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## Review of the rodent paleoparasitological knowledge from South America



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### ABSTRACT

Rodents (Mammalia, Rodentia) are a key mammalian group with a worldwide distribution. The relevance of rodents as hosts in parasitic life-cycles, also in those of zoonotic impact, has been fully recognized. Parasites have been found in ancient remains throughout the world. Paleoparasitology is the study of ancient parasites recovered from archaeological and paleontological sites and materials. This paper reviews the major research activities carried out in rodent paleoparasitology from South America, aiming to integrate data and generate prospects in this field of research. The presence of rodent parasites in ancient times can provide useful and valuable information, as rodent paleoparasitological data can be used from diverse point of views. Anthropologists, biologists, archaeologists, and paleontologists can use this data to reconstruct ancient events based on the parasite life cycles and on the biological requirements to maintain the transmission from host to host. Rodent paleoparasitology may provide a picture of the biodiversity of parasites in ancient times. Although rodent remains are generally present in ancient times, their recovery from archaeological and paleontological contexts is still exceptional.

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### 1. Introduction

Rodents (Mammalia, Rodentia) are a key mammalian group with a worldwide distribution, over 42% of all mammal species (Carleton and Musser, 2005). Their success is due to their small size, the short pregnancy and the ability to gnaw and to eat a wide variety of foods (Wilson and Reeder, 2005). Rodents are important in many ecosystems because they reproduce rapidly, and can function as food source for predators, as dispersors of seeds and as vectors of diseases. Some species are good ecological, climatological, and geographical indicators (i.e. Legendre et al., 2005; Hernández Fernández, 2006; Smith, 2012).

The relevance of rodents as hosts in parasitic life-cycles, also in those of zoonotic impact, has been fully recognized (Miyazaki, 1991; Perkins et al., 2005; Morand et al., 2006). Their role as reservoirs of zoonoses has long been known. Rodents are hosts to a number of ectoparasites such as lice, mites, and ticks, and can

transmit viral, bacterial and protozoan parasites to humans and animals (Soliman et al., 2001). In addition, they can harbour many different protozoan and helminthic endoparasites (Morand et al., 2006).

Parasites have been found in ancient remains throughout the world (Reinhard, 1990; Bouchet et al., 2003; Gonçalves Carvalho et al., 2003; Araújo et al., 2011). Paleoparasitology is the study of ancient parasites recovered from archaeological and paleontological sites and materials (Ferreira et al., 1979; Gonçalves Carvalho et al., 2003). It aims to provide additional information on parasites themselves (origin, history, evolution), on human and animal populations (paleopathology, sanitary conditions, lifestyles), and also on relationships among hosts, parasites and their environment (Reinhard, 1992; Bouchet et al., 2003; Le Bailly and Bouchet, 2010, 2013).

At the end of the 1980s, paleoparasitology added rodents as important material to be studied. The first research started on coprolites of the Brazilian endemic rodent *Kerodon rupestris* (Rodentia, Caviidae). Eggs and larvae of *Strongyloides ferreirai* and eggs of *Trichuris* sp. (roundworms, nematodes) were found in samples collected from archaeological layers dated from 8000 to 2000 BP from Brazil (Araújo et al., 1989). This paper reviews the

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major research activities carried out in rodent paleoparasitology from South America, aiming to integrate data and generate prospects in this field of research.

## 2. Sources and techniques used in ancient rodent parasitic studies

In some paleontological and archaeological sites from South America, coprolites are the most common source of paleoparasitological data. In southern Patagonia and Northeastern Brazil, coprolites are generally found by archaeologists and paleontologists dispersed in layers from rock-shelters and caves.

The study of coprolites presents some difficulties. When coprolites are collected from mummified bodies, their origin is clear. Commonly, coprolites are found free in sediment layers of archaeological and paleontological sites. The identification of the biological origin of the coprolites is mainly based on the knowledge of the feces of the local fauna and on morphometric characteristics associated with macro and microscopic examination (Chame, 2003).

In the 2000s, the study of raptor pellets and sediments opened up the possibility of new ancient rodent parasite sources of evidence (Fugassa, 2006a; Fugassa et al., 2007). Raptor pellets collected from archaeological sites are considered as good rodent material for parasitic studies (Beltrame et al., 2011).

Mummified bodies are rarely found in Brazilian and Argentinian archaeological sites. However, human and other animal mummies were recovered from archaeological sites from Perú. This allowed ectoparasite studies in rodent paleoparasitological data. The examination of mummies of the Guinea pig *Cavia porcellus* (Rodentia:

Caviidae) from Perú enabled the recognition of mites, fleas, and lice from ancient samples (Dittmar, 2000).

Rodent organic remains are examined by parasitological regular techniques after rehydration using a trissodium phosphate aqueous solution 0.5% ( $\text{Na}_3\text{PO}_4$ ) for 72 h (Callen and Cameron, 1960). Next, spontaneous sedimentation is recommended (Lutz, 1919; Araújo et al., 1998).

Technical improvements in Polymerase Chain Reaction (PCR) analysis added the possibility of studies with ancient DNA. Mitton (2012) achieved molecular detection of *Trichuris* spp. from samples of rodent coprolites from an archaeological site from Argentina from one egg. This technique has been also used with different tissues, offering a great spectrum of research for infectious diseases from archaeological samples. Bastos et al. (1996) used PCR to study the kinetoplast DNA (kDNA) of Chagas disease, *Trypanosoma cruzi*, from experimentally desiccated mouse tissue (heart, skeletal, muscle, spleen, and pancreas). The preliminary data suggest the application of this technique to detect *T. cruzi* in archaeological rodent material. On the other hand, the protozoan causative of toxoplasmosis (*Toxoplasma*) has not yet been detected in ancient remains, although successful recovery of its DNA has been accomplished from desiccated mouse tissues (Terra et al., 2004). The application of PCR to rodent paleoparasitological toxoplasmosis and Chagas disease research is a promising option.

## 3. Studies of ancient rodent parasites from South America

Records of ecto and endoparasites recovered from rodents from archaeological and paleontological sites of South America have been published chronologically (Table 1).

**Table 1**  
Summary of South America rodent paleoparasitological findings.

Locality	Date (yr B.P.)	Sample	Host	Parasites	Measurements ( $\mu\text{m}$ )	References
Piauí, Brazil	8000–2000	Coprolites	<i>Kerodon rupestris</i>	<i>Strongyloides ferreirai</i> <i>Trichuris</i> sp.	61.96 × 31.65 (N = 10)	Araújo et al. (1989)
Pedra Furada, Brazil	30,000–8450	Coprolites	<i>K. rupestris</i>	<i>Trichuris</i>	60–65 × 30–33	Ferreira et al. (1991)
Sitio do Meio, Piauí, Brazil	9000 yr	Coprolites	<i>K. rupestris</i>	<i>Trichuris</i> sp.	59–66 × 33 (N = 20)	Araújo et al. (1993)
El Yaral, Moquegua Valley, Perú	Chiribaya Culture	Mummies	<i>Cavia porcellus</i> (guinea pigs)	<i>Trimenopon hispidum</i> , <i>Gliricola porcelli</i> , <i>Ornithonyssus</i> spp., <i>Pulex simulans</i> <i>Eimeria macusaniensis</i>		Dittmar (2000)
Orejas de Burro 1, Santa Cruz, Argentina	3720–3978	Rodent coprolites	Unidentified			Fugassa and Barberena (2006)
Alero Mazquiara, Chubut, Argentina	s. XIX	Coprolites and sediments	Unidentified	Anoplocephalid <i>Trichuris</i> sp. Ascaridid <i>Capillaria</i> sp.	55–60 × 57.5–61.25 (N = 4) 66.25 × 52.5 53 × 35 65 × 35	Fugassa (2006b)
Cerro Casa de Piedra, Santa Cruz, Argentina	6540 ± 110	Raptor pellet	Unidentified	<i>Capillaria</i> sp.	37.5–42.5 × 63.75–68.75	Fugassa et al. (2007)
Cerro Casa de Piedra 7, Santa Cruz, Argentina	7920 ± 130	Coprolites	<i>Ctenomys</i> sp.	<i>Trichuris</i> sp. <i>Paraspidodera uncinata</i> <i>Eucoleus</i> sp.	60–67.5 × 30–37.5 57.5–67.5 × 45–50 (N = 24) 60–62.5 × 37.5–40	Sardella and Fugassa (2009a)
Alero Mazquiara, Chubut, Argentina	212 ± 35	Coprolites	Unidentified	<i>Monoecocestus</i> sp. <i>Pterygodermatites</i> sp. <i>Trichosomoides</i> sp.	50–62.5 × 50–62.5 (N = 30) 65–75 × 45–52.5 (N = 13) 62.5 × 62.5 (N = 5)	Sardella and Fugassa (2009b)
Alero Destacamento Guardaparque, Santa Cruz, Argentina	6700 ± 70–3440 ± 70	Coprolites		<i>Trichuris</i> sp. <i>Calodium</i> sp. <i>Eucoleus</i> sp. <i>Echinocoleus</i> sp. <i>Monoecocestus</i> sp.	57.5–70 × 30–35 57.5–70 × 33.75–47.5 50–55 × 22.5–35 (N = 85) 65 × 31.5 (N = 1) 48.75–70 × 47.5–70	Sardella et al. (2010)
Cerro Casa de Piedra, Santa Cruz, Argentina	2740 ± 100–3.990 ± 80	Raptor pellets	<i>Abrothrix</i> sp. and <i>Euneomys chinchilloides</i>	<i>Calodium</i> sp. <i>Trichuris</i> sp. taeniid	39.8 ± 2.2 × 67.2 ± 3.8 (N = 60) 60 × 35 (N = 1) 37.5 × 33.5 (N = 1)	Beltrame et al. (2011)
CCP 7	10,620 ± 40–9390 ± 40	Coprolites	Species of Caviomorpha	<i>Heteroxynema</i> sp. <i>Trichuris</i> sp.	87.5–107.5 × 45–62.5 (N = 30) 67.5–77.5 × 40–45 (N = 96)	Sardella and Fugassa (2011)

(continued on next page)

Table 1 (continued)

Locality	Date (yr B.P.)	Sample	Host	Parasites	Measurements ( $\mu\text{m}$ )	References
Cueva Huenul 1, Neuquén, Argentina	13,844 $\pm$ 75–1416 $\pm$ 37	Coprolites	<i>Lagidium viscacia</i>	<i>Heteroxynema viscaciae</i> <i>Viscachataenia quadrata</i> <i>Monoecocestus</i> sp.	133.39 $\pm$ 4.10 $\times$ 62.75 $\pm$ 4.48 (N = 90) 82.69 $\pm$ 5.44 $\times$ 91.73 $\pm$ 8.74 (N = 13) 59.15 $\pm$ 1.3 $\times$ 56.7 $\pm$ 1.5 (N = 4)	Beltrame et al. (2012)
Toca dos Coqueiros, National Park of Serra da Capivara, Brazil	5300 $\pm$ 50	Coprolites	<i>K. rupestris</i>	<i>Syphacia</i> sp.	101 $\times$ 35.7 (N = 1)	Vieira de Souza et al. (2012)
Cueva Huenul 1 and Perfil los Altares, Argentina	13,844 $\pm$ 75 to present	Coprolites	<i>L. viscacia</i>	Unidentified anoplocephalid	60–87 $\times$ 60–87 (N = 31)	Beltrame et al. (2013)
Los Altares Profile, Chubut, Argentina	2210 $\pm$ 70 yr B.P. to present	Coprolites	<i>L. viscacia</i> and <i>Microcavia australis</i>	<i>Heteroxynema viscaciae</i> <i>Helminthoxys</i> sp. Anoplocephalid 1 Anoplocephalid 2 Anoplocephalid 3	120–135 $\times$ 57.5–67.5 (N = 7) 77.5–92.5 $\times$ 45.0–52.5 (N = 17) 67.5–87 $\times$ 62.5–87 (N = 25) 80–92.5 $\times$ 70–87.5 (N = 15) 67.5 $\times$ 57.5 (N = 1)	Beltrame et al. (2014)

With respect to the endoparasites, the first paper referring to ancient rodent parasites dates from 1989, when Araújo et al. published the discovery of eggs and larvae of *S. ferreirai* (Nematoda: Strongylidae), and eggs of *Trichuris* sp. (Nematoda: Trichuridae) in coprolites of *K. rupestris* collected from archaeological sites from Piauí State, northeast Brazil (Araújo et al., 1989). *K. rupestris* is an endemic rodent living in rocky areas of Brazil. Coprolites were dated from 8000 to 2000 BP and were identified by comparison with recent feces of *K. rupestris*. The authors suggested that the species that were found could be a new or a known species of *Trichuris*, not yet described in this host. This paper stated that the parasitic fauna of South American wild animals is not completely studied, and new species of parasites can be found by examination of ancient material.

The second contribution was made when Ferreira et al. (1991) recovered eggs of *Trichuris* from coprolites of *K. rupestris* collected from Pedra Furada, Piauí State, northeast Brazil, from archaeological layers dated from 30,000 to 8450 BP. Moreover, more than 1000 fresh pellets from *K. rupestris* collected in their specific sites of defecation on the rocks were examined and were negative for *Trichuris*. This report suggests the existence of an unknown species of *Trichuris* parasitizing *K. rupestris* in the period from at least 30,000 to 8000 BP. The authors discuss the climatic changes that could be present in the region and the antiquity of the host–parasite relationships.

Araújo et al. (1993) also found eggs of *Trichuris* spp. in coprolites of *K. rupestris* dated at 9000 yrs B.P. collected in archaeological sites of São Raimundo Nonato, Piauí State, northeast Brazil. However, present day local rodents seem not to be infected by this parasite, suggesting its disappearance due to climatic changes.

The first study on rodents in Argentina was Fugassa and Barberena (2006) with the examination of sediments from the archaeological site “Orejas de Burro 1”, Santa Cruz province. The site consists of a multiple burial and archaeological levels with evidence of human activity. The burial was dated at 3720–3978 BP. Sediments from one human skeleton were examined for parasites and the macroscopic examination revealed the presence of rodent coprolites. These coprolites were negative for parasite eggs, but the protozoan *Eimeria macusaniensis* (Apicomplexa: Eimeriidae) oocysts were found. The authors discuss the presence of parasites as a source of information about the ecology of the human groups that occupied the cave, and ancient zoonoses. *E. macusaniensis* is a camelid parasite, probably found in the rodent coprolite due to contamination.

Sediments proceeding from the pelvic cavity of human and associated rodent coprolites from the archaeological site “Alero Mazquiarán”, Chubut Province, Argentina, were examined for

parasites, a rockshelter associated with the European contact, probably 19th century. Eggs of anoplocephalids platyhelminthes (flatworms), and the nematodes *Trichuris* sp., unidentified ascarid and *Capillaria* sp. (Nematoda: Capillariidae) were found (Fugassa, 2006b). The author discusses the probable contamination of sediments with rodent parasites.

Fugassa et al. (2007) reported the first study on regurgitated pellet belonging to a bird of prey from the archaeological site “Cerro Casa de Piedra” (CCP), Perito Moreno National Park, Santa Cruz Province, Argentina. CCP is a hill of volcanic origin, with a set of caves and rockshelters. Sample was dated at 6540  $\pm$  110 BP. Microscopic examination revealed the presence of eggs of *Capillaria* sp. attributed to a rodent ingested by the bird. Rodent hairs and a mite, *Demodex* sp., were also found. The author stated that pellets may provide a parasitological record of prey.

Rodent coprolites from CCP with an antiquity considered as 7920  $\pm$  130 BP were also examined (Sardella and Fugassa, 2009a). In this case, all samples were parasitized by nematodes: eggs of *Trichuris* sp. (Trichuridae), *Paraspidodera uncinata* (Aspidoderidae) and *Eucoleus* sp. (Capillariidae). Based on the macroscopical aspect of the feces and on the paleoparasitological results, coprolites were assigned to the South American endemic octodontid rodent *Ctenomys*, “tuco-tuco”. The first finding of *Paraspidodera* in Patagonian samples is discussed. This finding represents new evidence that strengthens the co-phylogenies between nematodes of this genus and *Ctenomys*, and discusses the value of parasites as tags in paleoparasitology.

Samples from the archaeological site “Alero Mazquiarán”, Chubut Province, Argentina, were also examined for parasites (Sardella and Fugassa, 2009b). This site is a rockshelter assigned to the interface of the Araucanian and Tehuelche cultures, dated at 212  $\pm$  35 BP. Rodent coprolites were positive for eggs of the flatworms *Monoecocestus* sp. (Cestoda: Anoplocephalidae), *Pterygodermatites* sp. (Nematoda: Rictulariidae), and *Trichosomoides* sp. (Nematoda: Trichosomoididae). In this study, the authors discuss the parasitic life cycles, the zoonotic importance of parasites, and the behavior of the aboriginal people.

Sardella et al. (2010) examined rodent coprolites from the archaeological site “Alero Destacamento Guardaparque” (ADG), Perito Moreno National Park, close to CCP. Coprolites were dated at 6700  $\pm$  70–3440  $\pm$  70 BP. A total of 582 parasite eggs were found in 47 coprolites. Parasites species were the roundworms *Trichuris* sp., *Calodium* sp., *Eucoleus* sp., *Echinocoleus* sp. and an unidentified capillariid (Nematoda: Capillariidae), and eggs of *Monoecocestus* sp. In this study, the specific affiliations of parasites, their zoonotic

importance, the rodent identity, on the basis of previous zooarchaeological knowledge, and the environmental conditions during the Holocene in the area are discussed.

Sardella and Fugassa (2011) also examined rodent coprolites from another layers of CCP dated at  $10,620 \pm 40$ – $9390 \pm 40$  BP. Eggs of the oxyurid nematode *Heteroxyxema* sp. (*Cavioxyura* sp.) (Nematoda: Heteroxyxematidae) and *Trichuris* sp. were observed. The rodent was identified as an unknown species of Caviomorpha (Hystricognathi) that lived during the Pleistocene transition in Patagonia. *Heteroxyxema* sp. is cited for the first time from ancient material. The authors discuss the finding of *Trichuris* and its relationships with environmental conditions.

The second contribution on raptor pellets was made by Beltrame et al. (2011). Samples come from CCP and were dated at  $2740 \pm 100$  and  $3990 \pm 80$  BP. It was possible to identify the rodent contents (bones and teeth) in the pellets. Rodents were identified as the cricetids *Abrothrix* sp. and *Euneomys chinchilloides*. Eggs of two nematodes *Trichuris* sp. and *Calodium* sp., and one taeniid cestode were found. This study increases the evidence that raptor pellets can be used as source of paleoparasitological information in archaeological sites. The authors also discuss the role of rodents as causative of possible zoonoses in ancient times.

The archaeological site “Cueva Huenel 1” (CH1), Neuquén Province, Argentina, was also studied for ancient rodent parasites. This is an archaeological cave that provides stratified sequences of archaeological and paleontological remains assigned from the Late Pleistocene/Early Holocene Transition to the Late Holocene period. Beltrame et al. (2012) examined rodent coprolites dated from  $13,844 \pm 75$  to  $1416 \pm 37$  BP. Feces were positive for the flatworms *Viscachataenia quadrata* and *Monoecocestus* sp. (Cestoda: Anoplocephalidae), and for the roundworm *Heteroxyxema* (*Cavioxyura*) *viscaciae* (Nematoda: Oxyuridae). The coprolites examined were attributed to *Lagidium viscacia* (Rodentia, Caviomorpha, Chinchillidae), called “vizcacha serrana or chinchillón”. The life cycles of these parasites was also discussed.

Paleoparasitological studies on coprolites of *K. rupestris* were also conducted by Vieira de Souza et al. (2012) in Brazil. Coprolites were collected from excavations at the archaeological site “Toca dos Coqueiros”, from Serra da Capivara National Park. Coprolites were dated at  $5300 \pm 50$  BP, and *Syphacia* eggs (Nematoda: Oxyuridae) were identified. The authors discuss this finding in ancient samples.

Eggs with morphological features attributed to an anoplocephalid cestode, *Andrya* or *Monoecocestus*, were found in samples collected from the archaeological site CH1 and from the paleontological site “Los Altares Profile” (LAP), Chubut Province, Argentina. It corresponds to an accumulation of sedimentary fill remnant of an ancient cave eliminated by road works, dated to Late Holocene. Coprolites were identified as belonged to *L. viscacia* and were compared with current feces of this rodent, where similar anoplocephalid eggs were found. These are the first findings of this anoplocephalid from faecal material from patagonic rodents (Beltrame et al., 2013). The authors discuss their life cycles and the importance of this kind of study.

Finally, other rodent coprolites from LAP were studied for parasites (Beltrame et al., 2014). Samples were positive for eggs of *Heteroxyxema* (*Cavioxyura*) *viscaciae*, for an unidentified oxyurid (attributed to *Helminthoxys*) (Nematoda: Oxyuridae), and for anoplocephalids with features of 3 morphotypes. Coprolites were dated at  $2210 \pm 70$  BP to present. Some of the rodent hosts were tentatively identified as *Microcavia australis* (Caviomorpha: Caviidae), the southern mountain cavy of South America, and others were attributed to *L. viscacia*, based on their morphology and the parasites found.

Respect to the ectoparasites recovered from ancient samples, the only reference is those of Dittmar (2000). Guinea pig (*C.*

*porcellus*) mummies were excavated at the archeological site “El Yaral”, Moquegua Valley, Southern Peru. It belongs to a complex of settlements dated to the coastal Chiribaya Culture. Thirty-two of the 112 studied guinea pigs were positive for arthropod parasitic remains: the lice *Trimenopon hispidum* and *Gliricola porcelli* (Mallophaga), mites of *Ornithonyssus* spp., and the flea *Pulex simulans* (Siphonaptera). Parasitic infestations of domestic livestock have always been a problem, not only involving the domesticated animals if not the human population to which they are associated. The author also discusses the health aspects of the presence of ectoparasites on humans and animals.

#### 4. Information provided by ancient rodent parasites

The presence of rodent parasites in ancient times can provide useful and valuable information, as rodent paleoparasitological data can be used from diverse points of view. Anthropologists, biologists, archaeologists, and paleontologists can use this data to reconstruct ancient events based on the parasite life cycles and on the biological requirements to maintain the transmission from host to host.

Rodent paleoparasitology may provide a picture of the biodiversity of parasites in ancient times. This review shows a wide diversity of rodent parasites collected from ancient sites studied in South America (Table 1). These findings are possible because caves and rockshelters are excellent sites of preservation of samples and parasitic remains.

With respect to nematodes, *Trichuris* spp. includes intestinal parasites of the caecum and colon of mammals, mainly humans, primates, pigs, ovines, goats, cervids, rodents, lagomorphs, African antelopes, marsupials, felids, and canids. They hatch in the small intestine of the definitive host and larvae migrate to the large intestine, where they reach the adult stage (Anderson, 2000). They act as geohelminths because infection involves ingestions of contaminated soils, and they also require climatic conditions in the soil to maintain infections inside the host. Consequently, climate aspects can be inferred when these parasites are found in archaeological sites (Araújo et al., 1993). There are reports of the findings of *Trichuris* spp. from *K. rupestris* from Brazil from at least 30,000 BP (Araújo et al., 1989, 1993; Ferreira et al., 1991). Nevertheless, coprolites of *K. rupestris* with more recent dating, from at least 400 years ago, were also positive for *Trichuris* sp. (Sianto, 2009; Vieira de Souza, 2013) as were samples collected in more humid regions of the Brazilian semiarid (Sianto et al., 2006). There are also reports of *Trichuris* from archaeological sites of Argentina from at least 8000 BP (Fugassa, 2006b; Sardella and Fugassa, 2009a, 2011; Sardella et al., 2010; Beltrame et al., 2011) and they continue today (Suriano and Navone, 1994; Rossin and Malizia, 2005; among others). Climate changes 10,000 years ago in the region could be the cause of the disappearance of *Trichuris* from Brazil. However, this helminth is found in the region today.

Cestodes are a ubiquitous group of intestinal and tissue parasites of all vertebrates, and are currently found in small mammals (Morand et al., 2006). The Anoplocephaline cestodes (Cyclophyllidea: Anoplocephalidae) represent a diverse group of parasites infecting both terrestrial mammals (placentals and marsupials) and birds from all major zoogeographic regions; however they are not commonly found from Central and South America (except for species of *Monoecocestus*). The most important radiation of anoplocephalines has been displayed in rodents and lagomorphs (Beveridge, 1994; Wickström et al., 2005). Intermediate hosts are oribatid mites ingested by their herbivorous definitive hosts (Beveridge, 1994). Parasites transmitted by arthropod vectors are restricted to the distribution area where the parasite and the arthropod are in close contact with the host. This implies that

parasite distribution is limited by favorable environmental conditions for the vector life cycle. Therefore, the presence of anoplocephalids in ancient samples can also provide information on the paleoenvironmental conditions in the period under study and on the local fauna.

Paleoparasitology should be combined with zooarchaeology in order to extend the information concerning rodent parasites. Another case that may be mentioned in this regard is *Spirurina*, which include a diverse group of nematodes that use intermediate hosts such as arthropods, insects, and crustaceans. Eggs of the genus *Pterigodermitis* were found in ancient samples from Alero Mazquiárán, and this finding represents the first worldwide (Sardella and Fugassa, 2009a).

Anoplocephalid cestodes were found in some archaeological sites from Patagonia, Argentina. Eggs of *V. quadrata*, *Monoecocestus* spp. and two unidentified anoplocephalids were found from samples examined (Fugassa, 2006b; Sardella and Fugassa, 2009b; Sardella et al., 2010; Beltrame et al., 2012, 2013, 2014). Anoplocephalid species are very difficult to identify from their eggs. Uterine morphology has played a key role in systematic and phylogenetic arrangements within this group. Eggs are not often taken into account at present to determine taxonomic differences among genera. Nevertheless, the importance of the study of anoplocephalid eggs is evident in paleoparasitological studies. Eggs are the most commonly parasitic remains found in coprolites, and generally are unique. It is necessary to improve the published descriptions and illustrations of eggs in most of the future taxonomic studies. This point is fundamental for future identifications not only of anoplocephalids, but also of all representative rodent parasites.

Species of oxyurid nematodes are monoxenic parasites that live in the digestive tract of various vertebrates and arthropods (Anderson, 2000). Oxyuroidea from vertebrates can be grouped into 3 families: Pharyngodonidae, Oxyuridae, and Heteroxyneematidae (Petter and Quentin, 2009). Heteroxyneematidae includes nematodes that evolved in sciuriform, caviomorph, and miomorph mammals. *Heteroxyneema* spp. was found in coprolites dated at  $10,620 \pm 40$ – $9390 \pm 40$  BP belonging to an unknown species of Caviomorpha (Hystricognathi) from CCP (Sardella and Fugassa, 2011). *Heteroxyneema viscaciae* (Heteroxyneematidae) is a parasite found in the caecum and large intestine from *L. viscacia* from Chubut Province, Argentina: it was first described by Hugot and Sutton (1989). *H. viscaciae* was also found in ancient coprolites assigned to *L. viscacia* from CH1 (Beltrame et al., 2012) and from the paleontological site LAP (Beltrame et al., 2014). In these studies, the presence of these eggs allowed the identification of the biological origin of the coprolites due to the specificity of this species.

This is another interesting contribution of the study of the rodent parasite eggs. In some archaeological and paleontological studies, is impossible to do the coprolite identification solely using their morphology. However, the knowledge of the local fauna and the paleoparasitological study can contribute to the rodent host identification.

Members of the genus *Syphacia* (Oxyuridae: Syphaciinae) are cosmopolitan and are frequently found in the caecum of rodents and lagomorphs (Hugot, 1988). This genus includes more than 60 species, of the around 20 species known from North and South America (Hugot, 1988; Vicente et al., 1997; Robles and Navone, 2007a, b; Robles et al., 2008). Species of *Syphacia* generally exhibit a co-evolutionary relationship with their hosts, with each *Syphacia* species showing specificity with the host genus (Hugot, 1988; Robles, 2010). Eggs of *Syphacia* were found in *K. rupestris* coprolites from Brazil, dated at 5300 BP (Vieira de Souza et al., 2012). Future studies on rodent coprolites can contribute to the

knowledge of the evolutionary patterns of *Syphacia* with their hosts.

Nematodes of the family Aspidoderidae parasitize hystricognath rodents. *Paraspidodera uncinata* was found in rodent coprolites from CCP. Species of *Paraspidodera* exhibit a high specificity for octodontid rodents of the genus *Ctenomys* in which they are usually present in high densities. *Paraspidodera uncinata* occupies a wide geographic range (Sardella and Fugassa, 2009a). Based on the macroscopical aspect of the feces and on the paleoparasitological results, coprolites were assigned to the South American endemic octodontid rodent of the genus *Ctenomys*. The finding of *P. uncinata* in Patagonian ancient samples extends its geographic range. This record also constitutes the first time this parasite species has been found in old material and represents new evidence that strengthens the co-phylogenies between *Paraspidodera* and *Ctenomys*, as proposed by Gardner (1991).

The finding of rodent parasites in ancient material can show the antiquity of the host–parasite relationships and in some, of the parasite losses through time. The parasitic fauna of South American wild animals is not completely studied. From the study of ancient material, new species of parasites can be found in archaeological and paleontological sites.

Another species cited for the first time from old and also for new material in Argentina is *Trichosomoides crassicauda*. It is a parasite of the rodent urinary system. Sardella and Fugassa (2009a) found this parasite in rodent coprolites from Alero Mazquiárán.

Rodents represent one of the most important sources of zoonoses for mammals, and their increasing density forced their dispersion to occur and brought them into closer contact with humans (Perkins et al., 2005). Anoplocephalids are parasites of zoonotic importance for animals and humans (Denegri et al., 1998). It is known that *Pterigodermitis* is parathenic in carnivores, with evidence of disease in humans (Anderson, 2000). Some species of the Capillaridae are also zoonotic. Capillarids were present at several sites (Fugassa, 2006b; Fugassa et al., 2007; Sardella and Fugassa, 2009a; Sardella et al., 2010; Beltrame et al., 2011). Dittmar (2000) found ectoparasites in mummies of guinea pigs. Ectoparasites are parasites of zoonotic importance and also are vectors of zoonotic pathogens.

The presence of zoonotic parasites can show that humans and other animals living in archaeological sites studied were exposed to parasitic zoonoses. Remains of rodents have been noted in human coprolites throughout history, and provide direct evidence of animal consumption (Reinhard et al., 2007). Rodent parasitic studies added to the archaeological studies can contribute to the knowledge of illness in ancient times. This review suggests that the sites under study, caves and shelters, could act as suitable environments for transmission of various types of parasites. Additional studies on zoonotic infections from the past will expand the knowledge on biological aspects of the health-disease processes and the co-evolution among parasites, animals, and human hosts.

Rodent bones are commonly found in archaeological and paleontological sites. Associated materials such as sediments and coprolites are an important source for paleoparasitological research. Results summarized in this review encourage archaeologists and paleontologists to recover coprolites and other possible sources of rodent parasite remains, because of the relevant information available.

Raptor pellets can be used as a source of paleoparasitological information (Beltrame et al., 2011). Pellets provide evidence of less digestible remains of their prey, such as scales, feathers, teeth, hair, and bones, most likely of rodent origin (Marti, 1987). Remains allowed recognition of the host in most cases.

Mummies are representatives of ancient populations and lives throughout the world (Bouchet et al., 2003). Parasite eggs and larvae found in mummy intestinal contents can be more easily identified than those found in coprolites or sediments. With mummies, the host is immediately known. As any other organic remain, mummified bodies may be found in any archaeological region. Rodent mummified bodies can be an important source for paleoparasitological data and should be studied in future research. Advances in the knowledge of the parasitism in rodents require continuing with the implementation of new techniques, mainly the molecular techniques, in order to extend the study of the parasitism itself, as well as to identify the biological origin of samples, that without doubt will broaden the interpretation of the results concerned with ancient materials.

## 5. Conclusions

As evidenced by the rodent paleoparasitological findings summarized above, an interesting paleoparasitological picture has been traced from South America archaeological and paleontological studied sites. Paleoparasitological research has increased over time and has made important contributions in several aspects. Although rodent remains are generally present in ancient times, their recovery from archaeological and paleontological contexts is still exceptional. As more materials and more sensitive techniques become available, as detection of parasite DNA and immunological antigen detection improves, more parasitic indicatives of ancient infections will be detected.

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