Part II - Parasite Remains Preserved in Various Materials and Techniques in Microscopy and Molecular Diagnosis

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Marcia Chame
Luciana Sianto

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16

Coprolite diagnosis, or who made the coprolite?

Marcia Chame • Luciana Sianto

When we find a lost pen drive, open it, and read some of the files, we can definitely speculate on the owner's personality. The data saved on it often suggest the person's profession, interests, places they have visited, family relations, and even a guess at their sex.

The same is true for biological remains found in nature, which are veritable data storage units. With focus, skill, and adequate techniques, we can learn and reconstruct a great deal from some samples. The object of our research may sound unheard-of or even disgusting. However, following any odd reaction upon initial impact, we find surprising information in the fecal remains left by individuals of any species. Such information extends beyond eating habits and items ingested in the last meals. The data contained in coprolites are like files that we can open and peruse, much like the chapters of this book.

For example, parasite findings reveal a set of adaptations by the coprolites' producers to the ecosystems in which they lived. If we succeed in reassembling the data like pieces in a jigsaw puzzle, they can tell us the evolutionary history, phylogeny, processes and paths in dispersal over time, and intricate food webs in the populations, vectors, and host species (Araújo, Rangel & Ferreira, 1993; Ley et al., 2008).

"Coprolite" (from the Greek *kopros*, feces, and *lithos*, rock) may sound odd. The name dates to the early 19th century, when the British Reverend William Buckland (1829a, 1829b, 1830), a geologist, paleontologist, and "dinosaur hunter" recognized naturally fossilized feces and coined the term. However, interest in the analysis of naturally preserved, fossilized, or simply desiccated feces only developed in the late 19th and early 20th centuries.

In Brazil, the first record of the term "coprolite" and the possibility of coprolites as objects of research dates to 1866, in comments by physician Otto Edward Henry Wucherer on a speech in 1865 by Benjamin E. Cotting, Secretary of Foreign Affairs of the Medical Society of Massachusetts and former member of the Agassiz Expedition to Brazil. Commenting on Cotting's speech at the Society's Annual Meeting, published in *Gazeta Médica da Bahia*, Wucherer (1866: 129) states:

...coprolites, petrified feces found inside and outside fossil animals, often reveal to us not only the nature of the ingestion, displaying parts of other animals that were consumed, but even the nature of the mucosal surface of the gut and prove that the ingestion was done in those times more or less as in our times.

From then on, the growing publication of scientific articles on coprolites (Harshberger, 1896) demonstrated that the understanding (albeit incipient) that the analysis of partially or totally undigested remains in human excreta can reveal habits and ecological data on prehistoric populations.

Finding coprolites during archaeological excavations requires expertise in their identification. Located in sedimentary layers, they must be distinguished from the surrounding soil by their shape and texture. This is not always a simple task, since such layers contain various shapes (not always obvious). Paleoparasitology also involves the finding of coprolites from extinct species such as dinosaurs, for which there are no parameters for comparison with the current fauna. Considering that the presence of phosphate in the feces facilitates their mineralization and preservation, the museum collections tend to contain more carnivore coprolites, naturally rich in phosphate and calcium from the bones and teeth of their prey.

Herbivores feces contain plant lignin and cellulose and require the minerals needed for better preservation from the environment. During mineralization or desiccation, the feces also serve as the habitat for many species. This colonization, typical of the decomposition process, can alter or distort the feces' original shape, drawing in external elements that contaminate the sample, such as insects, fungi, and mites, among others (Guerra et al., 2003; Dormont et al., 2007). The association of coprolites with artifacts, human or animal skeletons, or other remains can aid and facilitate the coprolite's on-site identification. The first difficulty for the study of coprolites results from the dispersal and preservation of the sedimentary layers. Problems arise mainly from geological processes, distinct modes of preservation of the coprolites, and lack of knowledge of the local fauna. Still, the dispersal and preservation of coprolites in the sedimentary layers (resulting from geological processes and distinct modes of preservation) lead to the first difficulty in studying this material. This includes not only the archaeological sites themselves but the usage areas around them, often combined with lack of knowledge on the local fauna. How to identify the coprolite's source? Was it human or animal? In the latter case, which species made it? This is not a recent problem, and many researchers have grappled with it. We are still searching for the best solution when we begin the analysis of a sample from an archaeological site or the soil. For the most precise and easiest identification of the remains, we need a clue to begin searching for our information. What universe of information and forms do we expect to find in the material that will allow us to infer who or what inhabited that place? What did they eat, which parasites did they harbor, which diseases may have existed in that setting, and which habits could be attributed indirectly to those populations?

The first research to identify the source of coprolites used the most obvious parameters, like their appearance and shape, after correlating them to recent fecal samples. Eames (1930) used this methodology to study coprolites from the extinct giant sloth, based on shape and food content. Likewise, based on the appearance and microscopic remains, Grzywinski (1959-1960) analyzed 36 coprolites from the 11th, 12th, and 13th centuries from Opole, Poland, including small ruminants (sheep and goats), dogs, horses, and probably pigs. Heizer & Napton (1969), however, mentioned the particular difficulty in identifying human and bear coprolites, emphasizing the need to systematize parameters for their identification.

During coprolite analyses, Callen & Cameron (1960) noticed that 0.5% trisodium phosphate solution, used to rehydrate samples, turned an opaque dark brown or black and gave off a fetid odor when the feces were from humans. This parameter was used from then on to diagnose human coprolites (Fry & Hall, 1969; Fry, 1970), which no doubt leads to errors of interpretation when applied to fecal samples from any region.

As the range of coprolite findings began to reflect the diversity of animal species (in addition to humans) that inhabited the study areas, other parameters were incorporated into the factors used jointly to elucidate the human origin of coprolites. Thus, Fry & Moore (1969), analyzing 142 coprolites collected at Hogup Cave, Colorado (USA) and dated $7,837 \pm 630$ to 650 ± 100 BP, included the samples' position in the site's archaeological context, findings of remains from plants that might already be undergoing domestication, and bones and charcoal as parameters for identifying the coprolite.

However, the color pattern in the rehydration solution is still an important parameter for identifying the coprolite, since other studies have corroborated the pattern of dark brown or black for humans, translucent yellow for herbivores, and translucent light brown for carnivores (Bryant & Williams-Dean, 1975).

In parallel with these studies, other researchers already identified problems with this standardization. For example, Wilke & Hall (1975) in California studied human material from 1,000 to 1,500 years ago and noted that some samples turned the rehydration solution lighter in color than the standardized solution. At the time, the researchers attributed this reaction to the fact that these samples were the driest among those examined.

As research and rehydration of coprolites and feces from other species proceeded, these patterns began to lose consistency. Tests by Fry (1976) with samples from zoo animals showed that feces of coatis (*Nasua* sp.) displayed the same staining attributed to human samples, associated with an omnivorous diet. Chame (1991), in a study of mammalian feces and coprolites collected from the archaeological region of São Raimundo Nonato in Piauí State, Brazil, identified feces and coprolites of non-omnivorous species that turned the rehydration solution opaque dark brown/black. The species included the collared anteater (*Tamandua tetradactyla*), an insectivorous species, and rock cavy (*Kerodon rupestris*), a rodent that feeds on tree leaves and bark.

Other parameters were incorporated, including the finding of parasites that were easy to identify down to the species level, which alone determined the coprolite's zoological origin, for example, findings of the nematodes *Enterobius vermicularis* and *Trichuris trichiura* published by Fry (1976), Araújo (1980), Ferreira et al. (1980, 1991), Araújo, Ferreira & Confalonieri (1981), and Rey (2008).

However, parasite diagnosis is not always simple or amenable to species identification. Jones (1982) questioned the identification of helminth eggs found in coprolites that were diagnosed by morphometric patterns, since alterations in the eggs' morphometry may have occurred during desiccation. Still, such changes were tested by Confalonieri (1983) in *Trichuris trichiura* and by Araújo (1987) in hookworms and did not occur to a significant extent.

The taxonomic literature still includes little work on egg morphometry and larval forms of helminth species and protozoan morphometry. Such research would allow the identification of coprolites and the parasites found in them. Taxonomic studies have focused basically on adult individuals and often overlook relevant information on the hosts, the number of individuals found during the necropsy, biocenosis, an accurate description of the collection site (both the site where the host was found and the specific place where the individuals were collected inside the host), the male/female ratio in findings, and other biologically and ecologically important information.

DIAGNOSIS OF HELMINTH EGGS

The accumulated parasitological analyses of coprolites have produced a large data set of egg measurements (length and width, with and without the operculum, when applicable). This allows distributional analysis of measurements for each species. This simple statistical treatment, among others, is essential for the identification of helminth eggs

from two similar species that may be present in the same sample (which may be suggested by a bimodal distribution in the sample's set of measurements). It also allows identifying the characteristic range and metric variation of the species or of some populations.

The identification of overlapping helminth egg measurements and morphological characteristics such as the appearance of the embryonic mass and presence of larvae, number of cuticles, type of shell, opercula, and other internal structures builds consistent parameters that can be used to identify helminth families, genera, and species. A clear example is the difficulty in identifying eggs from hookworm species and trematodes of genus *Echinostoma*, the eggs of which display a complex overlapping of sizes (Araújo, 1987; Chame, 1988; Sianto, 2004) (Graphs 1 and 2).

On the other hand, *Trichuris* egg morphometry provides a reliable parameter for approximate species diagnosis in this genus (Confalonieri, 1983; Ferreira et al., 1991). The same is true for some acanthocephalans.

Graph 1 – Variation in the range of length of *Echinostoma* eggs (Trematoda: Echinostomatidae) described in Brazil

* *Echinostoma* sp. found in mummified body in the Lapa do Boquete archaeological site, Peruáçu Valley, Januária, Minas Gerais, Brazil.

Source: Sianto (2004).

Graph 2 – Variation in the range of width of *Echinostoma* eggs (Trematoda: Echinostomatidae) described in Brazil

* *Echinostoma* sp. found in mummified body in the Lapa do Boquete archaeological site, Peruaçu Valley, Januária, Minas Gerais, Brazil.

Source: Sianto (2004).

The identification of a helminth egg often becomes confusing when one observes a range of similar shapes. In such cases, accurate observation of the morphological variations should concentrate on the possibility of a variation resulting from ontogenesis (Plate 1).

Plate 1 – Eggs of *Trichuris* sp. (Nematoda: Trichuridae) in different embryonic stages. Magnification 400x

* *Trichuris* sp (62-70 x 32-37 μ m) in coprolites from *Kerodon rupestris* (rock cavy) (Rodentia: Caviidae). Serra da Capivara National Park, Piauí, Brazil.

** *Trichuris* sp (54 x 27 μ m) in feces of *Cerdocyon thous* (crab-eating fox) collected in the Ipanema National Forest, Iperó, São Paulo, Brazil.

Photograph: Rita Soares Nunes.

Changes in eggs due to taphonomic processes, such as flattening or folding due to drying, are reasonably easy to detect when there are adequate numbers of eggs in the sample. However, it is common to observe the loss of membranes, cuticles, and shells and the opening of opercula, possibly caused by rehydration of the samples. In such cases, if it is not possible to find some eggs that prove these intermediate stages, identification may become impossible or even incorrect (Plates 2 and 3).

Plate 2 – Eggs of unidentified acanthocephalans (81-96.8 x 47-60 μm) in coprolites from collared anteater (*Tamandua tetradactyla*) (Pilosa: Myrmecophagidae) in different phases including complete breaking of the shell and exposure of the acanthor. Serra da Capivara National Park, Piauí, Brazil. Magnification 400x

Plate 3 – Ascarid eggs (69 x 39 μm with shell) (Nematoda: Ascaridae) in recent feces of *Kerodon rupestris* (rock cavy) (Rodentia: Caviidae) in different embryonic stages. Serra das Confusões National Park, Piauí, Brazil. Magnification 400x

(A) egg with mamillated thickened shell; (B) egg without shell, with a reduction of approximately 3 μm in both measurements.

DIAGNOSIS OF ANIMAL FECES

It is interesting that discussion of coprolite identification has lasted for so long, since feces had already been used since the early 20th century in biological studies of many mammalian species. Seton (1925) already noted that the shape and content of feces are excellent clues for identifying mammalian orders. Feces of species from the same order have characteristics that allow grouping them, and that reflect their peculiar anatomy. The shape of feces appears not

to be useful for diagnosing the family and genus. However, although it may appear contradictory, the shape of feces is a valuable tool for species diagnosis, as are the size and food content, which sometimes separate proximate species (Riney, 1957). Most authors still use feces as a research source, but most do not describe the criteria used for their identification (Eddy, 1961; Neff, 1968; Batcheler, 1975; Dzieciolowski, 1976; Floyd, Mech & Jordan, 1978; Johnson & Hansen, 1978; Von Gadow, 1978; Fitzgerald & Waddington, 1979; Strong & Freddy, 1979; Arthur III & Alldredge, 1980; White & Eberhart, 1980; Bailey & Putman, 1981; Dinerstein & Dublin, 1982; Andelt et al., 1987; Rogers, 1987; Fox & Smith, 1988; Hominger, Dale & Bailey, 1988; Cáceres et al., 2007).

However, ecological studies using feces as a primary research source have multiplied over time, meaning that they have been identified in some way (Welch, 1982; Mitchell et al., 1985; Rabinowitz & Nottingham, 1986; Patton et al., 1986; Green, 1987; Emmons, 1987; Lancia, Nichols & Pollock, 1996; Kohn & Wayne, 1997; Anacleto et al., 2007).

Meanwhile, some authors have studied parameters to characterize and identify fecal findings. Bowden, Andersen & Medin (1969) describe the feces of mule deer (*Odocoileus hemionus*) as a group of five or more units, generally with the same weight, size, consistency, shape, and color. Voth & Black (1973) used histological studies of plants ingested by small herbivores to characterize the feces of mountain beaver (*Aplodontia rufa*) according to size and weight.

Grant (1974) uses shape to differentiate the shape of *Megaleia rufa* (red kangaroo) fecal pellets from those of *Macropus giganteus* (gray kangaroo). The author compares feces collected from the colon of dead animals to pellets collected in the field and states that the results show considerable reliability, allowing their use to identify the two species of marsupials. According to other studies, such as Brunner, Lloyd & Comam (1975) with carnivores in Australia, it is not always possible to identify the scats of cats, dogs, and fox (*Vulpes vulpes*) by size, shape, and odor, but they estimate their diagnostic confusion at less than 5%.

The diameter of scats often facilitates their identification (Gree & Flinders, 1981; Danner & Dodd, 1982). Weaver & Fritts (1979) use diameter to distinguish between scats of *Canis latrans* (coyote) and *Canis lupus* (wolf) where the two species are sympatric. *Canis lupus* scats are greater than 3 cm in diameter, and the odds of identifying *Canis lupus* scats as *Canis latrans* are 4.9%. Like Huson & Davis (1980) in a study of droppings from *Rattus rattus* and *Rattus norvegicus*, they emphasize that the volume of food ingested can alter the size of feces.

Anacleto (2007), studying the eating habits of armadillo species (Dasypodidae) in the Mato Grosso *cerrado*, distinguish feces of *Prionomys maximus* (giant armadillo) from those of *Euphractus sexcinctus* (six-banded armadillo) by the shape, consistency, odor, and food composition, while the other species also require association with the remains of animals observed in the collection sites.

Bang & Dahlström (1974) made a huge contribution to solving the question when they published their illustrated field guide of tracks and signs of animals in Europe. The book also contains a detailed analysis of the shape, size, color, and food content of mammalian feces. Other field guides, although rarely mentioned in the scientific literature, are excellent aids for identifying animal feces from the region for which they were developed, and obviously also for coprolites, including the keys by Burt & Grossenheider (1976), Murie (1974), Halfpenny & Biesiot (1986), Russo & Olhausen (1987), Estes (1992), Walker (1996), Stuart & Stuart (1998), Lienbeberg (2000), and Kingdon (2001), among others.

In order to combine the existing information on the identification of feces and make it available in a scientific publication to support paleoparasitology, Chame (2003) conducted a morphometric compilation of the available data on feces of European, North American, and African mammals and original data from Brazil. This article's analysis corroborates observations by Seton (1925), with a classification of the shapes of feces from the orders of land

mammals. Many years of research experience with mammalian feces from the São Raimundo Nonato archaeological region in southeastern Piauí State, Brazil, allowed establishing a series of patterns for identifying feces, including other ecosystems (Plate 4).

Plate 4 – Shapes of feces from Brazilian land mammals

(A) *Puma concolor* (cougar), Serra da Capivara National Park, Piauí (PNSC, PI); (B) *Panthera onca* (jaguar), PNSC, PI; (C) *Cerdocyon thous* (fox), PNSC, PI; (D) *Leopardus* sp. (small spotted wildcats), PNSC, PI; (E) *Dasypus novemcinctus* (nine-banded armadillo), PNSC, PI; (F) *Lutra longicaudis* (neotropical river otter), Ipanema National Foresta, SP; (G) *Tayassu pecari* (white-lipped peccary), PNSC, PI; (H) *Tamandua tetradactyla* (collared anteater), PNSC, PI; (I) *Pecari tajacu* (collared peccary), PNSC, PI; (J) *Mazama* sp. (deer), PNSC, PI; (K) *Alouatta caraya* (black howler monkey), PNSC; (L) *Galea spixii* (yellow-toothed cavy), PNSC, PI; (M) *Kerodon rupestris* (rock cavy), PNSC, PI; (N) *Cebus libidinosus* (black-striped capuchin), PNSC, PI.

Other efforts have been made to determine the set of parameters and necessary measures for diagnosing the origin of coprolites. In addition to the work mentioned above, Chame et al. (1991) established a methodology for comparing recent feces and coprolites from the Serra da Capivara National Park in Piauí State, which allowed developing the issue from a regional approach. Reinhard & Bryant (1992) consolidated the systematization of a set of diagnostic parameters, and Jouy-Avantin et al. (2003) later proposed a detailed protocol of parameters for recording samples, including not only the date and location of the collection but a detailed external and internal description of the coprolites.

In addition to direct identification and microscopy, other techniques were developed to distinguish between feces of similar appearance, with methodological advances over previous proposals. In Mississippi, Major et al. (1980) analyzed biliary acids in feces to distinguish between scats from felids (*Lynx rufus*), canids (*Canis latrans* and *Vulpes vulpes*), raccoons (*Procyon lotor*), and domestic dogs and cats. According to these same authors, whatever the technique used to identify feces, it should allow distinguishing between morphometrically similar feces, the identification keys should be stable over time and resist chemical degradation, and analysis should be simple and relatively inexpensive.

According to Fernández, Corley & Capurro (1997), the composition of biliary acids in feces is specific and is thus especially useful for distinguishing between carnivore species. The authors developed a methodology to determine the origin of feces using chromatography layers from the biliary acid patterns. They tested the methodology in feces from cougars (*Felis concolor*) and jaguars (*Panthera onca*), two sympatric species in the Paraguayan Chaco, and found it the best technique for identifying feces from these two species.

Some immunological diagnoses, when specific, can also be effective for determining the origin of coprolites and parasites. An example is the detection of *Giardia intestinalis* in coprolites and feces using immunofluorescence techniques and ELISA (enzyme-linked immunosorbent assay), available in commercial kits (Gonçalves et al., 2004; Bailly et al., 2008).

The available techniques and methods now include molecular biology tools. The first studies of ancient DNA were done on bone and tissue samples. A case with great repercussion was the Tyrolean Iceman, whose DNA analysis verified his European origin (Poinar, 1999). However, analyses of coprolites by molecular methods are more recent and involve the detection of DNA fragments that are already extensively degraded, which requires a bit of luck. Currently, vestiges of ancient DNA have been recovered from coprolites, and their identification aids facilitates the latter's zoological identification, determination of food items consumed, and even the identification of parasites where these have not been preserved morphologically due to taphonomic processes.

With the same diagnostic objective, this methodology has made strides in ecological studies using feces as a sampling unit (Reed et al., 1997; Farrel, Roman & Sunquist, 2000; Fedriani & Kohn, 2001). Miotto et al. (2007a, 2007b) consider the results of this identification essential for studying the population dynamics of rare, threatened, or large species that are difficult to capture and indicate the technique's efficiency and accuracy.

The main concern when seeking to recover ancient DNA in coprolites involves the steps to avoid the sample's contamination with current DNA from the environment or from the researchers collecting and handling the sample, from the field to the laboratory.

Contamination should be avoided by using disposable and sterile material in all stages and processes involved in analyzing the sample. The laboratories should be specially prepared with clean equipment and environments. Analyses should be replicated, have a control group, and be performed in different laboratories for comparison and control. Proper packing of the sample is also essential, because after samples are removed from the archaeological site they can be exposed to variations in temperature, humidity, and other physical and chemical factors that can potentially degrade the molecular remains.

A solution for containing degradation is refrigeration of the sample, which requires planning and infrastructure proportional to the distance between the archaeological site (usually in a difficult-to-access rural area) and the laboratory, located in a large city. The conditions should be guaranteed during transportation from the field to the laboratory and in the installations of the biological collection responsible for the material.

Proper attention to these measures has produced encouraging results with coprolite specimens from various regions of the world. Sutton (1996) identified human coprolites as to the sex of the individuals that produced them, highlighting the importance of these results for studies aimed at distinguishing variations in diet between the sexes. Wood et al. (2008) identified coprolites of extinct bird species from New Zealand. Meanwhile, Gilbert et al. (2008) recovered human mitochondrial DNA from coprolites in Oregon, USA, thereby moving the dating of human occupation of North America back to 12,300 BP. The coprolites belonged to Amerindians that lived in the period prior to the Clovis culture, more than 11,000 BP. To guarantee the results' veracity, the samples were analyzed in different laboratories, and all the researchers handling the material had their DNA tested and compared to the results in order to rule out contamination.

DNA from *Enterobius vermicularis* and *Ascaris lumbricoides* has already been identified in Old World and New World human coprolites (Iñiguez et al., 2006; Leles et al., 2008), and DNA from chloroplasts of plants found in them was recovered by Reinhard et al. (2008), performing identification of plants with medicinal properties used by ancient populations. Since most coprolite specimens are not found together with skeletons, artifacts, and remains, the results described above show the potential of DNA analyses for zoological identification of coprolites, leaving no doubt as to their origin.

Although the techniques continue to improve, the first and perhaps most important diagnosis of a coprolite will certainly continue to be the decision by the field researcher to collect it into his rucksack or leave it in nature. At this moment, the shape, size, and visible food remains are undoubtedly the factors that influence this decision. Likewise, what else would lead us to pick up a lost pen drive, if not its size, shape, color, brand, make, and state of preservation, and above all the desire to unveil the secrets stored inside it?

IDENTIFICATION OF ZOOLOGICAL ORIGIN BY DIETARY STUDIES: THE MODEL FROM THE SERRA DA CAPIVARA NATIONAL PARK IN PIAUÍ, BRAZIL

Laboratories will probably not be able to conduct more sophisticated analyses of all the samples received, and the simpler methodologies will probably not become obsolete, at least for the initial workup. It is therefore useful to discuss how a set of basic information can provide an approximate diagnosis of the coprolite's origin, and how the sample can then be submitted to more in-depth investigation if it proves interesting.

However, in some situations the coprolite's identification is not conclusive with available methods, sometimes even with DNA analysis. One may also want more information beyond diagnosis of the origin, such as remains that may indicate the species' way of life.

In such cases, nothing is more comprehensive than studies on diet, since they position the coprolite's producer within its food web, reflecting the environment in which it lived. Thus, at least 50,000 years ago, coprolites were deposited in the sedimentary layers in the region that served as the birthplace of American humans – the Serra da Capivara National Park and its surrounding area in southeastern Piauí, now characteristic of the Brazilian semiarid region. The excavations launched there in the 1970s allowed the collection and study of a major sampling of coprolites, in addition to comparison with modern mammalian feces. The region underwent various climatic transformations

since then, from more humid periods, with forests and fields, to the present semiarid *caatinga* or scrub forest, thus influencing the occurrence of the species found there (Araújo et al., 1998) and preservation of the coprolites.

The elements in this transition can be observed in the macro and microfossils found in the coprolite specimens from the Serra da Capivara National Park in Piauí. The currently known vertebrate fauna in this site consists of 33 species of non-flying mammals, 24 bats, 208 birds, 19 lizards, 17 snakes, and 17 amphibians (Araújo et al., 1998). The most extensively studied coprolites are those of mammals, since they are the easiest to identify and the most likely to be confused with those of humans. Identification of coprolites from this region has been facilitated by the pioneering work of Chame (1988). However, their morphometry becomes useless when the coprolite is too degraded by taphonomic processes or destroyed during transportation.

Archaeology teams do not habitually draw or photograph coprolites in excavation layers, which would greatly facilitate the material's zoological identification, but would also doubtless increase their fieldwork time. Under such conditions, without the sample's shape and size, identification depends on studying food elements found in the coprolite. The composition and specificity of the food items obviously vary according to the target region, seasonality (as reflected by the food supply), and especially each group's eating and cultural habits. The work is thus greatly facilitated by knowing the dynamics of the region's occupation, factors limiting survival, and the local fauna and flora.

The most frequently found coprolite in the Serra da Capivara National Park is definitely from the species *Kerodon rupestris* (rock cavy). This medium-sized rodent inhabits rocky mountain ledges and has the habit of defecating in large dropping sites that last for generations and are used by various individual animals.

The analysis of macrofossils typically reveals abundant plant fibers, which tell little about the species in question. Microfossils show the greatest differences. Rock cavy droppings display a wealth of plant tissues not seen in other species and feature large amounts and good preservation. Charcoal fragments are common, possibly indicating that these animals consumed food scraps from humans. The feces are resinous due to the consumption of tree bark, such as angico (*Anadenanthera macrocarpa*), common in the region. Importantly, among the species of even-toed ungulates (deer and peccaries), the shape of feces from white-lipped and collared peccaries needs to be well-preserved, or they easily be confused with human feces. The main difference is the almost complete digestion of all the microscopic remains, which is not common in the microscopic examination of human feces.

Meanwhile, pellets from brocket deer (*Mazama* sp.) are rich in plant tissues. Microscopic examination shows entire plant structures and a wealth of small seeds and pollen (deer are flower eaters), but a slighter smaller variety of leaf epidermis than in feces of rock cavy, a leaf-eating species. Charcoal is also less common, although it does occur in some samples.

Coprolites from the collared anteater (*Tamandua tetradactyla*) are easy to identify, since the species feeds basically on termites and ants, the structures of which, such as pieces of chitin, heads, thoraces (sometimes whole), legs, and antennae are easily recognized in macrofossils. Fragments of other insects can also be observed under the microscope, although in smaller amounts.

Coprolites of small and large felines are easily identified macroscopically because they contain large amounts of hairs, bones, teeth, and occasionally feathers and a few arthropods (in small cats), in addition to their peculiar shape. Microscopic analysis of the diet shows virtually no microfossils, consisting basically of cell remains from digested foods, commonly referred to as debris.

Guard hairs, ingested during grooming, and the hair of consumed prey are key elements, allowing the specific identification of the diet's composition in these species (Figure 1).

Coprolites often show masses of leaves ingested to facilitate digestion and formation of the food bolus when there is excess hair and bones to eliminate (Plate 4, Figure A).

It is possible to find intact teeth and tiny mandibles, long bones of rodents, and armadillo claws and shells. Some coprolites from cougars or jaguars (*Puma concolor* and/or *Panthera onca*) from this region display a considerable amount of shellfish remains. The typical whitish color of coprolites from large cats is due to the important amount of calcium from ingested bones, which allows identification even when the coprolite is totally fragmented.

Figure 1 – Microscopic appearance of the diet in a coprolite from a small cat in the Serra da Capivara National Park, Piauí, with the presence of hair. Magnification 400x

Coprolites of wild canids display a characteristically brittle (“granola”-like) appearance (Plate 4, Figure C). They consist of large amounts of arthropod fragments, sometimes entire parts like the post-abdomen of a scorpion, feathers, bird claws and bones, scales, reptile claws and bones, and abundant seeds. The remains of small mammals are only found rarely. Due to these characteristics, these coprolites tend to crumble easily during transportation, but are still identifiable without major difficulties. The microfossils consist mostly of arthropod remains and plant tissues.

Primate coprolites (when dry) have a denser texture as compared to those of canids, due to their higher moisture content when excreted. Their composition varies from species to species due to eating habits. They all consist basically of fruits and leaves. However, coprolites of black howler monkeys (*Alouatta caraya*) display mostly intact seeds (they are seed dispersers), abundant plant epidermis remains (since they are basically leaf-eaters), and rarely arthropod remains

(Moura & McConkey, 2007). Coprolites of black-striped capuchins (*Cebus libidinosus*) have the same appearance, but are smaller. Intact seeds are infrequent (they are seed predators), arthropod and leaf remains are abundant, and small bones of amphibians or even small mammals, including bats, are common (Moura & McConkey, 2007; Falótico, 2008)

Coprolites of armadillos (Dasypodidae) are frequently confused in appearance with human coprolites, sometimes in both the macroscopic and microscopic analyses. There is a strong presence of Isoptera insect remains (ants and termites) and other arthropods in fecal samples of all armadillo species, in addition to plant remains, although amounts of the latter vary according to the species. An example is *Euphractus sexcinctus* (six-banded armadillo), which has the most varied feeding habits, including fruits and invertebrates, among species of Dasypodidae. In the other species, the differences are difficult to systematize such as to allow an approximation of the species.

It is important to recall the ant-eating habits of some human populations, which in some situations can complicate the diagnosis. In this case the diet does not apply to identification.

Human coprolites are definitely the greatest challenge. To positively identify a human coprolite without morphometry requires a detailed analysis of all the items found. Omnivorous eating habits mean that human coprolites can be confused with those of other animals. Attention to details, even subtle ones, can make the difference. Authors like Bryant & Willians-Dean (1975) and Ferreira, Araújo & Confalonieri (1980) report that the presence of charcoal in coprolites indicates human origin.

Unfortunately, this parameter does not apply to the coprolites studied in Piauí. Rock cavy, feline, canid, and deer coprolites also contain charcoal, so the simple finding of charcoal does not suffice to indicate the coprolite's zoological origin. A common structure in microscopic analysis of human samples is a kind of spherically-shaped fat. It is not possible to state whether it is really ingested and degraded fat, but it has served as a potential clue for identifying the material's human origin.

Figure 2 – Microscopic appearance (400x) of a human coprolite from Piauí, rich in plant remains, including starch and various charcoal fragments

Starch grains are a relevant finding in coprolite specimens. Starch ingestion indicates important food sources and reflects relevant aspects of a species' paleoecology.

However, finding starch in a sample should be interpreted with caution. In Brazil, commercially sold laboratory gloves are powdered with corn starch. Thus, in the attempt to avoid contamination of coprolites for DNA testing, contamination with starch occurs, which compromises diet studies in coprolites. Therefore, in both the field and the laboratory, gloves should be starch-free, since starch is light and disperses easily in the environment.

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