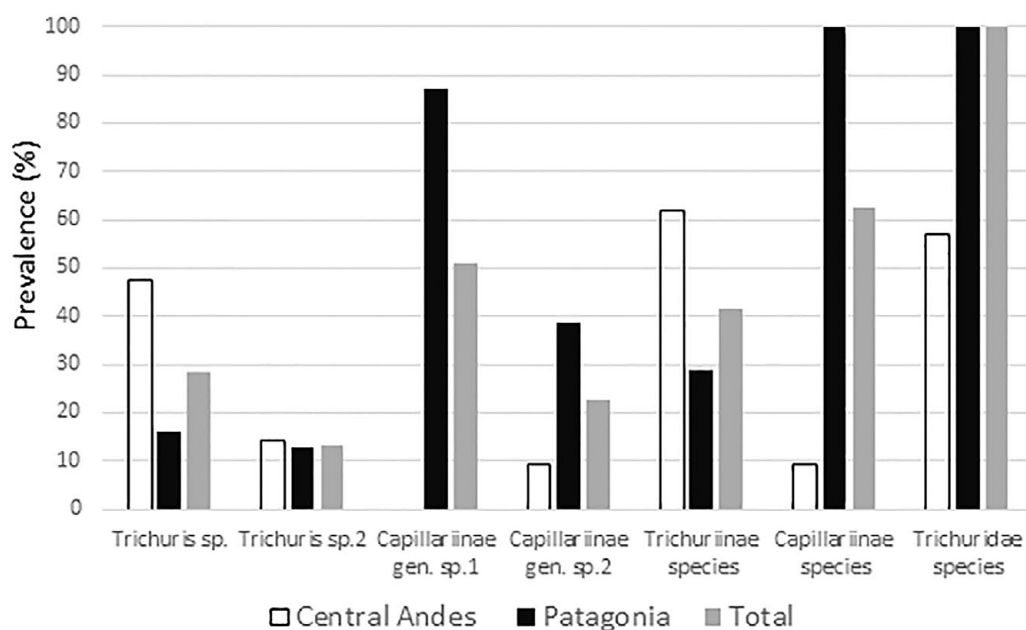


Figure 5. Prevalence of each species in Patagonia and Central Andes regions.

possible that this is due to the fact that their eggs have less requirements for their maturation. Another possible cause for its higher prevalence can be their life stories; these may involve intermediate hosts, paratenic hosts, or reservoirs – this, possibly supported by the apparent low specificity observed by Taglioretti *et al.* 2014 – that reduce the pressures coming from climatic restrictions.

Conclusions

Parasitological studies of archaeological remains confirmed the pre-Hispanic presence of a *Trichuris* species in SACs. The pre-Hispanic presence of a capillariid specific to SACs was also corroborated. Its inclusion by Aguirre and Cafrune (2007) is based on the evidence obtained from camelid mummies (Leguía *et al.*

1995), and its illustration is compatible with the eggs of Capillariinae gen. sp. 2.

Now, the richness of the native trichurid in SACs has been extended by the inclusion of *Trichuris* sp. 2 and Capillariinae gen. sp. 1. Modern *T. tenuis* and *Trichuris* sp. 2 have been proposed as sibling species where the former would have invaded and colonized SACs during the European colonization, and the latter – the native species – would derive from Pleistocene camelids. Regarding Capillariinae gen. sp. 1, the assignment of its eggs to *C. hepaticum* through their morphometric analysis was refuted. Capillariinae gen. sp. 3 remains excluded from the trichurid richness composition in SACs because a single egg was found in only one sample.

Likewise, the integration of parasitological and paleoecological information also allowed us to propose a possible origin for some of them. Although the present analysis is exploratory, it exposes patterns and suggests hypotheses that should stimulate future

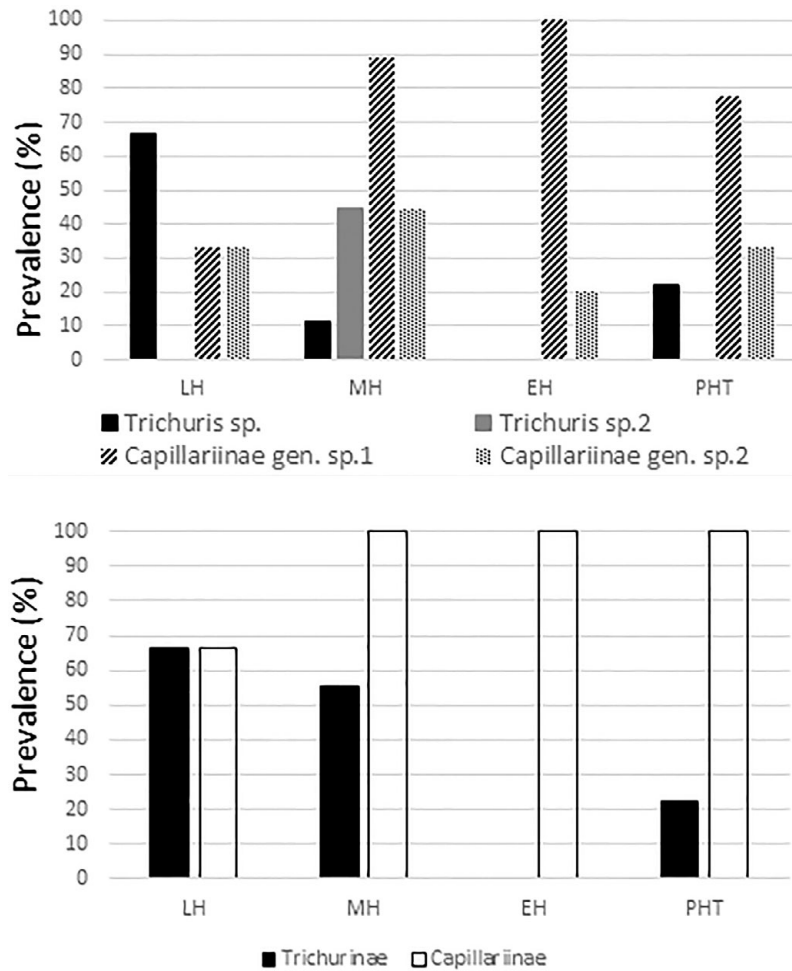


Figure 6. Trichurid prevalence through time in pre-Hispanic Patagonian SACs. (A) Prevalence of each species found, (B) Prevalence of each Subfamily, (LH) Late Holocene, (MH) Middle Holocene, (EH) Early Holocene, (PHT) Pleistocene-Holocene Transition.

research about the biogeographic history and current conservation status of SAC helminths. This information may be relevant, for example, to improve descriptions of the regional ecology during the Holocene and to identify threatened helminths that demand a place on conservation programs.

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