Part III - Parasite Findings in Archeological Remains: a paleogeographic view

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In South America, paleoparasitology first developed with studies in Brazil, consolidating this new science that reconstructs past events in the parasite-host relationship. Many studies on parasites in South American archaeological material were conducted on human mummies from the Andes (Ferreira, Araújo & Confalonieri, 1988). However, interest also emerged in parasites of animals, with studies of coprolites found in archaeological layers as a key source of ancient climatic data (Araújo, Ferreira & Confalonieri, 1982).

Callen & Cameron (1960) conducted pioneering studies in human coprolites from Huaca Prieta, Peru, dated to circa 5,000 BP, describing *Diphyllobothrium* sp. eggs. The authors demonstrated the usefulness of rehydrating coprolites in trisodium phosphate aqueous solution, a technique still widely used to recuperate desiccated material and allow microscopic examination of structures preserved in the fecal matter.

Paleoparasitology in South America began with isolated studies, mainly when archaeologists referred the material to parasitologist colleagues, who described the results, as commented by Ferreira, Araújo & Confalonieri (1988). Research groups developed gradually and interest grew in archaeological material, followed by studies in Chile (Arriaza, 1995), Peru (Ortega & Bonavia, 2003), and Argentina (Fugassa & Guichón, 2005). These three countries currently have dedicated research groups in paleoparasitology that collaborate with each other and with the group from the Oswaldo Cruz Foundation in Brazil. Colombian and Bolivian researchers have also participated in seminars and workshops like the international meeting in 2008 at the University of Tarapacá, Arica, Chile, headed by Bernardo Arriaza, with the theme paleoenvironment and paleoparasitology. Bolivian paleoparasitology began with Sotomayor, Burgos & Arango (2004) and Nancy Orellana, with her Master's thesis presented at the Oswaldo Cruz Institute in Rio de Janeiro, Brazil (Orellana, 2008).

The three meetings of the Paleopathology Association in South America, held in Rio de Janeiro, Brazil (2005), Santiago, Chile (2007), and Necochea, Argentina (2009), organized by Sheila Mendonça, Mario Castro, and Ricardo Guichón, respectively, featured symposia in paleoparasitology, with papers presented by students and experienced researchers.

Archaeology in South America has developed both in studies of the human groups that inhabited the Pacific Coast and the Andean Region (Silverman & Isbell, 2008) as well as in Patagonia and Brazil (Borrero, 2001; Pessis, 2003; Martin, 2005). Each new discovery demonstrates the growing need for exploration by specialists with multidisciplinary approaches.

Archaeological sites in South America feature those situated on the Pacific Coast of the Andean Region. Highly organized societies developed there, succeeding each other over time and finally dying out, mostly at the hands of the Spanish Conquerors. These societies were well-documented in reports from the time of the Conquest and by the archaeological record, due to the great interest they attracted. Importantly, there are still groups today that guard traditions from the ancient peoples, as the depositories of these ancient customs (Silverman & Isbell, 2008).

Less has been published on other lands of South America. Since the beginning of the colonial period, European chroniclers left the Atlantic Coast for various reasons and ventured out across forests and wilderness towards the other side of the continent. However, it was the archaeology of the peoples that inhabited Brazil before its discovery that highlighted the way of life and cultures of these peoples on the Brazilian and international research scene (Tenório, 1999; Gaspar, 2000; Gaspar et al., 2008; Martin, 2005; Prous, 2006; Neves, 2006). For example, recent studies have shown that even the forests had villages with large groups of individuals (Heckenberger, Petersen & Neves, 1999) that practiced diversified agriculture (Olsen & Schaal, 1999; Clarke et al., 2006; Montenegro, Avis & Weaver, 2008).

Controversies have arisen, for example with the wealth of findings in the archaeological sites of Serra da Capivara National Park in Piauí State, Brazil (Guidon, 2007). Dating on the human presence differs from the current wisdom, or rather, from what was conventionally accepted based on data from other regions (Lima, 2006; Neves, 2006; Silva & Rodrigues-Carvalho, 2006). Other sites with ancient dates, such as Monte Verde in Chile, were also featured in the discussion on the human presence in Prehistoric America (Dillehay, 2008). This new knowledge, added to established theories, confront and create new paths for understanding the evolution and dispersal of the human species, especially with new findings in South America (Guichón et al., 2006; Hubbe et al., 2007).

The peoples that inhabited the coast of Brazil were described in documents by the first European travelers that reached America. They also left abundant archaeological remains (Gaspar et al., 2008). These coastal peoples moved and interacted with those of the hinterland, in peaceful or belligerent relations, the latter intensified by the arrival of the Europeans (Medeiros, 2002). The historical documentation suggests hypotheses on the circulation of parasitic diseases in the Americas, before and after the great navigations, as discussed in this book. Paleoparasitological findings contribute scientific data to interpretations on each archaeological context.

Despite the conditions of preservation in a major part of South America, with a hot and humid climate and fauna and flora capable of taking advantage of all organic residues launched into the soil without leaving a trace, there is a considerable accumulation of data on the region's occupation, dating to remote times. Thus, it is not a general rule that a constantly hot and rainy climate impedes the preservation of organic archaeological remains capable of yielding data on the past. The neotropical region includes extensive areas with arid or semiarid climates and others with cold temperatures, thus favoring the preservation of organic remains. Organic remains from ancient populations were preserved even in the Amazon, which was believed to be impossible until recently (Neves, 2006, 2008).

Pizzi & Schenone (1954) made one of the first paleoparasitological findings in South America, in a pre-Columbian Chilean mummy. The authors made what have proven to be erroneous speculations on a possible South American origin of *Trichuris trichiura* infection, later discussed by Confalonieri (1988) in his thesis on this parasite's origin in ancestral humans and its introduction into the Americas.

Current findings from ancient South American sites are important for understanding prehistoric occupation of territories and peopling of the Americas. Paleoparasitology provides an evolutionary perspective on the interaction between parasites, human hosts, and the environment, contributing findings to various fields that study the past (Araújo et al., 2003).

The birth of Brazilian paleoparasitology had a strong influence on the organization of other similar groups in various parts of the world, leading to evolution and change in knowledge on parasitic diseases and infection in remote periods of humankind. Cockburn (1971) predicted this when he discussed the possibilities for studying diseases in ancient populations as a way of understanding prehistoric events, and even later in time, whenever written records or documents did not exist or had been lost.

Paleoparasitological data in South America are fascinating and varied. They provide clear evidence of prehistoric intestinal parasitic infections and overturn the classical concept by which these infections were brought to the Americas by the European Conquerors or the African slave trade. The data thus disprove established concepts according to which most so-called tropical diseases were brought to the Americas (previously blessed by a totally healthy environment) from Africa (Freitas, 1935; Carvalho, 2006). The picture emerging from the data are that tuberculosis and the most common helminth infections, such as ascariasis, hookworm, whipworm, and pinworm already infected indigenous groups in pre-Columbian America, ever since the first migratory waves in remote times, persisting in successive indigenous populations.

These parasitic infections probably existed at lower levels in pre-Columbian hunter-gatherer peoples, due to their nomadic habits and dietary characteristics, unfavorable to the maintenance of helminth life cycles or the transmission of certain bacteria, viruses, and other parasites. In some human groups, coprolite analysis has identified the ingestion of plants with anthelminthic properties (Chaves & Reinhard, 2003). The situation changed in farming and herding societies with the transmission of other parasites facilitated by human agglomeration (Reinhard, 1992).

Studies on parasitic infections in ancient populations can be compared to those in current indigenous peoples. This helps establish a continuum or sequence of events over time, reconstructing human history (Coimbra Jr. & Santos, 1992). Various research groups now study parasites in archaeological material from different countries of South America. Interpretation of the findings and their meaning for understanding the life of ancient peoples began to emerge in articles based on cooperation among the research groups. For example, studies in southern Patagonia have aimed to elucidate the living and health conditions of Patagonian indigenous peoples and the consequences of contact with early Europeans colonialists (Fugassa & Guichón, 2005; Casali, Fugassa & Guichón, 2006).

We will now summarize the parasite findings in South American archaeological material, highlighting the paleoparasitological record of each species or group of parasites. We aim not to provide an exhaustive record of the findings, because the list would be obsolete by the time this book is published. Rather, readers will find it useful as a record of how much information can be gleaned by finding a simple worm egg in preserved feces or a fragment of genetic material from a protozoan or bacteria in the mummified tissue of some individual that died thousands of years ago.

GEOHELMINTH INFECTIONS AND HELMINTH PARASITES AS MARKERS OF PREHISTORIC MIGRATIONS

Since most of the parasitic infections discussed here involve helminths, we will present details on those transmitted by soil contamination. These generally originated in ancient Africa, have parasitized humans since our pre-hominid ancestors, and reached the Americas with humans long before the Iberian navigators. They serve as interesting biological markers of prehistoric migrations (Araújo, Ferreira & Confalonieri, 1981; Araújo et al., 2008).

Geohelminth infections in humans are transmitted through soil contamination (Camillo-Coura, 1970, 1985a, 1985b). The most prevalent geohelminth species in the global population are *Ascaris lumbricoides*, *Trichuris trichiura*, *Ancylostoma duodenale*, *Necator americanus*, and *Strongyloides stercoralis*, followed by species from the family Trichostrongylidae, *Ternidens diminutus*, *Oesophagostomum brumpti*, and *Toxocara canis*. A third group includes helminths whose transmission can occur by other routes, but also by soil: *Enterobius vermicularis* (currently one of the most frequent helminth infections on all the continents), *Hymenolepis nana*, and *Echinococcus granulosus*. Cases of human infection with other species are much rarer, such as those of genus *Coenurus*, *Capillaria hepatica*, *Syngamus laringeus*, *Ancylostoma braziliense*, and others.

These parasites display complex life cycles, resulting from parasite-host-environment adaptations that occurred over a long evolutionary process. A detailed description would be both tiresome and repetitive, since they appear in easily accessible parasitology textbooks (Rey, 2008). Still, we will summarize some aspects that should help even the non-specialized reader to interpret their paleoepidemiological implications. The following outlines of their respective clinical presentations help understand possible health problems caused by these helminth infections.

Ankylostomiasis – Hookworms (*Ancylostoma duodenale* and *Necator americanus*)

The clinical presentation in hookworm infection in humans features different degrees of anemia and occasionally edema. Infected individuals lose blood through the stools due to the worms' attachment to the intestinal mucosa and the resulting microscopic ulcerations. The degree of anemia relates directly to the worm burden and inversely to the individual's iron replacement capacity.

Symptoms thus result from various factors including number of parasites (worm burden), the human hosts' nutritional status and diet, and the surrounding environment, with greater or lesser odds of constant infection.

Ancylostoma duodenale and *Necator americanus* can present indistinguishable clinical pictures, but with important differences in their biology, leading them to withstand greater or lesser environmental variation, thereby influencing their geographic distribution (Hoagland & Schad, 1978). *Ancylostoma duodenale* resists colder temperatures than *Necator americanus*, and its geographic distribution thus reaches higher latitudes.

Classic cases occurred during construction of the St. Gotthard Tunnel between Italy and Switzerland. In 1879, Edoardo Perroncito, Camillo Bozzolo & Luigi Pagliani identified infection with *Ancylostoma duodenale* (a species described by Angelo Dubini in 1843) as the cause of anemia in workers building the railway through the tunnel. The parasite maintained its life cycle inside the tunnel, where the temperature was higher and more constant than outside. Since the environment was closed with many individuals circulating and conditions favoring super-infection, workers presented extremely severe clinical conditions, some fatal (Peduzzi & Piffaretti, 1983).

Where prehistoric hookworm infection was prevalent, it may have particularly impacted cave-dwelling human groups that stayed inside their caves for long periods. El-Najjar et al. (1976), Stuart-Macadam (1992), Grauer (1993), and Rothschild (2002) raised this hypothesis, specifically related to porotic hyperostosis (characterized by bone marrow growth and thinning of the bony layer as a reaction to anemia), but the hypothesis requires more definitive evidence.

The number of hookworm eggs per coprolite or gram of latrine sediment in archaeological material in South America is small when compared to modern samples. Some samples show larvae in various stages of development which require morphological identification to avoid confusing them with free-living nematode larvae or other parasite species such as *Strongyloides stercoralis*.

The climatic conditions under which the dung was deposited may have facilitated egg eclosion and larval development. This explains finding the three larval stages in coprolites from the Gentio II Cave in Unaí, Minas Gerais State, dated to 3,500 BP (Ferreira, Araújo & Confalonieri, 1980). The semiarid climate of the *cerrado* and *caatinga* in Northeast Brazil leads to rapid water loss on the surface of excreted feces, while retaining some moisture inside. This allows egg eclosion and changes in larval stages but prevents them from migrating into the soil due to the dry outer crust. We tested this possibility in our laboratory by drying dog feces containing hookworm eggs in ovens for various periods of time, at 40-45°C. The larvae evolved to the infective stage without abandoning the fecal matter and were easily identified under the microscope after rehydration (Araújo, 1987).

Specific regional environmental conditions represent another key point in hookworm paleoepidemiology. Thus, *Ancylostoma duodenale* infection was diagnosed in 20% of the modern population in small villages around the Serra da Capivara National Park, but with no cases of infection with *Necator americanus*. The region is located in the so-called Northeast Brazilian "drought triangle" in semiarid southeastern Piauí State. A hot temperature but low relative humidity (depending on the season, rainy versus dry) hinders larval development in the soil in certain areas. The website of the Foundation of the Museum of the American Man (www.fumdham.org.br) provides climatic data on the Serra da Capivara National Park and surrounding area.

However, on-site observation and laboratory experiments have demonstrated that the use of water holes called *caldeirões* (literally "big caldrons") provided a source of infection and maintenance of local infection, with the necessary biological conditions for the parasite. The current villages grew around these reservoirs at the same sites chosen by prehistoric groups. Water flows around these natural reservoirs during the rainy season, and during the dry season humans and animals use them for water. They contain abundant feces, both prehistoric and modern. From past to present, they have acted as sites for contact between humans and animals, with parasitic infections transmitted over time, facilitated by the environment's microclimatic conditions and use by the species inhabiting the region, including humans. These "big caldrons" have thus been natural hookworm foci from prehistory to the present, perpetuating infection from the remote past to modernity in a 7,000-year continuum.

Other researchers have tested hookworm infectivity in numerically small human groups. Marasciulo (1992) simulated the transmission rate of parasitic infection by an infected individual with a male and female worm in a population of approximately 300 individuals, isolated from any outside contact. The entire population would be exposed to the parasite within one year, even under the most adverse semiarid climatic conditions. Attraction of human groups to the water holes would thus explain transmission. Larvae released in the feces would enjoy sufficient odds of finding new hosts.

The simulation provided a model for hookworm infection in prehistoric populations and concluded that a single infected individual in contact with a population of some 300 individuals could infect everyone within a year.

In prehistoric conditions, infected persons arriving by boat from Asia would be fully capable of contaminating humans already living in South America, especially under more favorable conditions for transmission (Figures 1 and 2).

Figure 1 – Caldeirão do Urubu, Serra Branca, Serra da Capivara National Park, Piauí State, Brazil. In this semiarid region in Northeast Brazil, humans and animals use reservoirs that retain rainwater throughout the year. The ground around the water hole tends to be wetter than the surrounding area, especially when people use the water to wash clothes and supply the local villages

Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

Figure 2 – Caldeirão (Water Hole), Serra da Capivara National Park, Piauí. When humans and animals use water from the reservoir, the soil becomes prone to transmission of hookworm larvae, since the site also contains human feces

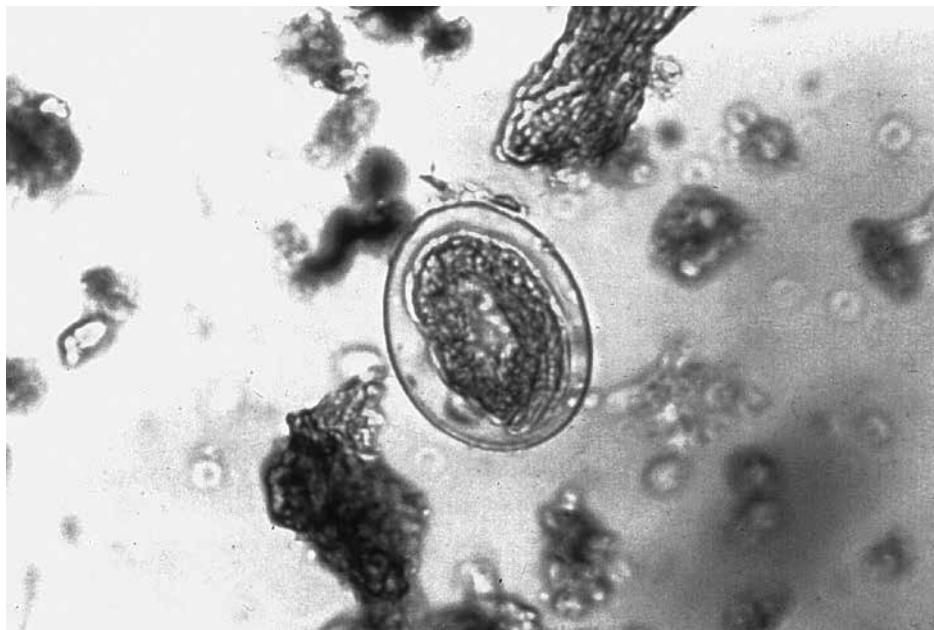Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

Human coprolites found in archaeological sites in South America (Figures 3 and 4) show the oldest dates for hookworm infection in pre-Columbian peoples. One of the oldest is in Piauí, in the Serra da Capivara National Park (Ferreira et al., 1987), at the Boqueirão da Pedra Furada site, dated by radiocarbon to 7,230±80 BP, and the Meio site, dated between 9,000 and 7,000 BP (Gonçalves, Araújo & Ferreira, 2003) (see Record of Archaeological Sites at www.fumdham.org.br).

Figure 3 – Human coprolite dated to 7,230±80 BP from the Boqueirão da Pedra Furada archaeological site, Piauí State

Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

Figure 4 – Hookworm egg from human coprolite dated to 7,230±80 BP, Boqueirão da Pedra Furada archaeological site, Piauí State

Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

The Boqueirão Soberbo archaeological site in Minas Gerais State yielded hookworm eggs in human coprolites dated between 4,905±85 and 1,325±60 BP. The Gentio II cave in the same state of Brazil also contained coprolites with hookworm eggs dated between 3,490±120 and 430±70 BP, collected from loose archaeological sediment and removed from inside a partially mummified body (Figure 5) found in the cave and dated to circa 2,500 BP (Ferreira, Araújo & Confalonieri, 1983).

Figure 5 – Partially mummified body from the Gentio II cave, Unaí, Minas Gerais State, Brazilian Institute of Archaeology, Rio de Janeiro

Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

The two regions have similar environmental conditions. Southeastern Piauí is located in the semiarid zone of Northeast Brazil, with rainfall limited to three to four months a year and different precipitation patterns for each season, with an annual average of 690 mm (Najar, Chame & Chaves, 2000). The *cerrado* of Minas Gerais shows similar conditions.

Despite the previous comments on favorable microenvironmental conditions for the transmission of hookworm infection, such conditions do not suffice to maintain *Necator americanus*. The life cycle of *Necator americanus* and *Ancylostoma duodenale*, studied in populations in India in regions subject to heavy monsoons (Schad et al., 1973; Hoagland & Schad, 1978; Nawalinski, Schad & Chowdhury, 1978a, 1978b), led to the conclusion that *Ancylostoma duodenale* adapts better to harsher environmental conditions and resists them better than *Necator americanus*. This explains the higher prevalence rates for *Ancylostoma duodenale* in semiarid regions of India when compared to *Necator americanus*, more prevalent in regions with a humid climate.

The hookworm species prevailing in prehistoric Piauí and Minas Gerais has not been identified thus far, but this may be possible using molecular biology. However, the conclusions from research in India could apply to the conditions in the *cerrado* in Minas Gerais and the Northeast *caatinga*, especially since *Ancylostoma duodenale* is still prevalent in the modern population, with no cases of *Necator americanus* reported (Marasciulo, 1992; Alves et al., 2003).

Precise data from Peru demonstrate *Ancylostoma duodenale* infection in a pre-Columbian population. Allison et al. (1974) found adult *Ancylostoma duodenale* worms still attached to the intestinal mucosa in a mummified body dated to 890 to 950 AD. Two records from Chile date to 6,100-3,950 BP in the Tiliviche site, Iquique, and 2,500-2,100 BP in Toconao Oriente, San Pedro de Atacama (Gonçalves, Araújo & Ferreira, 2003).

Another finding in Argentina dates closer to the European Conquest, between 1,000 to 500 BP, in the Encantado Valley (Gonçalves, Araújo & Ferreira, 2003). Other records of larvae and eggs consistent with hookworms in Patagonia belong to samples dated 8,920±200 BP, from the forest-steppe ecotone, one of the oldest on the American continent (Fugassa, 2006a, 2006b). Importantly, these findings correspond to the Early Holocene, when the relative humidity was higher than at present (Borrero, 1999).

By way of comparison, eggs from genus *Uncinaria* were found in canid coprolites dated to 6,540±110 BP (Fugassa et al., 2006). Although the human groups in this region were small, the intensive use of rock shelters may have served as foci for infection by these parasites.

The combined data from South and North America (Reinhard et al., 2001) confirm the antiquity of hookworm infection, probably resulting from introduction by individuals infected with *Ancylostoma duodenale* during remote times in the peopling of the Americas (Montenegro et al., 2006; Araújo, Ferreira & Confalonieri, 1981; Araújo et al., 2008).

Ascaris lumbricoides

South American archaeological sites have yielded only a few findings of *Ascaris lumbricoides* eggs in human coprolites (Gonçalves, Araújo & Ferreira, 2003). This appeared paradoxical, since *A. lumbricoides* is now one of the most highly prevalent intestinal helminths, and data also suggest that it occurred in ancient Europe (Bouchet, Harter & Le Bailly, 2003).

Data from molecular biology have recently changed this scenario. Although *A. lumbricoides* eggs are rarely found in organic material from archaeological sites in the Americas, Leles et al. (2008) succeeded in recovering the parasite's genetic material.

Ascaris lumbricoides infection existed in pre-Columbian peoples in the Andes and the Brazilian lowlands, as shown by molecular paleoparasitological data (Leles et al., 2008). The results show the importance of new techniques and recommend caution in interpreting negative data in paleoparasitology. For example, Fonseca Filho (1972) cited the absence (or low prevalence rates) of *A. lumbricoides* infection in populations of Melanesia and Micronesia to explain the transpacific origin of South American populations in prehistoric times. Some 60 to 70 years ago there was no record of *A. lumbricoides* infection in these Asian populations, but it did occur in South American indigenous peoples during the same period. The author thus used the "negative data" argument (namely absence of *A. lumbricoides* infection) as indicative of transpacific contact between Asians and South Americans in pre-Columbian times.

The negative data hypothesis was challenged by recent findings (although rare) of *A. lumbricoides* in South American archaeological material, combined with molecular paleoparasitology data (Leles et al., 2008). Contacts prior to the European Conquest require considerable further investigation, and parasitic infections can provide inestimable data to elucidate them.

For example, thus far Patagonia lacks any pre-Columbian record of *A. lumbricoides*. The only records are from 1584, corresponding to the first European settlement in the Strait of Magellan (Guichón et al., 2006). The finding suggests the probable European origin of a skeleton initially believed to be indigenous. To date, records of *A. lumbricoides* in Patagonia are consistent with predictions of low prevalence rates for this nematode among local indigenous peoples, characterized by small, highly-mobile bands. One can predict interesting findings of different lineages in *A. lumbricoides* and possibilities for using molecular techniques to identify those that were already present and others introduced during contact with Europeans.

Trichuris trichiura

Along with *Ascaris lumbricoides*, *Trichuris trichiura* was the most common parasitic infection in ancient Europe (Bouchet, Harter & Le Bailly, 2003). However, in pre-Columbian America, *Trichuris trichiura* eggs are common, while those of *Ascaris lumbricoides* are quite rare (Gonçalves, Araújo & Ferreira, 2003).

Trichuris trichiura and *Ascaris lumbricoides* eggs appear to show equivalent resistance to environmental conditions. However, *A. lumbricoides* eggs apparently suffer the effects of the taphonomic process more intensely than those of *T. trichiura*. Both have thick shells capable of maintaining an adequate inner microenvironment over sufficient time for larval evolution. Transmission is similar, by ingestion of eggs in food and water, but their internal cycles differ. While *A. lumbricoides* larvae pass through the bloodstream and lungs before reaching the adult stage in the small intestine, *T. trichiura* evolves directly in the intestine, with the eggs hatching as they pass through the stomach and releasing the larvae that reach the large intestine and attach to the mucosa to attain the adult stage.

Egg morphometry is an important diagnostic parameter. Eggs of *Trichuris* species can be distinguished by their size and shape, according to the species of hosts in the target region (Figure 6). Knowing the hosts and their given *Trichuris* species facilitates diagnosis of the coprolites' zoological origin (Chame, 2003). However, identification becomes more difficult when egg sizes from this parasite's species overlap in hosts with concurrent regional occurrence (Fugassa, 2006a).

However, in most cases, *Trichuris* egg morphometry is a diagnostic factor for species parasitizing humans, as exemplified in Europe (Jones, 1982; Fernandes et al., 2005) and in the Americas during the pre-Columbian period (Ferreira, Araújo & Confalonieri, 1980; Araújo, Ferreira & Confalonieri, 1981) and during the period of contact between Europeans and indigenous peoples (Fugassa, 2006b).

Figure 6 – *Trichuris trichiura* egg in coprolite from a mummy dated to the Brazilian colonial period, 17ᵗʰ century, Itacambira, Minas Gerais State, Brazil
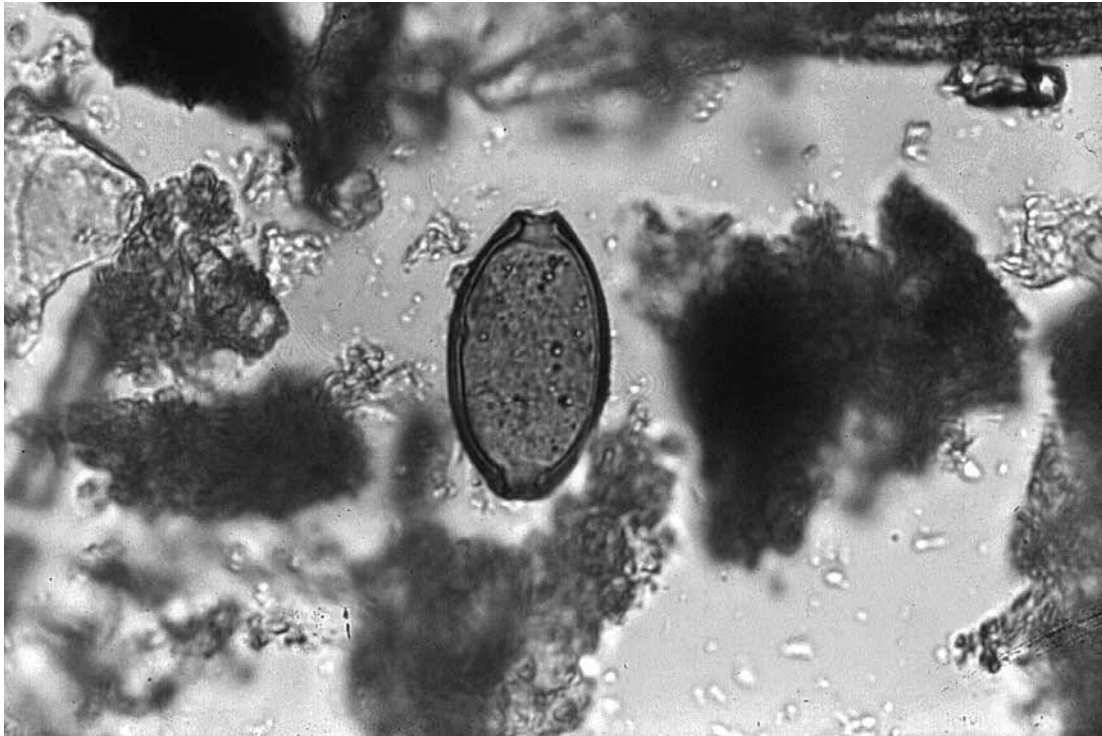
Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

Like *A. lumbricoides*, *T. trichiura* infection existed in prehistoric South America, but was much more prevalent than the former. *T. trichiura* findings in Brazil, Peru, and Chile showed the infection's wide territorial distribution (Gonçalves, Araújo & Ferreira, 2003). The oldest finding, from Minas Gerais, Brazil, dates between 8,000 and 7,000 BP, from the Lapa Pequena archaeological site (Gonçalves, Araújo & Ferreira, 2003).

In some situations, egg morphometric parameters from *Trichuris* species can distinguish between species of given hosts, particularly humans, but in other cases this is not possible. Fugassa (2006a) demonstrated that coprolites attributed to humans in Patagonia can contain *Trichuris* eggs with different morphometric patterns from the human host's *Trichuris* species. The case could be associated with eating uncooked rodents and thus represent false parasitism.

In the Nombre de Jesús archaeological site, the first Spanish settlement in Patagonia, the record showed *T. trichiura* eggs with dimensions consistent with those in eggs found in medieval Europe (Fernandes et al., 2005), agropastoral groups in pre-Columbian America, and the current population of Patagonia (Thienpont, Rochette & Vanparijs, 1979).

Studies on whipworm infection in current populations showed eggs measuring between 50.0-65.0 and 54.0-60.0 μm (Jones, 1982). In sediments collected from human skeletons in Santa Cruz, *Trichuris* eggs measured 51.25-62.5μm x 28.75-32.5μm, 61.75μm x 28.75μm, and 55.0-65.0μm (60.76±3.37; n=16) x 28.75-32.5μm (30.55±1.37; n=16). In coprolites attributed to humans, *Trichuris* egg measurements varied from 52.5-67.5μm (61.12±3.19; n=20) x 27.5-33.75μm (29.61±1.66; n=20) to 57.5-58.7μm (58.1±0.85; n=2) x 30-40μm (35±7.07; n=2). This means greater variability than is known for *T. trichiura*. This variability can be explained by methodological error, such as small samples or error in host identification, or by the biogeographic history of *Trichuris* sp. In this case, the morphometric

variability would assume an unknown species in indigenous groups or the presence of *T. trichiura* populations with eggs displaying different morphometric patterns, possibly due to some process of genetic drift.

False parasitism can occur both in humans and in canids and felines, namely, parasite eggs in transit after ingestion of animals infected with *Trichuris* species. Species have been described in rodents (Chart 1), so one should consider the possibility of cases of false parasitism in prehistoric populations. Rodents and other mammals from Patagonia show high specificity (Babero, Cattan & Cabello, 1975), as do hosts elsewhere in the world.

Chart 1 – *Trichuris* species in Patagonian hosts

Species	Length (μm)	Width (μm)	Host	Reference
Trichuris tenuis	46-50	28-30	Camelids	Chandler, 1930
T. bradleyi	57-65	29-34	*Octodon* sp.*	Babero, Cattan & Cabello, 1975
T. fulvis	65-72	28-31	*Ctenomys* sp.*	Babero & Murua, 1987
T. robusti	57-65	29-36	*Ctenomys* sp.*	Babero & Murua, 1990
T. chilensis	60-67	32-34	*Akodon* sp.*	Babero, Cattan & Cabello, 1976
T. bursacaudata	60-70	20-30	*Ctenomys* sp.*	Suriano & Navone, 1994
T. pampeana	50-60	20-30	*Ctenomys* sp.*	Suriano & Navone, 1994
T. myocastoris	53-60	30-34	*Myocastor coipus**	Barós, Majumdar & Mikailov, 1975
T. dolichotis	75	45	*Dolichotis patagonum**	Morini, Boero & Rodriguez, 1955

* Rodents.

The finding of *Trichuris* eggs with morphometric patterns consistent with the species *Trichuris trichiura* indicates that the sample was human in origin. This assertion is tested by molecular biology techniques (Leles et al., 2008), which can reach conclusions that are closer to reality than by morphological comparisons.

Trichuris eggs with larger measurements than usual have been found in humans. According to some authors (Dunn et al., 2002, Rinaldi et al., 2006), the size was closer to *Trichuris vulpis*, a specific parasite of canids and other carnivores which could occasionally parasitize humans. According to Yoshikawa et al. (1989), such findings could simply represent variations in the size of eggs from the same species identified in humans. Little current research has focused on this issue, but our laboratory is attempting to answer this question using molecular biology techniques. Leles et al. (2008) are testing protocols to answer the question of *Trichuris* sp. cross-infection versus size variation in *T. trichiura* eggs.

Trichuris trichiura, *Ascaris lumbricoides*, hookworm, and *Enterobius vermicularis* are among the oldest intestinal helminth infections in the human species. They shared significant moments in host species' evolution and probably underwent important changes in ancient times.

Both *T. trichiura* and *A. lumbricoides* eggs are highly abundant in medieval European material (Bouchet, Harter & Le Bailly, 2003). The same is not true for prehistoric America, although some specimens of these parasites have been found in pre-Columbian archaeological sites (Gonçalves, Araújo & Ferreira, 2003).

Preliminary data on Patagonia prior to the Europeans' arrival show abundant eggs of parasites of animals in human coprolites, representing either zoonotic diseases or simply parasite eggs in transit, called false parasitism.

A small group of Spaniards that occupied southern Patagonia in the 19th century showed *A. lumbricoides* and *T. trichiura* eggs in sediment collected in the pelvic region, thus differentiating them from the parasitic status of the local population (Fugassa, 2006a).

Enterobius vermicularis

Enterobius vermicularis infection was present 6,000 years ago in human groups that inhabited Tiliviche in northern Chile (Ferreira et al., 1989, Figure 7). South American archaeological material has yielded few eggs from this parasite. All of them thus far have been from organic remains of human groups that lived on the Pacific Coast (Patrucco, Tello & Bonavia, 1983; Ferreira et al., 1985; Araújo et al., 1985), with one rare, undated finding in Neuquén, northern Patagonia, Argentina (Zimmerman & Morilla, 1983).

Figure 7 – *Enterobius vermicularis* egg in pre-Columbian human coprolite from the Atacama Desert, Chile

Source: Ferreira & Araújo (2005).
Photograph: Paleoparasitology Laboratory (ENSP/FIOCRUZ).

Adult *Enterobius vermicularis* worms live in the human host's large intestine. From there, the gravid female pinworms migrate to the perianal region when the host is resting. Oviposition occurs there, causing intense itching from the worms' movement, causing hosts to scratch and destroy the worms, releasing large amounts of eggs. The eggs in turn contaminate the individual's hands, especially under the fingernails, facilitating both autoinfection and infection of new hosts. The eggs also disperse in the environment, and some are found on the surface of the individual's stools, contaminated during defecation.

Finding eggs in feces is thus fortuitous, requiring adequate methods to increase the odds of a positive diagnosis. Such methods include the use of adhesive tape to capture females and eggs in the perianal region, obviously not applicable to archaeological material (although one can scrape the region in mummified bodies in an attempt to

find pinworm eggs). In the case of coprolites, only luck would result in finding eggs, but one should search the sediments collected from the pelvic region in skeletons, with special attention to the sacral foramina after careful washing and collecting the material (Fugassa, 2006).

Further refinement of molecular biology techniques (Iñiguez et al., 2006) should also yield more precise data on the distribution of this parasitic infection in South America. Pinworm infection is prevalent in modern human groups in closed environments such as daycare centers, orphanages, and barracks, but its biological transmission characteristics means that it is scarcely dependent on the environment. Pinworm infection exists in all types of climates, wherever human groups occupy territories. It has been found in hunter-gatherers and sedentary groups in North America (Reinhard, Hevly & Anderson, 1987). The fact that it has not been found in the prehistoric populations that inhabited Brazil can only be explained by technical shortcomings or the scarcity of findings.

PARASITES OF ANIMALS IN HUMAN COPROLITES: DOMESTICATION AND CONTACT WITH WILD ANIMALS

Agriculture was not adopted in the New World in the same way as in the Old World. Various prehistoric populations either continued their hunting and gathering habits despite knowledge of agricultural techniques adopted by other groups in the same region, or used them concurrently (Diamond, 2002; Reinhard, 2006).

Pickersgill (2007) cites four independent areas with vestiges of the development of agriculture in the Americas: Southeast North America, Mesoamerica, Andean Region, and tropical lowlands of South America. Pre-Columbian crops included maize (*Zea mays*), beans (*Phaseolus vulgaris*), potatoes (*Solanum tuberosum*), manioc (*Manihot esculenta*), squash (*Cucurbita* spp.), and peanuts (*Arachis hypogaea*), among others (Martin, 2005; Pickersgill, 2007; Prous, 2006; Reinhard, 1990; Smith, 1997).

Domestication of animals in the Americas differed greatly from domestication in the Old World (Brothwell & Brothwell, 1971). Diamond (2002) explains this difference basically by local geography and climate. Most large herbivores were located in Eurasia, which was also the largest continent. The Americas were home to only a few large animal species that could be domesticated, especially after the mass extinction of mammals in the Late Pleistocene.

On the other hand, the large herds of Old World herbivores were migratory or occupied large areas. This forced human populations to shift constantly in search of game, sometimes across harsh areas or those used by other human groups, a phenomenon known as transhumance. Efforts at domestication thus produced advantageous results (Kormondy & Brown, 1998). Meanwhile, in the Americas, despite the existence of medium-sized and large social herbivores such as the Rocky Mountain goat (*Ovis canadensis*), American bison (*Bison bison*), and moose (*Alces alces*), among others in North America (Geist, 1985) there is no evidence that these species were ever domesticated, although they were hunted for food.

The domestication of animals in the New World occurred mainly in the Andean region and Mexico, where native groups domesticated ducks (*Cairina moschata*), turkeys (*Meleagris gallopavo*), guinea pigs (*Cavia porcellus*), and llamas (*Lama glama*) (from which they obtained milk and meat), and alpaca (*L. pacos*), used mainly for wool (Brothwell & Brothwell, 1971; Stahl, 2003).

Dogs were raised in Mexico for food (Wing & Brown, 1979), but they were not originally domesticated in the Americas. Dogs arrived already domesticated in the company of prehistoric human groups that entered the continent some 14,000 years ago (Savolainen et al., 2002).

Most native groups in the South American lowlands did not domesticate animals for food. In Brazil, for example, various indigenous groups kept wild animals as pets, or in the case of birds, to obtain feathers (Prous, 1992). Although there was no abundance of large social herbivores as in Eurasia, North America, and Africa, some of them such as the white-lipped peccary (*Tayassu pecari*), collared peccary (*Pecari tajacu*), and tapir (*Tapirus anta*) could have been domesticated. However, since these species used relatively small areas and were not migratory (Tiepolo & Tomas, 2006; Michalski & Peres, 2007), they were permanently available as food, in addition to the plentiful supply of fish in many regions (Melatti, 1993).

Unlike the Old World, in the New World there are coprolite samples available from populations of both hunter-gatherers and agriculturists. This allows expanding knowledge on the consequences of domestication of animals and especially plants as food sources for prehistoric populations, even though in different scenarios and situations.

In Brazil, there are only records of helminths of animals in human coprolites. Araújo, Confalonieri & Ferreira (1984) made the first discovery, namely *Trichostrongylus* sp. eggs associated with *T. trichiura* eggs in a mummified body from the colonial period. Gonçalves, Araújo & Ferreira (2003) found acanthocephalan eggs in material dated to 4,905-1,325 BP in Minas Gerais. Another parasite of animals was found in coprolites removed from a naturally mummified adult body in the State of Minas Gerais, dated to 1,200-600 BP and allowing the correct identification of *Echinostoma* sp. eggs and the certainty of their occurrence in humans (Sianto et al., 2005).

This parasite causes echinostomiasis, an endemic zoonosis in Asia that produces debilitating symptoms in infected individuals (Graczyk & Fried, 1998; Fry, 1970). Humans are infected by eating raw snails, fish, or amphibians, the parasite's intermediate hosts (Roberts & Janovy, 2009). This was the first record of *Echinostoma* sp. in humans in Brazil, and the finding enriched the data on the circulation of other zoonotic parasites in ancient peoples.

The helminths *Echinostoma* sp., *Paragonimus* sp., *Diphyllobothrium* sp., *Diphyllobothrium pacificum*, *Capillaria* spp., *Trichostrongylus* sp., and Acanthocephala species were etiological agents of zoonotic diseases in South American populations, considering the findings dated close to contact with Europeans.

McMichael (2004) argued that the transitions experienced by our ancestors, even in prehistory, such as descending from trees to the savannahs, the incorporation of meat into the diet, and more recently since the emergence of species *Homo sapiens*, the development and conquest of new territories and civilizations favored emergence of and exposure to infectious agents of animal origin. Armelagos, Brown & Turner (2005) analyzed the epidemiological transitions experienced by humankind and concluded that a new transition is currently taking place, in which parasitic infections that were common 10,000 years ago, at the time of the first transition (development of techniques for plant cultivation and domestication of animals), are reemerging, with the potential to cause huge economic impact. This reemergence can be explained by encroachment of the agricultural frontier on natural areas and parasites' resistance to conventional treatments.

Paleoparasitological findings provide important clues to human adaptive progress since prehistory, in addition to revealing eating habits of extinct populations and the domestication of animals. The data show that currently known zoonotic diseases have occurred in humans since prehistoric times. Knowing which parasites circulated in the past and their geographic distribution helps understand whether a zoonosis is emerging or reemerging (Mas-Coma, Bargues & Valero, 2005). Thus, the fact that *Dipylidium caninum*, *Capillaria* sp., and other parasites have not been found in human archaeological material in South America does not mean that they did not exist or that such infections did not occur.

Genus *Spirometra* (Cestoda) was recently identified in feline coprolites in the Serra da Capivara National Park, Piauí State, Brazil (Sianto, 2009). *Spirometra* sp. is the causative agent of sparganosis in humans, and one cannot rule out the possibility that this and other parasites were circulating in the prehistoric human population.

Few authors have conducted studies on archaeological material of animal origin. This could represent missed information, since the parasite's presence in the local fauna, associated with environmental and sociocultural factors such as diet and type of dwelling, could indicate the transmission routes of parasites to human populations.

The availability of more sensitive diagnostic techniques facilitates the identification of more parasitic infections from the past and recording of new paleoparasitological findings around the world. Further studies on zoonotic infections of the past will expand knowledge on biological and social aspects of the health-disease process and coevolution of parasites and animal and human hosts. In addition, identifying zoonotic diseases that affected ancestral peoples, understanding their transmission mechanisms and the biogeographic, ecological, cultural, historic, and social factors that affect this dynamic, can build predictive models to help control parasitic diseases soon after their emergence or prevent them from becoming public health problems.

Geographic, biotic, and abiotic factors from the environment (biocenosis) in which prehistoric populations lived and their cultural characteristics can be used to design models of predictability and transmission of parasite fauna in these groups. Studies include Martinson et al. (2003) and Reinhard (2008), based on models formulated according to the theory of natural nidality (Pavlovsky, s.d.; Silva, 1997). Such studies apply especially to zoonotic diseases, when biocenosis in certain natural ecosystems is well-defined (Silva, 1997). The following are examples of helminth parasites of animals found in human coprolites, discussing their significance.

SOUTHERN PATAGONIA

In Argentina, much of Southern Patagonia, including the provinces of Santa Cruz and Tierra del Fuego, is dominated by a steppe environment, while near the Cordillera an ecotone zone precedes the forest. Due to the harsh climate throughout most of the year, rock shelters became the predominant archaeological sites. Most samples examined so far come from rock shelters, cliffs, and caves.

Paleoparasitological findings in Patagonia were obtained from human and animal coprolites and sediment from areas of archeological occupation and showed a wide diversity of parasite species, with a predominance of capillarid eggs (Chart 2). Coprolites and sediments from caves and shelters yielded 15 nematode genera, including Trichostrongylidae, *Eucoleus* sp., *Toxocara* sp., *Physaloptera* sp., *Uncinaria* sp., possibly *Oesophagostomum* sp., and *Calodium* sp. (Moravec, 1982, proposed a new classification for the Capillariidae family, changing the genus *Capillaria* to *Calodium*) (Figure 8). The material also contained eggs of *Hymenolepis* sp. and *Monoecocestus* sp., in addition to eggs similar to genus *Taenia*. The protozoa included oocysts of Coccidia, among them *Eimeria* sp. (Figure 9), with the largest number of oocysts in the samples (Aschero 1981; Civalero & Aschero, 2003).

Figure 8 – *Calodium* (*Capillaria*) sp. egg in animal coprolite, Patagonia, Argentina

Photograph: Martín Fugassa.

Figure 9 – Oocyst, *Eimeria* sp., animal coprolite, Patagonia, Argentina

Photograph: MX Senatore.

These records suggest occupation not only by humans, but also by other species such as canids, camelids, felines, and birds of prey, depending on regional climatic conditions. Coprolites from these animals were found in archeological layers with important evidence of human occupation.

Although Patagonia measures some 800,000 km^2, with low apparent human density during the Holocene, the concentration and reutilization of caves and shelters by humans and other animals may have facilitated the exchange of parasite species. In Southern Patagonia, the demographic characteristics known thus far and the

biocultural habits of these groups suggest that zoonotic parasitism may have played a predominant role in the region's ancient epidemiology.

As mentioned previously, the paleoparasitological records of sediments and coprolites attributed to humans in Patagonia yielded eggs of *Trichuris* sp. with measurements consistent with *Trichuris trichiura*. As an alternative explanation, other species that parasitize rodents may have become zoonotic in ancient human groups in the region.

Chart 2 – Parasites of animal origin found in samples from Patagonia, South America

Sample	Archeological site	Host's zoological origin	Date (years BP)	Parasites found
European contact				
NJ-1	Nombre de Jesús, Cabo Vírgenes, Santa Cruz	Human	475 ± 45	*Ascaris lumbricoides*
NJ-2				*Trichuris* sp., *Eimeria macusaniensis*
NJ-3				*Trichuris* sp.
NJ-4				*Trichuris trichiura*, *Diphyllobothrium* sp.
M-84	Cerro Norte XI, Pali Aike, Santa Cruz		19th century	*Trichuris* sp., *Eucoleus* sp., *Calodium* sp., other capillarids, *Taenia* sp.
M-75, M-76	Alero Mazquiarán, Rio Mayo, Chubut	Rodent	212 ± 35	*Taenia* sp., *Monoecocestus* sp.*, *Pterygodermatites* sp.*, *Trichosomoides* sp.*
		Human		*Trichuris* sp., *Monoecocestus* sp.*
M-85	Cerro Norte III, Pali Aike, Santa Cruz	Sheep	Historic	*Toxocara* sp., *Strongyloides* sp., *Haemonchus* sp., *Trichostrongylus* sp., *Eimiera ovina*, *Mesocestoides* sp.
CF	Caleta Falsa, Península Mitre, Tierra del Fuego	Human	850	Capillarids, Anoplocephalidae?
LM	Las Mandíbulas, northern Tierra del Fuego		Historic	*Calodium* sp.
Late and Middle Holocene				
M-1	Orejas de Burro I, Pali Aike, Santa Cruz	Human	3565 ± 45	Capillarids, *Trichuris* sp., unidentified nematode larva
M-2*		Rodent		*E. macusaniensis*
M-2		Human		Capillarids, *E. macusaniensis*, *T. trichiura*, ascarid?
M-3		Waste	3490 ± 50	Capillarids, *Trichuris* sp., *E. macusaniensis*
M-6	La Arcillosa II, northern Tierra del Fuego	Waste	5205 ± 58	*Diphyllobothrium* sp., *Eimeria* sp.

Chart 2 – Parasites of animal origin found in samples from Patagonia, South America (continued)

Sample	Archeological site	Host's zoological origin	Date (years BP)	Parasites found
		Late and Middle Holocene		
M-8	CCP5, Perito Moreno National Park, Santa Cruz	Canid	6540 ± 110	*Eucoleus* sp., *Calodium* sp., outer capillarids, *Trichuris* sp., *Uncinaria* sp., *Physaloptera* sp., *Moniezia* sp., *A. lumbricoides*
M-24		Human?		*Calodium* sp., *Nematodirus* sp., hookworm
M-40		Feline		*Calodium* sp.
M-43				*Calodium* sp., Anoplocephalidae, *Trichuris serrata*, *Oesophagostomum* sp.
M-41		Bird of prey		*Calodium* sp., *Demodex* sp.
M-44		Human		*E. macusaniensis*, *Calodium* sp., other capillarids, *Nematodirus* sp.
M-46		Feline		*Calodium* sp., *Nematodirus* sp., *E. macusaniensis*, hookworm
M-47		Human		*Calodium* sp., other capillarids, *Habronema* sp., *E. macusaniensis*, *E. ivitaensis*
M-50				Acanthocephala, *Calodium* sp., Coccidia
M-21	CCP7, Perito Moreno National Park, Santa Cruz	Human	6150 ± 05	*Trichuris* sp., *Calodium* sp., *Eucoleus* sp., other capillarids, *E. vermicularis*
		Early Holocene		
M-22	CCP7, Perito Moreno National Park, Santa Cruz	Human	7880 ± 150	*Trichuris* sp., *Hymenolepis nana*, *E. macusaniensis*, *Calodium* sp., *Nematodirus* sp., *Physaloptera* sp., trematodes
M-11		Canid	7920 ± 130	*E. macusaniensis*, *Nematodirus* sp., *Calodium* sp.
M-9			8300 ± 115	*Trichuris tenuis*, *Eucoleus* sp., other capillarids, *Nematodirus* sp.

Chart 2 – Parasites of animal origin found in samples from Patagonia, South America (continued)

Sample	Archeological site	Host's zoological origin	Date (years BP)	Parasites found
Pleistocene-Holocene Transition				
M-39	CCP7, Perito Moreno National Park, Santa Cruz	Human	9730 ± 100	*Trichuris* sp., *Calodium* sp., *Nematodirus* sp., *E. macusaniensis*
M-37			8920 ± 200	*Ancylostoma* sp., *Calodium* sp. Anoplocephalidae
M-30				*Calodium* sp., *Nematodirus* sp.
M-34				*Eimeria* sp., *Calodium* sp., *Hymenolepis nana*
M-33			9640 ± 190	*Toxocara* sp., *Dipylidium* sp.
M-16		Camelid	9640 ± 190 – 9100 ± 150	*Eimeria* sp., *Nematodirus* sp., *Calodium* sp.
M-23		Canid	10530 ± 60	*Calodium* sp., other capillarids, *Moniezia* sp.?, *Nematodirus* sp.
M-36		Human	10530 ± 620	*Strongyloides* sp.
M-15		*Mylodon* sp. (giant ground sloth)	10530 ± 628	*Oxyuris equi*, cestode

* Source: Sardella & Fugassa (2009).

European contact generally led to epidemics of microparasites (smallpox, measles, tuberculosis, and influenza, among others). Osteological and ethnographic studies have shown the importance of nutritional deficiencies in indigenous peoples confined in missions in North America (Dobyns, 1993). The combination of various factors like the increase in the number of domestic animals, especially dogs, poor hygiene, increase in nutritional deficiencies and sedentarism, provided an ideal pathoecological scenario for the increase in enteroparasitic infections and the emergence of multiple parasitic infections. These scenarios should be considered in the paleoepidemiological reconstruction of these infections and provided the substrate in which other infectious diseases may have found a favorable niche during contact.

Eggs from nematode parasites of herbivores were also found, such as *Lamanema* sp. and *Nematodirus* sp. The larvae of these two parasites develop inside the eggs, making them resistant to drought, allowing survival of the larvae in pasture for up to two years (Leguía, 1999). Such characteristics may explain why many Patagonian coprolites only display this genus of herbivore nematode.

As observed by Navone & Merino (1989), the eggs of other nematode genera are delicate and undergo hypobiosis in the intestinal tract of guanacos during the winter, to synchronize oviposition under favorable climatic conditions. These parasites would thus be underrepresented in Patagonian coprolites due to taphonomic effects. Although fewer in number, eggs from these ascarids were found in canid, feline, and human coprolites, indicating the consumption of guanacos by these species of carnivores.

For human groups, the above-mentioned findings and those of *Eimeria* sp. are associated with the ingestion of viscera. One cannot rule out the possibility of human infections, since some cases have been reported at present (Taylor, Lathan & Woolhouse, 2001).

Trichostrongylidae infection causes enteritis that can include internal hemorrhage and hepatic lesions due to larval migration (Leguía, 1999). Although no cases of infection with *Lamanema* sp. have been described in humans, there are cases of parasitism with *Nematodirus* sp. (Rea et al., 2003). In humans, infections by other nematodes of herbivores are normally asymptomatic and only rarely cause diarrhea, bleeding, and secondary anemia (Atías, 1998). The latter author reports the formation of intestinal helminthomas or nodules due to nematodes of genus *Oesophagostomum* sp.

The presence of *Uncinaria* sp. and probable presence of *Toxocara* sp. indicate exposure to parasites that can cause atypical infections, since humans are not usual hosts. *Uncinaria* sp. larvae penetrate the skin, causing an infection known as cutaneous larva migrans or creeping eruption. The accidental ingestion of embryonated *Toxocara* sp. eggs produces larvae that lodge in various organs, called visceral larva migrans. Currently, parasites of genus *Toxocara* cause hundreds of cases of unilateral blindness in children in the United States, due to their intraocular localization (Robertson & Thompson, 2002).

Recently, human cases of intestinal infection have been reported with *Ancylostoma caninum*, another canid hookworm, raising the possibility of infection by this parasite in caves inhabited alternately by wild dogs and humans. In historical times, the late introduction of dogs among indigenous peoples in Patagonia would have exposed humans to this zoonosis with a higher than normal prevalence.

Hookworm eggs and larvae found in human coprolites from the Pleistocene-Holocene transition and other possible records prove important for various reasons: i) they provide data for discussing the introduction of hookworms into the Americas; ii) the disease associated with these helminths involves anemia and protein loss (Atías, 1998), which can correlate with hyperostosis in paleopathological examination; and iii) they allow inferring the region's environmental conditions during the respective time period. In this case, the record corresponds to forest expansion due to increasing humidity.

As mentioned previously, paleoparasitological findings in sediments and coprolites attributed to humans in Patagonia included *Trichuris* sp. eggs differing in size from those of *Trichuris trichiura*. An explanation is that other species that parasitize rodents may have become zoonotic in ancient human groups in the region.

Paleoparasitological findings of capillarids are rare in the Americas. In Brazil, in Lapa da Angélica IV, Goiás State, they were found in coprolites of wild animals (Confalonieri, 1988). Meanwhile, in Patagonia, the majority of the samples of free sediments and coprolites tested positive for capillarid eggs, with morphology consistent with *Calodium hepaticum* (*Capillaria hepatica*). Although the parasite is widely distributed in rodents (e.g., 60% prevalence in urban sewer rats), 44% of children in poor neighborhoods in Salvador, Bahia, Brazil, tested positive for *Calodium hepaticum* according to fluorescence (Assis et al., 2004).

Although the medical literature reports these parasitic infections as accidental or sporadic, such situations depend on both ecological and local socioeconomic conditions. Although it is recommended to discriminate the morphology of the eggs lodged in the vulvae of the females in these nematodes, due to differences between immature and totally developed eggs (Moravec, 2001), the reported findings refer to eliminated eggs, thus mostly mature. The observed morphological variability of eggs in sediments and coprolites is purportedly due to the presence of more than one capillarid species, although it could mean true parasitism or simply parasite eggs in transit.

Capillarid infections mostly represent accidental ingestion of eggs due to poor hygiene and contact with fecal matter. However, they could correspond to the consumption of infected prey as part of the eating habits of hunter-gatherers, although with less significance, since the eggs require a prior maturation period before becoming infective

for the new host, except in the case of *Calodium hepaticum*. Alternatively, some capillarid species, such as those that parasitize birds, have worms as their intermediate host (Moravec, 2001), which human groups in Patagonia could have consumed, thereby leading to infection.

Importantly, detailed morphometric studies are useful for producing statistical analyses. A more precise diagnosis allows better interpretation of the evidence. The combination of morphometric studies with light microscopy and scanning electron microscopy, statistical analysis, and modern comparative samples should allow progress in diagnosing this genus.

A hypothesis for the wide ecological distribution of parasites from this genus is that the success was due to species with a direct cycle, with numerous rodent species inhabiting the region as the reservoir. Findings in humans would be a combination of patent infections and ingestion of rodents. Capillarids are biologically resistant, even when exposed to different environmental conditions. As discussed, their eggs have been found in a wide range of contexts, including resistance to the application of palynological techniques using acids (Burry, personal communication).

Intestinal infections with *Pseudocapillaria philippinensis* can cause severe diarrhea and intestinal malabsorption syndrome, occasionally leading to dehydration and death (Atías, 1998). Parasitism of the respiratory tract with *Eucoleus aerophilla* or of the liver with *Calodium hepaticum* can cause severe disease in humans (Benenson, 1995; Miyazaki, 1991).

As for tapeworms, the most frequent paleoparasitological records in Patagonia were of Anoplocephalidae. These tapeworms parasitize reptiles, birds, and mammals and are more numerous in the latter group (Denegri et al., 1998). They are heteroxenous parasites that require oribatid mites as intermediate hosts. These mites are important components of the edaphic fauna, and their populations display daily and seasonal variations (Denegri, 2001). *Bertiella* sp. infection has been recorded in humans (Denegri, 2001). Rothman & Bowman (2003) report *Anoplocephala* sp. infection in gorillas. Infection with *Inermicapsifer madagascariensis* has been reported in Cuba and Africa (Frean & Dini, 2004; Soulsby, 1982). Taylor, Latham & Woolhouse (2001) include *Moniezia expansa* as a zoonotic species.

Current data on Anoplocephalidae in the Patagonian fauna mention *Moniezia expansa* in guanacos in the province of Chubut, Argentina (Beldomenico et al., 2003; Robles, personal communication), *Moniezia* sp. and *Thysanosoma actinoides* in sheep (Robles & Olaechea, 2001), *Moniezia* sp. in guanacos in Tierra del Fogo (Navone & Merino, 1989), and *Cittotaenia quadrata* in the southern viscacha (*Lagidium viscacia*), a rodent from southern South America (Denegri et al., 2003).

Findings of Anoplocephalidae in wild hosts from other regions of Argentina include species that accidentally ingest oribatid mites. For example, Martinez et al. (1999) report that among the most common tapeworm infections in Edentata, those involving Anoplocephalidae are important and caused by species of the genera *Anoplocephala*, *Paranoplocephala*, *Moniezia*, *Cittotaenia*, *Bertiella*, *Oochoristica*, *Mathevotaenia*, and *Monoecocestus*. Navone (1990) reported *Mathevotaenia surinamensis* in *Dasypus novemcinctus*, *Mathevotaenia matacus* in *Tolypeutes matacus*, and *Mathevotaenia diminuta* in *Chaetophractus vellerosus*, and Navone & Suriano (1992) reported genus *Mathevotaenia* in *Didelphys albiventris*. Sutton (1973) described *Monoecocestus myopotami* in *Myocastor coypus*, and Boero, Klusas & Boehringer (1967) detected *Monoecocestus hidrochoeri* in *Hydrochoerus hydrocoeris*.

Paleoparasitological findings provide evidence for evolutionary discussions. For example, according to Beldomenico et al. (2003), the presence of *M. expansa* in Patagonian guanacos could be due to interaction with sheep. If the eggs found in Patagonian coprolites (Fugassa et al., 2006) belong to a species from genus *Moniezia*, then the hypothesis

proposed by Beldomenico et al. (2003) would be less consistent and could be refuted by paleoparasitological studies of coprolites from Patagonian camelids.

Tenora (1976) contended that the cosmopolitan distribution of *Moniezia* was due to the domestication of animals. The findings could refute this hypothesis and allow that Anoplocephalidae were present in America long before European colonization. The finding of Anoplocephalidae in wild fauna from 6,000 BP raises the possibility that genus *Moniezia* was also present in pre-Columbian America.

Tapeworms identified in various archaeological and paleontological contexts belong to the genera *Taenia*, *Hymenolepis*, and *Diphyllobothrium* and are reviewed by Gonçalves, Araújo & Ferreira (2003). Bathurst (2005) reported finding *Diphyllobothrium* sp. and eggs attributable to the Taenidae family in a shell midden in Canada. For the Anoplocephalidae family, Hidalgo Arguello et al. (2003) recorded a single egg from *Anoplocephala perfoliata* in medieval tombs in Spain, although with measurements that were scarcely representative and with an image that was unclear as to the presence of hooks and the pyriform apparatus. Rodent coprolites found in the pelvic cavity of a human skeleton yielded numerous eggs attributed initially to *Moniezia* sp. (Fugassa, 2006b). The diagnosis was revised by Sardella & Fugassa (2009), concluding that it was *Monoecoestus* sp.

Finally, the observation of probable *Taenia* eggs in Cerro Norte XI, Patagonia, Argentina, is associated with European contact and probably indicates consumption of sheep, since the eggs are consistent in size and shape with *Taenia ovis* (Soulsby, 1982).

The presence of Anoplocephalidae in diverse archaeological samples from Patagonia suggests that the low representativeness of other cestodes such as *Taenia* cannot be attributed to problems of preservation. Other possible explanations should be investigated, related to epidemiological issues and diagnostic methodology.

As for tapeworm disease from Anoplocephalidae in Edentata, anoplocephalid infection with high worm burden can cause enteritis and diarrhea (Martinez et al., 1999). Infection with *Bertiella* (an anoplocephalid) in humans is generally asymptomatic, but cases have been recorded with intermittent diarrhea, gastroenteritis, decreased appetite, weight loss, general fatigue, and abdominal pain (Denegri & Perez-Serrano, 1997). Although anoplocephalid infection can cause weakness and predispose to various diseases, it is not expected to have left traces in ancient bones (for paleopathological studies).

Hymenolepis infection can be associated with enteritis (Atías, 1998) and other mild symptoms such as abdominal pain and weight loss (Benenson, 1995). Symptoms associated with taeniasis are mild and variable (Atías, 1998), and can include increased appetite, abdominal pain, headache, and nausea. Cestodes of genus *Diphyllobothrium* can cause systemic symptoms similar to those of taeniasis and occasionally lead to anemia (Atías, 1998), which can leave osteological traces such as porotic hyperostosis (Aufderheide & Rodríguez-Martín, 1998).

Many parasites found in coprolites could have been transmitted to humans by various routes, mainly through their water intake or accidental ingestion of contaminated foods or invertebrates due to unhygienic eating habits.

Currently, children are more susceptible to acquiring zoonotic diseases (Robertson & Thompson, 2002). However, in ancient human groups, contact with contaminated elements may have affected all age brackets, as described in ethnographic reports in Patagonia.

The estimation of exposure to zoonotic diseases should obviously consider the animal species that occupied the sites. The representation left in bones serves as an indicator of zoonotic diseases by handling and consumption of prey but not of zoonotic diseases by contact with species, since the zooarchaeological remains may only come

from consumption of prey, while the presence of animal coprolites is a more consistent indicator of the presence of animals in the same site occupied by humans. The caves in the Perito Moreno National Park (Santa Cruz, Argentina) were occupied by humans, large canids, felines like cougars, camelids, rodents, mustelids, and large birds of prey, as shown by analysis of coprolites and bird regurgitation pellets. Paleoparasitological studies on sediments from the fauna associated with sites occupied by humans produced evidence on the parasitic infections in animals, to which the humans were also exposed.

Most of the oldest sites in Patagonia are rock shelters and caves (Civalero & Franco, 2003) occupied by humans more than 10,000 years ago (Borrero, 2001), but also alternatingly by other animals. Even if the site was not used simultaneously by humans and canids, parasites could have persisted under specific environmental conditions, even for months or years. *Toxocara cati* and *T. canis* eggs can survive in the environment for months (Robertson & Thompson, 2002). Although there are no records of domestication in Patagonia, alternating occupation by humans and carnivores could have caused exposure to toxocariasis.

Likewise, *Uncinaria* sp. infection, described in carnivores and found in M-8, a canid coprolite from CCP5 (Perito Moreno National Park, Santa Cruz, Argentina), can cause skin lesions. More rarely, *Ancylostoma caninum* can infect the human intestine. Among the many zoonotic diseases caused by nematodes, modern cases have been reported of humans infected with *Trichuris vulpis,* a parasite of canids (Dunn et al., 2002). The authors call attention to the fact that similar cases may be missed by laboratories that fail to use egg measurements as diagnostic parameters. Paleoparasitology thus calls attention to possibilities in the realm of current parasitic infections, as shown by infections with parasites of animals.

According to the proposed models, although bands of hunter-gatherers were parasitized by fecal-borne species, even though at lower levels than in sedentary groups (Dillehay, 1991), the rock shelters displayed distinct scenarios. There are few records of typical fecal-borne parasites of humans (*Trichuris trichiura*, *Ascaris lumbricoides*, *Enterobius vermicularis*, etc.), but cases have been identified of less common fecal-borne enteroparasites, such as *Calodium* sp., *Ascaris* sp., and *Physaloptera* sp.

The hypothesis on the role of caves and rock shelters in Patagonia as centers of concentration for numerous species of enteroparasites and potentially for their dispersal should include not only helminths but also protozoa, viruses, and bacteria. The transition of Chagas disease from enzootic to zoonotic is an example that merits investigation (Ferreira et al., 2000).

The presence of numerous camelid coprolites in all layers of the archaeological sites suggests that these animals served as reservoirs for various parasitic infections, including those caused by bacteria. Camelids are reservoirs of *Trypanosoma cruzi* (Alcaíno & Gorza, 1999; Teixeira, Nascimento & Sturn, 2006), and if vector distribution allowed, the caves could have served as centers for the spread of Chagas disease. Food storage, the existence of latrines, consumption of undercooked meat, and long-term occupation of the caves would have produced ideal pathoecological conditions for spreading Chagas infection (Reinhard, 2005).

The paleoepidemiological models of sedentary versus nomadic, hunter versus farmer, terrestrial versus maritime, and pre-contact versus post-contact should be expanded experimentally to include rocky versus non-rocky, related to the habit of occupying rock shelters and caves. For example, in Patagonia, non-rocky includes the historical nomadic groups such as the Yámanas and Selk'nam, who lived in open-air shelters and tents. Thus, from the trophic point of view, occupation of the forest and ecotones with forest involves differences in the specific wealth and abundance of resources, especially plant resources, abundant in the western forests (Rapaport, Ladio & Sanz, 2003). This could

mean exposure to diverse parasites whose infective stages are found in the vegetation and to other parasites ingested with invertebrate intermediate hosts also existing there, such as orbatid mites.

The non-simultaneous development of paleoepidemiological models and paleoparasitological tests is a necessary strategy for reconstructing possible paleoepidemiological scenarios during different moments of the Holocene in Patagonia.

HELMINTH INFECTIONS ON THE PACIFIC COAST OF SOUTH AMERICA

In addition to infection with *T. trichiura*, *E. vermicularis*, and hookworms and the rare cases of infection with *A. lumbricoides*, parasitism by *Diphyllobothrium pacificum* is striking from the pre-Columbian period to the present on the Pacific Coast of South America (Ferreira, Araújo & Confalonieri, 1984; Gonçalves, Araújo & Ferreira, 2003). This zoonosis was described by Swiss parasitologist Jean Baer, who was called to Peru to study the parasites found in individuals with clinical intestinal symptoms. He identified the species *Diphyllobothrium pacificum*, a parasite of sea lions whose larvae contaminate saltwater fish and crustaceans (Baer, 1969). The presence of this parasite in the population is explained by the consumption of *cebiche*, a traditional raw seafood dish among the peoples of the Pacific Coast of South America.

When he saw examples of the prehistoric pottery in which the ancient peoples of the Pacific Coast served food, Jean Baer raised the hypothesis that they also suffered from this parasitic infection. Years later, when the parasite's eggs were found in Chilean coprolites dated to 4,000 BP, Ferreira, Araújo & Confalonieri (1984) commented that Baer's assumption was correct. Other researchers have also confirmed the parasite's presence in prehistoric peoples of the Pacific Coast (Callen & Cameron, 1960; Patrucco, Tello & Bonavia, 1983; Reinhard & Barnum, 1991; Reinhard & Urban, 2003).

Due to the wealth and diversity of the human cultures that inhabited the Pacific Coast of South America, paleoparasitology has contributed greatly to understanding the parasite-human host relationship. A recent example is the study by Arriaza et al. (2010) on the influence of climatic phenomena on parasitic infections. The authors show evidence that infection with *Diphyllobothrium pacificum* and *Anisakis* sp. probably had varying prevalence rates in prehistoric populations according to climatic oscillations resulting from the El Niño phenomenon.

The conclusion on intestinal helminths that infected prehistoric South American populations is that the archaeological record bears witness both to parasites introduced by human migrations since the peopling of the continent and others, acquired from animals with whom they lived (and with whom their descendants still live). These helminths include species that infect animals, but which can be transmitted to (and parasitize) humans.

It is interesting to examine modern human groups that maintain ancestral habits, like indigenous groups in some regions of Brazil. For example, cases of false parasitism by *Calodium hepaticum* (*Capillaria hepatica*) have been described when examining feces of persons that ingested animal viscera and eliminated eggs of these helminths (Coimbra & Mello, 1981; Carvalho-Costa et al., 2009). These are examples in which studies on ethnicity and health in both modern and prehistoric peoples show similar situations and can illustrate change or permanence in the disease profile over time.

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