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Pathoecology and the Future of Coprolite Studies in Bioarchaeology

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Coprolite Studies in Bioarchaeology

Human coprolites currently provide an expanding array of information about the diet, health, and ecology of prehistoric people in the Southwest, but for many years coprolites were not recognized or preserved, or they were not considered important and thus were not saved (Bryant and Dean 2006). With the expansion of archaeological field work during the last half of the twentieth century archaeologists have increasingly explored the "complete" potentials of sites, including the collection and analysis of geomorphologic, botanical, and faunal data. In some ideal habitats (e.g., very dry or frozen) this includes exploring the scientific potential of human coprolite studies. This is not easy to do: very few coprolites have what might be considered a "characteristic shape and size." In our experience, the majority of coprolites are usually fragmented, flattened by age, or in many cases are preserved as amorphous masses of various sizes similar in shape to "patties" left behind by cattle. These flat, amorphous human coprolites are especially common in sites used by foragers with diets very high in plant fiber. Coprolites and coprolite fragments are sometimes collected in situ during archaeological excavations, but most often they are found during screening, when dirt is being separated from artifacts. unrecognized, coprolites may be crushed into dust, along with clods of dirt, and their contents lost.

In the American Southwest the arid climate, protected sites, and dry rock shelters provide some of our best areas in North America for the preservation of human coprolites and the long record of biological history they help to reveal. Starting in the early 1960s with the pioneering efforts of Eric Callen

(1963) and Martin and Sharrock (1964), but especially in the seventies and eighties, coprolites were the focus of many interdisciplinary research theses and dissertations (Aasen 1984; Bryant 1969; Clary 1983; Edwards 1990; Fry 1969; Hall 1969, 1972; Kelso 1971, 1976; Napton 1970; Reinhard 1985a, 1988a; Sobolik 1988, 1991; Stiger 1977; Stock 1983; Van Ness 1986; Williams-Dean 1978). A large number of articles, chapters, and monographs were published as a result of this early work (Bryant 1974a, 1974b, 1974c; Bryant and Williams-Dean 1975; Callen and Martin 1969; Clary 1981, 1984, 1987; Cowan 1967; Cummings 1994; Fry 1977, 1980, 1985; Fry and Hall 1975; Fry and Moore 1969; Heizer and Napton 1969, 1970; Hevly et al. 1979; Hogan 1980; Holloway 1983; Kelso 1970; Lindsay 1980, 1983; Martin and Sharrock 1964; Moore et al. 1969; Napton 1969; Reinhard 1988b, 1992a; Reinhard and Clary 1986; Reinhard et al. 1985, 1987, 1988; Roust 1967; Scott 1979; Steele 1969; Winter and Wylie 1974). As summarized by Reinhard and Bryant (1992) these works explored the application of many fields to coprolite analysis including archaeopalynology, archaeobotany, archaeoparasitology, zooarchaeology, biochemistry, starch analysis, and phytolith analysis. (Phytoliths are microscopic mineral deposits produced by plants within their cells. Phytoliths are extremely durable and their morphologies are frequently specific to family, genus, and even species.)

Each research project offered new methodological innovations and several salient works came from this period. Williams-Dean's dissertation (1978) was a milestone in combining studies of modern feces with the contents of Archaic Period coprolites. She was also the first researcher to present a holistic dietary reconstruction including archaeopalynology,

archaeobotany, and zooarchaeology from the same coprolite series. Aasen (1984) pioneered the application of pollen concentration and anthracology to Basketmaker coprolites. Fry and Moore (1969) and Moore and Englert (1969) demonstrated that parasite eggs could be recovered from 10,000 year-old coprolites. Stiger (1977) and Fry (1977) integrated dietary and parasitological analyses to present a picture of pathology and diet for Pueblo and Fremont cultures. In this period, Bryant (1974a, 1974b, 1974c; 1975) emerged as the first coprolite specialist who fostered many graduate student studies at Texas A&M University (Bryant and Williams-Dean 1975; Edwards 1990; Jones 1988; Reinhard 1988a; Reinhard and Bryant 1992; Sobolik 1988; Stock 1983; Weir et al. 1988; Williams-Dean and Bryant 1975).

In other parts of the world, coprolite analyses were applied to bioarchaeology (Anderson 1967; Callen 1967; Weir et al. 1988) while in the Southwest coprolite analyses usually fell into the realm of paleoethnobotany and dietary reconstruction. However, there was considerable bioarchaeological influence on coprolite research at Texas A&M University and at Northern Arizona University which resulted in the application of coprolite studies to explaining osteological expressions of disease (Reinhard 1985a, 1988a). At the University of Utah and the University of Colorado, parasitology began to be incorporated in thesis research resulting in Fry's (1977) and Stiger's (1977) applications of parasitology to evaluate the symptoms that would have been suffered by prehistoric people. Bioarchaeologists were quick to incorporate the new coprolite data, especially archaeoparasitology, into their models of disease causation (Akins 1986; Merbs and Miller 1985; Stodder 1984, 1987; Stodder and Martin 1992).

Unfortunately, the numbers of theses and dissertations devoted to coprolite studies has declined during the last 15 years. Only four graduate research projects with a focus on Southwestern coprolites have been completed since 1991 (Androy 2003; Danielson 1993; Hansen 1994; Nelson 1999). Perhaps what is needed is a new theoretical approach that will attract young researchers to consider coprolite analyses and bring them "back into the laboratory." Bioarchaeology is a natural future host for coprolite research, providing that coprolite researchers in the Southwest can develop a conceptual framework applicable to bioarchaeology.

Pathoecology: A New Approach

Pathoecology is the study of the environmental determinants of disease (Martinson et al. 2003; Reinhard 2007a, 2007b). These include human factors such as

crowding, sanitation, hygiene, and trade. They also include biotic factors such as presence of pathogens, disease reservoirs, and intermediate hosts. Finally, physical factors such as climate and soil conditions can be studied. Pathoecology began to emerge in the Southwest with the establishment of a link between the emergence of parasitic disease and Ancestral Pueblo cultural development (Reinhard 1988b). Later, this approach was applied to the biarchaeological problem of the etiology of anemia resulting in porotic hyperostosis (Reinhard 1992a). From 1990 through 2000, much of the coprolite research, especially archaeoparasitology, shifted from the American Southwest to South America (Bouchet et al. 2003; Chaves and Reinhard 2006; Dittmar et al. 2003; Gonçalves et al. 2003; Iñiguez et al. 2003; Reinhard and Buikstra 2003; Reinhard and Urban 2003; Sianto et al. 2005), as research groups developed in Peru, Chile, and Brazil. The Escola Nacional de Saúde Pública, Fundação Oswaldo Cruz in Rio de Janeiro became a coprolite research hub for the Western Hemisphere. During this period new methods for diagnosing disease based on gross pathology, immunology, and molecular biology were developed and a paleoepidemiological approach also emerged (Aufderheide et al. 2004; Reinhard and Buikstra 2003).

Along with these new methods, Martinson et al. (2003) codified the concept of "pathoecology" to explain patterns of parasitic disease in archaeological sites in the Moquegua Valley of southern Peru. Martinson et al. (2003) showed that the parasitism at several villages was defined by occupation, trade, status, presence of domestic animals, and site location relative to fresh water access. In one village, which specialized in fishing, the inhabitants were parasitized by a tapeworm species, Diphyllobothrium pacificum that survives when fish is undercooked and then eaten. In another village further inland, where the main economy specialized in the herding of llamas, some of the herders may have suffered from dermatitis caused by a species of ectoparasites recovered in ancient llama coprolites. Trade also seems to have spread parasites. As fish was traded to inland groups, Diphyllobothrium infection spread inland to areas where agriculture was the main subsistence base. Overall lower levels of Diphyllobothrium infection are found in mummies from a higher status site, indicating that social status also impacted parasitism. Local site conditions also affected parasitism. The coastal site examined had no source of clean drinking water, which explains the evidence of fecalborne disease. The presence of domesticated guinea pigs and dogs in human habitations promoted the spread of Chagas disease. Population aggregation in sites occupied during Inca times was yet another factor (Santoro et al. 2003), since in populated areas

crowd diseases spread rapidly by person-to-person contact and fecal contamination.

In the late nineties, these pathoecological studies of past human populations in the Peruvian Andes began to influence Southwestern coprolite studies. The methods developed in South America were applied to a limited number of Ancestral Pueblo coprolites (Gonçalves et al. 2002, 2004; Reinhard et al. 2001) after the discovery that Ancestral Puebloans were infected by protozoa and hookworms. In combination with previous work (Reinhard 1990) these newer studies revealed that Ancestral Puebloans were infected with Giardia lamblia, (cause of "beaver fever"), Entomoeba histolytica (cause of amoebic dysentery), Trichuris trichura (whipworms), Ascaris lumbricoides (giant intestinal roundworms), Ancylostomidae (hookworms), Acanthocephala (thorny headed worms), Strongyloides stercoralis (threadworm), taeniid tapeworms, hymenolepidid tapeworms, Enterobius vermicularis (pinworm), ticks, lice, and possibly flukes. Relative to other parts of the Americas where there is excellent preservation and intensive archaeological research (central Mexico, northeastern Brazil, Chile, and Peru), the Southwest has evidence for a greater diversity of parasites infecting Ancestral Puebloans than any other known prehistoric culture. The variation, diversity, and prevalence of infections between pueblo sites is ideal for the application of pathoecology as an interpretive framework.

The pathoecological approach is exemplified in the comparative study of the parasite ecology of Salmon Ruins, New Mexico, occupied from A.D. 1088 to the mid-thirteenth century (Reed 2006; Reinhard 2008) and Antelope House (occupied from A.D. 500 to 1250) located in Canyon de Chelly, Arizona (Morris 1986; Reinhard 1996). Reinhard (1996; 2008) reviewed the pathoecology of the Pueblo III (A.D. 1100–1300) occupations of the sites. This study incorporates data on site ecology, subsistence, sanitation, food storage, and other data revealed by the archaeological work to explain the dramatic difference in parasitism between the two sites. The elevated levels of parasitism at Antelope House resulted in higher rates of anemia, as indicated by porotic hyperostosis in cranial vaults in the burials from Antelope House: 88 percent of subadults affected (El-Najjar 1986:219), compared to 43 percent in subadults from Salmon Ruin (Berry 1983). In essence, Antelope House was built in a canyon bottom location that was more conducive to the life cycles of a greater variety of parasites than Salmon Ruin located on a terrace above the San Juan River. The subsistence data from the coprolites verifies that Antelope House inhabitants used wet areas extensively for various economic activities and were thus exposed to wireworms and hookworms

(Reinhard 1985b; Reinhard et al. 1987). The sanitation system at Salmon Ruin was also more efficient at sequestering feces and therefore reducing the occurrence of infections from fecal remains.

Hugot et al. (1999) addressed pinworm infection and its variation among Southwestern sites. Pinworm is a crowd disease evident in 0 percent to 25 percent of coprolites from Anasazi sites. In modern clinics, tests reveal that only five percent of pinworm-infected patients pass pinworm eggs in the feces. If this equivalent rate was also present in ancient human populations, then the very high prevalence of pinworms at some sites begs explanation. Hugot et al. (1999) compared the pathoecological influences of site location and architecture against the prevalence of pinworm infection. They found that sites in caves had a higher prevalence of pinworm-infected coprolites than open sites. Large pueblos had a higher prevalence of infection than small pueblos. Large pueblos built in rock shelters had the highest prevalence of infection of any sites studied. Therefore, it appears that human crowding, combined with the pinworm's spread via airborne contamination, promoted infection to levels that were unprecedented and are unequaled in the modern clinical literature regarding pinworm infection.

The lessons learned from the Hugot et al. (1999) study should be important to bioarchaeologists interested in spread of airborne diseases such as tuberculosis. Since pinworm and tuberculosis infections are both airborne, one might anticipate that large communities, especially those in rock shelters like those with the highest pinworm rates, would also have been more prone to tuberculosis infection.

Applying the Nidus Concept in the Study of Prehistoric Health

A paper on Pueblo Health (Reinhard 2007a) proposes that bioarchaeologists adopt the concept of the nidus (Pavlovsky 1966) as a tool in reconstructing the pathoecology of infectious disease in prehistoric communities. The nidus is a geographic or other special area containing pathogens, vectors, reservoir hosts and recipient hosts that can be used to predict infections based on one's knowledge of ecological factors related to infection. Ecological factors include the presence of vectors, reservoir hosts, humans, and external environment favorable for the transmission of parasites. An individual nidus therefore reflects the limits of transmission of a given parasite or pathogen within specific areas of interaction: bedbugs in a bedroom, for example. Thus, a nidus is a focus of infection. A nidus can be as confined as a single room containing a bed and

with access to the room by rodents carrying plagueinfected fleas. However, a nidus can also be as large as the community and its surrounding area in which there is a transmission of hookworms.

Pueblos are a complex of overlapping nidi. For example, at Antelope House the grain storage and processing rooms could be identified as a nidus for tapeworm infections. The habitation rooms within the shelter formed a nidus for pinworm infection. The water sources were nidi for whipworm, *Giardia*, and amoeba infections. Finally, the defectaion and/or agricultural areas were nidi for hookworm and wireworm transmission.

Hymenolepis nana is a tapeworm that has only been recovered from agricultural sites and most commonly uses grain beetles as intermediate hosts and rodents as definitive hosts. Humans become infected when they eat food made with grain contaminated with beetles. The beetles and other insects become infected when they feed on the feces produced by infected rodents. Some grain beetles are quite small, only 2-3 mm long, therefore it is quite easy to overlook them when selecting grain for processing and eating. Alternatively, H. nana evolved a direct life cycle without intermediate hosts. Nevertheless, it is very likely that rodents and grain beetles in or around grain storage areas promoted the cycle of the tapeworm infections. Once humans processed the contaminated grain, human infection was promoted.

Hookworm and wireworm larvae penetrate the skin of humans. Nidi for these parasites probably were in agricultural fields and/or in or around toilet areas in the sites. The most common method to control for hookworms is to use footwear. Ancestral Puebloans wore sandals, but Behnke et al. (2000) document problems with the wearing of sandals among modern agriculturalists in Mali. They state (2000: 352) "soil sticks to sandals, making them uncomfortable and frustrating to wear when tilling soil, and risking damage. As a result of this practice, those who often wore shoes still became infected through bare skin." This same situation may have plagued Puebloan horticulturalists. Therefore, larval skin penetration could have occurred in cornfields. Schad et al. (1983) suggest another scenario for hookworm infection that is also applicable to Puebloan pathoecology. They found that in West Bengal, villagers defecated in areas around the village peripheries. People used the same areas day after day for this purpose. As a result, hookworm larvae proliferated in those areas and the time spent by humans in the contaminated areas was sufficient for hookworm infection. At Antelope House, hundreds of small concentrations of coprolites were found within the rock shelter. This pattern of coprolite remains shows that the Antelope House residents had a similar sanitation pattern as the people living in West Bengal, but used abandoned rooms rather than just peripheral regions around the village. Therefore, the nidi for hookworm and wireworm infections could have been in the peripheries of the village or in the abandoned rooms. Wireworm larvae were found in Antelope House dog coprolites (Reinhard 1985b, 1985c) suggesting that dogs were a reservoir within the Pueblo for wireworm infection.

By building a multi-room, stone-walled village within a rock shelter, Puebloans at Antelope House established a large nidus for the transmission of pinworm. Pinworms are transmitted both by hand-to-hand contact between humans and by airborn-dissemination when a population is occupying a closed space. The apartment-like pueblos with their closed spaces and stagnant air would have been ideal areas for the dissemination of eggs (Hugot et al. 1999; Reinhard 2007a). Proof for this is noted at Antelope House, which has one of the highest prevalences of pinworm infections due to airborne contamination.

Whipworm, Giardia, and amoebas are transferred in contaminated water, although hand-to-hand transfer of Giardia is known. This would have been a serious problem during a period of drought in the Canyon de Chelly region in Pueblo III times (Morris 1986; Reinhard 2007c). During the drought the number of Pueblos in the canyon grew as people moved closer to the remaining reliable sources of water in the canyon floor. As a result of overcrowding and poor sanitation the local water sources became contaminated and thus could be considered as nidi for fecal-borne diseases.

Parasites, Disease, and Ancestral Puebloan Demography

Parasitic infection does not always provoke disease. In fact, some parasite species rarely cause disease. Disease results from the pathogenicity and virulence of the parasite infection, combined with characteristics of the host. Virulence refers to a parasite's ability to multiply. Pathogenicity refers to the parasite's capacity to cause disease symptoms and mortality in host populations. Disease may be passed by vertical transmission, from parent to child, or lateral transmission from one human to another (except from parent to child).

Among the various worm types of parasites that infected Ancestral Puebloans, the most virulent included whipworms which have the potential for each female to lay as many as 20,000 eggs per day, and giant intestinal roundworms which lay 200,000

eggs per day. Perhaps the least virulent worm parasite was wireworm. Female wireworms lay only hundreds of larvae per day. However, the pathogenic potential of these worms is reversed. Whipworms and giant intestinal roundworms rarely cause debilitating long-term problems or death. In contrast, wireworms are more pathogenic. Wireworms enter the body by penetrating the skin. In their migration toward the intestine they work their way through the heart and lungs and can cause serious pathology in these organ systems. When they enter the intestine they plow through the intestinal mucosa and damage the intestinal tract. Mothers infected with wireworms can potentially infect their nursing babies in vertical transmission via breast milk. Whipworms and giant intestinal roundworms can be transferred only by fecal contamination of the environment. These are "geohelminths" which refers to parasites whose eggs need to mature to infective stage in soil. Of all the worm type parasites that infected the Ancestral Puebloans, only the wireworm and hookworm had the potential for vertical transmission.

The number of parasite species infecting a host population relates to their ability to combine into conditions that create a disease. If only one species of parasite infects a host population, then disease conditions are not likely to become a serious problem for that population. However, as more and more parasites become established in the host population, the population will begin to experience disease conditions caused by the symptoms and stress from the infection of multiple parasites. Therefore, it is important to document the diversity of parasite species found in a host population. One advantage of coprolite analyses is that they provide the potential for identifying the number and diversity of parasites that are infecting a single host (Reinhard et al. 1988). This potential should be fully explored in future coprolite work. Currently, the identification of multiple types of parasites found in a single coprolite is documented only for Antelope House.

The level and intensity of parasite-caused diseases in a population is affected by many conditions. These include the population's past experience with parasitic infection, nutritional and immune status, and the behavioral patterns of the population that increase or decrease risk. Two of these, susceptibility to infection and the nutritional needs of the host, can be assessed through examinations of the archaeological record. An example of this can be seen in the studies of sites in the American Southwest. A number of coprolite studies reported that the breadth of Ancestral Pueblo diets was generally nutritionally sound (Cummings 1994; Fry 1980; Minnis 1989). However, as early as 1992, Reinhard began finding coprolite evidence for substantial variation in the

consumption of wild plants at Ancestral Puebloan sites, suggesting that agricultural failures at some locations may have forced a much higher reliance on wild foods.

To test this assumption we compared the ancient diets reconstructed for the populations living at Antelope House and at Salmon Ruin to determine whether or not we could identify clues reflecting starvation in coprolite data (Reinhard 2008). These coprolite studies included identification and evaluation of starvation foods based on phytoliths (Reinhard and Danielson 2005), pollen concentrations (Reinhard et al. 2006a), and starch and macrofossils (LeRoy-Toren and Reinhard 2004; Reinhard 2008; Reinhard et al. 2006b; Sutton and Reinhard 1995). Data from both sites covered the time period during the recorded environmental deterioration in Pueblo III Canyon de Chelly (Reinhard 2004, 2008). We found that starvation foods, including yucca leaf bases and prickly pear pads, became very common foods at Antelope House but not so at Salmon and other Pueblo sites in Utah and New Mexico (Reinhard and Danielson 2005). Pollen concentrations in coprolites reveal that stored maize was eaten less often and in smaller quantities at Antelope House than at Salmon Ruins, and that people at Antelope House were relying more heavily on wild foods like cattail heads and horsetail stroboli. Finally, we found that starch grains were much less common in the coprolites from Antelope House than those found at Salmon Ruin. Macrofossil remains show the widest variety of wild plant use at Antelope House. When combined, all of these data support the apparent dietary impact of environmental deterioration in the Antelope House region of Canyon de Chelly, which undermined local agricultural yields and forced the residents to diversify and increase their reliance on wild plant foods (Reinhard 1996, 2008).

During that same stressful period a greater diversity of parasite species infected the population living at Antelope House. Some of these parasites. like hymenolepidid tapeworms and pinworms, are neither very virulent nor pathogenic but their presence suggests that the population, perhaps already suffering from various forms of malnutrition was generally in poor health. Whipworms were also present and although this parasite is virulent, it is not very pathogenic. Hookworm and wireworm infections were also common at Antelope House during this period. Neither of these is particularly virulent, but they both have the capability of vertical transmission from mother to fetus or newborn and the ability to infect the most susceptible portion of the population (infants) with regard to helminths. In addition, two species of diarrhea-causing protozoan parasites were found that are both highly virulent and pathogenic, Entomaeba histolytica and Giardia lamblia. Overall,

the image that emerges of the people living at Antelope House during this period is one of a physiologically stressed, highly infected population among whom some individuals in the poorest health were more susceptible to infection by many parasites.

The widespread infection levels indicated by the Antelope House coprolites raise other important questions, such as the level of interaction between the host's nutritional needs and parasitism and at what point those levels become critical or even lifethreatening. One example of this important relationship between nutritional needs and parasitism is discussed by Crompton and Whitehead (1993). In their discussion they constructed a model predicting the effects of hookworm infection on a non-pregnant vs. a pregnant woman. Their model predicts that hookworm infection will deplete stored iron in the host's body because of the hookworm's destruction of red blood cells thus reducing their density per milliliter of blood. Thus the effect of this iron depletion becomes much more acute in pregnant women because they must also provide iron for their growing fetus. Each hookworm in a person's body can consume 0.27 ml of blood per day (MacLeod 1988). After only 20 weeks of hookworm infection the host may show symptoms of hypochromic and macrocytic anemia.

A major problem among pregnant women is that the minor symptoms of hookworm infection are often indistinguishable from normal complaints of pregnancy such as epigastric pain, heartburn, etc. When the hookworm infection is more severe, the pregnant woman may show symptoms of a low grade fever, fatigue dyspnea, heart palpitations, flow murmurs, and anemia. In cases of heavy infection, constipation or diarrhea, jaundice, emaciation, cardiac failure, or pre-eclampsia can occur. If an infected woman survives labor, she often cannot recover easily from postpartum hemorrhage, which can contribute to maternal death. Overall, in hookworm-infected populations, the increased physiological needs of pregnancy put women at much higher risk.

When multiple infections occur in a pregnant woman, as they most probably did at Antelope House during this period of severe stress, serious consequences result. Of the parasites at Antelope House, hookworm, G. lamblia, and E. histolytica were the most serious challenges to maternal and infant health. In pregnant women hookworm causes severe iron deficiency anemia, nutrient malabsorption, alimentary bleeding, fatigue, diarrhea, preeclampsia, and heart failure in labor. E. histolytica and G. lamblia cause iron deficiency anemia, nutrient malabsorption, diarrhea, dehydration, and shock.

These parasites also cause problems for fetuses. Hookworm has a vertical transplacental infection mode and is associated with spontaneous abortion, still birth, and premature birth. Infants born to infected mothers often have a low birth weight. *E. histolytica* and *G. lamblia* infections of the mother also result in fetal reduced growth, low birth weight, abortion, still birth, and premature birth.

The presence of these three parasites in nutritionally stressed Puebloan populations is an important factor in the prevalence of porotic hyperostosis in Ancestral Puebloan skeletal assemblages, especially in concert with nutritional stress when changing environmental conditions resulted in reduced food and nutrient intakes (Reinhard 1992a). Long-term droughts, such as recorded in the Antelope House region resulted in an aggregation of human populations around the dwindling water sources. This in turn led to a proliferation of crowd diseases and diseases associated with contaminated water and inadequate sanitation. Bioarchaeologically, these phenomena are expressed as elevated levels of porotic hyperostosis in skeletal remains.

The Pathoecology of Chagas Disease in the Texas Archaic

Chagas disease, which is caused by the protozoan parasite *Trypanosoma cruzi*, has a multifaceted pathoecology. Its basic life cycle involves many species of reduviid bugs in the family Triatominae—winged insects called "kissing bugs" that act as vectors for the disease. The disease normally cycles among a wide variety of host animals including marsupials, edentates (such as the armadillo), carnivores, rodents, and bats. Humans most often become infected with *T. cruzi* when infected triatomines (assassin bugs) emerge nocturnally to feed on sleeping people (Reinhard et al. 2003; Schmidt et al. 2005).

The symptoms of Chagas disease are diverse. There are two stages of infection with distinct symptoms. In about 1 percent of cases, acute symptoms occur one to two weeks after infection. These include fever, fatigue, facial swelling around the bite site, and enlarged lymph glands. These symptoms last from four to eight weeks and then disappear. Chronic disease develops 10 to 20 years after initial infection in about one-third of infected people. Cardiac problems such as cardiomegaly, arrhythmia, and cardiac arrest are common indicators of the chronic stage of this disease. Problems with the digestive system, including megaesophagus and megacolon, are also symptoms of the chronic stage, which in some cases causes death.

Recently, oral transmission of Chagas disease has been discovered (Prata, 2001; Shikanai-Yasuda et al. 1991). This occurs when humans eat infected food that is either contaminated with the feces of infected triatomines, or they accidentally eat the infected bugs. Either can occur inadvertently in contaminated pro-

ducts that are processed into consumable foods. Another potential method of transmission for Chagas disease is eating the meat of infected animals when the meat has not been fully cooked.

Bioarchaeological diagnosis of Chagas Disease is based on gross pathology (Martinson et al. 2003) and molecular analysis (Aufderheide et al. 2004). A case of "megacolon" was discovered in a mummy found in a dry rock shelter located on the Texas-Mexico border in the lower Pecos area west of Del Rio (Reinhard et al. 2003). The Late Archaic age mummy was about 1,000 years old and the preliminary diagnosis of Chagas disease was verified by molecular tests (Dittmar et al. 2003). In an effort to understand why this might have happened during the Late Archaic period, a pathoecological reconstruction of the individual's lifestyle and Chagas disease ecology was attempted. Studies of the Lower Pecos region revealed that there are seven types of insects (tratomine vectors) that can carry Chagas disease. Four of these live in woodrat nests and feed primarily on woodrats. The mixture of rock and vegetation in the woodrat nests attracts the triatomines. Thus, the woodrat nest is the natural nidus for Chagas disease transmission. Human occupation of the rock shelters and caves in the region resulted in the accumulation of vegetal debris, including grass-lined beds. Other debris that attracted triatomines included rocks and vegetal remains from roasting agave and from the deposition of plant remains in trash. In essence, humans created artificial nidi in caves for the insects and thus increased the potential transmission of Chagas disease to humans. One of the most common animals killed and eaten by these Late Archaic cultures were woodrats that could easily be caught by women and children foraging for other foods. The unfortunate result of these actions was that people reduced the number of normal hosts for the insects by killing woodrats and then inadvertently constructed ideal alternative habitats in the middens and debris in and around their habitations.

A bioarchaeological examination of ancient skeletons recovered from the Lower Pecos region (Reinhard et al. 1989) reveals that over 40 percent of those people had abscesses. Analysis of human coprolite remains from these same rock shelters and caves suggests that woodrats may not have been completely cooked before being eaten (Reinhard et al. 2006c). These findings raise the possibility that Chagas infection could have been transmitted through consumption of infected animals. In this possibility, the protozoa in the blood of the woodrats may have entered the blood of the humans directly through oral lesions from abscesses. We also know that bedrock mortars and grinding stones were used in the same rock shelters and caves where the triatomines lived.

This raises the possibility that the actual insects or their feces could have been inadvertently ground and mixed into prepared foods, resulting in infection.

Megacolon is a very rare symptom of Chagas disease. The discovery of this one case suggests that many more Archaic age people were infected than previously suspected.

Insects and Insects and Parasitism in the Prehistoric Southwest

Some of the most intriguing pathoecological data come from areas and archaeological sites where ancient people ate the intermediate insect hosts that were carrying acanthocephalan—thorny-headed or spiny-headed worms—and tapeworms. In these cases, specific aspects of prehistoric diet or hygiene resulted in their infection.

Acanthocephala rarely parasitize humans in the modern world. Acanthocephala are named for their proboscis which is usually covered with spiny hooks that are often arranged in rings of horizontal rows. Using this proboscis, these worms attach themselves to the tissues of its host. The hooks on the proboscis pierce the intestinal wall of the host and allow the worm to derive nourishment while it also completes its life cycle.

Acanthocephalans have complex life cycles. Adults produce eggs that are released into the intestines of the host and thus become part of the host's feces. The feces are then eaten by an invertebrate and the dormant eggs hatch in the intermediate host. There, the acanthocephalan worm penetrates into the body cavity of the intermediate host and encysts. This then becomes the worm's infective cystacanth stage. When the invertebrate is then eaten by a vertebrate predator, such as a human, the cystacanth develops into a mature adult in the intestine.

We know that ancient Americans were infected because we have found acanthocephalan eggs in human coprolites. These finds are most common in the Great Basin from coprolites found at Archaic sites including Dirty Shame Rockshelter in Oregon (Hall 1977), Clyde's Cavern in Utah (Hall 1972), and Danger and Hogup Caves in Utah (Fry 1977) (for review see Reinhard 1990). Acanthocephalan eggs have also been recovered from Ancestral Pueblo coprolites found in sites located in Glen Canyon, Utah, and Black Mesa Arizona (Fry 1977; Gummerman et al. 1972:191; Reinhard 1990). The Ancestral Pueblo infections resulted from accidental or purposeful consumption of flour beetles, camel crickets, roaches, and perhaps other similar insects.

A different type of infection may have resulted from eating ectoparasites (parasites outside the body such as lice, fleas, and ticks). Fry (1977) and Napton (1969) found lice in human coprolites recovered from Danger Cave, Utah and Lovelock Cave, Nevada. Johnson et al. (2008) found a Dermacentor tick in a human coprolite from Antelope Cave, an Ancestral Pueblo Site in northwestern Arizona near the Virgin River. Apparently, the tick had been bitten off and swallowed and then became part of a coprolite. Fry (1977) presented a case suggesting that prehistoric people ate ectoparasites as a hygienic measure. This assumption makes good sense and we believe that Fry made a good case for this type of behavior.

Taeniid tapeworm eggs have been found in coprolites from Danger Cave, Hogup Cave, Glen Canyon, and Antelope Cave. The exact species of taeniid that is represented by these finds is unknown. In the modern world, humans are most commonly infected by two species, Taenia solium from pork and T. saginata from beef. These species of taeniids were almost certainly absent in the prehistoric New World because the host animals are native to the Old World. There is one other known taeniid that can infect humans, although it is much more common to find it as a parasite of dogs. This is Dipylidium caninum (cucumber tapeworm). D. caninum uses fleas and lice as intermediate hosts. Therefore, if a person ate fleas and lice, in an effort to prevent the ectoparasites from feeding on humans, it is possible they could have eaten an ectoparasite that had fed on an infected dog. Since there is coprolite evidence that prehistoric people did eat fleas and lice, we suspect that the taeniids eggs found in Southwestern human coprolites may be from D. caninum infections.

The Pathoecology of Dental Disease

The connection between dental disease and coprolite studies is obvious. The carbohydrates that are associated with dental caries such as starch can be recovered from coprolites in the form of starch grains. Fruits are represented in coprolites by seeds and epidermis. Habits that can cause dental fractures including cracking nuts or retouching stone tools with one's teeth are evidenced in coprolites in the form of nutshells and tiny chips of flint or obsidian. Abrasive plant foods full of tough fibers, such as yucca, agave, and prickly pear cactus pads, leave behind traces of fiber and phytoliths in coprolites. Finally, grit from grinding stones is often included in the resulting flour. When chewed, the grit tends to wear down the cusps on molar teeth. Grit has been found in coprolites.

From previous studies (Hartnady 1986; Hartnady and Rose 1991; Turpin et al. 1986) we know a lot about dental disease in the Lower Pecos region of Texas. Analysis of teeth from skeletal assemblages reveals that dental caries and extreme dental attrition led to abscesses and antemortem tooth loss (Turpin et al. 1986; Marks et al. 1985). The molars of these people tended to have smooth, polished occlusal surfaces and rounded occlusal margins from chewing tough fibers and grit in their foods. Some people had little or no enamel left on their front teeth. SEM analyses of the dentition of Lower Pecos peoples reveals microwear in the form of gouges, striations, and compression fractures in the polished enamel surfaces.

Hartnady (1986) and Turpin et al. (1986) completed separate studies of large samples from ancient teeth recovered from the Lower Pecos region spanning the full temporal range of the Archaic period (8,000 B.C. to A.D. 1000). They found that for many of those early inhabitants, by age 25 essentially all molars were lost, and by age 40 adults were virtually toothless.

Review of published dental pathology data indicates that dental caries, dental wear, abscesses, and tooth loss were much more significant problems for Archaic peoples in the Lower Pecos region than for contemporaneous groups living along the Texas coast, on the coastal plains, or on the Edwards Plateau (Reinhard et al. 1989). Several dietary explanations for the excessive dental problems in the Lower Pecos region have been proposed. Hartnady and Rose (1991) suggest that grinding stone grit was the main cause, while Turpin et al. (1986) suggest that a diet high in plant fiber or a dietary dependence on hard seeds was the primary cause.

Studies of human coprolites from the Lower Pecos region (Bryant 1969; Danielson 1993; Danielson and Reinhard 1998; Edwards 1990; Reinhard 1988a; Sobolik 1988, 1994; Stock 1983; Williams-Dean 1978) reveal important characteristics of prehistoric diet and shed light on the causes of dental pathology. Macroscopic remains in coprolites include fragments of shells from hard seeds and nuts including pecans, walnuts, mesquite and yucca seeds, and hackberries. Although some of those were probably broken open initially with stones, chewing on the hard fragments could have caused microfractures in teeth. Danielson and Reinhard (1998) explored one of the other potential causes, the high fiber hypothesis. They discovered high amounts of phytoliths in all of the Lower Pecos coprolites they examined; as much as 20 percent of the total volume of some Lower Pecos coprolites was composed of agave and prickly pear phytoliths. SEM studies revealed that the distance between the sharp chisel-shaped phytoliths embedded in agave fibers was the same as the distance between the parallel micro-striations observed on teeth of Lower Pecos region people (Danielson and Reinhard 1998). Those observations support the hypothesis that a high fiber diet including agave probably caused much of the Lower Pecos dental pathology. Although we cannot

be certain, it appears that grinding stone grit was not one of the major factors causing the high incidence of dental disease in these Archaic cultures of the region.

In a more recent study the same researchers (Reinhard and Danielson 2005) expanded the study of phytoliths to include coprolites from other parts of the Southwest including some hunter-gatherer sites in the northern Sonoran Desert, the Colorado Plateau of Utah, and three Ancestral Puebloan sites in Arizona, New Mexico, and Utah. Phytoliths from genera and species in the cactus and agave plant groups were as abundant in the Arizona and Utah hunter-gatherer coprolites as in the coprolites form Lower Pecos region sites. Although no human skeletal remains from these hunter-gatherer sites have been recovered, we suspect that if found the teeth of those people would show severe dental microwear and related dental disease, similar to the Archaic peoples of the Lower Pecos.

Cactus and agave phytoliths were also present in the coprolites from Ancestral Pueblo sites. Coprolites from Antelope House, northeastern Arizona, had the highest phytolith frequency followed by remains from Bighorn Sheep Ruin from Grand Gulch of Utah. Coprolites from Salmon Ruin in New Mexico had the lowest frequency of cactus and agave phytoliths of the Puebloan samples. In their earlier paper Reinhard and Danielson (1998) noted these phytolith data correlated with similar variations in dental wear reported from Ancestral Pueblo human remains. In summary, it appears that increased use of cactus and agave as foods is reflected in increased dental pathology and in dental wear patterns.

During the 1970s, when one of us (Reinhard) worked at Salmon Ruin, the abundance of worn out manos and metates led the archaeologists to speculate that the average Salmon villager probably "ate the grit from seven manos and three metates during his/her lifespan." In the analysis of coprolites from Salmon Ruin it is very difficult to determine whether or not the recovered grit came from grinding stones, from eating wind-blown sand, or from the exterior of the feces what were often deposited on sand and then sometimes covered with sandy soil. This problem can only be resolved through a careful study of the morphological similarity between the recovered coprolite grit and the composition of various grinding stones.

Coprolites and the Cannibalism Controversy

Any discussion of Southwest coprolite studies must address the world's most notorious coprolite which was deposited in a hearth at a small residential site in Cowboy Wash, Colorado by, some say, a cannibal (Billman et al. 2000; Diamond 2000; Dongoske et al. 2000; Lambert et al. 2000; Marlar et al. 2000a, 2000b). These publications focus on the discovery of disarticulated skeletons with butchery marks, human myoglobin residue in cooking pots, human bone fragments polished by boiling, and the occurrence of human myoglobin in one human coprolite. The coprolite was determined to be human based on the presence of human-linked digestive enzymes (Marlar et al. 2000a, 2000b). This human coprolite containing the remains of human muscle protein is considered the most convincing evidence of cannibal behavior in the Southwest.

None of the major protagonists in the debates about Anasazi cannibalism compared the results of the dietary analysis of the Cowboy Wash coprolite with any of the extensive published records of other Southwestern coprolites. The problem, as I (Reinhard) noted when the coprolite was first discovered and examined, is that the Cowboy Wash coprolite is absolutely abnormal in terms of its content. A recent essay (Reinhard 2006) addresses the central issue of what some have suggested was a case of droughtinduced cannibalism. This summary of the coprolite evidence for 10,000 years of subsistence in the American Southwest indicates that neither environmental collapse nor agricultural failure were ever associated with cannibalism or increased reliance on meat. Instead, the coprolite record documents that in times of stress the Ancestral Puebloans increased their reliance on the wild plants which had at one time been the primary diet of their hunter gatherer ancestors. Based on the coprolite evidence, there is no reason to assume that any of the Ancestral Puebloans would have altered their diet patterns at any time, even during periods of extreme stress, to systematically rely on eating the flesh of other humans.

It seems to us that the methods and conclusions presented by Marlar et al. (2000a, 2000b) were accepted as fact and reified before the method was tested or proven. For such a controversial discovery, an independent, blind study of the Cowboy Wash coprolites should have been performed. One problem with the original study is that a positive ELISA test will confirm the presence of a target protein even if it is present in very tiny amounts. It is a qualitative test without any type of quantitative measure. Thus, even very small amounts of a protein will result in positive outcomes. Previous studies using the ELISA test demonstrate this aspect. For example, Gonçalves et al. (2002, 2004) successfully used the ELISA method to identify the presence of parasitic protozoa proteins in coprolites, which would occur in very tiny amounts when a human was infected. Therefore, the most pressing question that should be asked is "how much

human muscle must be consumed before the ELISA test will confirm a positive result?" Would someone need to eat one milligram, or one gram, or as much as a kilogram of human muscle before the test would return positive results? We believe that this is the most important issue in this discussion. Consumption of one milligram does not imply the type of rampant cannibalism that has been suggested by some, such as Christy and Jacqueline Turner (1999) in their book Man Corn: Cannibalism and Violence in the Prehistoric American Southwest.

We believe that the issue of cannibalism must be addressed with cautious, hypothesis-driven research that takes into account many possibilities. For example, one possibility comes from ethnographic accounts that note the widespread use of ritualistic cannibalism. Records suggest that ritual cannibalism occurred among Native American groups where warriors either ate a small portion of a killed enemy, or a small portion of some departed relative. In both of these ritualistic cases the intent was to gain some type of magical benefit from eating a small portion of flesh; neither was an attempt to replace animal protein with human flesh!

Pathoecology and the Future of Southwestern Bioarchaeology

As demonstrated by our discussion of past studies, the combined theoretical approach to pathoecology combined with the data and methodologies derived from coprolite research are essential elements for Southwestern bioarchaeology. Currently, the greatest need is to refine certain areas of this research.

One area of research that needs strengthening is the study of paleonutrition. The forte of coprolite analysis is the potential to identify chemical, microscopic, and macroscopic remains of past human diets. The weakness of this approach at present is our inability to determine exactly how much of a potential food product was actually eaten! What does one seed, one piece of plant fiber, one leaf, or one fragment of a nut shell reflect? Does it mean a person ate only one tiny portion of each of these items, or do these data mean that these meager fragments are only slight traces of meals composed almost entirely of those items? Because we cannot determine the "quantity of food eaten," we can only interpret the nutritional value of a diet qualitatively. For example, the range of 40 foods discovered in a coprolite may include all the elements of a nutritionally sound diet. However, because we do not know the exact amounts that were actually eaten, we cannot verify that the represented diet was really nutritionally adequate. This is a problem that should be addressed in future research by experimental consumption of known amounts of traditional foods by volunteers and the controlled recovery and analysis of the volunteers' feces. The method for conducting this type of research, as it applies only to the flow of pollen that is eaten, was first developed by Kelso (1977; Kelso and Solomon 2006) and later by Williams-Dean (1978; 2006). Both used modern volunteers who ate specific diets and were able to record times and amounts of each component that was eaten.

If the quantification of paleodiets can be achieved, then the pathoecology approach can have important applications to ancient and modern Native American health. The combination paleonutritional and archaeoparasitological data will enable a more nearly precise estimation of the nutritional and physiological stresses experienced by the ancient populations we study. For modern populations, this approach could be very useful in addressing the origins of Type II diabetes in modern Southwestern Native Americans and whether it is more closely related to the influence of environmental (Bennett 1999) or diet (Neel 1999) change.

Archaeoparasitology is well developed, but its study needs to be applied broadly over wider regions of the American Southwest. The newest methods of using data from ELISA assay for protozoa parasites and broader searches for cryptic evidence of hookworm and wire worm infection in ancient groups could provide useful clues for interpreting the etiologies of osteological and dental indicators of stress including porotic hyperostosis, enamel hypoplasias, growth arrest lines, and periosteal reactions. These types of stress, which are recorded in skeletal remains, could be from physiological stresses caused by forms of parasitism or bacterial transmitted infections from the same types of entry routes.

We can make the link between dental caries, abscesses, and tooth loss and the types of foods that were eaten. What we need now is new research to explore the relationship between plant dietary abrasives (phytoliths and fibers), and processing dietary abrasives (grit from manos and metates) and the causation of microwear and dental pathology. This type of study is perhaps the most direct way where coprolite data and pathoecology are linked to bioarchaeology. It is potentially the most fruitful area of research because of the wide variation of diets at different times and in different environments throughout the American Southwest.

There are other potential bioarchaeological applications that can be gained from studies of coprolite analyses. Nevertheless, before bioarchaeologists can discover and apply these applications to answer questions, they will need to become familiar with the pathoecological approach to coprolite analysis. Once this "marriage" has been achieved, questions can be asked and testable hypotheses developed for coprolite studies.

In summary, we firmly believe that the field of bioarchaeology must broaden its scope to include coprology as one of its central tools. In essence, it must become the "host" for the further development of coprolite research.

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