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ANIMAL HELMINTHS IN HUMAN ARCHAEOLOGICAL REMAINS: A REVIEW OF ZOONOSES IN THE PAST

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SUMMARY

The authors present a review of records of intestinal parasitic helminths from animals in human archaeological remains, reported since the emergence of paleopathological studies. The objective was to relate paleoparasitological findings to geographic, biotic, and abiotic factors from the environment in which the prehistoric populations lived, and understand some aspects related to the process of human dispersion and biological and cultural evolution. Modification of eating habits and the incorporation of new cultural practices are analyzed from the perspective of zoonoses from prehistory to the present day, especially in Brazilian indigenous populations. Three tables identifying the helminths, their natural hosts, dates, and sites of archaeological findings complete this review. In conclusion, various zoonoses known today have occurred since antiquity, and these data, combined with studies on the emergence and reemergence of diseases, could make possible to compose scenarios for the future.

KEYWORDS: Coprolites; Paleoparasitology; Helminthiasis; Zoonoses; Ancient diseases.

INTRODUCTION

Parasites of animals may infect humans, and in some cases cause disease. On the other hand, false parasitism is also observed in individuals after eating infected animals with parasite species that are not able to infect humans. Therefore, the eggs pass with feces without causing infection, as recorded in indigenous groups[29]. In examining archaeological material one has to separate coprolites of human origin from others of animal origin. However, parasitism is a dynamic process, and changes may occur.

The finding of *Echinostoma* sp. in a mummified body from the pre-Colombian period in Minas Gerais State, Brazil[119] can be used as an indication of modifications in the parasite fauna in human groups over time. These modifications reflect possible variations in eating habits among prehistoric human groups, since hunter-gatherers ingested wild animals, thus becoming potential hosts for new parasites over the course of their evolutionary history[54].

Cases of animal parasites infecting humans were described in Europe, especially in the Neolithic and Medieval periods[71], and in Patagonia in the pre-contact period[45]. Evidence of the ingestion of small animals, consumed whole or in pieces, without cooking, described by REINHARD[103] in human coprolites, increased the interest in the investigations of animals used for food and as possible transmitters of parasites to humans.

The possibilities for the occurrence of parasitic helminths from wild animals in prehistoric human populations are wide and variable according to the local fauna and different habits and cultures around the world. The absence of many of these species today reflects the change in these parameters, especially since agriculture and domestication[32,54].

Thus, the interest in studying eating habits in past times and the interaction with intermediate, definitive, and paratenic hosts motivated a review of findings of helminths in archaeological material, situating them in time and space, as well as associating them with the living habits of ancient human groups.

The study of parasites in archaeological material has developed extensively in recent decades[40]. Since its emergence nearly a century ago, paleoparasitology has contributed empirical data on the presence of infections and clinical disease conditions among populations that have already disappeared from the Old and New Worlds. This science provides data on the evolution of parasites and their hosts, in addition to helping understand the occupation of territories and retracing migratory paths of prehistoric populations[2,4].

Paleoparasitological findings feature not only specific human parasites, inherited from ancestors, but also those acquired over the course of hominid dispersion and biological and cultural evolution[3]. Therefore, in paleoparasitology it is very important to know whether the coprolite is of human or other animal origin. Thus, the final diagnosis is

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based on evidences pointing to a true infection by a parasite or a false parasitism. A zoonosis may have occurred, i.e., a parasite of an animal may also have infected humans, and the paleoparasitologist has to deal with this possibility.

Rudolph Virchow coined the term zoonosis in 1855. Since then, other authors have attempted to define zoonoses and identify their causes, propelled by the early age of bacteriology that furnished data concerning their etiological agents and modes of transmission[73]. In the 1950s, the World Health Organization (WHO) issued its definition of zoonosis. The official concept (1959), adopted to this day, defines zoonosis as any disease or infection that is naturally transmissible from vertebrate animals to humans[73,88] and vice-versa. This transmission is possible since parasites can occur in hosts over the course of the evolutionary process, that is, there is a parasite specificity that restricts infections, but the latter can occur by evolutionary adaptation in new host species[9,54].

These various possibilities can include an accidental encounter between parasites and new hosts. Such encounters can generate new intraspecific relations (either successful or unsuccessful) and intermediate relations[91]. This fact can be exemplified by the sporadic finding of animal helminth eggs in human feces, merely meaning human consumption of some animal infected with the parasite and that the eggs passed through the human digestive tract together with the ingested food, without establishing a relationship and without even causing any damage to his health[38].

REINHARD[102] also refers to false parasitism, a relationship in which the parasite's lack of specificity with the individual that consumed it prevents the parasite from completing its biological cycle, developing, or multiplying inside this host; a large quantity of eggs in the feces would indicate true infection. The amount of eggs found in coprolites can vary according to the fragment of the sample used, the taphonomic processes involved, the diversity of parasites in an individual[40,102], environmental factors[63], and interaction between parasites that occupy the same habitat and that can express themselves in inter and intra-specific cooperation and/or competition[6,12]. COIMBRA Jr. & MELLO[29] report the consumption of raw rodent liver by indigenous peoples, in whom Capillaria eggs are eliminated for days, but without infection occurring.

When an animal parasite manages to establish itself in the human body, a true infection occurs, thus a zoonosis, whether or not the parasite succeeds in completing its life cycle. For example, human infection with larvae of *Ancylostoma caninum* or *Toxocara canis*, both canine parasites, cause infection and clinical manifestations, but the parasites do not complete their life cycle in the human host[105]. Another example is *Trichinella spiralis* infection. Humans become infected when they eat raw or undercooked meat of infected animals, especially pigs. There are ancient records of *T. spiralis* infection in Egypt from 3,220 years BP[30] (Before Present), Spain in the 19th century 19 AD[13] (Anno Domini), and Alaska from 440 ±70 BP[138]. Currently, in addition to *T. spirallis,* eight other species of the genus have been recorded in humans[99]. *Echinococcus granulosus* also fails to complete its cycle in humans but has been found in archaeological remains in the USA[79,89,132], Europe[11,21,100,130,131], and Middle East[5,137].

In this review we searched only for records of intestinal helminths. The article by GONÇALVES *et al*.[52] guided the research. We conducted a search in electronic databases (PubMed, Isi Web of Science, Scopus, Scirus, and Scielo) up to January 2008 and a search in indexing journals. The attempt was to verify all the existing records on paleoparasitology and related sciences that in some way had recorded the occurrence of animal intestinal parasitic helminths in human archaeological remains. We excluded findings of uncertain origin, but false parasitism was considered.

This review is expected to expand the knowledge on the occurrence of animal parasites in humans from an evolutionary perspective, from prehistoric periods, correlating them to the various regions of the world, chronology, and different habits between populations, thus contributing to the studies conducted today among special populations, like indigenous groups in Brazil.

Principal Zoonoses of the Old World (except East and Southeast Asia)

As shown in Table 1, the majority of findings of animal parasites in human archaeological material from the Old World are concentrated in Europe, where numerous latrines provide material for paleoparasitological analyses of practically the entire continent[18].

The first published studies containing zoonotic helminths were by SZIDAT[124], who found *Diphyllobothrium latum* eggs in material from Austria dated 1,500 years BP, followed by findings of *Dicrocoelium* sp. in material from England dated 1,100 AD[125]. In Germany, JANSEN & OVER[68] found *D. latum*, *Taenia* sp., and *Fasciola hepatica* eggs dated 100 BC - 500 AD. The paleoparasitological findings since then have always shown the presence of zoonotic parasites transmitted mainly by consumption of and/or contact with domesticated animals. The domestication of animals and plants favored an increase in the occurrence of parasitosis among human populations, as exemplified in specific regions. The increase in food production obtained through agriculture favored the agglomeration of individuals and consequently the occurrence of specific human parasites, transmitted by direct contact with environments and/or contaminated foods. In addition, the agricultural surplus was stored in deposits, increasing the potential risk of infection by contamination of the grain or other foodstuffs and by attracting animals like rodents[7,31,87], the natural hosts of various zoonoses affecting humans[92].

With domestication, humans kept animals close to them for consumption, like cattle, goats, and pigs, as well as companion animals like dogs and cats. ROCHA *et al.*[112] and FERNANDES *et al.*[37], studying material from Medieval European latrines, showed that specific human parasites like *Ascaris lumbricoides* and *Trichuris trichiura,* and animal parasites like *Ascaris suum* and *Trichuris suis*, that infect swine, appeared in association with each other, thus proving the close relationship between man and these animals, already demonstrated by archaeological records. This constant contact with animals facilitated the transmission of parasites, including zoonotic ones, that were previously acquired sporadically, like *Taenia* sp., *Capillaria* sp., and *Fasciola* sp., causing an increase in the number of animal parasite infections in human populations[8,15,16,18,19,34,35,36,37,61,62,67,68,71,86,110].

Still, little or nothing is known about the parasites that affected Old World populations before the domestication of plants and animals,

Table 1
List of animal intestinal helminths found in Old World human archaeological samples (except East and Southeast Asia)

Parasite	Natural Host	Country	Date
Dicrocoelium sp.	herbivore	Switzerland	5,384-5,370 BP[35]
		France	5,040-5,000 BP[35]
		Austria	2,000 BP[8]
		South Africa	Iron Age[33]
Dicrocoelium dendriticum		England	11th century AD[98]
		England	1100 AD[125]
		France	14th-15th century AD[14,15]
Fasciola sp.	ruminants and others herbivores	France	5,600 BP[35]
		Switzerland	5,384-5,370 BP[35]
		Germany	15th century AD[62]
		Egypt	2,400-2,300 BP[61]
		Nubia	2,700-2,300 BP[61] 4,400-3,750 BP[61] 2,275 BP-350 AD[61] 300-1,500 AD[61]
		Cyprus	7,600-9,500 BP[61] 10,500 BP[61]
Fasciola hepatica		France	32nd-25th century AD[19] 14th-15th century AD[15]
		Germany	4,500 BP[34] 2,100 BP - 500 AD[68]
		Austria	2,000 BP[8]
		Denmark	780-800 AD[86]
		Switzerland	5,900-4,900 BP[71]
Opistochiformes	carnivores	Switzerland	5,384-5,370 BP[35]
Opistorchis sp.	carnivores	Switzerland	5,900-4,900 BP[71]
Diphyllobothrium sp.	carnivores	France	5,600 BP[35]
		Switzerland	5,384-5,370 BP[35] 5,900-4,900 BP[71]
		Germany	15th century AD[62]
		Nubia Egypt Cyprus	2,700-2,300 BP[61] 2,400-2,300 BP[61] 9,600-9,500 BP[61]
Diphyllobothrium latum		France	5100-4400 BP[19] 15th-16th century AD[52]
		Germany	2,100 BP - 500 AD[68]
		Austria	1,500 BP[124]
		Israel	13th century AD[83]
		Norway	15th century AD[116]
		Belgium	18th century AD[52]

since most parasite findings in archaeological material date to after the introduction of agriculture as a means of subsistence. The oldest records of animal parasites in human archaeological remains are from the African continent and Middle East, already in agricultural societies, where eggs from the genera *Diphyllobothrium*, *Dicrocoelium*, *Taenia*, and *Fasciola* were found in material dating close to 10,000 BP in Israel, South Africa, and Egypt [33,61,81].

In Europe, the oldest records date to 4,500 year old *Fasciola hepatica* eggs found in human and cattle coprolites in Germany[34], and 3,900 - 2,900 BP, with *Dicrocoelium* sp., *Fasciola hepatica*, Opistorchiformes, *Diphyllobothrium* sp., *Taenia* sp., and *Dioctophyma renale* eggs found in archaeological material belonging to lacustrine communities in the Swiss and French Alps[35,36,71]. Although these findings are from communities that dominated farming techniques, they belong to the period in which the Pfÿn-Horgen transition occurred in the Neolithic (3,900 - 2,500 BC), when climate changes affected the production of cultivated grains, leading to subsistence crises. The population was thus forced to turn to the consumption of wild vegetables, and also hunting and fishing, often consuming raw items[35,36,71].

Table 1
Continuation

Parasite	Natural Host	Country	Date
Taenia sp.	bovines (*T. saginata*) pigs (*T. solium*)	Egypt	3,200 BP[110] 2,715-2,656 BP[61]
		Cyprus	10,500 BP[61] 6590±260 BP[61] 9,600-9,500 BP[61] 10,500 BP[61]
		Nubia	2,700-2,300 BP[61] 4th-5th century AD[61] 300-1500 AD[61] 4,400-3,750 BP[61] 2,275 BP-350 AD[61]
		France	5,100-4,400 BP[35,36] 17th-18th century AD[16]
		Germany	100 BC-500 AD[68]
		Austria	2,000 BP[8]
		Denmark	750-800 AD[86]
		Netherlands	1,370-1,425 AD[67]
		Switzerland	5,900-4,900 BP[71]
Capillaria spp.	several mammals and probably birds	Switzerland Belgium	5,900-4,900 BP[71] 16th century AD[37]
*Dioctophyma renale**	carnivores	Switzerland	5,900-4,900 BP[71]

East and Southeast Asia

In Asia, especially in Japan, findings are related mainly to parasites acquired through the consumption of raw fish, a cultural tradition that dates to prehistoric times, popularized with the emergence of sushi in the 4th century AD[65] (Table 2). *Clonorchis sinensis*, *Paragonimus* sp., *Metagonimus yokogawai*, and *Diphyllobothrium* sp. eggs have been found in fecal material from Japanese archaeological sites dated from 2,300 BP to the 12th century 12 AD[78]. Unlike Japan, in China, where foods are traditionally cooked before eating, *C. sinensis, Schistosoma japonicum*, and *T. solium* eggs have been found in archaeological remains dated from 2,300 BP to 2,100 BP[27,72,129,136]. In Korea, *C. sinensis* eggs have been found in human remains dated to 668 - 935 AD and 1,411 ± 42 AD[58,117]. A mummy from 1,650 - 1750 AD was also found with *Metagonimus yokogawai* and *Gymnophalloides seoi* eggs[118].

Currently, the main zoonotic helminths in the Asian population are still related to the consumption of raw fish and other seafood[25].

New World

Agriculture was not adopted at the same in the New World as in the Old World. Various prehistoric populations either continued their hunting-gathering habits - despite knowledge of farming techniques adopted by other groups in the same region - or used them jointly[32,103].

PICKERSGILL[97] reports four independent areas in which vestiges of agricultural development in the Americas by pre-Colombian groups can be observed: Southeast North America, Mesoamerica, the Andes region, and tropical lowlands in South America, with the cultivation of corn (*Zea mays*), beans (*Phaseolus vulgaris*), potatoes (*Solanum tuberosum*), manioc (*Manihot esculenta*), squash (*Cucurbita* spp.), and peanuts (*Arachis* hypogaea), among others, by pre-Colombian groups[74,97,101,102,122].

However, the domestication of animals shows major differences in comparison to the process that occurred in the Old World[22]. DIAMOND[31] explains this difference by local geography and climate, since the majority of large herbivores were located in Eurasia, while the Americas had few large species with chances of domestication, especially after the great extinctions of mammals in the Late Pleistocene.

Importantly, however, is that the great herds of Old World herbivores are migratory or occupy large areas, requiring continuous shifting of human populations to follow this resource, through areas that are sometimes inhospitable or used by other human groups, a phenomenon known as transhumance[139]. From this perspective, the investment in domestication brings advantageous results[70]. However, in the Americas, despite the existence of medium and large social herbivores like the Rocky Mountain Bighorn sheep (*Ovis canadensis*), American bison (*Bison bison*), moose (*Alces alces*), and others in North America[51], there is no evidence that these species were 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[22,123]. Dogs were also raised for food in Mexico[133], but domestication of the dog did not occur

Table 2
List of animal intestinal helminths found in human archaeological samples from East and Southeast Asia

Parasite	Natural host	Country	Date
Clonorchis sinensis	carnivores	China	2,300 BP[136] 2,167 BP[27,72]
		Japan	7^{th} - 9^{th} century AD[78]
		Korea	668-935 AD[60] 1411±42 AD[117] 16^{th}-17^{th} century AD[118]
Gymnophalloides seoi	Oystercatcher (*Haematopus ostralegus*)	Korea	16^{th}-17^{th} century AD[118]
Metagonimus yokogawai	dogs, cats, pigs and birds	Japan Korea	7^{th} century AD[78] 16^{th} - 17^{th} century AD[118]
Paragonimus sp.	mammals, mainly carnivores	Japan	3^{rd} century AD[78]
Schistosoma japonicum *	herbivores, carnivores, pigs and rodents	China	2,167 BP[72] 2,100 BP[129]
Diphyllobothrium sp.	carnivores	Japan	12^{th} century AD[78]
Taenia sp.	bovines (*T. saginata*) pigs (*T. solium*)	Japan	7^{th} century AD[78] 8^{th} century AD[78]
Taenia solium	pigs	China	2,167 BP[27,72]

on this continent. Dogs (already domesticated) came in the company of prehistoric humans when they arrived on the American continent some 14,000 years ago[115].

For most native groups in the South American lowlands, animals were not domesticated for food. In Brazil, for example, various indigenous groups kept wild animals either as pets or for plucking feathers in the case of birds[101]. Although there is no abundance of large herbivores in groups, like those that exist in Eurasia, North America, and Africa, some, like peccaries (*Tayassu pecari* and *Pecari tajacu*) and tapirs (*Tapirus anta*) could have been domesticated. However, since the browsing and grazing areas for these species are relatively small, they are not migratory. Other species such as wild pigs and capybaras live in large herds[80,127] and thus provide permanently available food, in addition to the abundant supply of fish in many South American lowland regions[81].

Unlike the Old World, in the New World there are samples of coprolites available from both hunting-and-gathering and farming populations, thus allowing to expand the knowledge on the possible consequences of the domestication of animals and especially of plants as alternative food sources in prehistoric populations, although in different scenarios and situations.

North and Central America

In North America, animal parasite findings in human coprolites are concentrated in the USA[42,43,44,55,56,57,58,59,84]. REINHARD[102] reviews the occurrence of parasites in the United States according to the geographic areas where they were found. The author showed that most of the findings are situated in the southern part of North America and Mexico, with Acanthocephala and Hymenolepididae eggs, among others. A peculiar case is the finding of eggs from *Moniliformis clarki*, an acanthocephalan transmitted by consuming insects, a common eating habit among North American indigenous peoples. For a long time Acanthocephala findings were attributed to false parasitism. However, the frequency of these findings in prehistoric material from the Americas in association with cultural customs favoring infection suggests that these parasites really infected these populations. However, this frequency may only reflect the preference or abundance of the available supply of insects for eating.

Data obtained by REINHARD[102], principally among the ancestral Pueblo of the United States (the ancient Anasazi), show that as occurred with Old World populations, the incidence of specific human parasites increased with the introduction of agriculture. Another episode that increased the occurrence of parasites in these populations occurred during an apparent ecological collapse which, similar to one that occurred in Europe[71], led the inhabitants of the last occupation of the Antelope House in Arizona to consume wild plants like cacti to replace the lack of cultivated crops. This strategy was also apparently adopted during dry seasons, when wild plants and also dogs, rabbits, whole rodents, lizards, and other animals were consumed[103].

In addition to the findings cited above, BOUCHET *et al*[17,20] found eggs from genus *Diphyllobothrium* in samples from Alaska.

South America

In South America, a zoonosis that is known to have occurred in a prehistoric population and that still exists in current-day populations in Peru and Chile is the presence of *Diphyllobothrium pacificum*. Swiss parasitologist Jean BAER[10], called to Peru to study parasites found in persons with an intestinal clinical condition, identified the species *D. pacificum* in the patients, a parasite of sea lions whose larvae contaminate saltwater fish and shellfish. The presence of this parasite in the population is explained by the consumption of a traditional dish by the Pacific coastal populations, *cebiche*, made with raw sea fish. BAER raised the hypothesis that the prehistoric populations also had this parasitosis, a fact confirmed years later when *D. pacificum* eggs were found in Chilean coprolites 4,000 years old by FERREIRA *et al.*[39], who commented on the coincidence in the findings. Other researchers also confirmed the presence of this parasite in prehistoric populations on the Pacific coast[23,93,106,108].

In Brazil there are only three records of animal helminths in human coprolites. The first was by ARAÚJO *et al.*[1], who found *Trichostrongylus* sp. eggs associated with *T. trichiura* eggs in a mummified body from the colonial period. GONÇALVES *et al.*[52] found Acanthocephala eggs in material dated 4,905 - 1,325 BP in Minas Gerais. But perhaps the most significant finding of a zoonosis in archaeological material in Brazil came from a paleoparasitological review of coprolite samples from a naturally mummified body in the State of Minas Gerais, Southeast Brazil, dated 600 - 1,200 BP, which allowed the correct identification of *Echinostoma* sp. eggs and the certainty of this parasite's occurrence in humans[119]**.** Echinostomiasis is an endemic zoonosis in Asia, that can produce debilitating symptoms in infected individuals[41,53]. Humans become infected by the ingestion of *Echinostoma* spp. larvae present in raw mollusks, fish, or amphibians, the parasite's intermediate hosts[111]. This is 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 populations.

Echinostoma sp., *Paragonimus* sp., *Diphyllobothrium* sp., *Diphyllobothrium pacificum*, *Capillaria* spp., *Trichostrongylus* sp., and Acanthocephala are the zoonotic helminths that have already been found in South American populations (Table 3). We only considered findings that dated up to close to contact with Europeans, since they are what we can positively classify as pre-Colombian. Thus, the current study excluded the findings by HORNE & TUCK[66] and FUGASSA[45], of *Taenia* sp. eggs in 17th-century material from Canada and 19th-century material from Argentina, since they are related respectively to the introduction of swine and beef cattle on the American continent after discovery.

Present Day

Currently, zoonoses caused by helminths have important impacts on human development around the world[49,77,92]. Recent publications have classified the majority of emerging or reemerging pathogens as zoonotic[88,126,135].

Nevertheless, records are rare on the occurrence of zoonoses among current native populations in Brazil. This is curious, since many Brazilian indigenous groups have maintained their traditional eating habits and continue to hunt and consume wild animals as their principal source of protein[81,85]. Many game animals are natural hosts of parasites, including helminths[46,64,109].

The explanation for this gap may lay in the fact that after contact with Brazilian national society, many indigenous communities have undergone social, economic, and environmental changes. Such changes have influenced the epidemiological profile of these groups, which have obtained easy access to antihelminthic drugs through indigenous health agents[120], often administered without any control. In addition, geographical restrictions imposed by territorial demarcation and transformation of semi-nomadic into sedentary behavior in the majority of the South American indigenous groups have contributed to fixing large groups, resulting in villages with high population densities and precarious sanitation, facilitating the transmission of specific human parasites that compete with those of animal origin[28,29,134].

Such data are provided by the publications by VIEIRA[128] and SILVA[120], both on intestinal parasitosis in Brazilian indigenous populations. In the literature review by VIEIRA[128] covering indigenous groups from throughout Brazil, *Hymenolepis* sp., *Taenia* sp., and *Capillaria* sp. were the only zoonotic helminths cited.

SILVA[120] conducted an extensive coprological analysis of the Suruí population, an indigenous tribe in the State of Rondônia in the Brazilian Amazon. Stool specimens were analyzed in two laboratories and were positive for the tapeworm *Hymenolepis diminuta* in 21/541 (3.9%) samples, and for *Capillaria* sp. in 28/541 samples (5.2%) of the specimens in this same set. A middle-aged woman's stool test showed eggs from *Dipylidium caninum*, a tapeworm rarely found in humans. *D. caninum* is a parasite of domestic and wild canids and felines that infects humans through the ingestion of an infected arthropod[92]. *D. caninum* and *Hymenolepis diminuta* have still not been found in paleoparasitological analyses. *Hymenolepis* spp. eggs were found in samples from the USA and Sudan[61,107], although the species were not identified and may be *H. nana*, specific to humans.

Many Brazilian indigenous groups consider viscera from animal, especially liver, a delicacy. The liver is consumed raw, and thus the presence of *Capillaria* sp. eggs in the feces of native Brazilian populations is not uncommon[24,29,50,113,114]. *Capillaria* sp. eggs have also been found in paleoparasitological analyses in Europe[7,37], but not in Brazil.

DISCUSSION AND CONCLUSION

Although in this review we adopted the World Health Organization's definition of zoonosis, we did not consider *A. lumbricoides* a zoonotic helminth as the WHO does. The *A. lumbricoides* cycle is direct and independent of another animal, and its origin is by the phylogenetic route, that is, descending from a common ancestor of humans and primates[3,4]. Parasites originating from the ecological route can be classified in two categories: (1) those that originated from other species and underwent modification over the course of the evolutionary process and became species-specific to humans (meaning that they differ from the original species) and (2) zoonoses. An example of the first category is the human immunodeficiency virus (HIV). MARX *et al.*[76] argue that AIDS is not a zoonosis, since the virus underwent modifications from the original version to infect humans, which goes against the concept of zoonosis as a disease naturally shared by animals and humans. Among the helminths, a good example is *H. nana*. According to the Pan-American Health Organization, some parasitologists classify the species that infects humans as *H. nana* var. *nana* and the species that infects rodents as *H. nana* var. *fraterna*, on grounds that there is a parasite host-specificity, justified by the lack of evidence of *H. nana* transmission from rodents to humans[92].

The parasitism phenomenon consists of dynamic relations within a natural evolutionary process as old as life itself[38]. An animal parasite that does not infect humans may begin to do so if pressure, genetic potentiality and plasticity allow it. The pressures for such an alteration can come from the environment itself, especially if the original hosts become scarce and thus its survival comes to depend on the incorporation of new hosts into its cycle[12,95]. A zoonosis occurs when these conditions appear. But if the alteration is so great that the parasite becomes totally specific to the new host[9,90], the outcome could be similar to HIV infection[76]. This may be

Table 3
List of animal intestinal helminths found in New World human archaeological samples

Parasite	Natural host	Country	Date
Echinostoma sp.	mammals and birds	Brazil	600-1,200 BP[119]
Paragonimus sp.	mammals, mainly carnivores	Chile	4,500 BP[56]
Trematode	nany vertebrates	Argentina	7880 ± 150[46]
Diphyllobothrium sp.	carnivores	Peru	5,000 BP[23]
		USA	1,400-1,700 AD[17]
Diphyllobothrium latum	carnivores	USA	2,300 BP-200 AD[102]
Diphyllobothrium pacificum	carnivores	Peru	10,000-4,000 BP[106] 4,700-4,850 BP[93]
		Chile	6,110-3,950 BP[39] 4,000 BP[105]
		USA	840 BP ± 40[20]
Taeniidae	?*	USA	6,500 BP[102] 6,200 BP[102] 4,000 BP[102] 300 BC-200 AD[102] 20 AD[102] 1100-1250 AD[102] 1250-1300 AD[102]
Capillaria spp.	several mammals and probably birds	Argentina	8920 BP to Modern Age[45]
Physaloptera sp.?	several vertebrates	Argentina	7880 ± 150[46]
Strongyloides sp.	canids and non-human primates	USA	500-1200 AD[57] 1075-1140 AD[102]
Trichostrongylus sp.	ruminants and other mammals	Chile Argentina USA Brazil	3,080-2,950 BP[52] 1,000-500 BP[52] 1,075-1,140 AD[102] 18th century AD[1]
Trichuris spp.	many mammals	Argentina	6540 ± 110 - 7920 ± 130 BP[46,47]
Acanthocephala	many mammals	USA	11,500 BP[44] 10,000 BP[44] 4,000 BP[44] 20 AD[44] 10,000-4,000 BP[42,44] 6,850 BP[56] 3,869 ± 60 BP[84] 20 ± 240 AD[84] 2,300 BP[58] 400-1,200 AD[58] 900-1,100 AD[55] 900-1300 AD[43,44]
		Brazil	4,905 ± 85-1,325 ± 60 BP[52]
		Argentina	6540 ± 110 BP[45]
Miniliformis clarki	many mammals	USA	12,000-10,500 BP[59] 10,000 BP[59] 8,400-6,856 BP[59] 6,800-6,300 BP[59] 6,300-7,900 BP[59] 4,000 BP[59] 3,869 BP[59] 20 AD[59] 600-900 AD[59]

*In this case both the host and parasite species are unknown.

taken as a general rule, as probably different responses occur from virus to other parasite organisms.

During human history, populations have faced different environmental conditions with biological and cultural adaptations. Scarcity of food and other resources necessary for survival, and also climatic and environmental changes have facilitated contact between humans and parasites, from animal origin or even not known to science, as evidenced by the work of LE BAILLY[71], FUGASSA[45], and REINHARD[103] in prehistoric populations of Europe, Argentina, and North America, respectively.

McMICHAEL[80] argues that the historical transitions experienced by our prehistoric ancestors when they climbed down out of the trees onto the savannahs, incorporated meat into their diet, and more recently since the emergence of *Homo sapiens*, the development of agriculture, and the conquest of new territories and civilizations favored the emergence of (and exposure to) infectious agents of animal origin. ARMELAGOS *et al.*[7] analyzed the epidemiological transitions experienced by humankind and concluded that we are undergoing a new transition, in which parasitic infections that were common 10,000 years ago, at the time of the first transition (with the development of techniques for cultivation of plants and domestication of animals), are now reemerging with the possibility of causing major economic impacts. The agricultural frontier's encroachment on natural areas and parasites' resistance to conventional treatments can explain this reemergence.

Paleoparasitological findings are important clues for knowledge on human adaptive progress since prehistory, in addition to revealing eating habits of extinct populations and the domestication of animals. The current study shows that various zoonoses known today have occurred since prehistoric times. The knowledge of which parasites circulated in the past and their geographic distribution helps understand whether a zoonosis is emerging or reemerging[77].

Thus, the fact that *D. 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 these infections did not occur.

We recently identified genus *Spirometra* (Cestoda) in feline coprolites from the Serra da Capivara National Park in Piauí State, Brazil (unpublished data). This parasite is the causative agent of sparganosis in humans, and one cannot ignore the possibility of this and other parasites circulating in the local human population. Few authors conduct studies with archaeological material of animal origin. This may represent a loss of information, since the parasite's presence in the local fauna, associated with environmental and socio-cultural factors like diet and type of dwellings, may indicate transmission routes for the parasites to human populations.

To the extent that more sensitive diagnostic techniques become available, more parasitic infections from the past are detected, and new paleoparasitological findings are recorded around the world. Additional studies on zoonotic infections from the past will expand the knowledge on biological and sociological aspects of the health-disease process and the co-evolution between parasites and animal and human hosts.

In addition, the identification of zoonoses that affected ancestral peoples, understanding their mechanisms of transmission and the factors affecting this dynamic (whether biogeographic, ecological, cultural, historical, or social), can help development of forecasting models to control parasitic diseases soon after their emergence or even to prevent them before they become public health problems.

Geographic, biotic, and abiotic factors from the environment in which prehistoric populations lived (biocenosis) and their cultural characteristics can trace models for the predictability and transmission of the parasite fauna in these groups, as done by MARTINSON *et al.*[75] and REINHARD[104], and are based on models grounded in the theory of natural foci[94,96,121]. These studies are especially applicable to zoonoses, since biocenosis in natural ecosystems is well defined[121], but they can also be applied to human-specific parasites.

Recent advances correlating the processes of fragmentation and isolation of natural areas to genetic loss, the interruption of gene flow between species, and the introduction of invasive exotic species in the wild fauna[26,69] can help compose prehistoric scenarios that favored the occurrence of animal parasites in humans, as well as drawing scenarios for the future.

RESUMO

Helmintos animais em vestígios arqueológicos humanos: revisão de zoonoses no passado

São revistos os registros de ocorrência de helmintos intestinais parasitos de animais em vestígios arqueológicos humanos, relatados desde o surgimento dos estudos paleopatológicos. Busca-se relacionar os achados em paleoparasitologia com fatores geográficos, bióticos e abióticos do ambiente em que as populações pré-históricas viviam, e com aspectos do processo de dispersão e evolução biológica e cultural humana. A modificação de hábitos alimentares e a incorporação de novas práticas culturais são analisadas sob o ponto de vista das zoonoses desde a pré-história até a atualidade, em especial em populações indígenas brasileiras. Três tabelas identificando os helmintos, seus hospedeiros naturais, datações e local dos achados arqueológicos complementam esta revisão. Conclui-se que várias zoonoses conhecidas hoje ocorrem desde a antiguidade e que estes dados, combinados a estudos de emergência e reemergência de doenças, podem auxiliar a compor cenários para o futuro.

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