



# Carnivore coprolites from “Gruta del Indio” site as source of paleoparasitological and paleoecological evidences (late Pleistocene-Holocene, Mendoza, Argentina)

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## Abstract

In the southern cone of South America, inhabit a large diversity of Neotropical carnivores. Carnivore coprolites are a valuable source of paleoecological and paleoparasitological information. The rock shelter Gruta del Indio (GI) is an emblematic archeological and paleontological site located from Mendoza, Argentina. Several studies were conducted at this site, which provided a stratified sequence spanning the last ~31 ky BP. The aim of this work was to study parasite remains found in coprolites assigned to carnivores from GI, with the purpose of contributing to the paleoecological knowledge of the site. Twenty coprolites were examined for parasites. Samples were rehydrated in a 0.5% water solution of trisodium phosphate, then homogenized, filtered, and processed by spontaneous sedimentation. The macroscopic remains were separated and dried at room temperature and were examined for diet analysis. All micromammal prey belonged to the Order Rodentia, and six histricomorphs could be identified. Also, bird bones, plant, arthropod, and hair remains were found. Five coprolites contained parasite remains, and eight nematode species were recovered. This is the first paleoparasitological study at this site, and the findings broaden the knowledge of the biogeographic history of the gastrointestinal helminths found. The obtained results evidence the importance of carnivore coprolite studies recovered from archeological contexts in the reconstruction of paleoecological scenarios. Also, the importance of carnivores for the dispersion of their own parasites and the parasites of their prey are discussed. These parasitological findings contribute with the study of the presence of potential parasitic zoonoses in the Holocene.

**Keywords** Paleoparasitology · Felids · Holocene · Helminth diet

## Introduction

South America shelters a wide diversity of wildlife. Among them, current terrestrial carnivores present a relatively high diversity, with 40 out of 245 species of the Order Carnivora

(Hunter and Barrett 2018). Further, the paleontological studies displayed that a rich diversity of carnivores inhabited the continent in the past (Prevosti and Forasiepi 2018).

In the southern cone of South America, inhabit a large diversity of Neotropical carnivores (Bárquez et al. 2006; Teta et al. 2018). Its presence in ancient times has been recorded in archeological and paleontological sites. Among the zooarchaeological materials of carnivores registered throughout time, the coprolites (mineralized or dehydrated scats) have a great relevance. Carnivore coprolites are a valuable source of paleoecological and paleoparasitological information (e.g., Bajdek et al. 2017; Beltrame et al. 2018a; Sianto et al. 2014). The data obtained from paleoparasitological studies is particularly useful for understanding the biological cycles of parasites in the past, the biogeographical history of the species, and the role played by the human and wildlife hosts through time (Araújo and Ferreira 2000; Araújo et al. 2003). From archeological sites of Argentina dated to the Pleistocene-Holocene transition to the late Holocene, carnivore coprolites

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were examined from a paleoparasitological point of view and a rich parasitic diversity were registered (e.g., Beltrame et al. 2018a, 2019a; Fugassa et al. 2009; Tietze et al. 2019).

The rock shelter Gruta del Indio (GI, thereafter) is an emblematic archeological and paleontological site located in the Monte Desert of central western Argentina. Several researches were conducted at this locality which provided a stratified sequence spanning the last ~31 ky BP (e.g., Lagiglia 1956, 1974; Semper and Lagiglia 1962–1968). GI has become one of the most important sources of evidence to infer the early human peopling of the CW Argentina and debate the possible or controversial coexistence between humans and Pleistocene megamammals (e.g., Borrero 2009; Forasiepi et al. 2010; García 1999, 2003a, 2003b; García and Lagiglia 1999; Neme and Gil 2008). Additionally, paleoenvironmental, paleoecological, and taphonomic studies that involve megamammals and micromammals were made (e.g., Dacar et al. 2001; D'Antoni 1983; Fernández and Pardiñas 2018; García et al. 2008; Martínez Carretero et al. 2013; Markgraf 1983; Zárate 2002). Despite the numerous research studies that have been conducted, paleoparasitological studies were not carried out at the present. The aim of the present work was to study parasite remains found in coprolites assigned to carnivores from GI site, with the purpose of contributing with the paleoecological knowledge of the site.

## Site context, material, and methods

### Studied site

The archeological and paleontological site GI is located close to the right margin of the Atuel river (Mendoza, Argentina) (34°35' S, 68° 22' W) (Fig. 1). The site is a large rock shelter whit 50 m wide and 12 m long that was eroded out of a basaltic outcrop, 20 m above the alluvial plain of the Atuel river (Semper and Lagiglia 1962–1968).

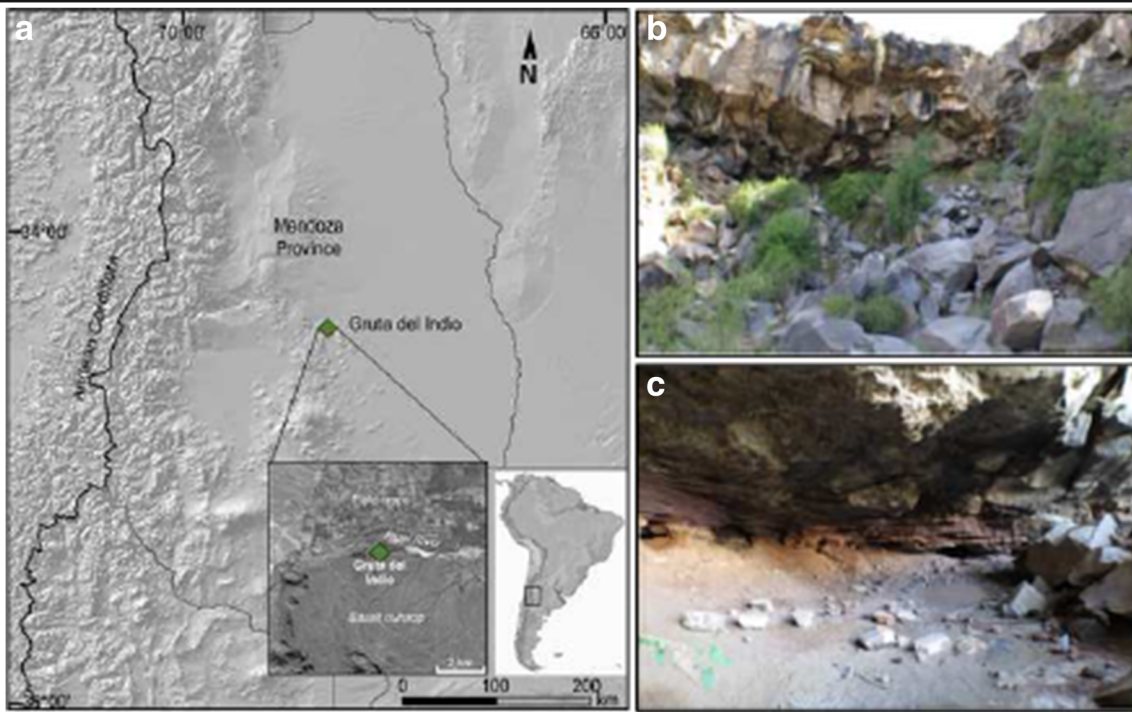
The regional vegetation belongs to the Monte Desert (Abraham et al. 2009; Cabrera 1976), which is included in the climatic region known as the South American Arid Diagonal (Bruniard 1982). It is exposed to the action of the Atlantic anticyclone, with a mean annual temperature about 15 °C and a mean annual precipitation ca. 350 mm. To the W and not far from GI, the regional landscape is characterized by large basaltic plateaus and volcanos, allowing the northern penetration of Patagonian biotic elements (Fernández 2012; Roig et al. 2000).

According to pollen sequence of GI, the Patagonian steppe was replaced by Monte Desert during the Pleistocene-Holocene boundary as a consequence of warmer and drier conditions (D'Antoni 1983; Markgraf 1983). Nonetheless, the small mammals and the plants contained in coprolites from cavid and chinchillid rodents, and extinct equids recorded in

GI, indicated overall stability under Monte conditions since at least 31 ky BP (Dacar et al. 2001; Fernández and Pardiñas 2018; García et al. 2008; Martínez Carretero et al. 2013).

The most recent cultural context, named “Atuel I”, is represented by pictographs on the walls of the rock shelter conducted by araucanized indigenous groups (Puelches and Pehuenches) during historical times (Semper and Lagiglia 1962–1968). The sedimentary profile shows four natural layers. The uppermost level, Layer 1, is between 20 and 40 cm depth (exceptionally up to 60 cm) and composed of yellowish brown loess-type sediment (Semper and Lagiglia 1962–1968). It was associated to “Atuel II” cultural context characterized by an incipient agriculture (maize, cucurbit and beans), chronologically placed between ca. 2.3 and 1.9 ky <sup>14</sup>C BP (Semper and Lagiglia 1962–1968). Layer 2 is between 40 and 100 cm depth (defined on the left side of the rock shelter). It presented the same type of sediment as above but friable. It also displayed a tephra band of 5 cm thick. This layer was linked to “Atuel III” preceramic cultural context where the rock shelter was mainly used for funeral activities associated to cordage, basketry, and bone tools between ca. 3.8 and 2.3 ky <sup>14</sup>C BP (Semper and Lagiglia 1962–1968). Layer 3 is between 70 and 110 cm depth (defined on the right side of the rock shelter) and included small fragments of basaltic rock fallen from the ceiling of the rock shelter. The upper part of this layer chronologically placed between ca. 11 to 8 ky <sup>14</sup>C BP was related to the oldest cultural context so-called “Atuel IV”, allied with extinct megafauna identified as *Myiodon* sp., *Macrauchenia* sp., and *Hippidion* sp. (García 2003a; García and Lagiglia 1999; García et al. 2008; Semper and Lagiglia 1962–1968). It is expected that the first occupations in GI were the consequence of short-term events, associated with groups that would be exploring the local landscape (Iniesta et al. 2020). The lower part of Layer 3 range from ca. 31 to 11 ky <sup>14</sup>C BP presents megafauna remains assigned to *Myiodon* sp. and *Hippidion* sp. (García 2003a; García and Lagiglia 1999; García et al. 2008; Long et al. 1998; Semper and Lagiglia 1962–1968), although they are not associated with human occupation because these findings did not show taphonomic evidences of human processing (Borrero 2009). Layer 4 is 20 cm thick, which exhibits a dark sand and gravel deposit with neither cultural nor faunal remains (García et al. 2008; Martínez Carretero et al. 2013).

Although the remains of megamammals and micromammals were analyzed in detail (e.g., Borrero 2009; Fernández and Pardiñas 2018; Forasiepi et al. 2010; García 2003a, 2003b; García et al. 2008; Martínez Carretero et al. 2013), there is a lack of taphonomical knowledge about the medium and large-size mammals recovered from GI (e.g., Semper and Lagiglia 1962–1968). This makes it difficult or impossible to know the human



**Fig. 1** **a** Geographic location from Gruta del Indio site, Mendoza, Argentina; **b** Outside rock shelter; **c** Inside rock shelter

paleo diets and the possible interactions between human and fauna since the first occupations.

## Methodology

Twenty coprolites assigned to carnivorous from GI were examined for parasites. The samples belong to three temporal units (Layer 1 = ca. 2.3–1.9 ky  $^{14}\text{C}$  BP; Layer 2 = ca. 3.8–2.3  $^{14}\text{C}$  ky; and Layer 3 = ca. 31–8 ky  $^{14}\text{C}$  BP) (Table 1). The examination consisted of an external observation of feces (morphology, size, and color) according to Chame (2003). Samples of 1 g of the interior of each coprolite were processed by rehydration in 0.5% water solution of trisodium phosphate (TSP) in plastic tubes for 72 h, followed by homogenization, filtered and processed by spontaneous sedimentation (Lutz 1919). Samples were preserved in 70% ethanol. Twenty slides of each sample were made with one drop of sediment and one drop of glycerin and then were examined at 100X and 400X using light microscopy. The recovered parasitic remains were measured and photographed. Broken eggs were discarded. Egg dimensions and morphologies were compared with data from the literature.

Next, to study the macroscopic remains, each of the remaining samples was rehydrated in 0.5% water solution of TSP in glass containers for at least 72 h. Then, the samples were disaggregated with a sterile scalpel, and the macroscopic remains were separated and dried at room temperature. Remains were observed under a stereomicroscope for diet analysis. Taxonomic identifications of micromammal were made on cranial and dental remains, through comparisons against modern specimens belonging to

the mammal collection of Grupo de Estudios en Arqueometría (FIUBA, Buenos Aires, Argentina) and specific literature (e.g., Fernández et al. 2011; Pearson 1995). Rodent taxonomy used here follows Patton et al. (2015). Since fragmentary remains of the caviomorph *Ctenomys* (tuco-tuco) are very difficult to identify at species level, they were characterized only to the generic level.

The skeletal remains contained in the coprolites were taphonomically studied following the four categories of digestive corrosion (light, moderate, heavy, and extreme) on bones (Andrews 1990) and teeth (Fernández et al. 2017). According to Andrews (1990), the corrosion marks on the surfaces of bones are observed on proximal epiphysis of femur and distal epiphysis of the humerus. However, taking into account the small sample size, the corrosion will be registered in all bones. In case of the few remains of bird recovered from some coprolites, the digestive corrosion was recorded following Bochenski and Tomek (1997). Digestive corrosion is considered the greatest signature of predation of small mammals recovered from archeological and paleontological sites (e.g., Andrews 1990; Fernández et al. 2017; Montalvo and Fernández 2019).

## Results

Table 1 presents the layer, dates, measurements, parasites, and macroscopic remains of each studied coprolite. The macroscopic remains included in this table are as follows: plants

**Table 1** Layers, dated, cultural period, measurements, parasites, and macroscopic remains found in carnivore samples from Gruta del Indio site, Mendoza, Argentina. Plant remains [abundance: (+) scarce, (++) little, (+++) abundant, and (++++) very abundant]

Layer	Dates (ky BP)	Cultural period	Coprolite	Macroscopic remains			Parasite remains			
				Length	Width	Sizes (mm)				
				Arthropod exoskeleton		Vertebrate prey identified				
				Plants presence	Hairs					
1	2.3–1.9	Atuel II	G11			Negative	–	–	Positive	
			G12	+++	29,91	17,24	Negative	–	–	Positive
			G15	++	42,80	15,46	Negative	Tangles, gray and blacks	Indet. Sigmodontinae	Positive
			G16	+	27,93	14,74	Negative	Tangle, black and white	Indet. Sigmodontinae and Passeriformes	Negative
			G18	+	19,58	16,28	Negative	Tangle, browns	–	Negative
			G19	++	44,78	22,03	Negative	Blacks, browns and gray	<i>Graomys griseoflavus</i>	Negative
			G112	++	54,78	31,02	Positive	Tangles, browns and gray	<i>Ctenomys</i> sp.	Positive
			G113	+	57,19	23,41	Positive	Gray	<i>Phyllotis xanthopygus</i>	Negative
			G114	++	29,67	16,83	Positive	Black and gray	<i>Ctenomys</i> sp., <i>Galea leucoblephara</i> , indet. Sigmodontinae, and indet. bird	Negative
			G115	++	32,99	19,15	Positive	Gray	Indet. Rodentia	Negative
			G116	++++	34,46	17,57	Negative	Gray	Indet. Sigmodontinae	Positive
			G117	++	37,07	14,33	Positive	Yellow and light brown	Indet. Bird	Negative
			2	3.8–2.3	Atuel III	G118	++	18,39	14,59	Negative
G119	++	31,03				17,85	Negative	White and gray	Indet. Caviomorpha	Negative
G120	+	25,14				18,46	Negative	Light browns and dark browns	<i>Calomys musculus</i>	Negative
G110	+++	43,98				21,19	Positive	Browns	<i>Calomys musculus</i> and indet. Sigmodontinae	Negative
G111	++	65,63				13,97	Negative	Light brown and dark brown	Indet. Rodentia	Positive
G13	++	17,52				15,45	Negative	Gray and browns	<i>Microcavia australis</i>	Negative
G14	+++	22,57				17,16	Positive	–	–	Negative
3	31–8	Atuel IV	G17	+	26,01	16,98	Negative	Grays and browns	<i>Galea leucoblephara</i> Indet. Sigmodontinae Medium-sized raptor bird <i>Galea leucoblephara</i>	Negative



[(+) scarce, (++) poor, (+++) abundant, and (++++) very abundant], exoskeletons of arthropods, hairs, and the vertebrate prey identified of each examined coprolite. These remains were indicative of a carnivorous or omnivorous diet. After rehydration, all samples showed a dark coloration and an intense odor, typical of carnivorous fecal material.

The morphology of the studied coprolites is shown in Fig. 2. Seventeen samples presented skeletal remains such as teeth, maxillae, mandibles, bone of extremities, and other diverse skeletal bones (Tables 1 and 2). In some cases, prey identification was possible. All prey identified as micromammal (< 1 kg) belonged to the Order Rodentia. The histricomorphs include the lowland yellow-toothed cavy *Galea leucoblephara* (Caviidae, Caviinae), the southern mountain cavy *Microcavia australis* (Caviidae, Caviinae), and the tuco-tuco *Ctenomys* sp. (Ctenomyidae, Ctenomyinae). The miomorph species contain the gray leaf-eared mouse *Graomys griseoflavus* (Cricetidae, Sigmodontinae), the yellow-rumped leaf-eared mouse *Phyllotis xanthopygus* (Cricetidae, Sigmodontinae), and the

drylands vesper mouse *Calomys musculus* (Cricetidae, Sigmodontinae). Bird bones of Passeriformes and other types possibly belonging to a raptor bird were also found (Table 1).

Most coprolites contain all bones and teeth fractured and digested (Table 2). Few skull remains were recorded, including two fragments of maxillae (GI8) and one broken mandible (GI7). Unidentified fragments were important in several coprolites (GI2, GI5, GI8, GI9, GI12, GI14, GI16, and GI18). The remains with evidence of digestive corrosion were mainly assigned to light and moderate categories (Table 2), although several coprolites had bones and teeth with heavy corrosion (GI8, GI9, GI10, GI11, GI13, GI15, and GI18) and two coprolites (GI11 and GI13) yielded bones with extreme digestion.

Microscopic observations revealed that five coprolites contained remains of parasites. A total of eight nematode species were recovered. The coprolites positive for parasites and measurements of the eggs found are shown in Table 3.

Two different nematode eggs were found in coprolite GI1. In one case, the egg was oblong and brown, with a thick and striated wall, with a subterminal and notorious operculum, and

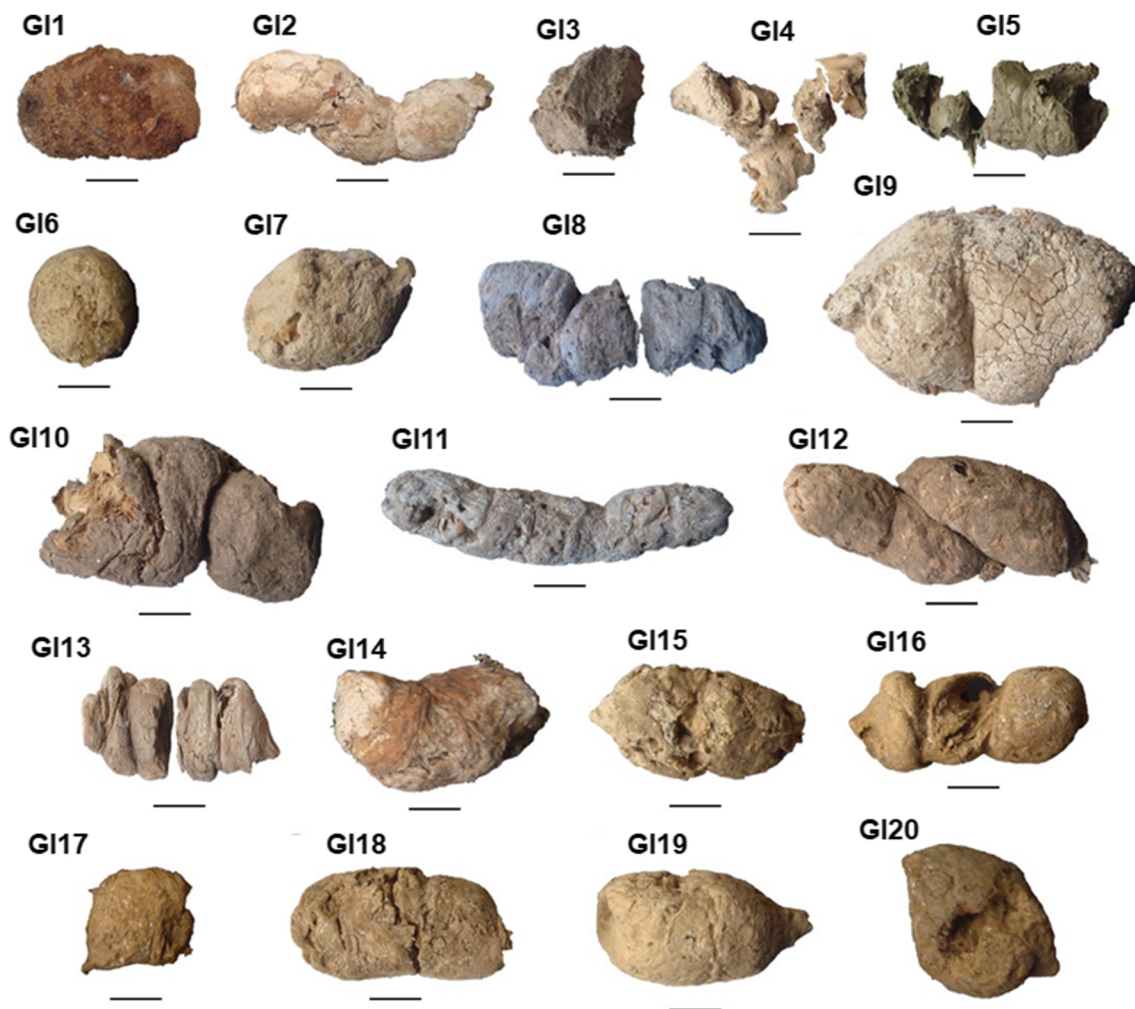


Fig. 2 General appearance of coprolites from Gruta del Indio site, Mendoza, Argentina. Bar: 1 cm

**Table 2** Breakage and categories of digestive corrosion in carnivore coprolites from Gruta del Indio site, Mendoza, Argentina

		Fracture		Digestive corrosion									
				Absent		Light		Moderate		Heavy		Extreme	
		<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%	<i>N</i>	%
G12	Incisor ( <i>n</i> =5)	5	100	0	0	3	60	2	40	0	0	0	0
	Vertebra ( <i>n</i> =2)	0	0	0	0	1	50	1	50	0	0	0	0
	Metapodial ( <i>n</i> =2)	2	100	2	100	0	0	0	0	0	0	0	0
	Fragment indet. ( <i>n</i> =19)	19	100	9	47	5	26	5	26	0	0	0	0
	Femur ( <i>n</i> =1)	1	100	0	0	1	100	0	0	0	0	0	0
G15	Humerus* ( <i>n</i> =1)	1	100	0	0	1	100	0	0	0	0	0	0
	Fragment indet. ( <i>n</i> =9)	9	100	0	0	5	56	4	44	0	0	0	0
G17	Mandible ( <i>n</i> =1)	1	100	0	0	0	0	1	100	0	0	0	0
	Molar ( <i>n</i> =2)	0	0	0	0	0	0	2	100	0	0	0	0
G18	Maxilar ( <i>n</i> =2)	2	100	0	0	2	100	0	0	0	0	0	0
	Incisor ( <i>n</i> =2)	2	100	0	0	2	100	0	0	0	0	0	0
	Molar ( <i>n</i> =6)	0	0	0	0	2	33	4	67	0	0	0	0
	Vertebra ( <i>n</i> =2)	0	0	0	0	2	100	0	0	0	0	0	0
	Femur ( <i>n</i> =1)	1	100	0	0	1	100	0	0	0	0	0	0
	Tibia ( <i>n</i> =1)	1	100	0	0	0	0	0	0	1	100	0	0
	Fragment indet. ( <i>n</i> =7)	7	100	0	0	2	29	5	71	0	0	0	0
G19	Incisor ( <i>n</i> =1)	1	100	0	0	0	0	1	100	0	0	0	0
	Fragment indet. ( <i>n</i> =5)	5	100	0	0	0	0	4	80	1	20	0	0
G110	Vertebra ( <i>n</i> =2)	1	50	0	0	0	0	2	100	0	0	0	0
	Scapula ( <i>n</i> =1)	1	100	0	0	0	0	1	100	0	0	0	0
	Fragment indet. ( <i>n</i> =9)	9	100	0	0	2	23	4	44	3	33	0	0
G11	Molar ( <i>n</i> =3)	2	67	0	0	0	0	2	67	1	33	0	0
G12	Molar ( <i>n</i> =1)	1	100	0	0	1	100	0	0	0	0	0	0
	Fragment indet. ( <i>n</i> =8)	8	100	0	0	0	0	0	0	0	0	8	100
G113	Incisor ( <i>n</i> =3)	3	100	0	0	3	100	0	0	0	0	0	0
	Molar ( <i>n</i> =5)	2	40	0	0	0	0	5	100	0	0	0	0
	Vertebra ( <i>n</i> =1)	0	0	1	100	0	0	0	0	0	0	0	0
	Femur ( <i>n</i> =1)	1	100	0	0	0	0	0	0	0	0	1	100
	Tibia ( <i>n</i> =1)	1	100	0	0	0	0	1	100	0	0	0	0
	Astragalus ( <i>n</i> =1)	0	0	1	100	0	0	0	0	0	0	0	0
	Metapodial ( <i>n</i> =3)	0	0	0	0	3	100	0	0	0	0	0	0
	Tibiotarsus* ( <i>n</i> =1)	1	100	0	0	–	–	–	–	–	–	–	–
	Tarsometatarsus* ( <i>n</i> =1)	1	100	0	0	–	–	–	–	–	–	–	–
Fragment indet. ( <i>n</i> =40)	40	100	10	25	15	37.5	11	27.5	4	10	0	0	
G14	Fragment indet. ( <i>n</i> =4)	4	100	0	0	4	100	0	0	0	0	0	0
G115	Astragalus ( <i>n</i> =1)	0	0	0	0	1	100	0	0	0	0	0	0
	Matapodial ( <i>n</i> =2)	2	100	0	0	0	0	1	33	2	67	0	0
	Phalange ( <i>n</i> =6)	5	83	0	0	2	33	4	67	0	0	0	0
G116	Fragment indet.* ( <i>n</i> =8)	8	100	0	0	–	–	–	–	–	–	–	–
G118	Vertebra ( <i>n</i> =1)	1	100	0	0	0	0	0	0	1	100	0	0
	Tibia ( <i>n</i> =1)	1	100	0	0	0	0	0	0	1	100	0	0
	Fragment indet. ( <i>n</i> =2)	2	100	0	0	0	0	2	100	0	0	0	0
G120	Incisor ( <i>n</i> =2)	2	100	0	0	2	100	0	0	0	0	0	0
	Molar ( <i>n</i> =1)	0	0	0	0	1	100	0	0	0	0	0	0

\*Bird remains, all with evidence of digestive corrosion in the category of rounded (sensu Bochenski and Tomek 1997)

**Table 3** Parasitic remains, quantity, and measurements of the eggs found in carnivore coprolites from Gruta del Indio site, Mendoza, Argentina

Coprolite	Eggs ( <i>n</i> )	Size ( $\mu\text{m}$ )						Parasite eggs
		Length			Width			
		Min	Max	Med	Min	Max	Med	
GI1	1	137.5			62.5			<i>Helminthoxys</i> sp. (Oxyurida: Oxyuridae)
	1	57.5			35			<i>Physaloptera</i> sp. (Spirurida: Physalopteridae)
GI2	1	55			30			Spirurid (Spirurida)
GI9	3	42.5	50	45.8	35	37.5	36.6	<i>Toxascaris leonina</i> (Ascaridida: Ascarididae)
	83	62.5	77.5	71.3	32.5	45	39.5	Oxyurid (Oxyurida: Oxyuridae)
GI10	8	62.2	77.5	69.7	35	40	33.1	<i>Trichuris</i> sp. (Trichinellida: Trichuridae)
	1	132.5			72.5			<i>Heteroxyxynema viscaciae</i> (Oxyurida, Heteroxyxynematidae)
	1	47.5			35			<i>Toxascaris leonina</i> (Ascaridida: Ascarididae)
GI15	5	52.5	65	59.5	30	35	33	<i>Trichuris</i> sp. (Trichinellida: Trichuridae)
	1	57.5			37.5			Oxyurid (Oxyurida: Oxyuridae)

was embryonated. The measurements were 137.5  $\mu\text{m}$  in length and 62.5  $\mu\text{m}$  in width. The identity of egg was attributed to the genus *Helminthoxys* sp. (Oxyurida, Oxyuridae) (Fig. 3a). The other egg was oval with a thick and smooth wall and was embryonated. The measurements were 55  $\mu\text{m}$  in length and 30  $\mu\text{m}$  in width. The egg was assigned to *Physaloptera* sp. (Spirurida: Physalopteridae) (Fig. 3b).

A nematode egg was found in coprolite GI2. The egg presented an oblong shape, with a thick and smooth wall, and was embryonated. The measurements were 57.5  $\mu\text{m}$  in length and 35  $\mu\text{m}$  in width. The egg was identified as a spirurid (Spirurida) (Fig. 3c).

Eggs of parasites assigned to two species of nematodes were found in coprolite GI9. Some eggs ( $n = 3$ ) had a round shape, with a thick and mamillated wall, and were embryonated (Fig. 3d). The average measurements were 45.8  $\mu\text{m}$  in long and 36.6  $\mu\text{m}$  in wide. The eggs were assigned to *Toxascaris leonina* (Ascaridida: Ascarididae). Nematode eggs ( $n = 83$ ) with an oblong shape, with thin walls, and the presence of operculum on one side was also found. The average measurements were 71.3  $\mu\text{m}$  in long and 39.5  $\mu\text{m}$  in wide. The eggs were attributed to an indeterminate oxyurid (Oxyurida: Oxyuridae) (Fig. 3e).

In coprolite GI10, parasite eggs attributed to three species of nematodes were found. Some eggs ( $n = 8$ ) were lemon-shaped, with smooth surface and plug-shaped structures at their ends. The eggs were assigned to *Trichuris* sp. (Trichinellida: Trichuridae) (Fig. 3g). The measurements were 69.7  $\mu\text{m}$  in long and 33.1  $\mu\text{m}$  in wide. Eggs with an oblong shape, thick-walled, embryonated, with one rounded pole and the other one sharp were also observed. The presence of plaques was observed at the sharp end of the egg. The measures were 132.5  $\mu\text{m}$  in length and 72.5  $\mu\text{m}$  in width. The eggs were assigned to *Heteroxyxynema (Cavioxynema) viscaciae*

(Oxyuroidea, Heteroxyxynematidae) (Fig. 3f). Another egg, with a round shape, thick-walled, with mamillated surface, and embryonated, was found. The measurements were 47.5  $\mu\text{m}$  in long and 35  $\mu\text{m}$  in wide. The egg was assigned to *T. leonina* (Ascaridida: Toxocaridae) (Fig. 3d).

Coprolite GI15 presented two nematode species. Some eggs ( $n = 5$ ) were lemon-shaped, with smooth surface and polar plugs. The measurements were 59.5  $\mu\text{m}$  in length and 33  $\mu\text{m}$  in width. The eggs were assigned to *Trichuris* sp. (Trichinellida: Trichuridae) but were attributed to another species to that found in sample GI10 (Fig. 3h). Finally, one oblong egg ( $n = 1$ ), with thin walls and with an operculum on one side, was also observed (Fig. 3e). The measurements were 57.5  $\mu\text{m}$  in length and 37.5  $\mu\text{m}$  in width. This egg can be attributed to an indeterminate species of oxyurid, similar to that found in GI 9.

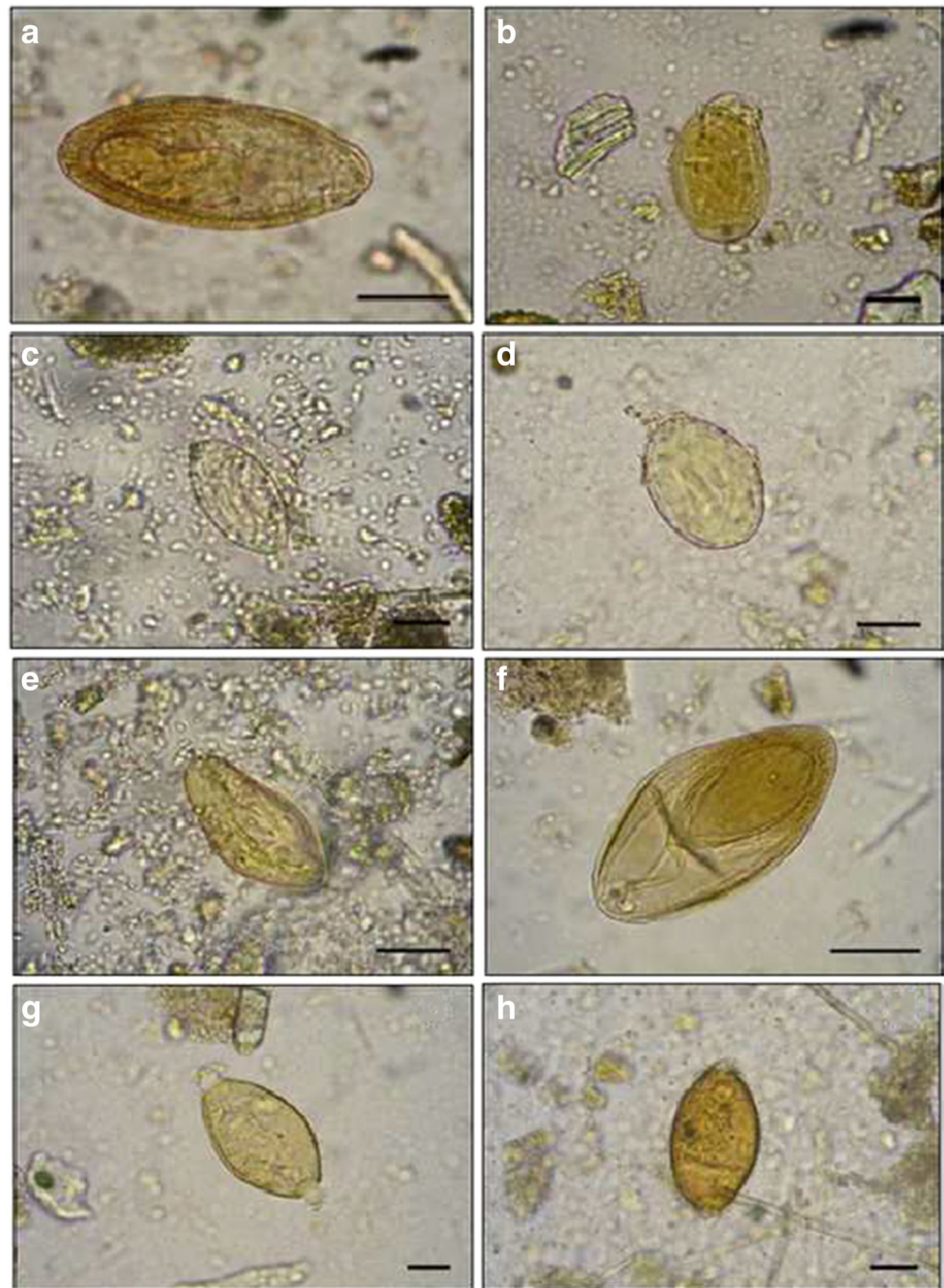
## Discussion

From an ecological approach, due to the wide home range and the trophic level, carnivores are keystone species. Carnivores play a critical role in the dispersion of parasite species of their prey (e.g., micromammals, reptiles, birds) and their own parasites in the environment, through the dispersion of diverse infectious stages through the scats (Moleón et al. 2015; Vieira et al. 2008). Besides, carnivores have an important role in the maintenance and spread of many zoonotic parasitic diseases (Otranto and Deplazes 2019).

Carnivore scats can be identified based on morphological characteristics and usually contain remains of their prey such as hairs, feathers, and bones (Montalvo et al. 2007; Palacios 2007). The constrictions are one of the morphological characteristics of the carnivore scats and allow differentiate between



**Fig. 3** Helminth eggs found in carnivore coprolites from Gruta del Indio site, Mendoza, Argentina: **a** *Helminthoxys* sp. (Oxyurida: Oxyuridae) Bar: 40  $\mu$ m; **b** *Physaloptera* sp. (Spirurida: Physalopteridae) Bar: 20  $\mu$ m; **c** indet. Spirurid (Spirurida) Bar: 20  $\mu$ m; **d** *Toxascaris leonina* (Ascaridida: Ascarididae) Bar: 20  $\mu$ m; **e** indet. Oxyurid (Oxyurida: Oxyuridae) Bar: 30  $\mu$ m; **f** *Heteroxytnema viscaciae* (Oxyurida: Heteroxytnematidae) Bar: 40  $\mu$ m; **g** *Trichuris* sp. (Trichinellida: Trichuridae) Bar: 20  $\mu$ m; **h** *Trichuris* sp. (Trichinellida: Trichuridae). Bar: 20  $\mu$ m



canid and felid scats. In general, the felid scats present marked and close constrictions, with strangulations and well-defined segments and one of the extremities especially tapered (Fig. 2, e.g., GI9, GI10, GI13, and GI16), while the canid scats have separated and less marked constrictions with a characteristic pointed end (Fig. 2, e.g., GI11, GI15, GI18, and GI19). The diameter of the scats also allows to identify large felids from small and medium-carnivorous. The measurements of the small and medium-sized carnivore scats range from 11 to 18 mm in diameter, while for large felid scats, the average diameter is 25 mm or more (Palacios 2007; Chame 2003).

From South America, large felid scats with diameters greater than 2.5 cm can be identified as belonging to jaguar, *Panthera onca*, or puma, *Puma concolor* (Chame 2003). Their scats are usually deposited in rock shelters and caves where these large felids frequently have its lairs and latrines (Martín and Borrero 1997; Martín 2008; Montalvo et al. 2007). In the particular cases of the coprolites GI9 and GI10, their morphology and size suggested that correspond to a large carnivore. *P. concolor* is the only large size carnivore inhabiting currently in this area, although *P. onca* lived in the area until historical times (Lehaman-Nitsche 1907). Morphometric patterns



cannot distinguish puma scats from jaguar ones due to their similar characteristics (Emmons 1997). The scats of large carnivores can sometimes be totally white as a result of high calcium content as a consequence of the ingestion of bones (Palacios 2007). In sample GI9, it can be observed the whitish coloration (Fig. 2). In the high Andean areas of Argentina and southern Chile, a high consumption of ungulates and camelids along with medium-sized preys has been recorded as a substantial part of the diet of big felids (Cajal and Lopez 1987; Franklin et al. 1999). A higher consumption of small rodents was recorded in protected areas in southern Chile, in Argentinean Patagonia (histicomorph and myomorph rodents) and in the Paraguayan Chaco. Nonetheless, the importance of rodents in terms of biomass consumed is minor (Montalvo et al. 2007). The bone material of the largest mammals included in the diet of big felids is represented by unidentifiable fragments, which indicate extensive bone breakage with strong evidence of digestion such as thinning, superficial degradation, polishing of prominent areas, and presence of holes. The small mammals, on the other hand, are the ones that show the greatest integrity in the entire total sample, which suggests that the prey was swallowed entirely without chewing (Montalvo et al. 2007). This explains the findings of coprolites G9 and GI10, which mainly include bones of small mammals from light to heavy digestive corrosion (Table 2). *P. concolor* is a broad-spectrum opportunistic predator, and its diet varies with the seasons and between each individual. It feeds on lizards, hares, rodents, birds, and even large herbivores, such as guanacos, increasing the weight of their prey with the latitude increase (Rau and Jiménez 2002; Walker et al. 2010). Given the wide distribution and habitat diversity of *P. onca*, this carnivore is an opportunistic predator whose diet reflects the available prey community of a particular area (Hayward et al. 2016). The diet is diverse, with at least 85 species listed as prey, with a range from more than 200 kg to small rodents (Weckel et al. 2006). In this study, *Ctenomys* sp. and indeterminate Rodentia bones remains were found, understanding this finding as part of this carnivore diet. Also, arthropod remains, vegetal tissues, and hairs were observed. These findings suggest an omnivorous diet of these felids.

The other coprolites analyzed in this study could be assigned to small or medium-sized carnivores based on characteristics morphological, taphonomic, and diet (Tables 1 and 2, Fig. 2). The diameter sizes of these scats are smaller than those of the big carnivores mentioned above (Table 1). Also, several of the samples present a whitish coloration (Fig. 2, GI2, GI8, GI11, GI13, and GI19), linking this with the consumption of prey that provide high-calcium content. Among the small carnivores species inhabiting the study area, may include the wild cats *Leopardus colocolo* and *Leopardus geoffroyi*, the skunk *Conepatus chinga*, and the Pampas gray fox *Lycalopex gymnocercus*, which feed mainly on rodents

(Redford and Eisenberg 1992; Wilson and Reeder 2005). These small carnivores yield bone and tooth modifications with high proportion of breakage and digestive corrosion, embracing all the proposed categories, because their chews crush their prey before ingesting it, contrary to what is observed in large carnivores like *P. concolor* (see Montalvo and Fernández 2019, and references therein). In coincidence, the skeletal remains contained in the smaller studied coprolites were severely broken and digested (Table 2).

This is the first paleoparasitological study from Atuel river basin. Paleoparasitological examinations of samples revealed the presence of eight nematode species. Two species of the genus *Trichuris* sp. were found in this study. Trichurid parasites, commonly known as “whipworms”, are found worldwide, but at a higher frequency in tropical and subtropical environments. This nematode has a direct life cycle, where the host acquires the infection by ingestion of eggs from the soil. They host various mammals and marsupial hosts, for example, ruminants, rodents, primates (including humans), canids, minks, wolves, foxes, jackals, coatis, skunks, ferrets, weasels, raccoons, pumas, cats, seals, pigs, and horses (Anderson 2000). This parasite is located in the caecum and colon of the host. The larval stages of *Trichuris* sp. cause hemorrhages and local edema, causing bacterial infections. They are expelled abroad along with feces, and their embryonic development takes place in the external environment (Anderson 2000). Previous studies in Holocene environments from Patagonia reported *Trichuris* spp. in coprolites of rodents, deer, camelids, megamammals, and carnivores (Fugassa et al. 2009, 2010; Sardella et al. 2010; Beltrame et al. 2017, 2018b, 2020, among others). So, this finding extends the past distribution of *Trichuris* sp. to the studied area.

False parasitism (or pseudoparasitism) occurs when a parasite which does not normally utilize a host for the perpetuation of its lifecycle is found in that host incidentally. In the case of carnivores, due to the fact that they are top predators, pseudoparasitism is a common finding, as their prey (e.g., small mammals, reptiles, and birds) may be infected by such parasites.

The finding of Oxyuroidea eggs in carnivore coprolites is associated with consumption of parasitized prey, due to the fact that carnivores are not natural oxyurid hosts. Oxyurid species are monoxenic parasites that live in the posterior third of the digestive tract of various vertebrates and arthropods (Anderson 2000). Infection occurs when eggs are ingested with contaminated food or water. They are incubated in the small intestine and subsequently develop into their adult state by moving into the colon (Adamson 1989; Anderson 2000; Petter and Quentin 1976). The Heteroxynematidae family includes species that evolved in sciuriform rodents, caviomorphs, and myomorph. The eggs found in coprolite GI10 were assigned to *H. viscaciae*, parasite of the mountain vizcacha *L. viscacia* (Caviomorpha: Chinchillidae) (Hugot

and Sutton 1989a). Therefore, the finding of this parasite in coprolites assigned to *P. concolor* or *P. onca* is associated with a pseudoparasitism, due to the ingestion of *L. viscacia*, giving information about possible trophic relationships between these felids and *L. viscacia* in samples dated to 3800–2300 years B.P. The presence of *H. viscaciae* from Patagonia has been reported in the current samples of *L. viscacia* from Chubut province (Hugot and Sutton 1989a) and in ancient samples from archeological and paleontological sites (Beltrame et al. 2012, 2016, 2019b). Furthermore, it was found in felid coprolites assigned to *P. concolor* or *P. onca* from Cueva Galpón, an initial late Holocene mortuary site from northeast Patagonia (Beltrame et al. 2019a).

The genus *Helminthoxys* includes ten nominal species, all of them parasites of neotropical caviomorphs (Hugot and Sutton 1989b). Several studies have demonstrated the high specificity of these oxyurids with the host, with a parallel relationship with their phylogeny (Hugot 2003). A recent study documented the presence of *Helminthoxys effilatus* from the Cueva Peligro archeological site, Chubut, for the last 1200 years in samples assigned to *M. australis* (Beltrame et al. 2019b). Furthermore, the presence of *Helminthoxys caudatus* in coprolites samples assigned to *M. australis* from the Somuncurá Plateau Protected Natural Area (Patagonia, Argentina) was also reported (Beltrame et al. 2018b). Due to the fact that the host range of this genus seems to be strictly restricted to the Hystricomorphs (Hugot 2003), the presence in carnivore samples could be associated with the predation of hystricomorphs.

Additionally, unidentified oxyurids also were found in two carnivore coprolites studied. The morphometry of the eggs found is similar to that of *Enterobius vermicularis* (Oxyuridae, Oxyurida), which is known as a human parasite. One possible explication to the presence of this parasite in carnivore coprolites could be related to coprophagy, in close contact with humans and their feces. A recent study (Lino et al. 2018) reports the presence of *E. vermicularis* in pre-Columbian coprolites from Brazil, associated possibly with foxes and raccoons. However, future studies are needed in order to confirm the oxyurid species found.

Parasitic species of the family Ascarididae (“ascarids”) cause among the most widespread and important zoonotic infections. Ascarididae eggs are released in large numbers through the feces of the hosts. In favorable environmental conditions, they develop in infectious larvae. It also contributes to the existence of parathenic hosts, mostly rodents, an important item of carnivore diet that may have larval stages. Parathenic hosts ingested by a carnivore transmit the larvae and then mature in the wall and lumen of the intestine of the definitive host. Eggs become infectious in the soil (Anderson 2000). The definitive hosts of *T. leonina* are both feline and canine species, usually found in the small intestine of cats, dogs, lions, mountain lion, tigers, foxes, coyotes, jackals,

and other wild felids and canids around the world (Levine 1968; Strube et al. 2013). Current studies in South America have found the presence of *T. leonina* in wild and domestic felines from Brazil (Vieira et al. 2008), in different fox species from Chile (Acosta-Jamett et al. 2018; Aguilera 2001; Jiménez et al. 2012; Okulewicz et al. 2012) and in *P. concolor* from Argentina (Moleón et al. 2015), among others. In this study, *T. leonina* eggs in samples assigned to *P. concolor* or *P. onca* were found and provide the evidence of the presence of this specie in ancient times from this study area. These findings are important to discuss the possible role of carnivores as potential agents of transmission of zoonotic parasites in the past.

*Physaloptera* sp. and one unidentified spirurid were found. These parasites are located in the digestive tract of amphibians, reptiles, birds, and mammals. They have indirect life cycles and were described in mountain lion, lynx, badger, raccoon, fox, skunk, and coyote, around the world, and are very common in cats (Ramos et al. 2010). The life cycle includes intermediate hosts (orthoptera and coleoptera) or parathenic hosts, such as reptiles and amphibians (Anderson 2000). Carnivores can become infected after eating organisms with infective larvae. The adult stage is found in the esophagus, in the gastric mucosa, and in the small intestine (Anderson 2000; Ortlepp 1922) and produces gastritis, edema, and ulcers (Naem and Asadi 2013). In some cases, were found in humans (Mohamadain and Ammar 2012). *Physaloptera* sp. has been identified in prehistoric coprolites belonging to canids from archeological sites from Patagonia (Beltrame et al. 2018a; Fugassa et al. 2006; Fugassa et al. 2018) and human coprolites from the archeological site Cueva de los Muertos Chiquitos from Mexico (Cleeland et al. 2013). In this study, the presence of Physalopteridae provides information on the possible presence of zoonotic diseases to which ancient populations were exposed.

Zoonoses, any disease or infection that is naturally transmissible from vertebrate or invertebrate animals to humans and vice versa, are currently considered one of the most important threats for Public Health worldwide. In the past, numerous zoonoses also were present (Beltrame et al. 2018a, 2019a; Sianto et al. 2009; Tietze et al. 2019). Today, carnivores have important public health relevance due to their potential impact in the epidemiology of many zoonotic parasitic diseases (Otranto and Deplazes 2019). Nevertheless, carnivores also acted like zoonotic parasite reservoirs in ancient times (Beltrame et al. 2018a). Some parasitic taxa such as *T. leonina* and *Physaloptera* sp. found in this work are considered potentially zoonotic (Mohamadain and Ammar 2012; Okulewicz et al. 2012), although its presence in humans is very rare. In the other hand, the presence of the zoonotic specie *E. vermicularis* must be confirmed. Egg resistance to both chemical and climatic factors influences egg viability in the environment over long periods of time. Soil type, ambient

temperature, and humidity are the main factors that determine the time it takes an egg to develop to the infective stage (Sommerfelt et al. 2006). There are strong cultural and biological evidences of the presence of hunter-gatherers from the early Holocene of GI (Period Atuel IV, 11–8 ky <sup>14</sup>C BP) and late Holocene (Period Atuel III, 3.8–2.3 ky <sup>14</sup>C BP and Period Atuel II, 2.3–1.9 ky <sup>14</sup>C BP) (e.g., Fernández and Pardiñas 2018; Lagiglia 2002; Neme and Gil 2008; Semper and Lagiglia 1962–1968). The archeological resolution allowed to show temporal ranges where humans and carnivores were found together in Layer 1 (Atuel 2), Layer 2 (Atuel III), and upper Layer 3 (Atuel IV). Although it is not a direct indication of the synchronic occupation of the site, it provides evidences of their presences from GI. In this way, the possibility of exposure to zoonotic diseases in humans due to environmental contamination with eggs of zoonotic species can be related. Therefore, it can be inferred that the hunter-gatherers that inhabited the area in the past were potentially exposed to these parasitic diseases.

The six histricomorph rodents found in carnivore coprolites were previously recorded from sieved sediments of GI, reflecting Monte Desert biome typically linked to drier and warmer conditions (Fernández and Pardiñas 2018). All the identified rodent species prey was present through the Holocene. The prey recorded in the carnivore coprolites was in relation to the availability through the Holocene registered by Fernández and Pardiñas (2018). Additionally, the finding of *H. viscacia* eggs displays the presence of *L. viscacia*. This suggests that the carnivore coprolites are a good tool to complement studies on rodent diversity.

## Conclusion

The rock shelter GI is an emblematic archeological and paleontological site where numerous researches were performed. This is the first paleoparasitological study in this site. Therefore, the present findings broaden the knowledge of the biogeographic history of the gastrointestinal helminths found. Results in the present study evidence the importance of carnivore coprolite studies in the reconstruction of paleoecological scenarios. The paleoparasitological studies of carnivore coprolites are an important source of knowledge concerning the parasites diversity in ancient times. Additionally, it contributes with the identification of the parasites of the prey consumed by these top predators and improves the knowledge of past food webs. The paleoparasitological findings suggest the importance of carnivores for the dispersion of their own parasites and also the parasites of their prey. In the other hand, when the parasite species found have the potential to infect humans, the parasitological findings contribute with the study of the presence of parasitic zoonoses in the Holocene. This is the case of the taxa

*T. leonina* and *Physaloptera* sp. found in this study, considered potentially zoonotic. Finally, we believe it is relevant to continue expanding the number of paleoparasitological studies, to provide complementary information to previous studies carried out in the studied region.

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