Review

Food, parasites, and epidemiological transitions: A broad perspective

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ABSTRACT

Pathoecology provides unique frameworks for understanding disease transmission in ancient populations. Analyses of Old and New World archaeological samples contribute empirically to our understanding of parasite infections. Combining archaeological and anthropological data, we gain insights about health, disease, and the way ancient people lived and interacted with each other and with their environments. Here we present Old and New World parasite evidence, emphasizing how such information reflects the different ways ancient populations exploited diverse environments and became infected with zoonotic parasites. It is clear that the most common intestinal helminths (worm endoparasites) were already infecting ancient inhabitants of the New World prior to the European conquest, although not so intensely as in ancient Europe. The first paleoepidemiological transition from hunting–gathering to agriculture did not change the zoonotic infection pattern of people in the Americas. However, the same transition in Europe resulted in increased zoonotic parasitism with parasites from domestic animals. Therefore, there is a demonstrable difference in the impact of the first paleoepidemiologic transition in the Americas compared to Europe.

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1. Introduction

Pathoecology, as defined by Martinson et al. (2003), is the study of parasitism in context of culture and environment. In a paleopathological sense, the evolution of *Homo* was an entirely new adaptive process. Typically, parasitism is derived from the coevolution of vertebrate hosts with parasites in a specific environment (Gandon et al., 2008). With humans, however, adaptive behavior strategies could be developed to accommodate this interaction. With the genus *Homo*, there evolved a capacity for symbolic thought that resulted in an enormous diversity of cultural

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adaptation to an equally diverse array of environments on a global scale. Thus, cultural evolution produced a variety of behaviors that enabled humans to adapt all environments and to spread the planet in hundreds of ecological niches, each with its own array of parasites. Therefore, throughout the early radiation of *Homo*, symbolic thought and flexible cultural evolution had adaptive value in coping with the endemic parasites encountered in diverse environments (Donald, 1993). This is especially true of food-borne parasites which were encountered as people adapted gastronomically to new and different fauna. In the New World archaeological record, we can see these processes at play.

The paleopathology of infections disease has been viewed as passing through distinct "paleoepidemiologic" transitions. Barrett et al. (1998) asserted that there are three pathoecologic phases and two major paleopaleoepidemiologic transitions. They proposed a "Paleolithic Age Baseline" of human infection and stated that during the Paleolithic times, human populations existed as small bands of nomadic foragers. The small and diffuse human groups could not support many infectious agents. This is the original state of human parasitism. With regard to pathoecology, this has been supported by analyses of coprolites (Reinhard, 1988, 1990; Reinhard et al., 1985). From this Paleolithic baseline, human populations experienced new infectious disease challenges with the Neolithic revolution. Therefore, the first epidemiologic transition was that between the Paleolithic and Neolithic. For Europe, the first epidemiologic transition established a pattern of high prevalence of disease that lasted in all regions for centuries. Barrett et al. (1998) asserted that permanent settlements, accumulation of human waste, animal domestication, and agricultural practices increased contact with a variety of parasites. The Industrial Revolution, according to Barrett and colleagues, saw the control of infectious diseases and the emergence of chronic, noninfectious challenges. This is the second epidemiologic transition. In the archaeoparasitological record, this is seen in a reduction of contexts that contain parasite remains and a reduction of the diversity of parasite species. For the Americas, the "Paleolithic Age Baseline" is represented analogously by Paleo-Indian and Archaic periods. The Neolithic revolution is represented by Formative cultures and their subsequent periods. We are comparing the evidence of food-borne parasites between the Americas and the Old World of Europe with some reference to the Old World of Asia. We are presenting our review following the transition sequence established by Barrett et al. (1998).

For this paper, we are focusing on cultural dietary adaptations, or gastronomy in the broadest definition of the word. Therefore, we review the literature for Europe and the Americas with specific interest in parasitic evidence that is directly related to food choice and preparation. The data set comes from a variety of sources including mummies, coprolites, burial sediments, and latrines. Taphonomically, these data sources are not equal. Methods have been refined over several decades to recover parasite remains efficiently from these sources (Reinhard et al., 1986). However, the best methods cannot recover ephemeral remains from contexts, such as open middens, that are prone to decomposition. Ephemeral remains include larvae and delicate eggs. In our combined experience, there is significant decomposition of remains from latrines by fungi and arthropods as described by Reinhard et al. (1986). In contrast, coprolites exhibit the best preservation. Mummies (Reinhard and Urban, 2003) and sediments from sacra (Fugassa et al., 2008a) also show excellent preservation of delicate eggs. Of the range of nematode, cestode, and trematode eggs recovered from archaeological sites from these sources, pinworm eggs, hookworm eggs and larvae and threadworm larvae are differentially susceptible to decomposition in latrines. However, they preserve well in mummies and coprolites. In coprolites found in archaeological layers larvae may have abandoned feces before desiccation be completed. Those nematodes that have infective larvae, such as

hookworms and threadworms, are rare in latrines and this may be due to poor preservation conditions. The delicate eggs of pinworm have been rarely found in latrines, partly because of decomposition and partly because few pinworm eggs are passed in feces relative to geohelminths. As of this writing, thousands of parasite samples from hundreds of sites have been analyzed from Europe, Asia, North America and South America. This provides a data base that can show the general relation between diet and parasitism for these areas. Archaeoparasitology and paleoparasitology are terms used hereafter interchangeably. The first term is mainly used in association with human remains while the other has a broader spectrum, also referring to animal parasites. Both refer to parasite infections, not necessarily to diseases.

2. Parasite migration to the New World

Ancient populations arrived in the New World with an array of tightly coevolved human-specific parasites that adapted to *Homo* early in that genus's evolutionary history (Araújo et al., 2008). Thus, over ten thousand years ago human groups in South and North America hosted the intestinal helminths pinworm (*Enterobius vermicularis*), hookworm (*Ancylostoma duodenale/Necator americanus*), whipworm (*Trichuris trichiura*), and rarely roundworm (*Ascaris lumbricoides*). The head louse (*Pediculus humanus*) is also a human parasite found in South and North American archaeological sites. Intestinal worm and louse eggs have been found associated with humans in archaeological sites dated as early as 10,000 years ago. Therefore, some common human parasites already infected prehistoric human populations in the Americas long before historic immigrants from Europe and Africa. However, all the parasites cited above (head lice, whipworm, hookworm, and roundworm) ultimately have an African origin, probably coevolving with remote *Homo* ancestors. Based on mitochondrial DNA (mtDNA) data, human head lice (*P. humanus*) separated from Chimpanzee head lice (*Pediculus schaeffi*) about 5.6 million years ago (Reed et al., 2004). The world's oldest known direct head louse association – nits on human hair – was found at a 10,000 year old archaeological site in northeast Brazil (Araújo et al., 2000). The intestinal helminths mentioned above and head lice were dispersed by human migrations to other parts of the world whenever and wherever climatic conditions allowed maintenance of the parasites' life cycles. Parasitological data showed that some of these parasites, especially hookworm, roundworm, and whipworm were introduced before 10,000 years ago by routes other than the Bering Land Bridge between Siberia and Alaska (Araújo et al., 2008). Pinworm and head lice, by contrast, were able to complete their life cycles in cold conditions of Arctic and may therefore have been introduced by groups migrating across the Bering Land Bridge (Araújo and Ferreira, 1995).

3. Diet and parasitism in the New World

In the New World, dietary patterns played a key role in defining parasitology in ancient people from the Paleolithic onward through the Formative and until Columbian contact (Reinhard, 1990, 1992a). Zoonotic parasites normally exist in animals but can be transmitted to humans. New studies that compare parasite diversity show that zoonotic parasites were taxonomically more diverse and with highly varied life cycles compared to human specific parasites in New World prehistoric agriculturalists (Jiménez et al., 2012; Cleeland et al., 2013). In other words, Native Americans exposed themselves to a greater variety of zoonotic parasites with a greater variety of life cycles than human-specific parasites. This was demonstrated by studies of a single site in northern Mexico. There, four zoonotic species were present, transferred by consumption

of grain beetles, fleas and amphibians. In comparison, three human-specific species were present, one with a direct anal-oral cycle and two fecal transmitted species. This Formative site, Cueva de los Muertos Chiquitos, is a microcosm of the parasitic state in the prehistoric Americas before and after the first paleoepidemiologic transition. Zoonotic parasitism dominated before and after the first paleoepidemiologic transition. In the same region, Archaic period coprolites have been analyzed as reviewed by Reinhard (1990). Fluke eggs consistent with *Echinostoma* were found. Eggs of the same type were recovered from the maize-dependent site of Cueva de los Muertos Chiquitos. Therefore, at least this zoonotic infection occurred before and after the first paleoepidemiologic transition. Interestingly, as evidenced in this area, two species of tapeworm were added to the human parasite spectrum after agriculture. One is a zoonosis associated with dogs, and the second with grain storage.

Reviews of parasite evidence from New World archaeological sites show that zoonotic infections from wild reservoirs were diverse and common (Beltrame et al., 2010; Fugassa and Beltrame, 2009; Fugassa et al., 2010, 2011; Moore et al., 1969; Reinhard, 1990; Sianto et al., 2009). In addition, diverse flukes and tapeworms infected prehistoric Americans, varying across local resources and varied continental ecologies (Fry, 1977; Gonçalves et al., 2003; Reinhard, 1990, 1992a; Sianto et al., 2009). Indeed, the majority of parasite species found in prehistoric New World site have animal origins (Gonçalves et al., 2003; Reinhard, 1990). Humans intruded into the endemic life cycles of a variety of parasites. By eating the parasites' normal intermediate hosts, whether invertebrates or vertebrates, people became infected. Thus, prehistoric American parasitism was defined by dietary habits from the Paleo-Indian and Archaic periods onward.

A case reported by Sianto et al. (2005) showed unusual eggs of a parasite identified as *Echinostoma* sp., along with hookworm eggs in a human coprolite from 1200 years ago in Brazil. In this area, humans can be involved in the *Echinostoma* sp. life cycle if they ingest raw mollusks, the invertebrate host. In Asian countries today *Echinostoma* sp. is an important public health problem, but the infection had never been reported in the Americas either in modern or ancient times when Sianto and her colleagues published their work. Carefully distinguishing true from false parasitism, the authors argued for true parasitism due to the large number of eggs recovered from the coprolite and the nature of the parasite life cycle, which implies intermediate host ingestion, and the presence of adult worms in the human intestine passing eggs. Thus, the parasitological record anticipates possible cases of echinostomiasis among current traditional groups in South America. Subsequently, a different *Echinostoma* species was found in the Cueva de los Muertos Chiquitos.

Moniliformis clarki is a classic case of an animal parasite that was recovered from human coprolites in Utah (USA) 10,000 years ago (Fry, 1977; Moore et al., 1969) on into Formative times. It is a thorny-headed worm, or acanthocephalan, related to the genus *Moniliformis moniliformis* that can cause significant discomfort in infected humans. In the Great Basin region it was a consistent parasite of Archaic hunter-gatherers throughout prehistory (Reinhard, 1990). Ingestion of insects, probably camel crickets, is implied in its transmission. Fry (1977) encountered the species in Formative sites in Glen Canyon, Utah. Moore et al. (1969) discussed the possibility of transmission by ingesting arthropods, linking true parasitism in humans to the evolutionary history of the parasite. Reinhard (1990) reviewed the many finds of acanthocephlans in Oregon, Utah and Colorado and concluded that these were true infections. Another thorny-headed worm genus, *Macracanthorhynchus* was recently reported (Fugassa et al., 2011; Jiménez et al., 2012). In this case, humans adapted by consuming a natural anthelmintic, sagebrush tea (*Artemisia* sp.) (Fugassa et al., 2011; Reinhard et al.,

2012). This discovery is from agricultural Ancestral Pueblo coprolites. Habitual ingestion of raw or poorly cooked insects contributed to what seems to have been a common infection by thorny-headed worms from hunter–gatherer to Formative agricultural times (Fry, 1977; Fugassa et al., 2011; Moore et al., 1969). Most importantly, thorny-headed worm infection was present on both sides of the agricultural revolution in the region and indicates that the first paleoepidemiologic transition did not affect infection with acanthocephalan species. This is because insects were an abundant food source for Paleo-Indian, Archaic, and Formative cultures in North America.

The reason for the continuation of zoonotic infection across the transition relates to the fact that people found small animals to be good food sources both before and after agriculture. The reliance on small animals for food in the Americas is borne out by zooarchaeological analysis of coprolites (Reinhard, 1992b, 2008; Reinhard et al., 2007). Ancient diets of the Southwest consistently included small vertebrates (Reinhard et al., 2007). Over 80% of preagriculture coprolites and almost 50% of coprolites from agricultural sites contained small animal bones. Eating small animals, no doubt incompletely cooked, expanded the diversity of parasitism in two ways; exposure to parasites by direct ingestion of the vertebrate host and exposure of humans to vectors of the parasite. The latter case has been documented for hunter–gatherers of Texas who selectively hunted wood rats and ate them in an incompletely cooked state (Reinhard et al., 2003, 2007). This exposed them to mucocutaneous transmission of the trypanosomes that cause Chagas disease by eating infected animals. Also, by reducing the normal vertebrate host number for the trypanosomes, the triatomine bug vectors increasingly infested human cave habitations and expose humans to the typical life cycle of trypanosomes (Reinhard et al., 2003). Thus, a New World exploitation of rodents resulted in new paleoepidemiological complications of Chagas disease (Reinhard et al., 2003).

In South America, Chagas disease can be characterized as zoonosis due to animal domestication, including dogs and guinea pigs. A very ancient association of humans with animal parasites is exemplified by Chagas disease. Paleoparasitological data showed that the protozoan *Trypanosoma cruzi* infected South American populations by 9000 years ago, first recorded in Chile's Atacama desert (Aufderheide et al., 2004). Infection was also present among inhabitants of the Brazilian lowlands 7000 years ago (Fernandes et al., 2008; Lima et al., 2008), changing the paradigm that hypothesized an origin in the Bolivian highlands (Araújo et al., 2009; Ferreira et al., 2011).

Food availability affected zoonotic parasite prevalence over time. An example of this is the prevalence variation of fish tapeworm infection exhibited among mummies from different Chinchorro cemeteries in Arica, Chile. *Diphyllobothrium pacificum* is a parasite with a curious history. Jean Baer first described the parasite in living Peruvians, highlighting morphological distinctions with another species, *Diphyllobothrium latum* (Baer, 1969). *D. latum*, infects humans in the northern hemisphere and has a life cycle involving terrestrial mammals, freshwater crustaceans and fish (Baer, 1969). The life cycle of *D. pacificum* may include marine crustaceans, fish and sea mammals, while also infecting humans. Baer described cases from Peru, characterized by abdominal discomfort, diarrhea, and general weakness, and the finding of parasite proglottids (segmented parts of the parasite's body) in feces. Baer hypothesized that ancient inhabitants were also infected by *D. pacificum*. He was unaware that Callen and Cameron (1960) had discovered *Diphyllobothrium* eggs in ancient coprolites from coastal Peru, ironically proving Baer's hypothesis correct even before Baer developed the hypothesis. Subsequent research showed that *D. pacificum* was the most common parasite among prehistoric cultures in Peru and Chile at all time periods and across
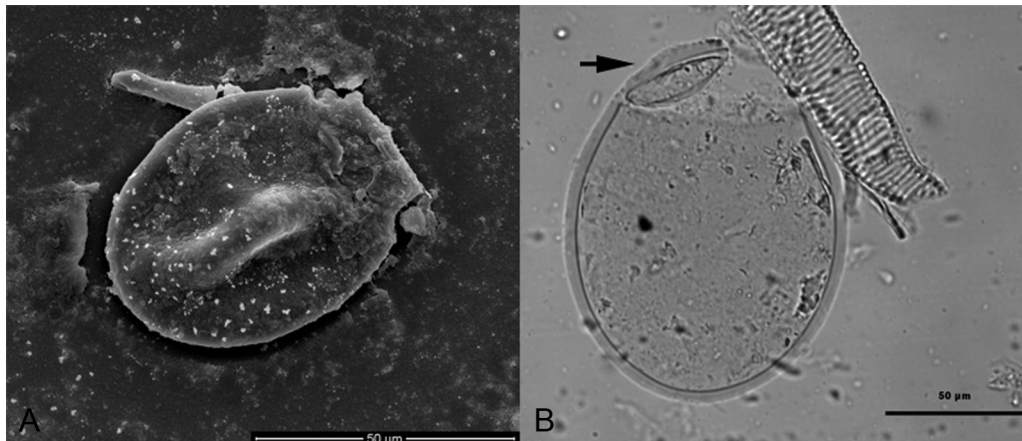
Fig. 1. *Diphyllobothrium pacificum* from human remains, Chinchorro mummies, Chile. These mummies date between 4000 and 5000 years ago. (A) Scanning electron microscopy showing eggshell layout and (B) bright field microscopy showing the operculum (arrow).

both paleoepidemiologic transitions as the infection is common today (Araújo et al., 1983; Ferreira et al., 1984; Patrucco et al., 1983). Reinhard and Urban (2003) discussed aspects of the infection among Chinchorro people from the extreme north of Chile dated between 4000 and 5000 years ago. These findings illustrate the persistence of food habits from prehistory to today (Fig. 1). However, Arriaza et al. (2010) demonstrated a relationship between prevalence of *D. pacificum* infections in the past and ENSO (El-Niño Southern Oscillations) events, which influence the abundance of fish as intermediate host species, alternating with other helminth parasitoses. They noticed that one cemetery exhibited a high level of parasitism while another had none. They were able to relate the prevalence variation to El Niño or ENSO phenomena. Ocean water temperature variation alternatively opened or closed coastal fishing waters to the fish species that host the tapeworm. The use of marine food resources in relationship to climate fluctuation thus influenced *D. pacificum* prevalence from Chinchorro times, nearly 6000 years ago. ENSO phenomena influence *D. pacificum* prevalence even to the present day. This shows that in some regions, climatic variation was at least as important as behavior in defining infection prevalence.

Prehistoric parasitism in the Americas challenges researchers with the sheer diversity of extraordinary parasites in the archaeological record. Some parasites are quite widespread due to common human activities. For example, New World agriculture and food storage patterns further promoted zoonotic parasites by establishing environments for food pests and their parasites. Hymenolepidid tapeworms parasitized people from the Southwest USA (Reinhard, 1992b), Mexico (Jiménez et al., 2012) and the Andes (Santoro et al., 2003). These tapeworms commonly infect rodents as the definitive hosts and grain beetles as intermediate hosts. By ingesting grain with grain beetles, humans became infected as well (Reinhard, 2008).

The analysis of zoonotic parasites is confounded by dietary patterns that resulted in the ingestion of animal parasite eggs. Thus, ancient people's coprolites and intestines may contain eggs from two distinctive sources: adult parasites in the intestines and food sources that simply pass through the digestive system. Paleoparasitological studies from Patagonia (Fugassa and Beltrame, 2009), the Arizona desert (Reinhard, 1990, 1992a) and the semi-arid regions of Brazil (Sianto et al., 2009) report animal parasite eggs in human coprolites. This suggests one of two alternative explanations: true parasitism with established infections or false parasitism whereby helminth eggs pass through the intestinal tract without infecting the human host (Sianto et al., 2005). Whether true infections or false infections, the presence of the eggs shows

that humans interacted with parasite life cycles of animals, therefore making humans susceptible to infection. This is especially evident in Patagonia through the work of Martin Fugassa and his colleagues (Fugassa and Barberena, 2006; Fugassa et al., 2008a,b, 2009, 2010) who frequently find parasites of animals in human coprolites (Fugassa and Beltrame, 2009; Fugassa et al., 2010). Some regions of the Americas today produce clinically bizarre parasites. For example, a recent case of *Calodium hepaticum* eggs passing through in feces was recorded in a woman living in the Amazon region (Costa et al., 2009). Her daughter gave her a carcass of a tapir that she ate everyday for more than a week. At the time of coproscopy, *C. hepaticum* eggs were found, initially in great numbers, declining a few days after the end of animal consumption, and finally disappearing. This phenomenon has a documented prehistoric counterpart. Fugassa et al. (2010) found *C. hepaticum* eggs in human and animal coprolites from Patagonian archaeological sites, indicating close contact between this parasite and humans during the Pleistocene–Holocene transition (13,000–9000 years ago), thus demonstrating a long history of false parasitism.

Changes in diet and parasitism can result from imperial expansion as shown by archaeological recovery of both parasites and food remains (Vinton et al., 2009; Santoro et al., 2003) for the Chilean Pacific coast. Vinton and her colleagues analyzed Inka Late Period (AD 1400–1532) and the pre-Inka Late Intermediate Period (AD 1100–1400) coprolites. In the Late Intermediate Period, the study area was occupied by farmers dispersed along the valley in very small communities. The Inka reorganized the population into large population centers. Santoro et al. (2003) noted an increase in *D. pacificum* and pinworm in the Late Inka Period. Vinton et al. (2009) noted a decline in maize during the Inka Period. This suggests that as maize became less abundant as a key food source, the people turned to fishing as an alternative dietary resource. This case exemplifies how different subsistence strategies can be associated with distinctive parasitological profiles as suggested by previous researchers (Ferreira et al., 1989, 1985).

4. Diet and parasitism in the Old World

Animal domestication established zoonotic parasites in the Old World. Le Bailly's (2005) study of parasite infections from the Neolithic period to the Middle Ages in Europe revealed changes in foods coinciding with climate conditions. Dietary changes were documented through pathoecology, which indicated shifting patterns of food choice. As a consequence, new parasites begin to infect humans. Zoonotic parasites were derived both from eating infected

animals, and also by eating plant foods contaminated with intermediate stages of domestic animal parasites.

Gonçalves et al. (2003) summarize the distribution of the lancet liver fluke, *Dicrocoelium dendriticum* in human remains. This parasite is associated with a variety of domestic animals including sheep, pigs and cattle. The oldest dates from Switzerland and France are about 5000 years ago. Later, from the Roman age onward, they are found in Austria and England. These cannot be said to be true infections. Human false infection is a consequence of eating raw or undercooked animal liver. Eggs pass through the human digestive tract unchanged. Humans can become infected with adult worms only If they eat ants infected by the larval stage of the parasite. Le Bailly and Bouchet (2010) summarize the history of infection with *D. dendriticum*, that is passed by ingestion of infected ants. This was a relatively common trematode parasite of Old World people, but whether true infection occurred is unknown. The best case for a true infection is the Iron Age Roman mummy, Zweeloo Woman (Searcey et al., this volume). In Zweeloo Woman, eggs were found in the liver. Without a doubt, Zweeloo Woman was truly infected with lancet liver flukes (see also Searcey et al., this volume).

Fasciola hepatica, the sheep liver fluke, was a common trematode in ancient humans. Humans become infected by eating vegetation contaminated with infective cercaria. Gonçalves et al. (2003) summarize the archaeological distribution of this species. It is the most common trematode parasite in north central Europe from 5600 years ago onward to the Medieval period. Like the lancet liver fluke, *F. hepatica* is a parasite associated with animal domestication after the first paleoepidemiologic transition. For archaeological context, Bouchet et al. (2003a) described parasite transmission, which they associate with watercress intake. Although able to infect humans, this parasite is primarily a parasite of herbivores, and it is always difficult to discriminate a human infection from an animal infection, especially when the eggs are found in archaeological sediments such as trash midden samples where animal feces may have been deposited. However, in latrine, mummy, or burial contexts, the find of eggs signals human infection (Dittmar and Teegen, 2003).

Food practices in Europe after the first paleoepidemiologic transition resulted in zoonotic infections. But compared to the Americas, the diversity of parasites was low. This is probably due to the fact that after the first paleoepidemiologic transition, Europeans focused on a limited spectrum of domesticated animals and therefore were not exposed to a wide variety of terrestrial animal parasites. In contrast, New World cultures were dependent on a greater variety of wild vertebrates and invertebrates both before and after the first paleoepidemiologic transition.

Research in Korea and Japan show a great diversity of parasites derived from food animals. From Japan, Matsui et al. (2003) reported Yokogawa flukes (*Metagonimus yokogawa*), liver flukes (*Clonorchis sinensis*), the beef or pork tapeworms (*Taenia* spp.), fish tapeworm (*Diphyllobothrium* sp.), and the lung fluke (*Paragonimus* sp.). From Korea, a variety of researchers reported *M. yokogawai*, *Paragonimus westermani*, *Gymnophalloides seoi* and *Taenia* eggs f in mummies (Lee et al., 2011; Seo et al., 2009; Shin et al., 2009a,b, 2011). Thus, food related parasites were very well established in Asia. These came from a diet that included substantial amounts of fish, crustacea, and meat. There is no doubt that much more exciting data will emerge from continued work in Korea and Japan.

5. Contrasts in paleoepidemiologic transitions, Old World and New

Parasitological data from Europe have been reviewed by several authors, including Bouchet et al. (2003b), Le Bailly and Bouchet (2010), and Reinhard and Pucu (2013). Reviews have covered human remains dating from before the Neolithic period to the

nineteenth century. For European cultures, the results indicate the existence of distinct first and second paleoepidemiological transitions with the emergence of parasitic disease and progressive exacerbation of infections from the early Neolithic until the Industrial Revolution. Bouchet et al. (2003b) and Le Bailly and Bouchet (2010) argue that zoonotic parasitism may have ebbed and flowed over the centuries in Europe associated with periods of famine, when people turned to a broader range of dietary resources. During such times, humans were infected with parasites when ingesting infected raw fish, for example. Other parasites of animals, able to adapt to the human host, were also found, suggesting close contact between the species and the use of natural resources. There is strong evidence that the first epidemiologic transition, associated with increased prevalence of infectious diseases and poor sanitation, occurred in Europe (Barrett et al., 1998; Le Bailly and Bouchet, 2010). This is characterized in the parasitological record by ubiquitous infections with geohelminths (soil transmitted helminths) (Reinhard and Pucu, 2013). By contrast, zoonotic infections from wild reservoirs become less common as zoonotic infections from domesticated reservoirs increases (Bouchet et al., 2003b; Le Bailly and Bouchet, 2010).

For the Americas, the first paleoepidemiologic transition is not well defined archaeologically. Especially for zoonotic parasites, there seems to be no or very little change in diet-related parasitism. Prehistoric Native Americans subsisted on a great variety of terrestrial and aquatic vertebrates and invertebrates, with each prey species having its own array of parasites potentially infective to humans. This is the source of diversity of helminths in the prehistoric New World. But as far as the first transition, the only distinct parasitic change after agriculture is an enigmatic epidemic of pinworm infection among Ancestral Puebloans (Reinhard, 1988) and frontier Mesoamericans (Jiménez et al., 2012), as well as Inkas (Santoro et al., 2003).

In the New World, ubiquitous geohelminth infections did not become established until Colonial times (Leles, 2010; Leles et al., 2010). Indeed, the first and second paleoepidemiological transitions, as witnessed by parasitology, occurred nearly simultaneously in the Americas (Reinhard and Pucu, 2013).

6. Agriculture practices—indirect influence of subsistence on parasitism

Indirectly, agriculture had a strong impact on the state of pathoecology. In some areas, parasites overwhelmed *Homo*'s capacity for cultural evolution. This was true after the establishment of urban life and multi-tiered complex societies. In such societies, parasites proliferated among the lowest tiers of society and resulted in a vast reservoir of infection for all levels of the society. This is best seen in the European archaeological record where food-borne parasites were replaced as a major health hazard by filth-borne and crowd parasites. This is extensively reviewed and discussed by Reinhard and Pucu (2013). They summarize the archaeological studies of parasites and found that fecal-borne parasites were ubiquitous in European societies from the Iron Age onwards. They support Jones (1985) assertion that fecal-borne parasites were the common urban background fauna by medieval times.

Helminth eggs from archaeological remains of the Old World and the New World show intriguing contrasts. Whereas great numbers of *A. lumbricoides* and *T. trichiura* eggs have been found in most archaeological sites in Europe, these eggs are rare in the pre-Columbian Western Hemisphere (Gonçalves et al., 2003; Leles et al., 2010; Reinhard and Pucu, 2013). A variety of conditions in the ancient Americas hampered these parasites' ability to infect new susceptible hosts (Reinhard, 1988, 1990; Reinhard and Pucu, 2013). Finding explanations for this difference is a focus of current

and future research at the Fundação Oswaldo Cruz and the University of Nebraska-Lincoln. These explanations include, for Native America, an abundance of medicinal plants, more open habitations, less population concentration, absence of the humoral theory of medicine, fecal avoidance, and other behaviors. In Europe, by contrast, after the first paleoepidemiologic transition people were aggregated in communities without sanitary facilities and in close contact with domesticated animals. Importantly, it is likely that the humoral theory limited the response to disease. The failure of European medicine to recognize the contagion theory until remarkably late in history made populations there intellectually susceptible to infection as reviewed by Reinhard and Pucu (2013). This failure encouraged the use of human feces as agricultural fertilizer. Under such conditions, fecal-borne parasites proliferated, including *A. lumbricoides* and *T. trichiura*.

Agriculture, especially irrigation cultivation, increased the risk of vector borne disease. A full discussion of this topic is beyond the page limitations of this article. But it is worth highlighting an example such as malaria in Italy. During Renaissance times malaria, caused by *Plasmodium falciparum*, was prevalent in southern Europe. *P. falciparum* is a protozoan parasite originally from Africa, which infected people in southern Italy during this period, and it has been implicated in the deaths of members of the Medici family (Fornaciari et al., 2010). Malaria epidemics and severity were directly linked to agricultural cycles, environmental cycles and the distribution of pernicious malaria caused by *P. falciparum* versus the milder form caused by *Plasmodium vivax* (Snowden, 2006).

7. Summary

Paleoparasitological studies indicate that people living in the Americas have been infected by a variety of parasites over time. Some parasites originated in an environment occupied or transformed by humans, while others were acquired from wild or domesticated animals. Additional parasite species undoubtedly were introduced directly by humans during early migrations from Africa via Asia. These parasite species had their origin in African human ancestors, and are called heirloom parasites. By recovering heirloom parasites in archaeological sites it was possible to trace prehistoric human migrations (Araújo et al., 2008).

Therefore, pre-Columbian New World populations were infected by parasites that were introduced into the Americas by ancient prehistoric migrations. Other parasites were acquired from the environment, especially by ingesting raw or undercooked meat of wild animals. With the European invasions that began in the late 18th century, however, an enormous change occurred. Unknown parasites, especially viruses and bacteria, were introduced, causing a tremendous impact upon Native Americans (Desowitz, 1997/1998; Ujvari, 2008). Some of these included parasites associated with European domestic animals. The lancet fluke, sheep liver flukes, pork tapeworm, beef tapeworm and other parasites arrived at this time. In some regions, people were obliged to live in settled villages, with increased population density. On the Brazilian coast, for example, prior to the conquest, the Tupi occupied a vast territory (Noelli, 2008). With the Portuguese colonization, the Indians either were assimilated or escaped into the interior. As the Portuguese reproduced architectural models of Old World Middle Ages on the Brazilian coast, aggregating people without sanitary measures (Fisher et al., 2007), intestinal helminth parasite loads increased (Edler, 2011).

Another instructive example is offered by Chagas disease. Although infection by *T. cruzi* was common among North and South American prehistoric groups, prevalence rates varied according to lifeways. Caves and rock-shelters, for example, were ideal ecological niches for triatomines (triatomines are vectors of Chagas

disease, transmitting *T. cruzi* after blood sucking) and small mammal reservoirs. Therefore, pre-Columbian people who used caves and rock-shelters were more commonly exposed to *T. cruzi* transmission than those living in villages. However, following European immigrations, Chagas disease transmission spread throughout the continent when Europeans, especially Portuguese, introduced mud and daub dwellings, to which *Triatoma infestans*, and other vector species, adapted well (Araújo et al., 2009; Ferreira et al., 2011). Chagas disease patterns thus changed and increased during colonial times, and rural intra-household transmission became characteristic of the disease.

According to Perrin and Herbreteau (2010), human parasites are most abundant in the Palearctic realm, while the Neotropics and Australia are parasite poor. They explain low diversity in parasite species in the Neotropics and Australia because these regions were colonized relatively recently, compared with other areas. The conclusions proposed by Perrin and Herbreteau (2010) agree with paleoparasitological data (Dittmar, 2010). Human helminth parasites acquired evolutionarily in pre-*Homo* times were introduced into the Americas with the first migrants, both crossing the Bering Land Bridge or following alternative routes (Montenegro et al., 2006; Araújo et al., 2008). The first humans in the Americas occupied new environments, in which they were exposed to other parasites. However, when Europeans arrived, epidemiological patterns changed, prevalence rates of old diseases were altered, and the burden of disease increased.

With specific regard to food and parasitism, the reduced reliance on domesticated animals and increased reliance on wild animals in the prehistoric Americas produced a distinct pathoecological picture relative to Europe. In the Americas, a diversity of flukes, tapeworms, acanthocephalans and nematodes derived from wild animals make up the majority of species that infected humans. In contrast, flukes and tapeworms of domestic animals dominate European pathoecology after the first paleoepidemiologic transition. However, these parasites are far less common then fecal borne parasites in Europe.

References

Araújo, A., Ferreira, L.F., Confalonieri, U.E.C., 1983. Eggs of *Diphyllobothrium pacificum* in pre-Columbian human coprolites. Paleopathology Newsletter 41, 11–13.

Araújo, A.J.G., Ferreira, L.F., 1995. Oxiuríase e migrações pré-históricas. História, Ciências, Saúde-Manguinhos 2, 99–109.

Araújo, A.J.G., Ferreira, L.F., Guidon, N., Freire, N.M.S., Reinhard, K., Dittmar, K., 2000. Ten thousand years of head lice infection. Parasitology Today 16, 269–270.

Araújo, A.J.G., Jansen, A.M., Reinhard, K., Ferreira, L.F., 2009. Pathoecology of Chagas disease: a review. Memorias do Instituto Oswaldo Cruz 104, 9–16.

Araújo, A.J.G., Reinhard, K.J., Ferreira, L.F., Gardner, S.L., 2008. Parasites as probes for prehistoric human migrations? Trends in Parasitology 24, 112–115.

Arriaza, B.T., Reinhard, K., Araújo, A.J.G., Orellana, N.C., Standen, V.G., 2010. Possible influence of the ENSO phenomenon on the pathoecology of diphyllobothriasis and anisakiasis in ancient Chinchorro populations. Memorias do Instituto Oswaldo Cruz 105, 66–72.

Aufderheide, A.C., Salo, W., Madden, M., Streitz, J., Buikstra, J.E., Guhl, F., Arriaza, B.T., Renier, C., Wittmers, L.E., Fornaciari, G., Allison, M.J., 2004. A 9,000-year record of Chagas' disease. Proceedings of the National Academy of Sciences of the United States of America 101, 2034–2039.

Baer, J.G., 1969. *Diphyllobothrium pacificum*, a tapeworm from sea lions endemic in man along the coastal area of Peru. Journal of the Fisheries Research Board of Canada 26, 717–723.

Barrett, R., Kuzawa, C.W., McDade, T., Armelagos, G.J., 1998. Emerging and re-emerging infectious diseases: the third epidemiologic transition. Annual Review of Anthropology 27, 247–271.

Beltrame, M.O., Fugassa, M.H., Sardella, N.H., 2010. First paleoparasitological results from Late Holocene in Patagonian Coprolites. Journal of Parasitology 96, 648–651.

Bouchet, F., Guidon, N., Dittmar, K., Harter, S., Ferreira, L.F., Chaves, S.M., Reinhard, K., Araújo, A.J.G., 2003b. Parasite remains in archaeological sites. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 47–52.

Bouchet, F., Harter, S., Le Bailly, M., 2003a. The state of the art of paleoparasitological research in the Old World. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 95–101.

Callen, E.O., Cameron, T.W.M., 1960. A prehistoric diet revealed in coprolites. New Scientist 8, 35–40.

Cleeland, L.M., Reichard, M.V., Tito, R.Y., Reinhard, K.J., Lewis, C.M., 2013. Clarifying prehistoric parasitism from a complementary morphological and molecular approach. Journal of Archaeological Science, http://dx.doi.org/10.1016/j.jas.2013.03.010.

Costa, F.A.C., Silva, A.G., Souza, A.H., Moreira, D., Souza, C.J., Valverde, D.L.D., Jaeger, J.G., Martins, L.H., Meneses, P.P., Araujo, V.F.D., Boia, A.M.N., 2009. Pseudoparasitism by Calodium hepaticum (syn. Capillaria hepatica; Hepaticola hepatica) in the Negro River, Brazilian Amazon. Transactions of the Royal Society of Tropical Medicine and Hygiene 103, 1071–1073.

Desowitz, R., 1997/1998. Who gave Pinta to the Santa Maria? Tracking the devastating spread of the lethal tropical diseases into America. In: Harvest Book. W.W. Norton & Company, NY, 264 p.

Dittmar, K., 2010. Palaeogeography of parasites. In: Morand, S., Krasnov, B.R. (Eds.), The Biogeography of Host–Parasite Interactions. Oxford University Press, pp. 21–29.

Dittmar, K., Teegen, W.R., 2003. The presence of Fasciola hepatica (Liver-fluke) in humans and cattle from a 4,500 Year old archaeological site in the Saale-Unstrut Valley, Germany. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 141–143.

Donald, M., 1993. Précis of origins of the modern mind: three stages in the evolution of culture and cognition. Journal of Behavioral and Brain Science 16, 731–791.

Edler, F.C., 2011. Medicina no Brasil Imperial: Clima, Parasitas e Patologia Tropical. Fiocruz Editora, Rio de Janeiro, p. 298.

Fernandes, A., Iñighez, A., Lima, V.S., Souza, S.M.M., Ferreira, L.F., Vicente, A.C., Jansen, A.M., 2008. Pre-Columbian Chagas disease in Brazil: Trypanosoma cruzi I in the archaeological remains of a human in Peruaçu Valley, Minas Gerais, Brazil. Memorias do Instituto Oswaldo Cruz 103, 514–516.

Ferreira, L.F., Araújo, A.J.G., Confalonieri, U.E.C., Nuñez, L., 1984. The finding of eggs of Diphyllobothrium in human coprolites (4. 100-1. 950 BC) from Northern Chile. Memorias do Instituto Oswaldo Cruz 79, 175–180.

Ferreira, L.F., Araújo, A.J.G., Confalonieri, U.E.C., Nuñez, L., 1989. Infecção por Enterobius vermicularis em população agro-pastoris pré-colombianas de San Pedro de Atacama, Chile. Memorias do Instituto Oswaldo Cruz 84, 197–199.

Ferreira, L.F., Filho, B.M.R., Araújo, A.J.G., Confalonieri, U.E.C., Nuñez, L., 1985. Infecção por Enterobius vermicularis em população pré-colombianas no Chile. Cadernos de Saúde Pública 1, 112–113.

Ferreira, L.F., Jansen, A.M., Araújo, A., 2011. Chagas disease in prehistory. Anais da Academia Brasileira de Ciências 83, 1041–1044.

Fisher, C.L., Reinhard, K., Kirk, M., DiVirgillio, J., 2007. Privies and parasites: the archaeology of health conditions in Albany, New York. Historical Archaeology 41, 172–197.

Fornaciari, G., Giuffra, V., Ferroglio, E., Gino, S., Bianucci, R., 2010. Plasmodium falciparum immunodetection in bone remains of members of the Renaissance Medici family (Florence, Italy, sixteenth century). Transactions of the Royal Society of Tropical Medicine and Hygiene 104, 583–587.

Fry, G.F., 1977. Analysis of Prehistoric Coprolites From Utah. University of Utah Anthropological Papers, n. 97. University of Utah Press, Salt Lake City, 45 pp.

Fugassa, M., Barberena, R., 2006. Cuevas y zoonosisantiguas: paleoparasitologíadel sitio Orejas de Burro 1 (Santa Cruz, Argentina). Magallania (Punta Arenas) 34, 57–62.

Fugassa, M.H., Beltrame, M.O., 2009. Zoonotic parasites from caves and rock shelters during the Middle Holocene in Patagonia: new evidences associated to felines. Memorias do Instituto Oswaldo Cruz 104, 1177–1180.

Fugassa, M.H., Beltrame, M.O., Bayer, M.S., Sardella, N.H., 2009. Zoonotic parasites associated with felines from the Patagonian Holocene. Memorias do Instituto Oswaldo Cruz 104, 1177–1180.

Fugassa, M.H., Beltrame, M.O., Sardella, N.H., Civalero, M.T., Aschero, C., 2010. Paleoparasitological results from coprolites dated at the Pleistocene-Holocene transition as source of paleoecological evidence in Patagonia. Journal of Archaeological Science 37, 880–884.

Fugassa, M.H., Reinhard, K.J., Johnson, K.L., Gardner, S.L., Vieira, M., Araújo, d.C.A., 2011. Parasitism of prehistoric humans and companion animals from Antelope Cave, Mojave County, Northwest Arizona. Journal of Parasitology 97, 862–867.

Fugassa, M.H., Sardella, N.H., Guichón, R.A., Denegri, G.M., Araújo, A., 2008a. Paleoparasitological analysis applied to skeletal sediments of meridional patagonian collection. Journal of Archaeological Science 35, 1408–1411.

Fugassa, M., Taglioretti, V., Gonçalves, M., Araújo, A., Sardella, N.H., Denegri, G.M., 2008b. Capillaria spp. eggs in Patagonian archaeological sites: statistical analysis of morphometric data. Memorias do Instituto Oswaldo Cruz 103, 104–105.

Gandon, S., Buckling, A., Decaestecker, E., Day, T., 2008. Host-parasite coevolution and patterns of adaptation across time and space. Journal of Evolutionary Biology 21, 1861–1866.

Gonçalves, M., Araújo, A.J.G., Ferreira, L.F., 2003. Human intestinal parasites in the past: new findings and a review. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 103–118.

Jiménez, F.A., Gardner, S.L., Araújo, A., Fugassa, M., Brooks, R.H., Racz, E., Reinhard, K.J., 2012. Zoonotic and human parasites of inhabitants of Cueva de Los Muertos Chiquitos, Rio Zape Valley, Durango, México. Journal of Parasitology 98, 304–309.

Jones, A.K.G., 1985. Trichurid ova in archaeological deposits: their value as indicators of ancient feces. In: Fieller, N.J.R., Gilbertson, D.D., Ralph, N.G.A. (Eds.), Paleobiological Investigations: Research Design, Methods and Data Analysis, BAR International Series 266. Brit. Archaeol. Rep., Oxford, pp. 105–114.

Le Bailly, M., 2005. Evolution de la relation hôte/parasite dans les systèmes lacustres nord Alpins au Néolithique (3900–2900 BC), et nouvelles données dans la détection des paléoantigènes de Protozoa. Ph.D. Dissertion. Université de Reims Champagne-Ardenne.

Le Bailly, M., Bouchet, F., 2010. Ancient dicrocoeliosis: occurrence, distribution and migration. Acta Tropica 115, 175–180.

Lee, H.-J., Shin, D.H., Seo, M., 2011. Discovery of Taeniid eggs from A 17th century tomb in Korea. Korean Journal of Parasitology 49, 327–329.

Leles, D., 2010. Paleogenética e paleoepidemiologia de Ascaris sp. (Linnaeus 1758) e Trichuris sp. (Roederer 1761). PhD Dissertation. Escola Nacional de Saúde Pública-FIOCRUZ. Fundação Oswaldo Cruz, Rio de Janeiro, p. 161.

Leles, D., Reinhard, K.J., Fugassa, M., Ferreira, L.F., Iñiguez, A., Araújo, A., 2010. A parasitological paradox: why is ascarid infection so rare in the prehistoric Americas? Journal of Archaeological Science 37, 1510–1520.

Lima, V., Iñighez, A., Otsuki, K., Ferreira, L.F., Araújo, A., Vicente, A.C., Jansen, A.M., 2008. Chagas disease in ancient hunter–gatherer population, Brazil. Emerging Infectious Diseases 14, 1001–1002.

Martinson, E., Reinhard, K.J., Buikstra, J.E., Dittmar, K., 2003. Pathoecology of Chiribaya parasitism. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 195–205.

Matsui, A., Kanehara, M., Kanehara, M., 2003. Pathoecology in Japan—discovery of toilet features. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 127–136.

Montenegro, A., Araújo, A., Eby, M., Ferreira, L.F., Hetherington, R., Weaver, A.J., 2006. Parasites, paleoclimate and the peopling of the Americas: Using the hookworm to time the Clovis migration. Current Anthropology 47, 193–200.

Moore, J.G., Fry, G.F., Englert, E., 1969. Thorny-headed worm Infection in North American prehistoric man. Science 163, 1324–1325.

Noelli, F.S., 2008. The Tupi expansion. In: Silverman, H., Isbell, W.H. (Eds.), Handbook of South American Archaeology. Springer, pp. 659–669.

Patrucco, R., Tello, R., Bonavia, D., 1983. Parasitological studies of coprolites of pre-Hispanic Peruvian populations. Current Anthropology 24, 393–394.

Perrin, P., Herbreteau, V., 2010. Biogeography, humans, and their parasites. In: Morand, S., Krasnov, B.R. (Eds.), The Biogeography of Host–Parasite Interactions. Oxford University Press, New York, pp. 41–57.

Reed, D.L., Smith, V.S., Hammond, S.L., Rogers, A.R., Clayton, D.H., 2004. Genetic analysis of lice supports direct contact between modern and archaic humans. PLoS Biology 2, e340, 1972–1983.

Reinhard, K.J., 1988. Cultural ecology of prehistoric parasitism on the Colorado Plateau as evidenced by coprology. American Journal of Physical Anthropology 77, 355–366.

Reinhard, K.J., 1990. Archaeoparasitology in North America. American Journal of Physical Anthropology 82, 145–163.

Reinhard, K.J., 1992a. Parasitology as an interpretive tool in archaeology. American Antiquity 57, 231–245.

Reinhard, K.J., 1992b. Patterns of diet, parasitism, and anemia in prehistoric west North America. In: Stuart-Macadam, P., Kent, S. (Eds.), Diet, Demography, and Disease: Changing Perspectives on Anemia. New York, Aldine de Gruyter, pp. 219–258.

Reinhard, K.J., 2008. Parasite pathoecology of chacoan great houses: the healthiest and wormiest ancestral puebloans. In: Reed, P.F. (Ed.), Chaco's Northern Prodigies. Salmon, Aztec, and the Ascendancy of the Middle San Juan Region after AD 1100. University of Utah Press, Salt Lake City, pp. 86–95.

Reinhard, K.J., Ambler, J.R., McGiffie, M., 1985. Diet and parasitism at Dust Devil Cave. American Antiquity 50, 819–824.

Reinhard, K., Confalonieri, U.E.C., Herrmann, G., Ferreira, L.F., Araújo, A., 1986. Recovery of parasite remains form coprolites and latrines: aspects of paleoparasitological tehcnique. Homo 37, 217–239.

Reinhard, K., Fink, T.M., Skiles, J., 2003. A case of megacolon in Rio Grande Valley as a possible case of Chagas disease. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 165–172.

Reinhard, K.J., Pucu, E., 2013. Comparative parasitological perspectives on paleoepemiological transitions: Americas and Europe. In: Zuckerman, M.K. (Ed.), Moving the Middle to the Foreground: Interdisciplinary Approaches to Examining the Second Epidemiological Transition. Wiley-Blackwell Publishing (in press).

Reinhard, K.J., Szuter, C., Ambler, J.R., 2007. Hunter–gatherer use of small animal food resources. International Journal of Osteoarchaeology 17, 416–428.

Reinhard, K., Urban, O., 2003. Diagnosing ancient Diphyllobothriasis from Chinchorro mummies. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 191–193.

Santoro, C., Vinton, S.D., Reinhard, K., 2003. Inca expansion and parasitism in the Lluta valley: preliminary data. Memorias do Instituto Oswaldo Cruz 98 (Suppl. 1), 161–163.

Searcey, N., Reinhard, K.J., Egarter-Vigl, E., Maixner, F., Piombino-Mascali, D., Zink, A.R., van der Sanden, W., Gardner, S.L., Bianucci, R., 2013. Parasitism of the Zweeloo Woman: Dicrocoeliasis evidenced in a Roman Period Bog Mummy. International Journal of Paleopathology 3, 224–228.

Seo, M., Shin, D.H., Guk, S.M., Oh, C.S., Lee, E.J., Shin, M.H., Kim, M.J., Lee, S.D., Kim, Y.S., Yi, Y.S., Spigelman, M., Chai, J.Y., 2009. Gymnophalloides seoi eggs from the stool

of a 17th century female mummy found in Hadong, Republic of Korea. Journal of Parasitology 94, 467–472.

Shin, D.H., Chai, J.Y., Park, E.A., Lee, W., Lee, H., Lee, J.S., Choi, Y.M., Koh, B.J., Park, J.B., Oh, C.S., Bok, G.D., Kim, W.L., Lee, E., Lee, E.J., Seo, M., 2009a. Finding ancient parasite larvae in a sample from a male living in late 17th century Korea. Journal of Parasitology 95, 768–771.

Shin, D.H., Lim, D.S., Choi, K.J., Oh, C.S., Kim, M.J., Lee, I.S., Kim, S.B., Shin, J.E., Bok, G.D., Chai, J.Y., Seo, M., 2009b. Scanning electron microscope study of ancient parasite eggs recovered from Korean mummies of the Joseon Dynasty. Journal of Parasitology 95, 137–145.

Shin, D.H., Oh, C.S., Chai, J.Y., Lee, H., Seo, M., 2011. Enterobius vermicularis eggs discovered in coprolites from a medieval Korean mummy. Korean Journal of Parasitology 49, 323–326.

Sianto, L., Chame, M., Silva, C.S.P., Gonçalves, M., Reinhard, K., Fugassa, M., Araújo, A., 2009. Animal helminths in human archaeological remains: a review of zoonoses in the past. Revista do Instituto de Medicina Tropical de Sao Paulo 51, 119–130.

Sianto, L., Reinhard, K., Chame, M., Chaves, M.B.G., Mendonça, S., Gonçalves, M., Fernandes, A., Ferreira, L.F., Araújo, A., 2005. The finding of *Echinostoma* (Trematoda: Digenea) and hookworm eggs in coprolites collected from a Brazilian mummified body dated 600–1,200 years before present. Journal of Parasitology 91, 972–975.

Snowden, F.M., 2006. The Conquest of Malaria: Italy, 1900–1962. Yale University Press, New Haven, Connecticut, 304 pp.

Ujvari, S.C., 2008. The history of the dissemination of microorganisms. Estudos Avançados 22, 171–182.

Vinton, S.D., Perry, L., Reinhard, K.J., Santoro, C.M., Teixeira-Santos, I., 2009. Impact of empire expansion on household diet: the Inka in Northern Chile's Atacama desert. PLoS ONE 4, e8069, http://dx.doi.org/10.1371/journal.pone.0008069.