Coprolite Analysis: A Biological Perspective on Archaeology

Karl J. Reinhard
University of Nebraska at Lincoln, kreinhard1@mac.com

Vaughn M. Bryant Jr.
Texas A&M University

Follow this and additional works at: http://digitalcommons.unl.edu/natrespapers

Part of the Natural Resources and Conservation Commons

http://digitalcommons.unl.edu/natrespapers/46

This Article is brought to you for free and open access by the Natural Resources, School of at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Papers in Natural Resources by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.
The most remarkable dietary remains recoverable from archaeological contexts are coprolites. Coprolites are desiccated or mineralized feces that are preserved in sheltered and open sites in arid regions, primarily in the New World. These dietary remains are remarkable from several perspectives. They typically contain a variety of macroscopic and microscopic remains that form interrelated data sets for the reconstruction of diets. Because contexts containing coprolites are typified by excellent preservation, the remains coprolites contain tend to be in better states of preservation than dietary remains recovered from nonfecal deposits. Coprolites also contain the well-preserved remains of intestinal parasites and pathogens which affected prehistoric health. Thus, coprolites provide excellent evidence of diet and disease for arid regions.

Today, coprolites are recovered from caves, open sites, mummies, and occasionally from burials. Latrine deposits and trash middens are another source of coprolite data, even when individual coprolites are not identifiable in the soil matrix. Our paper offers a history of coprolite research, critically examines the types of data which can be recovered from human coprolites, evaluates interpretive value of coprolite data, and summarizes current directions in coprolite studies.

History of Coprolite Analysis

The term *coprolite*, first coined by Buckland (1829), comes originally from the paleontological literature and was initially applied to mineralized dinosaur feces. Currently, the term refers to
feces and mummy intestinal contents preserved by desiccation (Callen and Cameron 1960; Callen 1965; Heizer and Napton 1969; Bryant 1974a; Fry 1977, 1980, 1985; Turpin et al. 1986). Thus, the term coprolite encompasses fecal material preserved either by mineralization or desiccation, from both paleontological and archaeological contexts.

Coprolite studies have gone through three historical phases. The first began in 1829 when the term was coined, and ended in 1960 when Callen began intensive coprolite analysis and standardization of analytical techniques. This early phase is characterized by diverse pioneering efforts by a number of individuals. The second phase began in 1960 with Callen's early analyses and ended with his death in 1970. It was during this period, largely due to Callen's efforts, that techniques were developed, specialized studies of pollen, parasites, and macrofossils were initiated, and wide interest in coprolite analysis was first sparked. This period laid the foundations for current coprolite research. The last phase began in 1970 and extends to the present. It is characterized by refinement in techniques and broader applications of coprolite analysis to archaeological questions.

Harshberger (1896) was the first to realize the potential value of human coprolite analysis. He suggested that seeds and bones found in prehistoric feces offer clues to ancient diet. Later, Young (1910) examined macroscopic plant remains in human coprolites from Salts and Mammoth caves in Kentucky. A variety of macroscopic plant remains were also recovered from intestinal contents of mummies in Nubia (Jones 1910). Netolitsky (1911, 1912) identified a number of dietary components in coprolites from Egyptian mummies including macroscopic plant remains and animal bone. Although not from coprolites per se, Warren (1911) examined the visceral area of an English, Bronze Age skeleton and found a variety of edible seeds. Loud and Harrington (1929) were the next to report on the analysis of human coprolites. From their study of fecal remains found in Lovelock Cave, Nevada, they suggested that prehistoric diet patterns included a variety of wild seed types and plant fibers. Macroscopic plant food remains were found in coprolite material from the Newt Kash Hollow Shelter in Kentucky (Jones 1936) and in dried fecal remains found in a mummy recovered from a rock shelter site in Arkansas (Wakefield and Dellinger 1936). Wakefield and Dellinger's study was a landmark in coprolite research in that chemical and microscopic analyses of fecal remains were undertaken and the data were related to prehistoric health.
By the late 1950s there was a growing interest in coprolite research. Sperry and Fonner completed a study of macroscopic plant and animal constituents of human coprolites from Danger Cave (Jennings, 1957). This was the first study to include hair and feather analysis. Webb and Baby (1957) looked at a few human coprolites from caves in eastern Kentucky and found evidence of sunflower and goosefoot seeds as well as insects. MacNeish (1958) noted that human coprolites recovered from sites in Tamaulipas, Mexico, contained maguey fibers, squash seeds, insect fragments, and pieces of snail shells.

It was during this initial period that the search for parasites in the archaeological record began. The first evidence of prehistoric parasitism was derived from the study of the colon contents of mummies. In the New World, an Inca mummy provided the first evidence of ancient parasitism (Pizzi and Shenone 1954) in the form of *Trichuris trichiura* (whipworm) eggs.

During the 1960s there were a number of new studies conducted on human fecal materials. Coprolite analysis during this period was dominated by Callen, who emerged as the first coprolite specialist. Callen and Cameron (1960) reported their analysis of human coprolites recovered from Huaca Prieta, an open midden on the coast of Peru. Callen then published the account of his analysis of human coprolites from the Ocampa caves of Tamaulipas, Mexico (Callen 1963). Later, he reported on the completed analysis of additional human fecal materials recovered from several Peruvian archaeological sites (Callen 1965). Callen completed three other studies and had begun a fourth before his untimely death in 1970.

The analysis of over 100 human coprolites from Tehuacán, Mexico, was of critical importance to archaeology because it dealt with diet changes before, during, and after the period of early plant domestication in Mesoamerica (Callen 1967a, 1968). Callen (1969) also became the first person to examine the contents of human feces from Middle Paleolithic (ca. 75,000 B.P.) age deposits. The last report published before his death (Callen and Martin 1969) reported the diet patterns of the prehistoric peoples who lived in Glen Canyon, Utah. In 1970, he began the analysis of human feces recovered from rock shelter and cave deposits near Ayacucho, Peru, but, unfortunately, died of a heart attack in the field before that study could be completed (Bryant 1974c).

Concurrent with Callen, other researchers began to recognize the importance of human coprolite analysis. A series of reports resulted

In the mid-1960s Martin and Sharrock (1964) introduced a new concept to the study of human feces; pollen analysis. In their initial study of 54 human coprolites from the Glen Canyon area they found that the pollen contents of coprolites could provide information relative to the understanding of prehistoric diet, seasonal camp site occupation, and insights into the use of specific plants (such as juniper) which are not otherwise represented in coprolite samples. Soon, other pollen analyses of human coprolites followed. These included the studies in southwest Texas (Bryant 1969; Bryant and Larson 1968; Riskind 1970), the Great Basin (Napton and Kelso 1969; Hall 1972); and from Kentucky (Bryant 1974b; Schoenwetter 1974).

In Europe, the study of ancient latrine deposits was providing clues on the extent and spread of Medieval parasitism (Gooch 1983; Jones 1985; Pike 1975; Taylor 1955). Latrine studies demonstrated that fecal remains could be recovered from archaeological sites, even though no distinct coprolites remained. Although occasional studies of latrine soils were attempted in the Americas (Hevly et al. 1979; Reinhard et al. 1986), coprolite analyses have remained a primary source of New World parasite evidence.

The years since 1970 have seen a refinement in coprolite analysis and interpretive techniques. New macrofossil quantification techniques were developed by researchers such as Yarnell (Watson and Yarnell 1966), Bryant (1974a, b, c), Fry (1977, 1985), and Minnis (1989). In addition, macrofossil analysis expanded to include the identification of mollusk remains (Jones 1988a) and detailed descriptions of faunal remains (Czaplewski 1985; Reinhard 1985a, 1988b; Sobolik 1988a; Williams-Dean 1978). Comparative analysis of coprolites from different sites and regions was also developed (Fry 1977, 1980; Gasser 1982; Minnis 1989; Reinhard 1988a, 1990; Reinhard and Jones n.d.; Sobolik 1988a; Stiger 1977) as well as studies of dietary
change through time at one site [Minnis 1989; Hall 1977; Stock 1983; Reinhard, Jones, and Barros n.d.].

Pollen analyses of coprolites have also undergone pronounced refinement. Methods for interpreting dietary versus environmental pollen taxa were developed [Bryant 1974a, 1974b, 1986; Clary 1984; Scott 1979; Williams-Dean 1978]. Experimental studies of pollen movement through the human digestive tract were examined by Kelso [1976] and later by Williams-Dean [1978]. Kelso [1976] and Aasen [1984] worked with pollen concentration techniques in feces and coprolites, but it has been the recent studies by Reinhard et al. [1991] and Sobolik [1988b] that have given us a better understanding of how to use concentration values to document the prodigious amount of pollen present in coprolites.

Coprolite research has expanded to include study of phytoliths [Bryant 1974a; Bryant and Williams-Dean 1975; Reinhard 1985a], mycology [Reinhard 1985b; Reinhard et al. 1989], acarology [Kliks 1988], microbiology [Stiger 1977; Williams-Dean 1978], nutrition [Reinhard 1988b; Reinhard, Jones, and Barros n.d.; Sobolik 1988a], and chemistry [Fry 1977; Moore et al. 1984; Bercovitz and Degraff 1989].

In the 1970s and 1980s, archaeoparasitology laboratories were established in Brazil, Chile, Peru, the United States, Canada, England, and Germany. This resulted in a proliferation of work as reviewed by Ferreira et al. [1988], Horne [1985], and Reinhard [1990, 1992]. Parasitological extraction and quantification techniques were evaluated [Reinhard et al. 1988] and theoretical frameworks were forged [Ferreira et al. 1988; Herrmann and Schultz 1986; Reinhard 1990]. Regional overviews have been published for the Great Basin [Fry 1977, 1980], the Colorado Plateau [Reinhard 1988a; Reinhard et al. 1987], northern Europe [Herrmann 1986], Peru [Patrucco et al. 1983], Brazil [Ferreira et al. 1988] and North America [Reinhard 1990].

Coprolite Components

Several types of dietary remains can be recovered from coprolites and form discrete data sets. Once analyzed, these can be integrated in a holistic reconstruction of diet and disease. For archaeologists to employ coprolite data effectively, they must be familiar with the types of information that can be recovered, how that infor-
Biological Components

Bacteria and Virus. Bacteria in coprolites can be identified through examination of dead bacteria and through culturing live bacteria. A search for nonactive bacterial remains in prehistoric coprolites from Utah was conducted by John Moore (Fry 1977:24). Through gram staining, he was able to identify cocci bacteria, but not the rod type.

Culturing live bacteria from coprolites has been difficult. Wakefield and Dellinger (1936) were the first to attempt to culture microorganisms from coprolites; they were followed by Tubbs and Berger (1967). These early attempts at agar culturing were unsuccessful. Colvin, working in conjunction with Stiger (1977:45), used a different culturing technique which resulted in the growth of viable bacteria isolated from Anasazi coprolites (ca. A.D. 1240) excavated from Hoy House in Mesa Verde, Colorado. The bacteria they cultured were cyst-forming anaerobic types in the genus Clostridium. Colvin's success in culturing bacteria from coprolites is attributed to his technique of heat shocking the culture media. This process kills the vegetative bodies of modern bacterial contaminants and stimulates the growth of encysted, ancient spores (Stiger 1977).

The preservation of bacteria differs between cyst-forming, anaerobic gut bacteria and noncyst-forming species. Cyst-forming bacteria such as Clostridium can be recovered and identified from coprolites. However, noncyst-forming, pathogenic bacteria such as Salmonella and Shigella are susceptible to decay in the postdepositional environment and cannot be identified.

Viral study of coprolites has been attempted only once. Williams-Dean (1978) submitted several Hinds Cave coprolites (ca. 7,000 B.P.), for analysis. One specimen contained biologically active viral organisms of an unknown strain which was never identified. Not enough information is available to assess the ease in recovery of virus remains from coprolites or to assess their interpretive value.

Fungus. Fungal hyphae and spores are well preserved in coprolites. They provide insights into the preservation conditions of coprolites. Occasionally they also provide dietary data. Interpreting these remains is hampered by the lack of taxonomic keys for fungal spores.
Mycological studies have proven useful in evaluating the desiccating conditions leading to coprolite preservation (Reinhard 1985a, b, c). Sometimes the presence of fungal spores provides dietary information. Spores from the hypogeous mucoralean fungus *Endogone* in coprolites from Dust Devil Cave, Utah, suggested prehistoric consumption of rabbits and other small rodents (Reinhard 1985b). *Endogone* grows on the roots of grasses where it produces packets of spores that are eaten by rabbits and rodents that disseminate the spores in their feces. Apparently, the consumption of rabbit/rodent viscera by humans resulted in the release of the spores in human feces.

In other studies, the distinctive spores of rust fungus have been found in horticulturalist coprolites (Reinhard and Jones n.d.; Reinhard et al. 1989), indicating that maize was parasitized by this fungus. An attempt to culture fungal spores from 20 coprolites from the Salmon Ruin, New Mexico, for evidence of the fungus *Coccidioides immitis* was made (Reinhard 1985a). None of the 20 samples tested positive for the fungus.

**Pollen.** Pollen is excellently preserved in coprolites and provides evidence of dietary components that are not evident in macroscopic analysis. For example, pollen analysis of coprolites from southwest Texas reveals that for over 6,000 years the prehistoric peoples living in that region ate a diet containing a considerable proportion of flowers and/or flower buds from plants such as *Yucca*, sotol (*Dasylirion*), *Agave*, cactus (*Cactaceae*), and mesquite (*Prosopis*) (Bryant 1969; Riskind 1970; Stock 1983; Williams-Dean 1978; Reinhard 1988b; Sobolik 1988b; Reinhard et al. 1991). Analysis of Anasazi coprolites indicates consumption of flowers from a variety of plants including beeweed (*Cleome*), prickly pear (*Opuntia*), horsetail (*Equisetum*), cottonwood (*Populus*), squash (*Cucurbita*), and cattail (*Typha*) (Aasen 1984; Clary 1984; Williams-Dean 1978).

Background and economic pollen in human coprolites can be used to infer seasonality. If a coprolite contains high percentages of economic pollen from plants which bloom only during the spring and/or summer, then that season of the year can be inferred as being the time of year when the coprolite was deposited. This information can then be used to suggest seasonal use of archaeological sites. Background pollen also can be used to infer season of deposition. When background pollen is abundant, one can infer that the coprolites were deposited during the pollination period of spring, summer, or early...
fall. When background pollen is absent, a cold season deposition can be inferred.

In rare cases, pollen in human coprolites may be used to make limited generalizations about the paleoenvironment. Local vegetation composition will change when, and if, the climate changes or is altered by human activity. If background pollen from key indicator plant types, such as pine or spruce, are present in the coprolites from one time period but absent in the coprolites from an earlier or later time period, then the absence may reflect local or regional ecological changes. However, a great deal of caution should be used not to over-interpret climatic changes based solely upon pollen spectra in human coprolites. Humans are highly mobile and selective. As such, human coprolites represent the ingestion of food and water that may, or may not, reflect only the key pollen types in the immediate area of their camp site.

**Phytoliths.** Phytoliths occur in many kinds of plants and are especially frequent in regions where available water sources are rich in dissolved silicates and calcium (Esau 1965). Silica and calcium are deposited in plant tissues in the form of calcium salts and anhydrides of silica in crystalline form. When deposited, they occur in a variety of basic crystalline shapes. They can be concentrated in special idioblast cells or be dispersed throughout the plant tissue (Piperno 1988). When plant tissues are eaten, many of the phytoliths are liberated during chewing and digestion. Phytoliths then pass through the human body, essentially unchanged, and can be isolated and described from coprolites. Interestingly, the acidic environment of the upper alimentary tract does not drastically alter calcium oxalate phytoliths, but acidic extraction techniques destroy them [Dennis Danielson, University of Nebraska, current research].

Bryant (1969) was the first to separate and analyze the phytolith component from coprolite samples, followed much later by Reinhard (1985a). When examining coprolites collected at Conejo Shelter in southwest Texas, Bryant noticed a large number of whitish crystals mixed with the macrofossil component. After some experimentation, he found that these plant crystals could be separated using heavy density separation techniques. In that initial study he was unable to identify many of the phytoliths as coming from specific plants. However, druse-shaped phytoliths from cacti species were
noted as well as one type of rhombohedral crystal which came from *Agave lechuguilla*.

Reinhard (1985a) noted that the most abundant microscopic component in hunter-gatherer coprolites from Dust Devil Cave, Utah, was phytoliths. After comparing the phytoliths from coprolites with phytoliths from modern plants in the area, he was able to tentatively identify prickly pear (*Opuntia*) and *Yucca* phytoliths in the coprolites.

Recent studies of phytoliths from southwest Texas near Conejo Shelter (Jones and Bryant, in press) reveal that four species (*Opuntia lindheimeri*, *O. phaeacantha*, *O. leptocaulis* and *Echinocactus texensis*) contain uniquely shaped druse phytoliths. We predict that future coprolite analysis will determine which cacti groups were being collected and eaten by specific prehistoric peoples.

Phytoliths preserve well in coprolites and will be an important source of dietary information in the future when phytolith analyses are routinely performed on coprolites. Phytoliths provide evidence of dietary components that are not evident in pollen or macroscopic study.

**Parasites.** Parasite remains, most commonly eggs and larvae of helminths, provide important diet and disease information. Helminths include nematodes (roundworms), trematodes (flukes), cestodes (tapeworms), and acanthocephalans (thorny-headed worms). Protozoa cysts are also recoverable from coprolites (Faulkner et al. 1989). Parasite eggs preserve well through the alimentary tract and do not decay in the postdepositional environment.

Eggs of parasites possessing intermediate host life cycles can be used to identify dietary habits (Reinhard 1992). Human coprolites recovered from sites along the Pacific coast of Chile (Ferreira et al. 1988) and Peru (Callen and Cameron 1960; Patrucco et al. 1983) contained the eggs of the fish tapeworm, *Diphyllobothrium pacificum*. Marine fish are intermediate hosts for this parasite and humans are infected by eating uncooked fish. The consistent find of *D. pacificum* eggs indicates that fish were commonly consumed along the western coast of Peru and Chile. Additional dietary inferences can be derived from finds of taeniid eggs in ancient Egyptian mummies and acanthocephalan eggs in Great Basin coprolites. Taeniid infection was derived from the consumption of beef and pork. Acanthocephalan infection indicates consumption of insects and/or rodents.
Some parasites are health threats and others proliferate in unsanitary conditions. Hookworms (Ancylostomidae) are dangerous to humans. To find hookworms in coprolites indicates a health menace to prehistoric peoples (Ferreira et al. 1988; Faulkner et al. 1989). Pinworms proliferate in conditions of poor sanitation. The numerous finds of pinworm eggs in Southwest horticulturalist coprolites compared to hunter-gatherer coprolites indicates that living conditions became pronouncedly less hygienic in horticultural villages (Reinhard 1988a, 1990).

Ectoparasites (ticks, mites, lice, and fleas) are occasionally found in human coprolites (Fry 1977). Callen (1967a) found ticks in 6,000 year old coprolites from Mexico, and Fry (1977) found lice and lice eggs (Pediculus humanus) in 3,000 year old human feces from Danger Cave, Utah. The records of ectoparasites provide useful clues about the types of parasites that infected prehistoric people and also tell us how far back in time human-parasite associations existed and the geographical range of specific parasites.

Seeds, Leaves, and Other Plant Remains. Seeds are indicators of diet and, sometimes, of food preparation techniques. Seeds have a hard outer coat called the testa that is resistant to human digestive processes and is defecated almost unchanged. The shape and surface morphology of most testa are diagnostic and are used to identify the species of the plant eaten. Even after grinding and mastication, many types of testa are identifiable.

Some seeds are used as dietary staples, for example maize (Zea mays), amaranth (Amaranthus), goosefoot (Chenopodium), or wheat (Hordeum). Other seeds are swallowed with their fruit; examples include the seeds of melons, squash (Cucurbitaceae), chili peppers, tomatoes (Solanum), grapes (Vitis), cactus fruits (Cactaceae), or blackberries (Rubus). The seeds of fruits containing large pits, such as peaches, plums, and dates, are not usually swallowed with the fruit. Thus, flotation study of middens is a better source of data for fruit pits than coprolite analysis. Legume seeds present special problems of interpretation. Usually, the seeds are completely or near completely digested. Sometimes, if the seeds were not prepared in a way that tears the seeds, the empty seed coats are recovered from coprolites. However, in cases where the seed coats are ground or heavily masticated, evidence of seed consumption (i.e., beans) is lost in coprolites and must depend on flotation data from nonfecal depos-
its. There are exceptions to the legume problem. In Peru, where peanuts were consumed, although the seeds are completely digested, pod fragments are recovered from coprolites.

Plant leaves are not commonly found in human coprolites, and when present they generally are masticated into small fragments. Ethnographic reports suggest that certain types of leaves were either chewed or mixed with other foods and then eaten. Small, chewed leaf fragments are generally so altered in shape and structure that there is little left to identify. Often, the only statement that can be made about leaves from coprolites is that they were from a monocot or dicot plant, as determined by the leaf venation pattern. The analysis of leaves from coprolites is an area that requires continued refinement. Currently, leaves of dietary value are better studied through flotation of nonfecal midden deposits.

Roots, tubers, and bark are not commonly found in human coprolites. Bryant (1974a) noted that out of a total of 43 Late Archaic human coprolites in southwest Texas only 4 contained any traces of chewed bark and that in 1 of those 4 the major food had consisted of bark. Fry (1977) found dogwood (*Cornus*) bark in several prehistoric coprolites from Hogup Cave, Utah. Neuman and Holloway (1989) identified fern rhizomes in a Great Basin coprolite. Roots and bark are difficult components to identify in human coprolites, largely because of the lack of taxonomic keys for such remains. The problem of identification becomes even more complicated if bark or root fragments were pounded or masticated. Again, flotation data can provide important corroborative data regarding consumption of bark or roots.

*Vertebrate Remains.* Quill bases, down feathers, and other types of feather fragments sometimes appear in coprolites. Small feathers and feather fragments are easy to identify based on barbs and barbules on the edges of feathers. Based upon barbule patterns, Napton and Brunetti (1969) identified feather fragments of water fowl such as grebes, herons, geese, and mudhens from Lovelock Cave coprolites. The bones of these same waterfowl species were found in nonfecal deposits of Lovelock Cave (Napton 1969). Other coprolite studies noting the occurrence of feathers include Callen (1967a), Callen and Martin (1969), Fry (1977), Yarnell (1969), and Sobolik (1988a).

Numerous coprolite studies show that when small animals are eaten, such as snakes, lizards, rodents, birds, and fish, the bones are
eaten with the meat. This occurs because the bones of these animals are too small to be separated from the meat before eating; as a result many identifiable bone and bone fragments are defecated. Bryant (1974a) found that 21 of 43 coprolites from southwest Texas contained the bones of small reptiles, birds, mammals, or fish. Earlier studies by Callen (1967a), Douglas (1969), Yarnell (1969), Fry (1977), and later studies by Williams-Dean (1978), Stock (1983), Sobolik (1988a) and Reinhard (1988a) have noted small animal bone in coprolites of prehistoric cultures.

Some small animal bones are completely digested in the intestine (Jones 1986a). Those bones that remain in coprolites can be easily sorted into categories such as fish, reptile, bird, or mammal based upon density and morphological features. If diagnostic bones are present, precise taxonomic identification is possible (Reinhard, Ambl er, and Szuter n.d.). The bones of larger animals such as deer, antelope, and elk are rarely eaten. Meat protein from large animals is digested rapidly and little evidence of its presence is ever found in coprolites. Thus, zooarchaeological study of nonfecal deposits is the best source of information concerning consumption of large animals.

During the butchering of large animals a few hairs will loosen and adhere to the meat. Unlike meat, hairs are very resistant to digestion and remain unaltered when defecated in feces. Hairs are often diagnostic and many can be identified to precise species. Today, the precision of the scanning electron microscope facilitates taxonomic identifications of animal hairs. In sites from Tehuacán, Mexico, Callen (1967a) was able to identify a large number of animals that were eaten based upon the hairs he found in coprolites. Williams-Dean (1978) and Sobolik (1988a) provided similar data from southwest Texas coprolites.

Small shell fragments sometimes appear in human coprolites. While opening shellfish, small chips of shell are often broken off and are later eaten along with the meat. Shell fragments are not significantly altered by the human digestive system and are expelled in feces (Jones 1988a). When analyzed, these shell fragments can sometimes be identified to genus or species. Coprolites from Chile contain gastropod shells and opercula and indicate that small snails were consumed whole (Reinhard and Barnum 1991). Eggshell fragments are also found in human coprolites (Stiger 1977). Eggshell fragments can be segregated from other types of shell, but precise identification to species is often difficult or impossible.
Animal scales fall into two broad groups: fish and reptile. Fish scales are generally fairly round and have patterns of small concentric growth rings. Reptile scales are pointed at one end and lack growth rings. As evidenced by analyses of prehistoric human coprolites (Bryant 1969; Yarnell 1969; Jones 1988a; Sobolik 1988a; Reinhard n.d.), both types of scales pass freely through the human digestive system and at times are an abundant component of coprolite specimens. Identification of fish or reptile scales depends on an adequate comparative reference collection. For example, in Sobolik's (1988a) study from Baker Cave, Texas, and Heizer and Napton's (1969) analysis from Lovelock Cave, Nevada, fish that were eaten as food were identified to the family, genus, and in some cases even to the species level by their scales in coprolites.

**Insects.** Coprolite evidence demonstrates that insect consumption has great antiquity. Remains of insects in prehistoric human coprolites come from Mexico (Callen 1967a), Utah (Fry 1977; Hall 1972), Arizona (Reinhard 1988a), Colorado (Stiger 1977), Texas (Bryant 1969; Williams-Dean 1978; Stock 1983; Sobolik 1988a; Reinhard, Jones, and Barros n.d.), Kentucky (Yarnell 1969), Nevada (Heizer and Napton 1969), and Peru (Weir and Bonavia 1985).

Insects have hard, chitinous exoskeletons that are undigestible. Some exoskeletons, such as those of grasshoppers and beetles, are easy to recognize, but other remains, especially larval stages of insects, are difficult to identify.

Insects found in human feces can come from two sources: (1) insects eaten as part of the diet, and (2) coprophagous insects. The types of insects that are generally eaten will vary depending on local availability and the preferences of different ethnic groups. Other groups of insects feed on feces or lay eggs in feces. Some of these coprophagous insects and their empty egg and pupae cases are recovered during coprolite analyses but should not be viewed as dietary components.

**Mineral and Chemical Components**

**Sand, Grit, and Flakes.** Sand and grit can become attached to feces when they fall at the time they are excreted or can come from eating soil or foods containing soil. Callen and Martin (1969) reported that coprolites from Utah contained considerable amounts of grit. Weir
et al. (1988) noted the same thing in Peruvian coprolites. Earlier, Callen and Cameron (1960) suggested that high levels of sand and grit in coprolites might come from the eating of soil as seasoning, or from the eating of soil for its suspected curative powers. Grit in coprolites could be introduced through the eating of stone-ground seeds, from meat or plant foods roasted on hot coals, or from the drinking of silt-laden water.

Occasionally, small flakes of stone occur in prehistoric human coprolites. Ethnographic studies of Australian aborigines (Gould 1968) and of certain American Indian groups (Hester 1973) suggest that such stone chips may result from the practice of using one's teeth to retouch the cutting edges of stone tools. Fry (1977) found tiny chips of obsidian and chalcedony in several prehistoric human coprolites from Hogup Cave, Utah. Nissen (1973) found a similar occurrence of small obsidian chips in a prehistoric human coprolite from Bamet Cave, California.

**Charcot-Leyden Crystals.** Rarely, coprolites contain masses of Charcot-Leyden crystals. These small crystals form in the human intestinal tract as a result of severe diarrhea. Heizer and Napton (1969) reported that one of the Lovelock Cave, Nevada, coprolites contained these types of crystals. This led them to suggest that some early inhabitants might have suffered from intestinal amebiasis resulting from infection by the parasite *Entamoeba histolytica*. To date, this is the only known record of Charcot-Leyden crystals being found in prehistoric coprolites.

**Chemical Components.** Chemical analyses of coprolites have been conducted beginning with Wakefield and Dellinger's (1936) element analysis of cave coprolites found with burials in the Ozark Mountains. Their analysis noted that the specimens were low in nitrogen and surprisingly high in calcium. Fry's (1977) analysis of coprolites from Danger and Hogup Caves is the most extensive yet conducted. His analysis of basic chemical components (nitrogen, potassium, calcium, and sodium) showed that prehistoric levels were within the extreme ranges of normal, modern feces. The only exception was sodium, which was very high in the prehistoric samples. Fry (1977) believed the high sodium values resulted from consumption of sodium-rich plants and drinking water.
Fry (1977) also reported on a series of other chemical tests which John Moore conducted on a group of Utah coprolites. These included: bilirubin and blood testing, which were attempted but produced negative results; and tests for hydrolyzed fat, which were negative in all but two of the Glen Canyon coprolites recovered from mummies and one of the coprolites from Danger Cave. Other related chemical analyses include amino acid analysis of coprolites from Lovelock Cave by Lin et al. (1978).

Biochemical analysis of coprolites has become more common in recent years. Moore et al. (1984) has continued to search for new ways to use gas chromatography in coprolite studies and now believes he can identify certain coprolite plant components by modifications of his gas chromatography method. Bercovitz and Degraff (1989) have successfully extracted steroids (testosterone and estrogen) from sloth coprolites to determine the sex of the animals that produced them. Lin et al. (1978) extracted steroids from Lovelock Cave coprolites.

We have completed preliminary gas chromatographic studies of coprolites. The data derived from these show that many break-down products are formed by the alteration of molecules in the postdepositional environment. Thus, molecular "noise" is introduced into the coprolite chemical record. The interpretive impact of this noise must be evaluated by further study.

**Identifying Coprolites**

Coprolite analysts will admit that human fecal material is often difficult to identify with assurance. In certain cases, it is difficult to distinguish human from nonhuman coprolites, especially with crushed or fragmented samples. Another complicating factor is the great variety of shapes and sizes of human feces. Depending upon the diet and the interval between bowel movements, human feces can appear as large segmented pellets, cylindrical masses, or as amorphous pads resembling the dung of some large herbivores such as cow and bison. In general, the only coprolites that are certainly of human origin are those extracted from human mummies or burials.

In general, coprolite identification must take place on four distinct levels: (1) during excavation, (2) during the initial examination,
(3) during the chemical reconstitution phase, and (4) during the analysis of coprolite contents. Initial recognition of coprolites occurs during excavation, and observations made by the archaeologist at this time are essential to meaningful analysis. For example, coprolite associations with latrine deposits indicate probable human origin. Also at this stage, preliminary sorting of human versus nonhuman coprolites can be made based on morphology and size.

After excavation but prior to chemical reconstitution, major determinations as to human versus nonhuman coprolites can be made. As in the field, size and shape of the coprolites are useful in separating human from nonhuman coprolites. In addition, examination of visible inclusions also allows for identification of human coprolites. Carnivore coprolites can be identified by their hard outer coating of dried intestinal lubricant secreted as protection for the intestinal wall.

The rehydration process can provide hints as to human origin of coprolites. The color of the rehydration fluid and the degree of translucency are used by some coprolite analysts as an indicator of coprolite origin (Fry 1977). It is generally thought that coprolites from nonhumans turn the trisodium phosphate solution pale white, light brown, or yellow-brown, while the solution remains translucent. Human specimens will often turn a trisodium phosphate solution dark brown or black and opaque. Experimentation by Fry (1977) indicated that only feces of humans and the coati (Nasua nasua), turn a trisodium phosphate solution black and make it opaque. However, recent reevaluations of rehydration color have challenged Fry's original work (Chame et al. 1989; Holden 1990). Studies of South American mammalian feces (Chame et al. 1989) indicate that the black color is not associated strictly with human coprolites. Four nonhuman taxa in the orders Edentata, Artiodactyla, and Carnivora were found to turn rehydration solution black and opaque. However, in general, most of the other 18 species tested produced light brown or brown coloration. Holden (1990) reports that black, opaque rehydration color can result from rehydration of ancient plant tissue as well as coprolites and concludes that the color of the rehydration solution is determined by age and amount of organic material in the samples.

Some of our recent studies indicate that although most human feces darken a trisodium phosphate solution, they do not always do so. The occurrence of parasite eggs from Enterobius vermicularis (pinworm) in coprolites was used as a guide to compare rehydration colors in coprolites from the Antelope House (Reinhard 1988a). Since
this is an exclusive parasite of humans, we knew feces containing the eggs should be of human origin. Using the presence of eggs as a guide, we found that coprolites with eggs turned the rehydration solution a variety of colors from translucent yellow through shades of translucent brown to opaque black. In another analysis of 100 coprolites from Dust Devil Cave, Utah, Reinhard (1985a) found that rehydration color correlated to dietary components, especially the presence of bone and seeds. Therefore, although a black and opaque rehydration color is a useful tool for identifying human coprolites, it cannot be considered a definitive test for human origin.

Odor is another clue sometimes used at this level of identification. Human coprolites sometimes produce an intense odor when reconstituted. However, this cannot be considered a fail-safe test. We have also discovered that the odor produced by coprolites seems to be partly determined by environmental factors. For example, some coprolites, such as many of those from the Colorado Plateau, produce little or no odor. By contrast, coprolites recovered from caves in the Great Gypsum Plain of west and southwest Texas are some of the most odoriferous we have ever encountered. The difference may be linked to the high magnesium and sulfide content of the drinking water in areas of west Texas (Holloway 1985) and its absence in the waters of the Colorado Plateau.

At the final level, during the actual analysis of a coprolite's contents, human coprolites can often be separated from nonhuman coprolites. Humans tend to favor an omnivorous diet and often eat prepared foods. As such, human coprolites tend to include a wide range of diverse components such as charcoal, cracked and ground seeds, snail and clam shell fragments, bird eggshells and feathers, insect chitin, bone fragments, mammal hair, and plant fibers. Sometimes a few of these items might appear in nonhuman coprolites, yet very rarely will such a variety be found in a specific nonhuman coprolite.

**Problems with Early Hominid Coprolites**

Recognition of human coprolites from ancient hominids, such as those from Australopithecus, Homo erectus, and Homo sapiens neanderthalensis, presents unusual problems. Although rare, coprolites of great antiquity have been recovered and analyzed from archaeological sites in the Olduvai Gorge, caves in South Africa, Terra Amata and Lazaret, France.
Coprolites of suspected hominid origin were recovered from sites in the Olduvai Gorge of Kenya and date in excess of 1 million B.C. (Leakey 1971). Lewis Napton examined those coprolites and reported that when placed in 0.5% trisodium phosphate the specimens did not emit an odor, did not dissolve, and did not color the solution. However, based on the coprolite contents, Napton concluded they might be of hominid origin (Leakey 1971).

In the late 1970s Bryant was asked by Philip Tobias to examine a small fossilized coprolite recovered from one of the fossil hominid sites in South Africa. He encountered the same problems which plagued Napton’s study of the Olduvai Gorge material. The South African coprolite was fossilized with calcium and did not react with the usual reagents we use to process coprolites. After all the standard laboratory attempts failed, the coprolite was gently broken open and examined. Bryant did not find any seeds or other plant material, although there were tiny fragments of broken bone. No other types of remains could be identified and no attempt to dissolve the coprolite and search for fossil pollen or phytoliths was made. Although positive identification as to the source of that coprolite was impossible, the shape and size were within the size range of coprolites produced by small hominids (i.e., South American Indians ca. 4–5 feet tall).

Callen (1969) received and examined four coprolites from Lazaret, France, archaeological deposits associated with the cultural remains of Homo sapiens neanderthalensis. During his analysis Callen encountered many problems. The Lazaret coprolites did not darken the reconstitution solution or produce any type of fecal odor. On the other hand, based on their contents of charcoal, bone fragments, hair, and other debris, Callen reported that at least two of them were of probable human origin.

Bryant conducted a pollen analysis of the two Lazaret coprolites Callen believed to be of human origin (Callen 1969). The pollen contents of these two Neanderthal-age coprolites were meager and consisted of only a few pollen grains (less than 10 per sample) of common plants which are so ubiquitous in geographical distribution that no definitive statement could be made about possible seasonality, environmental setting, or diet. The fossil pollen found in those two specimens included Chenopodium types, grass, composites, oak, and elm. Although care was taken not to contaminate these samples, it is possible such few pollen grains could have been modern in origin.
During the 1970s, Trevor-Deutsch and Bryant (1978) conducted an examination of suspected fecal samples 400,000 years old found in association with Homo erectus remains at the site of Terra Amata in southern France (de Lumley 1966). The analysis of those samples revealed the presence of small fragments of marine shells, sand grains, flecks of charcoal, and a few animal hairs. However, no seeds, bones, fibers, or other organic residues were found. When placed in a trisodium phosphate solution the samples produced a weak, musty smell, and only a few specimens produced even the faintest tint of color. We finally concluded the samples probably were not fossilized coprolites but instead were worm casts formed in the beach sand at Terra Amata shortly before the site was occupied by Homo erectus. Other suspected coprolites from this same site (de Lumley 1969) were analyzed in France. That study mentions the presence of fossil Genista pollen which the analyst suggests indicates a spring or summer occupation of the site (de Lumley 1969).

In each study where the coprolites of ancient hominids have been examined, the resulting analyses have raised a number of important questions: (1) What should a human coprolite contain after tens of thousands of years of weathering? (2) How does time alter the color and odor-forming substances in human coprolites? And (3), do the apparent differences in data reflect different digestive patterns between earlier and later species or subspecies of humans?

Sampling Coprolites

The main goal in sampling a coprolite collection is to select a diverse sample with as many defecations by as many different individuals as possible. In sites that have a broad time chronology and/or several identified latrine areas, achieving sample diversification is done by sampling many separate proveniences. In sites where the span of occupation is short, or where only one latrine area is discovered, achieving sample diversification is more difficult.

The first type of site includes Hinds Cave, southwest Texas, Turkey Pen Cave, Utah, and Huaca Prieta, Peru. These sites were excavated in thin, artificial, or natural levels. Fortunately, at least one coprolite was recovered from each level or distinct stratum. The coprolites from these sites were later examined and sample diversification was achieved on a vertical scale.
Obtaining a diversified set of specimens on a horizontal scale is easiest when many separate latrines are excavated from the same site. The Anasazi village site of Antelope House (A.D. 600 to 1270) is one such example. At that site, hundreds of different areas contained fecal deposits. Diversification was achieved by sampling separate fecal deposits of different spacial and temporal affinities (Reinhard 1985a, 1988a; Williams-Dean 1986; Fry and Hall 1986).

Salmon Ruin, located in northwestern New Mexico, is an example of the second type of site. It was occupied during a fairly brief period (A.D. 1088 to ca. 1250) and contained only one latrine area suitable for study. In order to optimize sample diversity, coprolites were selected from alternate levels in alternate grid squares within the one latrine. Thus, from a latrine area containing an estimated 4,000 coprolites, diversity was achieved by horizontal/vertical sampling over a large area (Reinhard et al. 1987; Reinhard 1988b).

Sample Size

There are generally two questions usually asked about the size of coprolite samples: (1) How many coprolites should be examined from a site to obtain a reliable dietary reconstruction? And (2), how much of each coprolite should be processed and analyzed to obtain an accurate record of that specimen’s contents?

Studies have revealed that diet components are often fairly uniform within a coprolite series (Bryant 1974a; Williams-Dean 1978; Stock 1983; Fry 1985; Reinhard 1988a; Sobolik 1988a). This knowledge is being used to reduce the number of coprolites that researchers believe must be examined in order to identify the primary food components. However, we acknowledge that larger numbers of specimens must be examined to understand the full dietary diversity.

To answer the first question of how many coprolites must be examined, we recommend considering two limiting factors: the total number of specimens available for analysis, and the amount of time/money required to complete the study. In studies which are limited by a time/money factor, a useful approach is to concentrate the analysis on determining only the major food items. Studies of large series of coprolites indicate that usually 80–90 percent of the most common food components are found after 15–20 coprolites in a series have been examined (Reinhard 1988b). Thus, a minimum sample
size of 20 coprolites appears to be sufficient to identify the major dietary items. However, parasite analysis requires more extensive sampling simply because only 1–30 percent of coprolites in a series contain parasite eggs. A minimum sample size of 50 coprolites for horticultural sites and 100 for hunter-gatherer sites is recommended for parasite study.

The second question pertains to the amount of each coprolite that must be processed to obtain an accurate characterization of that specimen. For most studies it is important to examine a fairly large fragment (>5 gr) of each coprolite in order to obtain a representative number of dietary components. Usually, it is sufficient to cut a coprolite in half along its longest axis and analyze one of the halves. In studies of coprolites from Conejo Shelter, Bryant (1974a) found that the halves processed from each specimen ranged in weight from 10 to 72 grams. When coprolite samples are fragmented or when one-half of a coprolite is smaller than 5 gr, one must adopt a different strategy. Perhaps a number of fragments from the same specimen should be combined and in some cases perhaps the whole specimen will need to be processed if the total size is quite small.

Sampling Privies and Mummies

The sampling of soils from latrines, living surfaces, and trash middens provides a new avenue to the exploration of parasitism and diet at historic sites and promises to be an important area of research in the future (Deagan 1989). Sampling of latrine areas, living surfaces, and trash middens already is widespread in Europe (Jones 1985; Herrmann 1986, 1987; Herrmann and Schultz 1986; Pike 1975). Sampling and analysis techniques were largely developed by the Environmental Archaeology Unit at the University of York in England. Meanwhile, in the New World, latrine analyses have been attempted in the past but have only recently gained increased interest. Soils have been analyzed successfully from both prehistoric latrine deposits (Hevly et al. 1979) and historic latrine deposits (Bryant 1982; Fries et al. 1990; Reinhard 1990; Reinhard et al. 1986). Pollen, parasite eggs, and seeds are well preserved in latrines.

The study of latrine soils expands the application of coprolite methodological techniques. Examination of soils from latrines, trash middens, and other locations where feces are likely to have been
deposited can provide similar data to that provided by actual coprolite specimens. Importantly, Jones (1985) has developed techniques that allow a researcher to recognize a fecal-contaminated soil by calculating the concentration of parasite eggs in soil samples.

The analysis of colon contents from mummies also provides valuable data. However, sampling problems are lessened when working with mummified colon contents. For example, in mummy analyses one can be certain that organic materials in the colon region are of human origin. In addition, by sampling different areas of the digestive tract, different meals can be identified in a single mummy (Reinhard and Hevly 1991). Finally, studies of mummies are useful because it is possible to examine differential disease and dietary patterns between sexes and ages of individuals because mummies can usually be identified to sex and age.

Mummy intestinal contents have provided important dietary, parasitological, and pharmaceutical data. Analyses of mummies in Chile, Peru, and Brazil have revealed the earliest South American evidence of prehistoric parasite infection (Horne 1985). Similarly, mummies from Europe and North America reveal infection with a variety of parasites (Jones 1986b; Reinhard 1990). Palynological and macrobotanical analysis of colon contents found in a Mimbres-age burial in New Mexico revealed evidence that the individual consumed a tea made from willow (Salix) for its medicinal properties (Shafer et al. 1989). Additional dietary studies have been derived from the analyses of mummies recovered from Arizona (Fry 1977), the Lower Pecos region of west Texas (Turpin et al. 1986), the Ozarks of Arkansas (Wakefield and Dellinger 1936), Ventana Cave in Arizona (Reinhard and Hevly 1991), and coastal regions of Peru (Callen and Cameron 1960).

Interpretive Value of Coprolites

The dietary representation of any given coprolite series is affected by cultural, depositional, and analytical factors. These factors affect the interpretive value of coprolites in reconstructing prehistoric behavior.

Seasonality is a major bias in coprolite analysis. Many coprolite series, especially hunter-gatherer coprolites, represent seasonal or short period occupations. Consequently, dietary data represent re-
The size of 20 coprolites appears to be sufficient to identify the major dietary items. However, parasite analysis requires more extensive sampling simply because only 1–30 percent of coprolites in a series contain parasite eggs. A minimum sample size of 50 coprolites for horticultural sites and 100 for hunter-gatherer sites is recommended for parasite study.

The second question pertains to the amount of each coprolite that must be processed to obtain an accurate characterization of that specimen. For most studies it is important to examine a fairly large fragment (>5 gr) of each coprolite in order to obtain a representative number of dietary components. Usually, it is sufficient to cut a coprolite in half along its longest axis and analyze one of the halves. In studies of coprolites from Conejo Shelter, Bryant (1974a) found that the halves processed from each specimen ranged in weight from 10 to 72 grams. When coprolite samples are fragmented or when one-half of a coprolite is smaller than 5 gr, one must adopt a different strategy. Perhaps a number of fragments from the same specimen should be combined and in some cases perhaps the whole specimen will need to be processed if the total size is quite small.

**Sampling Privies and Mummies**

The sampling of soils from latrines, living surfaces, and trash middens provides a new avenue to the exploration of parasitism and diet at historic sites and promises to be an important area of research in the future (Deagan 1989). Sampling of latrine areas, living surfaces, and trash middens already is widespread in Europe (Jones 1985; Herrmann 1986, 1987; Herrmann and Schultz 1986; Pike 1975). Sampling and analysis techniques were largely developed by the Environmental Archaeology Unit at the University of York in England. Meanwhile, in the New World, latrine analyses have been attempted in the past but have only recently gained increased interest. Soils have been analyzed successfully from both prehistoric latrine deposits (Hevly et al. 1979) and historic latrine deposits (Bryant 1982; Fries et al. 1990; Reinhard 1990; Reinhard et al. 1986). Pollen, parasite eggs, and seeds are well preserved in latrines.

The study of latrine soils expands the application of coprolite methodological techniques. Examination of soils from latrines, trash middens, and other locations where feces are likely to have been
deposited can provide similar data to that provided by actual coprolite specimens. Importantly, Jones (1985) has developed techniques that allow a researcher to recognize a fecal-contaminated soil by calculating the concentration of parasite eggs in soil samples.

The analysis of colon contents from mummies also provides valuable data. However, sampling problems are lessened when working with mummified colon contents. For example, in mummy analyses one can be certain that organic materials in the colon region are of human origin. In addition, by sampling different areas of the digestive tract, different meals can be identified in a single mummy (Reinhard and Hevly 1991). Finally, studies of mummies are useful because it is possible to examine differential disease and dietary patterns between sexes and ages of individuals because mummies can usually be identified to sex and age.

Mummy intestinal contents have provided important dietary, parasitological, and pharmaceutical data. Analyses of mummies in Chile, Peru, and Brazil have revealed the earliest South American evidence of prehistoric parasite infection (Horne 1985). Similarly, mummies from Europe and North America reveal infection with a variety of parasites (Jones 1986b; Reinhard 1990). Palynological and macrobotanical analysis of colon contents found in a Mimbres-age burial in New Mexico revealed evidence that the individual consumed a tea made from willow (Salix) for its medicinal properties (Shafer et al. 1989). Additional dietary studies have been derived from the analyses of mummies recovered from Arizona (Fry 1977), the Lower Pecos region of west Texas (Turpin et al. 1986), the Ozarks of Arkansas (Wakefield and Dellinger 1936), Ventana Cave in Arizona (Reinhard and Hevly 1991), and coastal regions of Peru (Callen and Cameron 1960).

Interpretive Value of Coprolites

The dietary representation of any given coprolite series is affected by cultural, depositional, and analytical factors. These factors affect the interpretive value of coprolites in reconstructing prehistoric behavior.

Seasonality is a major bias in coprolite analysis. Many coprolite series, especially hunter-gatherer coprolites, represent seasonal or short period occupations. Consequently, dietary data represent re-
source exploitation for a specific time of year. Therefore, although coprolites provide exceptionally detailed dietary data, these data usually represent only seasonal exploitation, and one must resist generalizing year-round dietary patterns from coprolites alone.

The demographic sample represented by a coprolite series is unknown. Thus, one cannot assume that the dietary data revealed in a coprolite series are representative of all ages and sexes of the population. It is conceivable, for example, that coprolites from any given hunter-gatherer cave site over-represent one sex or another, or even one age grade over other age grades. Thus, the dietary patterns represented by coprolites may be skewed.

After deposition, the coprolites may begin to decompose. When decomposition reaches an advanced state, all that remains for the archaeologist are compact layers of organically rich soil. Even coprolites that retain identifiable shapes in archaeological matrices can be decomposed to the point that only animal bone and shell remain.

It is almost certainly the case that coprolite sampling error over-represents older individuals and those that enjoyed healthy intestines (Reinhard 1988a). This is due to two sources of sample error: in the field, and in the laboratory. Diarrheal stools are very common in coprolite collections, but rarely studied. With extreme cases of watery diarrhea, the feces desiccate to form very thin crusts in archaeological deposits that are very difficult or impossible to recover from the field. Once in the laboratory, coprolite analysts tend to select formed, cylindrical coprolites for study. This helps to insure that human coprolites are studied, but diarrheal stools, as well as those defecated by infants and children, are not included in the sample. This neglect of diarrheal and subadult coprolites has an especially strong impact on parasitological data since the young and sick are more likely to be parasitized. We suggest that the sampling process should include all coprolite morphological forms and not be biased by the perception of healthy, human stools. After all, cylindrical stools are the norm for modern North Americans, but this morphological type was not the norm for many prehistoric cultures.

In the final analysis, the value of coprolite analysis depends on how many types of analysis are carried out on a coprolite series. Certainly, analysis of all types of remains listed above is costly. However, to optimize data recovery from coprolites, we suggest that macrofloral, macrofaunal, pollen, phytolith, and parasite analyses be
completed. These data sets can then be integrated into a comprehensive reconstruction of the diet.

Coprolites in Dietary Reconstruction

Paleoethnobotanical studies of nonfecal archaeological deposits through flotation and palynology provide important information regarding detailed use of plant and animal species. For dietary studies, flotation and pollen studies of nonfecal remains tend to be more ambiguous than coprolite remains because of contaminant seeds and pollen in the soil matrix. Often, only items that show evidence of human activity, such as parched seeds, are counted by flotation researchers. Coprolite researchers face reduced problems of contamination. The items recovered from the fecal matrix can be safely assumed to be of dietary origin. Because coprolites contain remains that were actually consumed and defecated, they provide a stronger data base than nonfecal flotation and palynology.

Gasser's (1982) comparative study of flotation and coprolite data highlighted another difference between macroscopic coprolite and flotation data. Many fragile items that are susceptible to decomposition in an open site are better preserved in coprolites. This is because coprolites generally come from contexts ideal for preservation. Consequently, in general coprolites provide evidence of a greater range and better representation of fragile dietary items. Miksecek (1987) noted discontinuity between coprolite data and bulk sample data from the Tehuacan Valley. He attributes the differences to the increased difficulty in identification of items in coprolites. This is probably partially correct, but in general differences in representation are due to the fact that flotation and bulk samples contain many items that are discarded in the process of food preparation. Thus, one is more likely to find chewed leaf bases, nut shells, and other processing debris in bulk samples that are absent in coprolites. Flotation data can be used in conjunction with coprolites to reconstruct year-round diet. For example, flotation data from Dust Devil Cave represented warm season plant use, while the coprolites were apparently defecated in the winter (Reinhard 1988b). The midden provided information regarding the spectrum of plants harvested and processed at the cave year round, while the coprolites provided insight into which of these were stored for winter consumption.
The interpretive power of any line of evidence is increased when augmented with other lines of evidence; this is certainly the case with coprolite analysis. In our opinion, the combination of coprolite data with trace element, carbon isotope, and nitrogen data derived from bone analysis holds the greatest potential of revealing general and specific dietary patterns.

Stable carbon isotope and trace mineral analysis data, derived from bone and mummified tissue, provide important information regarding general lifetime dietary patterns. These techniques provide data regarding the consumption of different classes of food (i.e., C-3 plants, C-4 plants, legumes, marine animals, terrestrial animals, etc.), but coprolites provide evidence of specific plants and animals eaten. Together, chemical study of bone and biological study of coprolites present a complete picture of prehistoric diet. Although in its pioneering stages (Farnsworth et al. 1985), we feel that this combined approach will be particularly effective in the future, especially in mummy studies where coprolites and bone samples can be recovered from the same individual. This integrative approach to coprolite and bone studies from mummies is currently being investigated by Aufderheide, Buikstra, and Reinhard in the analysis of Peruvian remains.

With trace mineral analysis, diagenesis strongly affects the elemental composition of bone and can often diminish the accuracy of such study (Aufderheide 1989). There are also preliminary indications that microbial activity can alter isotopic signals and thereby confuse archaeological interpretation. These are not problems with the biological study of fecal residues, so coprolite analysis is of particular importance in substantiating trace element work. The incorporation of coprolite and trace element data was pioneered by Weir et al. (1988), and current research by Reinhard and Aufderheide with Chilean mummies indicates that with remains that do not undergo significant diagenetic change, trace element and coprolite data can be effectively used to reconstruct general and specific dietary patterns.

Coprolite data are of greater interpretive value when incorporated with flotation and faunal data. This provides a clearer idea of how well diet is represented in coprolites. The incorporation of coprolite data with bone chemical data is especially important. A long-term dietary picture is revealed by the chemical analysis, the specifics of which are filled in by coprolite analysis. Continued mummy studies will undoubtedly benefit from this approach.
Behavioral Inferences from Coprolite Data

Jerome et al. (1980) described the relationships between diet and technology, social organization, physical environment, and social environment. Because coprolites directly reflect subsistence, coprolite analysis has a critical role in the reconstruction of prehistoric lifestyles. Although not all aspects of culture discussed by Jerome et al. (1980) can be determined from coprolite data alone, some can. It is possible to use coprolite data to examine prehistoric food technology, physical environment, and nutrition.

Food Technology

Food technology involves the recognition of plant and animal food resources, developing harvesting techniques, and developing food preparation techniques. For example, a common dietary plant food utilized by hunter-gatherers in Mexico, the American Southwest, and southwest Texas was Agave. Some parts of the plant could be eaten without specialized preparation. Other parts, however, are inedible without intense preparation. The recovery of great quantities of Agave pollen in coprolites from as far south as Frightful Cave in northern Mexico (Bryant 1974a) and from sites in southwest Texas (Bryant 1969; Riskind 1970; Williams-Dean 1978; Sobolik 1988a; Reinhard et al. 1991) demonstrates the consumption of flowers or a tea derived from Agave flowers. The eating of Agave flowers requires no special harvesting or preparation techniques since flower eating requires only a memory of where flowering stands are likely to occur.

However, other evidence indicates harvesting and preparation of vegetative portions of the plant. The recovery of Agave fibers, plant leaf epidermis, and phytoliths in coprolites demonstrates that the thick basal bulbs of the Agave plant and the bases of individual leaves were eaten (Bryant 1974a; Bryant and Williams-Dean 1975; Reinhard 1988b; Sobolik 1988a). Agave bulb bases and leaf bases are not edible when raw because they contain many alkaloids that taste bad. Ethnographic records (Castetter et al. 1938) and our own experiments show that an effective way to prepare these plant parts for eating is roasting the bulbs and leaf bases in earthen ovens or steam- ing pits for various periods of time ranging from two to four days.

The collection, preparation, and cooking of Agave in earthen ovens
are not simple tasks. One must possess a technical knowledge that includes: (1) how and when to harvest *Agave* to obtain the maximum amount of nutrition, (2) how to prepare an effective roasting pit, and (3) when it is best to uncover the fully cooked *Agave*. Thus, when we recover evidence of *Agave*, other than pollen, complex harvesting and preparing procedures are implicated.

Other plant species found in coprolites also implicate approximate techniques of harvesting and preparation. Cactus and sotol plants were other staples utilized in most of the same regions where *Agave* was being used. The picking and eating of cactus and sotol flowers, or the picking and eating of cactus fruits, require no specialized technology. Collecting and cooking cactus pads and sotol leaf bases require more complex techniques much like the techniques associated with *Agave* because cactus pads and sotol leaf bases also contain alkaloids and tough fibers. They need to be roasted or steamed like *Agave* bulbs and leaf bases to soften the fibers and neutralize many of the alkaloids.

Coprolites recovered from the colons of mummies found in caves in the Ozark Mountains of Arkansas (Wakefield and Dellinger 1936) contain fragments of acorn shells. This finding indicates that the early people of that region had developed techniques for leaching tannin from acorns and thus turning inedible acorns into rich sources of edible carbohydrates. In other parts of North America, such as the Lower Pecos region in Texas, the same level of acorn preparation technology cannot be inferred since many of the oak species that are present produce "sweet" acorns that lack the bitter tannin and can be eaten raw or roasted.

Food preparation techniques can sometimes be inferred from seed remains in human coprolites. Callen (1967b) found that some of the millet seeds in coprolites from Mexico had been prepared by pounding while others had been split open by rolling them back and forth on a grinding stone. In prehistoric coprolites from southwest Texas, Bryant (1969) noted that some of the eaten cactus seeds had been broken open by pounding or grinding. Some of the broken cactus seeds in those coprolites were also charred, suggesting they were ground, roasted, and then eaten. The presence of *Chenopodium* seeds in coprolites deposited in winter at Dust Devil Cave suggests a knowledge of seed gathering, grinding, drying, and storage techniques (Reinhard et al. 1985). The finding of maize pollen grains that
have been cracked and broken in a tearing manner tells us that maize kernels, with pollen attached, were ground with a mano and metate before being eaten (Bryant and Morris 1986).

Macroscopic remains of maize also indicate various maize preparation techniques. Aasen (1984) was able to identify several techniques of maize preparation including roasting and grinding. Exceptionally fine grinding typified prehistoric maize preparation in Durango, Mexico (Reinhard et al. 1989).

Animal exploitation also requires specialized harvesting techniques. In the Lower Pecos region of southwest Texas, prehistoric coprolites contain the remains of small fish, many of which are too small to have been caught in a net or on a hook and line (Bryant 1969; Williams-Dean 1978; Sobolik 1988a). Cultural deposits, in the same archaeological sites containing the coprolites, are often full of Mexican buckeye (*Ungnadia speciosa*) seeds. Mexican buckeye seeds are poisonous and do not occur in human coprolites. Experiments show that these seeds, when ground and placed on the surface of small pools of water, create a potent fish poison (Adovasio and Fry 1972). The combined presence of tiny fish bones and scales in coprolites (Reinhard, Jones, and Barros n.d.; Sobolik 1988a; Williams-Dean 1978) and the occurrence of Mexican buckeye seeds in the deposits of the same sites suggest that the technological knowledge of how to use these seeds as fish poisons was known and utilized.

**Physical Environment**

Coprolite studies can offer clues about the physical environment through the types of microfossils and macrofossils they contain. The abundance and percentages of microfossils such as the background pollen of spruce, pine, juniper, and oak suggest certain types of broad environmental settings. Likewise, economic pollen types such as cactus, agave, mesquite, and sotol can indicate that the people who produced the coprolites were living in a semi-arid or arid environment. Phytoliths are yet another type of microfossil that can be used to infer the presence of certain plants as well as certain types of environmental settings.

Plant macrofossils such as maize kernels, pinyon or cactus seeds, the bones of ecologically specific mammals and fish, the feathers of birds that occupy certain types of habitats, and the remains of regionally important insects often appear in human coprolites. Once iden-
tified, these remains serve as clues to the habitats occupied by those who produced the coprolites. For example, Fry (1985) found that coprolite remains reflected adaptations to different ecological areas in the Great Basin region including the lacustrine environment of Lovelock Cave and the desert environment of Danger and Hogup caves. He used the presence of waterfowl and fish bones and an abundance of water plants in Lovelock Cave coprolites to infer that those people utilized a lake shore environment. At Danger and Hogup caves, Fry found desert plants and the halophyte *Allenrolfea* (pickle weed), indicating a dry physical environment with soils of high salt content. In similar studies, the physical remains found in coprolites from areas of southwest Texas, such as those examined by Williams-Dean (1978), Stock (1983), and Sobolik (1988a), revealed a stable desert habitat for that region covering a span of 9,000 years.

Current Directions in Coprolite Studies

The role of coprolite analysis in tracing dietary changes concurrent with cultural change has been the main focus of coprolite analysis for much of its history. With the onset of Callen's research in the early 1960s, coprolite studies focused mainly on questions of dietary composition and changes in diet through time with the introduction of cultivated plants (Callen 1967a). This orientation has been adopted and modified by recent researchers. Recent coprolite comparative evaluation of hunter-gatherer and horticultural parasitism (Reinhard 1988a) is an outgrowth of Callen's approach to dietary adaptation (Callen 1967a). Fry (1980) used coprolites to focus on regional variations in desert diet, and to answer broad questions of cultural adaptation as expressed in the similarities and differences between desert and lacustrine habitats in the Great Basin. Minnis (1989) used coprolite data to define regional trends in Anasazi diets. The last two decades of coprolite studies from southwest Texas have focused on a 9,000 year record of dietary and cultural stability exhibited by the hunter-gatherer cultures who occupied sites such as Hinds Cave (Edwards 1990; Reinhard, Jones, and Barros n.d.; Stock 1983; Williams-Dean 1978), Conejo Shelter (Bryant 1974a), and Baker Cave (Sobolik 1988a). Coprolite studies from Peru have also focused on dietary modifications over time. Callen and Cameron (1960) were the first to report on Peruvian diets. Later, Weir et al. (1988) studied
dietary change in the central coast region of Peru from preceramic through early formative times, and Jones's (1988a) most recent work reported on the dietary practices in the coastal region during preceramic times.

Copolites are also becoming an important data base for studies of prehistoric morbidity and mortality. In the past, these topics were explored solely on the basis of skeletal remains. Although some early coprolite studies noted the presence of pathogenic disease organisms, these studies were rarely included in discussions of prehistoric health. Now, coprolite studies are recognized as a new way of assessing the levels of infectious disease in prehistoric populations (Reinhard 1988b; Weir and Bonavia 1985) and are incorporated in skeletal studies (Akins 1986; Kent 1986; Walker 1985).

In general, coprolite analyses can provide data that are relevant to at least three classes of osteological data: (1) dental disease, (2) metabolic/nutritional stress, and (3) infectious disease. As discussed by several researchers, dental disease in prehistoric peoples is mainly a result of food preparation techniques and the types of food eaten (Reinhard, Jones, and Barros n.d.; Turpin et al. 1986). Three aspects of coprolite study are relevant to dental disease. First, the amount and kind of dietary abrasives in the diet can be identified by macrofossil plant analysis, bone analysis, and phytolith analysis. Second, the degree of dental attrition caused by abrasives derived from grinding stones can be evaluated. Third, nutritional evaluation of diets derived from coprolite study can be used to assess the potential of dental decay. Diets rich in carbohydrates and natural sugars can cause dental caries and tooth loss as noted by Turpin et al. (1986), who relate the high frequency of dental caries and tooth loss to the frequent consumption of sugar-rich prickly pear fruits.

Infectious disease is directly mirrored in parasite remains from coprolites, specifically by helminth parasites (Horne 1985; Reinhard 1988a) and protozoan parasites (Faulkner et al. 1989). Coprolite analysis provides quantitative data regarding specific intestinal pathogens of humans. In fecal analysis, identification of a parasitic pathogen is easily accomplished by morphological or immunological examination of the recovered organism. Also, because common parasites are recovered that do not necessarily leave osseous traces, it is possible to carry out more complete comparative paleopatological studies from fecal remains (Herrmann 1986; Jones 1985; Reinhard 1988b, 1990).
Nutritional studies are a fairly new avenue of research in coprolite research (Reinhard 1988b; Reinhard, Hamilton, and Hevly 1991; Sobolik 1988a). Using nutritional values derived for prehistoric food plants, coprolite analysts reconstruct qualitative nutritional profiles for prehistoric peoples. Nutritional analyses from coprolites have also been used to assess the overall diet of prehistoric groups who suffered from anemia (Reinhard 1988b, n.d.).

Coprolite remains can also offer data useful in the study of paleopharmacology. For example, coprolite studies from the Rustler Hills area of west Texas reveal that *Larrea* (creosote bush) was probably being used to treat diarrhea (Holloway 1985), that *Salix* was probably used as an analgesic in the Mimbres area of New Mexico (Shafer et al. 1989), and that *Ephedra* (mormon tea) was probably used as a diuretic at Bighorn Cave in western Arizona and in the Rustler Hills (Reinhard, Hamilton, and Hevly 1991). These examples demonstrate yet another avenue of research derived from coprolite analysis. In addition, plant macrofossils, specially *Chenopodium* seeds, may have had anthelmintic value to peoples of the Southwest and Mexico (Reinhard et al. 1985).

**Summary**

The wealth of information recoverable from the study of human coprolites continues to expand as we learn new applications and new techniques of analysis. Fossil pollen trapped in coprolites is being used to gain clues about diet preferences, possible seasonality of site occupancy, and paleoenvironmental conditions. Phytoliths indicate plant types that were eaten by prehistoric cultures even when no macrofossil remains of those plants are present. Parasites found in human coprolites are now being used to infer the history and spread of parasite infection in the New World, types of animals that were killed and eaten, and prehistoric health status. Coprolite data are now used by bioarchaeologists to evaluate prehistoric morbidity and mortality.

Plant macrofossils are being used to reconstruct dietary histories of prehistoric populations and to provide a basis for nutritional studies of these groups. In addition, information provided by plant remains is also being used to explain high ratios of dental caries and tooth loss in some populations. More recently, the study of paleo-
pharmacology has relied upon the coprolite record for clues about the ancient use of possible medicinal plants and the diseases they may have cured.

Bones, hair, feathers, shell, scales, and other items relate to the animals collected and eaten by prehistoric groups. These data also offer clues about habitat environments in the collection area where coprolites are found, about the potential types and diversity of animals used as food, and about levels of technological development as evidenced by possible harvesting techniques.

The search for and analysis of steroids and occult blood in human coprolites are fairly new, yet offer exciting new potentials for future studies. Eventually we should be able routinely to use steroids from coprolites to derive quantified information broken down by sex. With that degree of data sophistication we will be able to examine possible gender differences in food eating habits, health, and nutrition for specific prehistoric cultural groups.

In spite of the vast amount of knowledge that can be derived from the analysis of human coprolite data, too few researchers recognize or save human coprolites or other evidence of human excrement. Even those coprolites that are saved often sit in storage for years awaiting analysis. Today there are still too few scientists trained in the techniques of coprolite extraction and analysis, but there is hope that this situation will change in the near future.

REFERENCES

Aasen, D. K.

Adovasio, J. M., and G. E. Fry

Akins, N. J.
Ambro, R. D.

Aufderheide, A. C.

Bercovitz, A. B., and S. L. Degraff

Bryant, V. M., Jr.
1969  Late Full-glacial and Post-glacial Pollen Analysis of Texas Sediments. Ph.D. diss., Department of Botany, University of Texas, Austin.

Bryant, V. M., Jr., and D. L. Larson

Bryant, V. M., Jr., and D. Morris
Bryant, V. M., Jr., and G. Williams-Dean

Buckland, W.

Callen, E. O.

Callen, E. O., and T.W.M. Cameron

Callen, E. O., and P. S. Martin

Castetter, E. F., and W. H. Bell
1942 *Pima and Papago Indian Agriculture*. Albuquerque: University of New Mexico Press.

Castetter, E. F., W. H. Bell, and A. R. Grove

Chame, M., L. F. Ferriera, A. Araujo, and U. Confalonieri

Clary, K. H.
1984 Prehistoric Coprolite Remains from Chaco Canyon, New Mexico: Inferences for Anasazi Diet and Subsistence. M.S. thesis, Department of Biology, University of New Mexico, Albuquerque.
Cowan, R. A.
1967  Lake-Margin Ecological Exploitation in the Great Basin as
Demonstrated by an Analysis of Coprolites from Lovelock Cave,
University of California Archeological Survey Reports, no. 70.

Czaplewski, N.
1985  Bone Remains from the Dust Devil Cave Feces. Appendix H in
Recovery of Helminths from Prehistoric Feces: The Cultural
M.S. thesis, Department of Biological Sciences, Northern
Arizona University, Flagstaff.

Deagan, K.
1989  Historical Archaeology: Tracing the Waste Makers. Archaeology
42:56–62.

de Lumley, H.
d'anthropologie prehistorique de Monaco 13:29–51.

Douglas, C. L.
1969  Analysis of Hairs in Lovelock Cave Coprolites. In Archaeological
and Paleobiological Investigations in Lovelock Cave, Nevada:
Further Analysis of Human Coprolites, edited by R. Heizer and
Papers, Special Publication, no. 2.

Edwards, S. K.
1990  Investigations of Late Archaic Coprolites: Pollen and Macrofossil
Remains from Hinds Cave [41 VV 456], Val Verde County, Texas.
M.A. thesis, Department of Anthropology, Texas A&M University.

Esau, Katherine

Farnsworth, P., J. E. Brady, M. J. DeNiro, and R. S. MacNeish
1985  A Re-evaluation of the Isotopic and Archaeological
Reconstructions of Diet in the Tehuacan Valley. American
Antiquity 50:102–16.

Faulkner, C. T., S. Patton, and S. S. Johnson
1989  Prehistoric Parasitism in Tennessee: Evidence from the Analysis
of Desiccated Fecal Material from Big Bone Cave, Van Buren


Fries, C. R., D. K. Beidleman, and J. F. Custer
1990  Analysis of Parasites from 19th-century Privy Contents in
Fry, G. E.


Fry, G. E., and H. J. Hall


Fry, G. E., and J. G. Moore

Gasser, R. E.

Gooch, P. S.

Gould, R. A.

Hall, H. J.
1972 Diet and Disease at Clyde’s Cavern, Utah. M.A. thesis, Department of Anthropology, University of Utah, Salt Lake City.


Harshberger, J. W.

Heizer, R. F.

California Archaeological Survey Report, no. 70.


Jennings, J. D. 1957 *Danger Cave*. Salt Lake City: University of Utah Anthropological Papers, no. 27.
Jerome, N. W., G. H. Pelto, and R. F. Kandel
1980 An Ecological Approach to Nutritional Anthropology. In 
Nutritional Anthropology: Contemporary Approaches to Diet 
and Culture, edited by N. W. Jerome, R. F. Kandel, and G. H. 

Jones, A.K.G.
1985 Trichurid Ova in Archaeological Deposits: Their Value as 
Indicators of Ancient Feces. In Paleobiological Investigations: 
Research Design, Methods, and Data Analysis, edited by N.J.R. 
Symposia of the Association for Environmental Archaeology, no. 
5b. Heslington: British Archaeological Reports International 
Series, vol. 266.

1986a Fish Bone Survival in the Digestive Systems of the Pig, Dog, and 
Man: Some Experiments. In Fish and Archaeology: Studies in 
Osteometry, Taphonomy, Seasonality, and Fishing Methods, pp. 
Series, no. 294.

1986b Parasitological Examination of Lindow Man. In Lindow Man: 
The Body in the Bog, edited by I. Stead, J. Bourke, and D. 

Jones, E. W.
1910 Mode of Burial and Treatment of the Body. In The Archaeological 
Cairo: National Printing Department.

Jones, J. G.
1988a Middle to Late Preceramic (6000–3000 B.P.) Subsistence Patterns 
on the Central Coast of Peru: The Coprolite Evidence. M.A. 
thesis, Department of Anthropology, Texas A&M University.

1988b A Simplified Procedure for the Extraction of Silica and Calcium 

Jones, J. G., and V. M. Bryant, Jr.
n.d. Preliminary Study of the Taxonomy of Some Texas Cacti 
Phytoliths. In Phytoliths and Taxonomy, edited by G. Rapp and 
S. Muhlenhouser. Minneapolis: University of Minnesota Press, 
forthcoming.

Jones, V. H.
1936 The Vegetal Remains of Newt Kash Hollow Shelter. In 
Rockshelters in Menifee County, Kentucky, edited by W. S. Webb 
and W. D. Funkhouser, pp. 147–65. Lexington: University of 
Kentucky Reports in Archaeology and Anthropology, vol. 3.
Kelso, G.  

Kent, S.  

Kliks, M. M.  

Leakey, L.S.B.  


Loud, L. L., and M. R. Harrington  

MacNeish, R. S.  

Martin, P. S., and E. W. Sharrock  

Miksecek, C. H.  

Minnis, P. E  

Moore, J. G., B. K. Krotoszynski, and H. J. O'Neill  

Napton, L. K.  

Napton, L. K., and O. A. Brunetti


Netolitsky, F.


Neumann, A., and R. Holloway


Nissen, K.


Patrucco, R., R. Tello, and D. Bonavia


Pike, A. W.


Piperno, D.


Pizzi, T., and H. Schenone


Reinhard, K. J.


1992 Parasitology as an Interpretive Tool in Archaeology. American Antiquity, in press.


Reinhard, K. J., D. L. Hamilton, and R. H. Hevly

Reinhard, K. J., and R. H. Hevly

Reinhard, K. J., R. H. Hevly, and G. A. Anderson

Reinhard, K. J., and J. G. Jones

Reinhard, K. J., J. G. Jones, and R. P. Barros

Reinhard, K. J., S. A. Mrozowski, and K. A. Orloski

Riskind, D. H.

Roust, N. L.

Schoenwetter, J.

Scott, Linda

Shafer, H. J., M. Marek, and K. J. Reinhard
1989 A Mimbres Burial with Associated Colon Remains from the

Sobolik, K.  
1988a The Prehistoric Diet and Subsistence of the Lower Pecos Region, as Reflected in Coprolites from Baker Cave, Val Verde County, Texas. M.A. thesis, Department of Anthropology, Texas A&M University.  

Stiger, M. A.  

Stock, J. A.  

Taylor, E. L.  

Trevor-Deutsch, B., and V. M. Bryant, Jr.  

Tubbs, D. Y., and R. Berger  

Turpin, S. A., M. Henneberg, and D. H. Riskind  

Wakefield, E. E, and S. C. Dellinger  

Walker, P.  

Warren, S. H.  

Watson, P. J., and R. A. Yarnell  
1966 Archaeological and Paleoethnobotanical Investigations in Salts
Karl J. Reinhard and Vaughn M. Bryant, Jr.


Webb, W. S., and R. S. Baby


Weir, G. W., R. A. Benfer, and J. G. Jones


Weir, G. W., and D. Bonavia


Williams-Dean, G.


Yarnell, R. A.


Young, B. H.