

2012

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Reinhard, Karl and Araujo, Adauto, "Synthesizing Parasitology with Archaeology in Paleopathology" (2012). *Karl Reinhard Papers/Publications*. 64.

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# Synthesizing Parasitology with Archaeology in Paleopathology

Karl J. Reinhard and Adauto Araújo

Parasites furnish information about present day habits and ecology of their individual hosts. The same parasites hold promise of telling us something about host and geographical connections of long ago. They are simultaneously the product of an immediate environment and a long ancestry reflecting associations of millions of years. Eventually there may be enough pieces to form a meaningful language which could be called parascript—the language of parasites which tells of themselves and their hosts both of today and yesterday. (Harold Manter 1966:70)

## Introduction

Parasitology is the study of organisms that are symbiotic with other organisms. In this form of symbiosis, the parasite species by definition benefits from the interaction while the host is harmed to some degree. In actuality, some parasites benefit their hosts. The animals traditionally studied by parasitologists range from protozoa to arthropods, and include all types of internal and external worms. Ticks, fleas, lice, and a variety of insects that transmit parasites are also studied by parasitologists. Recently, a more holistic view of parasitism appeared, including bacteria and viruses. In essence, parasitology is the study of a certain kind of biological relationship that is very common in the natural world.

Humans host hundreds of parasite species. The details of the relationship between any parasite species and humans are defined by culture. Archaeology is the study of past humans and human culture. Therefore, archaeoparasitology is the analysis of parasitism based on archaeological evidence. As defined by Reinhard (2000a) and Reinhard and Araújo (2007), archaeoparasitology derives data from physical evidence such as artifacts, documents, and art. In addition, ecoartifacts such as coprolites, sediments, and human remains provide direct evidence of parasitism. Fisher et al. (2007) provide a holistic example of archaeoparasitological

reconstruction of Albany, NY, based on analysis of medical documents, artifacts such as medicine bottles, archaeochemical analysis of sediments for evidence of medicines, reconstruction of sanitation, and direct analysis of parasite eggs from various domestic contexts. In addition, archaeopalynology (Chaves and Reinhard 2006) and archaeobotany (Reinhard et al. 1985) reveal evidence of medicines used to treat parasitic disease symptoms. In short, archaeoparasitologists sift through every imaginable type of archaeological residue that can provide any insight into the culturally defined relationship between human hosts and parasites. In doing so, we decipher the unique parascript specific to human-parasite cultural evolution.

## The Americas and Archaeoparasitology

Archaeoparasitology is a fusion of archaeology and parasitology (Horne 1985). In North America archaeoparasitology began with excavations by archaeologists such as J. Richard Ambler, Robert Heizer, Cynthia Irwin-Williams, Jesse Jennings, Don Morris, Art Rohn, Steve Mrozowski, and Harry Shafer. These archaeologists, among others, recognized the importance of coprolites for detailed data regarding diet and disease. Each of them focused graduate students and parasitologists on analysis of coprolites. Thus, the distinct linkage of parasitological data to archaeological questions

comes from these researchers who took the relevant remains from the field into the laboratory.

In the Great Basin, Robert Heizer (Hester 1982) and Jesse Jennings (Aikens 1999) were prolific field researchers. Jennings and his students excavated coprolites from Danger Cave, Hogup Cave, Cowboy Cave, Dirty Shame Rockshelter, and other lesser known sites, including a number of sites in Glen Canyon. They were the first to analyze coprolites for dietary and parasite evidence collaborating with a parasitologist, John Moore. Heizer excavated in the Great Basin of Nevada and directed the California Archaeological Survey at the University of California at Berkeley. He promoted the interdisciplinary analysis of coprolites, especially those from Lovelock Cave. The late 1960s and the decade of the 1970s saw a shift of focus from the Great Basin to the Ancestral Pueblo region of the Colorado Plateau. National Park Service archaeologists Art Rohn and Don Morris excavated coprolites from Mug House, Mesa Verde, and Antelope House, Canyon de Chelly, respectively. Cynthia Irwin-Williams (Wormington and Agogino 1994) also excavated coprolites from Salmon Ruin, and J. Richard Ambler, a student of Jennings, excavated coprolites from the region of Navajo Mountain and Glen Canyon.

Beyond the Ancestral Pueblo homeland, Harry Shaffer, Vaughn Bryant, Donny Hamilton, and other Texas archaeologists were excavating coprolites from west Texas. Hundreds of coprolites were recovered from Hinds Cave, Baker Cave, and other rockshelters in the region. These researchers collaborated with parasitologists and directed research into prehistoric parasitism among Texas hunter-gatherers (Reinhard 1990).

Steve Mrozowski pioneered the scientific study of latrine sediments from historic sites (Reinhard et al. 1986). He promoted the study of parasite eggs from latrine sediments. His focus was on the integration of parasitological, palynological, and macrobotanical evidence with historical documentation of urban development (Mrozowski 2006). Thus, Mrozowski's efforts inspired the search for evidence of parasitism in industrializing societies.

Because archaeologists directed the research, parasitological data addressed archaeological problems in North America (Reinhard 1992a). In a broad sense, the archaeological questions focused on zoonotic parasitism related to hunter-gatherer dietary practices, zoonotic diseases from domestic animals, increase in human-specific crowd disease among farming peoples, transhumance patterns, cultural contact, paleopharmacology related to anthelmintics (vermifuges),

development of sanitation, and the overall health of prehistoric peoples adapting to a diversity of arid environments. Thus, the sponsorship of parasitological research by archaeologists resulted in a distinct focus of archaeoparasitology on human questions.

## Archaeoparasitological Studies

There have been distinct phases to archaeoparasitology: exploratory (1910 to 1974), population (1976–1987), and synthesis of archaeology and parasitology (1987 onward). The exploratory phase was most influenced by the archaeologists noted above. Studies of ancient parasites, like many fields of paleopathology, began as series of isolated case studies. In this exploratory phase, the discoveries were by themselves noteworthy, and sometimes sensational, due to the novelty of recovering parasites from archaeological remains. The exploratory period was rapidly supplanted by a period of population comparison over geographic regions, again influenced by these same archaeologists. The synthesis phase was represented by the synthesis of “parasitological theory” and archaeology. Parasitological theory generated theoretical frameworks that were used to interpret archaeological parasite remains.

## Early Exploration

The exploratory phase began with the first parasitological study of archaeological remains in the Old World (Horne 1985). Ruffer (1910) reported the find of blood fluke eggs in Egyptian mummies. In *Diseases in Antiquity*, Brothwell and Sandison (1967) added parasitology as a distinct part of paleopathology. Sandison (1967) described the relevance of the field to paleopathology, summarizing evidence from art and literature. Taylor (1955) described the value of parasite examination of latrine sediments in medieval England, and Lambrecht (1967) summarized the evidence for the evolution of African sleeping sickness from South African ecological data. Alongside parasitological study, W.H.S. Jones (1967) examined ancient Greek texts to describe the antiquity of malaria in Greece. Later, direct evidence of parasites was presented from latrine excavations in Denmark (Nansen and Jørgensen 1977) and England (Pike 1975). Samuels (1965) analyzed coprolites from Mesa Verde, Colorado, and established protocols for laboratory analysis. Pike (1968) published the results of analysis of parasitological examination of Roman sites and showed the value of eggs in making cultural interpretations regarding ancient sites.

These discoveries stimulated the interest of American archaeologists. Coprolites from Great Basin sites were the focus of defining publications in the exploratory phase. Heizer and Napton (1969) summarized the analyses of coprolites from Lovelock Cave, Nevada. At this site, archaeoparasitological study revealed no evidence that hunter-gatherer lifeways limited parasitism in some areas (Reinhard 1988). The antiquity of parasites was demonstrated by Fry and Hall (1969), Fry and Moore (1969), and Moore et al. (1969). In contrast to Lovelock Cave, Utah Great Basin hunter-gatherer coprolites were positive for zoonotic and human-specific parasites. Fry and Hall (1969) reported the discovery of pinworm eggs in a 10,000-year-old coprolite from the Great Basin of Utah. Moore et al. (1969) reported the discovery of acanthocephalans, also in the Great Basin, in 10,000-year-old coprolites. These early coprolite discoveries were sensational enough to be published in *Science*. Following Pike's 1968 paper in *Nature*, such publications illustrate that the novelty of ancient parasite discoveries was so impressive that isolated case studies were published in the most prestigious outlets. This inaugurated a line of research that focused on the search for zoonotic parasites, especially among hunter-gatherer remains.

Exploratory work in South America was also sensational. Allison et al. (1974) published the remarkable discovery of adult hookworms in a prehistoric Peruvian mummy. Eggs were recovered from the intestinal lumen and adult hookworms were found adherent to the intestinal mucosa. This was followed by a series of discoveries of hookworms in Brazil (Araújo et al. 1981; Ferreira et al. 1980, 1983). These discoveries contradicted the prevailing conventional wisdom that hookworm was a historic introduction into the New World. The work of all of these pioneering researchers established parasitology as a part of paleopathology.

### **Comparison Between Populations**

Population studies emerged in 1976 as students of Jennings, Ambler, Shafer, and Bryant began their careers. Gary Fry (1977, 1980) and Henry Hall (1972, 1977) completed their graduate work on coprolites from the southwestern US. They established standard protocols for coprolite analysis that were followed by subsequent researchers. They also completed comparative studies for hunter-gatherer sites and Ancestral Pueblo sites in the Great Basin and the Colorado Plateau. Reinhard (1985a, b, 1988) built his work on Cockburn's (1971) theory and defined the archaeoparasitological

transition from hunter-gatherer populations to farming communities. Cockburn proposed that species that occasionally infected hunter-gatherer became major health hazards in agricultural communities. Cockburn also postulated a decline in food-borne zoonotic infections with agriculture. Both of these hypotheses were verified by coprolite analysis. Thus, archaeoparasitology was established in population studies in arid North America (Reinhard 1992b).

Population studies began in other regions from the 1970s onward. In Brazil, Luiz Fernando Ferreira directed Adauto Araújo and Ulisses Confalonieri in a search for parasites in South American remains. Their work resulted in the definition of the distribution of ascarid, whipworm, and hookworm infections. In Peru, Duccio Bonavia working with archaeologists Raul Patrucco and Raul Tello analyzed series of coprolites (Patrucco et al. 1983) and defined the antiquity of parasites in that region. In England, AKG Jones (1979; 1982; 1983, 1985; 1986; Jones and Nicholson 1988; Jones et al. 1988) built on pioneering work by Pike (1967, 1975), Sandison (1967), and Taylor (1955) to explore regional distributions of parasites in medieval urban settings from England to Norway. He defined methods and theory for parasitological investigations of latrine sediments. By comparing the egg quantities between archaeological deposits, he was able to document variation associated with different site functions. He also showed that parasite eggs were part of the normal medieval urban background fauna and, thus, exposure to parasite infection was an unavoidable aspect of medieval life. Furthermore, Bernd Herrmann (1985, 1986) developed a quantitative analysis of German medieval villages to trace the distribution of parasite species.

Researchers of the population phase had diverse theoretical perspectives. Jones' theoretical framework emerged from environmental archaeology as practiced in the 1980s at the University of York's Environmental Archaeology Unit, established formally in the mid-1970s. It was composed of a variety of specialists who sought to integrate diverse biological data sets to establish solid, holistic interpretations from archaeological deposits. In addition, theoretically, Herrmann and Schulz (1986) defined the interpretive variables at play that described parasite egg spectra in latrine sediments. These included the social group or groups that used specific latrines, the demographic makeup of those groups, differential egg production between species, and the effects of soil chemistry and decay organism on egg preservation.



Horst Aspöck at the University of Vienna pioneered archaeoparasitology in Austria (Aspöck, 2000). He and his colleagues first analyzed parasite eggs from Otzi, the Iceman (Aspöck et al. 1995, 1996). Later, they published a summary of the antiquity of parasite infection in central Europe (Aspöck et al. 1999). *Trichuris trichiura* is the most ancient parasite and has been dated as early as 5,500 years ago, with *Ascaris lumbricoides* and the hookworm *Ancylostoma duodenale* being dated to 3,500 years ago, the fish tapeworm, *Diphyllobothrium*, and the sheep liver fluke, *Fasciola hepatica*, to 5,100 years ago, and the taeniid tapeworm and the lancet liver fluke, *Dicrocoelium dendriticum*, dated to 2,000 years ago.

In Japan, Matsui and his colleagues explored the antiquity of parasitism from Jomon context to medieval times (Matsui et al. 2003). This was an interdisciplinary team that included experts in parasitology, zooarchaeology, palynology, and archaeobotany. Within a few months of research, they identified a range of parasites including ascarid roundworms, whipworms, Yokogawa flukes, Chinese liver flukes, and the beef or pork tapeworms. By integrating the parasite evidence with the other areas of expertise, they identified the use of anthelmintics and related patterns of diet to disease, and immigration of people to Japan from other countries. The development of sanitation in Japan was defined.

### *A Synthesis of Parasitology and Archaeoparasitology*

Overviews of parasitological theory are presented by Price (1980) and Brooks and McLennan (1993). Synthesis of parasitological theory and archaeological practice emerged over a long period of time. The process was sporadic as archaeological investigations recovered appropriate material for different aspects of the synthesis.

Perhaps most essential was a demonstration that prehistoric patterns fit the epidemiological features of modern parasitic infection. Parasites are over-dispersed in natural populations. This means that a very small percentage of hosts harbor the majority of parasites. In parasitological terms, this phenomenon is best described by the negative binomial distribution (Anderson 1993). In order to validate the paleo epidemiological value of archaeoparasite data, this distribution had to be demonstrated with archaeological remains. Mummies of the Chiribaya culture of Peru were selected for study. Previously, Mumcuoglu and Zias (1988) had found lice nits in ancient louse combs. Reinhard and Buikstra (2003) were able to quantify

infection on an individual basis by calculating the maximum number of eggs and nits cemented to hair shafts on the scalps of mummies. Lice nits and eggs were quantified in 147 mummified individuals (Reinhard and Buikstra 2003). The distribution of nits and eggs on Chiribaya hosts reflected the negative binomial. This supports the statistical value of parasitological data when large numbers of human remains can be evaluated.

Beyond the epidemiological consistency of archaeological data, other purely detailed epidemiological work was undertaken. Until the 1980s, theories of parasitology and epidemiology played small roles in the investigations of ancient parasitism. However, this changed with the incorporation of the theoretical constructs of Cockburn (1971) and Pavlovsky (1966), as reviewed by Reinhard (2008) and Reinhard and Bryant (2008). Aidan Cockburn's perceptions about the sources of disease directed the development of parasitological study of Archaic and Ancestral Pueblo sites in the Southwest US. Cockburn (1967, 1971) proposed that the evolution of infectious diseases was determined by the evolution of human social complexity. Cockburn's theories motivated Reinhard (1985a) to test Cockburn's ideas with archaeological remains. Reinhard viewed the prehistoric Southwest as an ideal experimental setting because there were several stages of cultural development represented by archaeological sites: hunter-gatherers with varying dietary strategies, dispersed horticultural hamlets, and large agricultural villages. Reinhard (1985a, 1992 b) compared the parasitic picture of Colorado Plateau Archaic peoples to Ancestral Puebloan sites. He reified some of Cockburn's theories that occasional infections in hunter-gatherers became major health hazards in agricultural populations. Reinhard (1988) included the following explanations of why parasitic disease arose in Ancestral Puebloans relative to earlier hunter-gatherers. Parasitism was limited in hunter-gatherers due to small band size, its mobility, diffuse regional populations, and presence of natural anthelmintics. Hunter-gatherer parasitism was promoted by the consumption of uncooked meat and insects. Parasitism was promoted in Ancestral Puebloan communities by contaminated water sources, concentrated populations, a more sedentary life, apartment-style living, establishment of large latrines, activities centered on water (agriculture), and activities that expanded wetlands, including irrigation of all types.

The work of E.N. Pavlovsky (1966), an epidemiologist, had a less immediate influence on archaeoparasitology. Pavlovsky developed the "doctrine of

nidity,” deriving the term from the word “nidus” (plural “nidi”), which means “nest.” (Many subsequent researchers synonymize “nidus” with the Latin “focus”). The doctrine of nidity establishes that each infection results from the favorable overlap of host factors, parasite factors, and environmental factors, at the very least. The nidus is the specific area or focus of that interaction that results in infection. The key concept of nidity is that disease transmission has its own natural habitat. Thus the nidus exists under definite conditions of climate, vegetation, soil, and favorable microclimate in which host, pathogens, vectors, and reservoirs are associated as a biocenosis. The nidus can be permanent or seasonal. Humans can acquire a natural-nidal disease of animals when they occupy or pass through biocenoses of that infection. Pavlovsky applied the doctrine of nidity to explain the transmission of plague, tularemia, leptospirosis, arboviruses, tick-borne relapsing fever, and other diseases.

The term pathoecology was coined by Karl R. Reinhard in 1974 (K.R. Reinhard 1974a, b). K. R. Reinhard, as an epidemiologist who worked on the history of infectious diseases in modern populations, applied pathoecology to the integrative study of historic climate and health records to define the impact of climate variability on health patterns. Because statistically rigorous epidemiological data were not available for these early historic periods, K. R. Reinhard (1974a) suggested the term “retrospective pathoecology” for application to reconstructing the ecology of past disease. The nidus concept, combined with the concept of pathoecology, is especially useful in exploring infectious disease transmission evidenced in archaeological sites.

As proposed by Martinson et al. (2003), Reinhard (2008), and Reinhard and Bryant (2008), nidi can be discerned in careful excavations in combination with ecological reconstruction. Nidi can be as finite as a *Giardia*-contaminated water point, or a single cave where cooking debris left by humans creates the biocenosis for Chagas disease transmission, or as large as a human feces-contaminated agricultural field where hookworms complete embryonation in irrigated soil and accomplish infection of sandal-wearing farmers.

Another basic parasitological theoretical concept relates to souvenir and heirloom parasite taxa. Originally defined by Sprent (1969), these concepts are widely used by other parasitologists. Heirloom parasites evolved from ancestral parasite species hosted by primate common ancestors of modern apes and humans and even earlier mammalian ancestors. This follows the Fahrenholtz’s rule (Price 1980), which states

that the evolution of parasites parallels the evolution of their hosts. Therefore, the phylogeny of some parasite taxa is congruent with the phylogeny of their host taxa. Thus, heirloom parasites have very ancient evolutionary origins.

Souvenir parasites are those acquired relatively recently in human prehistory through the breakdown of ecological, behavioral, or geographical barriers between humans and a parasite species. Sprent (1962, 1969) specified animal domestication as a main source of souvenir parasites. Parasitological evidence from archaeological sites shows that heirloom parasites such as hookworm, whipworm, pinworm, and a few other species do have a *pre-Homo sapiens* origin. The majority of parasites in archaeological sites are geographically circumscribed souvenir species. Such souvenirs include thorny-headed worms in the Great Basin (Moore et al. 1969), intestinal flukes in Brazil (Sianto et al. 2005), ticks in northwestern Arizona (Johnson et al. 2008), and fish tapeworm infection on the Pacific coast of Chile and Peru (Callen and Cameron 1960).

Archaeoparasitology contributed to understanding the evolution of the strategies of parasites. Until the 1990s, the general notion was that parasites evolved over time to have benign relationships with their hosts and to develop a high degree of host specificity. Parasitological work eventually showed that a high degree of host specificity is lacking in most parasites of humans. Of the 342 species of helminths clinically known to infect humans (Crompton 1999), only the beef tapeworm, pork tapeworm, hookworm, pinworm, whipworm, and ascarid roundworm exhibit high specificity to humans. The other hundreds of helminth species that infect humans also infect other host species. Most recently, Johnson et al. (2009) presented phylogenetic and experimental support of the hypothesis that host specificity is an ancestral condition. Generalists evolved from specialist ancestors. Agosta et al. (2010) present a case that there are pulses of generalization as parasites switch hosts. They assert that climate changes and large-scale ecological perturbations drive the mixing of species that increases rapid host switching. Both perspectives are borne out in the archaeological record. The majority of parasites found in the archaeological record are opportunistic species that are generalists and therefore infect a variety of hosts. Humans became infected with them when they intruded into nidi where these parasites existed. In short, humans create their own ecological perturbations when they move into a new environment and change it through exploitation, agriculture, or animal

domestication. In these situations, zoonotic parasites switch to humans. In contrast, the human-specific parasites, such as hookworm, pinworm, and whipworm have been shown to be very ancient human-specific species, dispersed in antiquity throughout the prehistoric world with human migrations. Interestingly, it was once thought that *Ascaris lumbricoides* evolved in humans from the pig species *Ascaris suum*. The discovery of ascarid eggs in 30,000-year-old human coprolites shows that humans were infected before pig domestication and therefore this human-specific parasite has an ancient evolutionary history with humans. Even the human-specific tapeworms noted above evolved in ancient times, before the evolution of the genus *Homo*. Phylogenetic and ecological analysis shows that these tapeworms evolved from interaction between hominids and suids a million years ago (Hoberg 2006).

In an evolutionary context, Ferreira and his colleagues based their work on the parasitological theories of the times presented by Fonseca (1972) and Manter (1967), who argued that the Arctic would prevent the entry of pathogens into the New World with human migrations. According to the theory of heirloom and souvenir parasites, the most common modern parasites of humans, such as giant roundworm, whipworm, hookworm, and various flukes and tapeworms, would have been absent in the New World because they could not have survived the migration of humans to the New World. By analyzing mummies and coprolites, Ferreira's researchers discovered abundant evidence of hookworm and whipworm infection (Araújo et al. 1981; Ferreira et al. 1980, 1983), disproving the hypothesis that a Beringean cold filter prevented the entry of parasites (Araújo et al. 2008).

The use of archaeological parasites to evaluate parasitological theory leads to a single conclusion from several perspectives. The evolution of heirloom, human-specific roundworms and tapeworms occurred very early in hominid evolution. The overwhelming number of helminth parasites known from the archaeological and clinical literature are generalist souvenir parasites that opportunistically infected humans as humans intruded into a variety of diverse nidi.

Archaeoparasitology has redefined our perceptions of the emergence and introduction of parasites into the New World. Hookworm was once thought to have been introduced into the New World with African slaves. As reviewed by Cox (2002), this perception persisted for many years but has been dispelled by hookworms recovered from archaeological sites.

Another example of paradigm shift resulting from archaeological data is represented by investigation of Chagas disease as reviewed by Araújo and colleagues (2003, 2009). Chagas disease was once thought to have emerged in Andean cultures after animal domestication, but the growing body of evidence shows that Chagas disease was distributed in North and South America before agriculture. There are similar paradigm shifts for many other species (Reinhard 1990, 1992a; Sianto et al. 2005, 2009).

## Parasites and Paleopathology

Barrett et al. (1998) painted a picture of the state of human parasitism from a paleopathological perspective in broad-brush strokes. In their review, they define three paleoepidemiological transitions, two of which occurred in the remote past. These include a rise in infectious diseases associated with the Neolithic Revolution, and a shift from infectious to chronic disease mortality associated in industrialized societies. Both of these followed a Paleolithic pattern of low levels of parasitism in dispersed hunter-gatherer groups. Using archaeoparasitological data, we can fill in the details of these transitions, especially using archaeological data from the Americas. New World archaeology provides an ideal "laboratory" for the recovery of parasites marking the transitions noted by Barrett et al. (1998). Since hunter-gatherer, Neolithic, and industrial sites have been excavated for parasitological data, further details can be added from Old World archaeological work.

Barrett et al. (1998) note that "long-term coevolutionary relationships between hominids and a heirloom parasite imply a good match between the parasite's mode of transmission, virulence, and lifecycle, and the lifestyle and demographics of early foraging bands" (Barrett et al. 1998:251). They suggest that pinworm and lice would be among the oldest of human parasites. These extremely intimate parasites of humans would easily migrate to, and stay established in, human populations in any biome. The archaeoparasitological work bears this out. Pinworm (Reinhard 1990) and lice (Araújo et al. 2000) arrived in the New World with Paleolithic migrations. Interestingly, whipworm, wireworm (*Strongyloides stercoralis*), and hookworm also arrived with the earliest pre-Clovis migrations (Araújo et al. 2008). *Ascaris lumbricoides* has also been found in Paleolithic coprolites in France (Bouchet et al. 1996). The combined data shows that all



of the heirloom, human-specific roundworms developed before or during Paleolithic times. The data also show that souvenir, generalist parasites also infected Paleolithic hunter-gatherers. Thorny-headed worms and tapeworms are also found to have infected hunter-gatherer bands more than 10,000 years ago in Utah (Fry 1977). However, as suggested by Barrett, early populations were too small and dispersed to be chronically infected. This is borne out in New World archaeology by the fact that most hunter-gatherer coprolite series are nearly parasite-free (Reinhard et al. 1985; Reinhard 1992b). Therefore, for many parasite life cycles, hunter-gatherer behavior limited transmission only for those parasite species that were tightly coevolved with humans. The evolutionary pressure on human evolution has also been explored for some parasites. Lambrecht (1980, 1985) presented a particularly convincing case that forms of African sleeping sickness had a differential role in the evolution of human resistance to the disease in different regions of Africa.

The "Neolithic Revolution" is represented in the Americas by many horticultural sites excavated in drier regions. These sites contained mummies and coprolites, which have been extensively studied. In reviews of parasitic data, it is clear that horticulture and sedentism did not by themselves result in a rise in parasitism. The level of parasitism depended on a variety of factors including village plan, construction and location, use of irrigation versus dry farming, population concentration, and the use of outdoor space (Hugot et al. 1999; Reinhard 1990, 1992b, 2007, 2008; Reinhard and Bryant 2008). Prevalence and species diversity increase is associated with drought and environmental collapse. The diversity of parasites among horticulturalists increased over hunter-gatherers and included evidence of intestinal flukes, lung flukes, hymenolepidid tapeworms associated with grain storage, tapeworms from uncooked meat, thorny-headed worms from insects, wireworms from human-dog association, dog tapeworm cyst disease, giardiasis, amoebiasis, body lice, and crab lice. Strangely, fecal-borne helminthiasis represented by whipworm and ascarids was relatively rare in the horticultural societies of the Americas. This can be explained by use of anthelmintics and behavioral patterns (Leles et al. 2010). Therefore, although the general picture of "Neolithic" parasitism is variable, there are sites that show a dramatic increase in parasitism diversity, especially associated with development of empires (Santoro et al. 2003) and environmental perturbations (Reinhard 2007). Bone pathology such as porotic hyperostosis is additionally associated with sites with high parasite diversity (Reinhard 2007).

The impact of early industrial societies can be evaluated by analysis of latrine sediments from historical sites in the Americas. The arrival of Europeans resulted in the introduction of fecal-borne helminthiasis. Whipworm and ascarid eggs are present in latrines from every town and city from the Colonial Period onward (Fisher et al. 2007; Raymer and Reinhard 2006; Reinhard et al. 1987; Reinhard 1990, 2000b). Fisher et al. (2007) studied in detail the emergence of fecal-borne parasitism from colonial times to the 20th century in Albany, New York, and showed that fecal-borne geohelminths dominated. Infection peaks in the working class neighborhoods in the 19th century. Other work shows that parasitism in cities such as New York (Reinhard 2000b) and Philadelphia (Raymer and Reinhard 2006) was extremely common. Unpublished reports on file with Reinhard show decreased parasitism in smaller towns, and absence of parasitism in rural farms. Therefore, the archaeological data recovered from a variety of sites supports the general picture of the emergence of parasitic disease proposed by Barrett et al. (1998).

## Current Centers for Archaeoparasitology

Archaeoparasitology training has foci in Canada and the United States. In keeping with the foundations of the field, training is offered in archaeology or parasitology programs. Allison Bain (2001) earned her doctorate at the Université Laval, Quebec, and currently teaches in the environmental archaeology focus in the archaeology doctoral program at the same university. Her dissertation focus was on methods of recovery and interpretation of parasite eggs and insect remains. Rhonda Bathurst earned her doctorate from McMaster University and is currently on staff at the University of Western Ontario (Bathurst 2005a, b). The work of these two archaeoparasitologists is innovative in method, application, and interpretation. Bain (2001) offers a comparative evaluation of diverse processing and quantification methods and an overview of the Significance of archaeoparasitology, especially in historic contexts. Bathurst (2005a, b) integrates zooarchaeology and archaeoparasitology through an innovative auger test system at a variety of coastal sites. In the United States Susan Jacobucci is an archaeopalynologist and archaeoparasitologist trained at the University of Massachusetts, Boston, and currently works at the Andrew Fiske Memorial Center for Archaeological Research, University of Massachusetts, Boston, directed by Steve Mrozowski (Gallagher et al. 2007). Her



integration of pollen and parasite analyses builds on a long-standing tradition (Hevly et al. 1979; Reinhard et al. 1986). At the University of Nebraska, Lincoln, archaeoparasitology is taught at the School of Natural Resources and the Manter Laboratory of Parasitology. In the near future, the Manter Laboratory will archive archaeoparasitological samples to preserve important specimens for future researchers.

Independent of these centers of training, US archaeological contractors are offering services in archaeoparasitology. Some of the work by these individuals is substandard because of inadequate training. The more common errors we see in the archaeological “gray literature” is misdiagnosis of parasite species and failure to quantify the remains in a meaningful way. Therefore, the emergence of contract archaeoparasitology threatens the integrity of the field. Archaeologists would be wise to employ only those individuals who have graduate training in archaeoparasitology.

Europe has several active laboratories. Andrew K. G. Jones is in the process of returning to parasite research at York Archaeological Trust. Jones and students have been working in Pompeii, Italy, and have recently found human helminth eggs in calcareous “tufa-like” deposits that accumulated inside waste pipes and at the entrance to deep rubbish disposal pits dug before the eruption of the volcano Vesuvius in 79 CE. Parasite eggs, fly puparia, fish bones, and even sherds of pottery have been in these materials. The work shows that Romans were infected with parasites, even after the use of complicated sanitation systems become common. It is noteworthy that three research groups have been established in France. At the University of Perpignan, Claude Combes, and Henry de Lumley have analyzed archaeological coprolites collected from sites in the Old World. Françoise Bouchet has also established her laboratory at the University of Reims. She has trained several doctoral and postdoctoral students from France and Brazil including Sophie Dommelier-Espejo, Stephanie Harter, Matthieu Le Bailly, Gino Chaves da Rocha, and Marcelo Gonçalves. Matthieu Le Bailly has a new position at the University of Franche-Comté, where the French Scientific Centre has enabled him to establish a new parasitology lab.

One of the most active centers for archaeoparasitology is in South Korea at the Anthropology and Paleopathology Lab, Seoul National University College of Medicine — <http://shinpaleopathology.blogspot.com/2009/11/publications-and-other-achievements.html>. In cooperation with archaeologists from the Foundation for the Preservation of

Cultural Properties, Chungnam Institute of History and Culture, Hangang Institute of Cultural Heritages, and the Seoul Museum of History, parasitologists are examining a variety of archaeological deposits including from privies, in tombs, and within mummified remains. Their papers cover methodological issues, address interpretive problems, and approach the knotty problem of differential preservation of parasite remains in tombs. Seo et al. (2009) and Shin et al. (2009) provide literature reviews of the many papers that have come out of the Korean archaeoparasitological collaborations during recent years. Their work is characterized by refined diagnostic techniques combined with meticulous association of parasites with well-illustrated archaeological contexts. This excellent integration of parasitology and archaeology sets the ideal standards for such research.

Brazil has the longest history in archaeoparasitology (Chapter 40). By the end of the 1970s Luiz Fernando Ferreira and colleagues had published their first contribution to the study of parasites in ancient material, naming it *Paleoparasitology, a contribution to the study of parasites found in archaeological material in Brasil* (Ferreira et al. 1979). After this pioneering work, they committed to the study of parasites in archaeological and paleontological material, aiming to contribute to the study of the origin and evolution of infectious diseases, not only in humankind, but also in other animals. With the development of their studies, and collaboration with other research groups, a network was established, mainly with the University of Nebraska-Lincoln and with the Laboratoire de Paléoparasitologie, at the University of Reims, in France. The collaboration among these three laboratories was very productive, with researchers and students participating in diverse scientific events, both of parasitology, such as those organized by the American Society of Parasitologists, the North American Congress of Parasitology, Federación Latinoamericana de Parasitología, Sociedade Brasileira de Parasitologia, as well as the Paleopathology Association, American Anthropological Association, International Council for Zoo archaeology, and the World Congress of Mummy Studies.

In South America three other laboratories have appeared recently. In Argentina, Ricardo Guichón, a bioanthropologist, and Martín Fugassa, a parasitologist, have created a laboratory of paleoparasitology in the Universidad Nacional de Mar del Plata, dedicating their studies to the Patagonian region. They are studying infectious diseases among prehistoric groups in Patagonia, and the impact of new parasites on native populations when Europeans arrived to establish new

colonies. Methodological contributions include examination of museum-curated sacra for parasites and the comparative analysis of burial sediments.

At the University of Tarapad., Arica, in Chile, Bernardo Arriaza has created an archaeoparasitology research line to recover parasites in prehistoric populations who lived on the north coast of Chile. He is combining archaeology, anthropology, and parasitology to understand the life of people who lived in the Atacama Desert, especially the Chinchorro (Arriaza et al. 2010).

In Peru there is a recent proliferation of archaeoparasitology centers. Sonia Guillen at the Centro Mallqui has long fostered archaeoparasitological research (Holiday et al. 2003; Dittmar et al. 2003). Jane Wheeler, now of CONOPA (an independent Peruvian institution primarily dedicated to scientific research and development of the South American camelids, established in 2001), conducted extensive parasitological examinations of mummified llamas at San Marcos' Faculty of Veterinary Medicine in Lima. Her PhD student, Eva Casas, coauthored the definitive work on llama archaeoparasitology (Leguia and Casas 1999). Since 2007 two new laboratories have been established. Ines Garate at the Universidad Nacional Mayor de San Marcos has begun analysis of archaeological remains for parasites, and Luis Huaman has included archaeoparasitology in his Paleobotany laboratory at the Universidad Peruana Cayetano Heredia. There, parasitology is taught as part of a holistic analysis of plant remains to reconstruct ancient diet, environment, and disease.

By the end of the 1990s the laboratory at Fiocruz in Rio de Janeiro started to apply molecular biology techniques to ancient parasitological materials (Bastos et al. 1996; Ferreira et al. 2000) contemporaneously with research in Arica, Chile (Guhl et al. 1999). In addition, molecular biology techniques began to be used, mainly in Chagas disease research (Aufderheide et al. 2004). In North America, Dittmar et al. (2003) confirmed the diagnosis of Chagas disease in a mummified body with megacolon described by Reinhard et al. (2003). However, PCR technique was also applied to detect helminth infection in sediments and coprolites (Iñiguez et al. 2003; Leles et al. 2008, 2010) as performed by Loreille et al. (2001), Loreille & Bouchet (2003). The South Korean research is also sequencing *Ascaris lumbricoides* and *Trichuris trichiura* DNA, and the *T. trichiura* data have been published (Oh et al. 2010). Researchers at the University of Nebraska-Lincoln have also begun collaboration with the University of Oklahoma's Molecular

Anthropology Laboratories to recover ancient DNA from coprolites. Preliminary work focusing on gut bacteria has been published. (Tito et al. 2008) and analysis of helminth DNA is ongoing.

## Conclusion

The interdisciplinary interest in archaeoparasitology has created contributions in several areas. Work in the exploratory period and population study phases contributed to understanding the prehistoric distribution of parasites and established an idea of the relative parasite burden different cultures experienced in prehistory. These phases focused primarily on archaeological problems such as transhumance (including migrations), resource exploitation, anthelmintic parasite control, sanitation, and other issues. The synthesis phase integrated archaeological data into developing parasitological theory established by Sprent and others. Archaeoparasitology was especially relevant to defining which parasites are heirloom species and which are souvenir species. These data also contributed to understanding the parasite adaptation dichotomy of generalists and specialists. The field has also contributed to epidemiological and paleopathological theory as defined by a variety of authors. Cockburn's ideas regarding the evolution of pathogens was particularly well adapted to evaluation through archaeoparasitology. The more recent construct presented by Barrett and colleagues regarding stages of pathogen emergence is also conducive to testing through laboratories of archaeoparasitology. Of all theories, Pavlovsky's nidus concept is particularly adaptable to archaeology today. The individual nidi of prehistoric habitations can be defined in archaeological space and the pathogens can be recovered. Through archaeological method and paleopathological/epidemiological data, archaeoparasitology has made its most meaningful contributions and will continue to do so as a synthetic field.

**Acknowledgments** — The final version of this chapter benefited greatly from discussions with the University of Nebraska parasitology faculty and students. In particular, Dan Brooks, John Janovy, Scott Gardner, and Mary Lou Pritchard provided comments on broad aspects of theory and also small errors in detail. We are all intellectual descendants of Harold Manter, who founded parasitology at the University and our evolutionary perspective on parasites and hosts.

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