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# Chemistry, mineralogy and microbiology of termite mound soil eaten by the chimpanzees of the Mahale Mountains, Western Tanzania

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ABSTRACT. Subsamples of termite mound soil used by chimpanzees for geophagy, and topsoil never ingested by them, from the forest floor in the Mahale Mountains National Park, Tanzania, were analysed to determine the possible stimulus or stimuli for geophagy. The ingested samples have a dominant clay texture equivalent to a claystone, whereas the control samples are predominantly sandy clay loam or sandy loam, which indicates that particle size plays a significant role in soil selection for this behaviour. One potential function of the clays is to bind and adsorb toxins. Although both termite mound and control samples have similar alkaloid-binding capacities, they are in every case very high, with the majority of the samples being above 80%. The clay size material ($<2\ \mu m$) contains metahalloysite and halloysite, the latter a hydrated aluminosilicate ($Al_2Si_2O_4 \cdot nH_2O$), present in the majority of both the termite mound soil and control soil samples. Metahalloysite, one of the principal ingredients found in the pharmaceutical Kaopectate$^{TM}$, is used to treat minor gastric ailments in humans. The soils commonly ingested could also function as antacids, as over half had pH values between 7.2 and 8.6. The mean concentrations of the majority of elements measured were greater in the termite mound soils than in the control soils. The termite mound

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soils had more filamentous bacteria, whereas the control soils contained greater numbers of unicellular bacteria and fungi.

KEY WORDS: geophagy, soil ingestion, termite mound soil, toxin adsorption

## INTRODUCTION

Geophagy has been observed in a diverse number of species throughout the world, such as mountain gorillas (Fossey 1983, Mahaney *et al.* 1990); colobus monkeys (Oates 1978); moustached tamarins (Heymann & Hartmann 1991); ungulates (Kreulen 1985, Mahaney *et al.* 1996a); elephants (Ruggiero & Fay 1994); Holstein cross cattle (Mahaney *et al.* 1996a); geese (Wink *et al.* 1993); and even humans (Aufreiter *et al.* 1997, Geissler *et al.* 1997, Johns & Duquette 1991, Vermeer 1966). Although the exact stimulus, or stimuli, for this behaviour in animals is not known it is suspected that these soils may offer nutritional benefits (Geissler *et al.* 1997, Johns & Duquette 1991, Kreulen 1985, Mahaney *et al.* 1990, Vermeer 1966) or have medicinal properties (Huffman 1997, Mahaney 1995a, 1996a, b) as they do for humans. Recently the possibility that primates incorporate non-nutritive, often toxic, chemical elements into their diet for treatment of disease has received wide attention (see Huffman 1997).

A number of scientists have repeatedly concluded that geophagy functions through: (1) adsorption of toxic plant compounds onto the surface of clay particles (Johns & Duquette 1991, Oates 1978, Wink *et al.* 1993), or absorption in the interlayer space of swelling clays (White & Hem 1983); (2) possible mineral supplementation (Davies & Baillie 1988, Heymann & Hartmann 1991, Hirabuki & Izawa 1990, Johns & Duquette 1991, Mahaney *et al.* 1990, Oates 1978); and (3) the clay minerals in the soil possibly alleviating stomach upset or relieving diarrhoea (Davies & Baillie 1988, Kreulen 1985, Mahaney *et al.* 1995b, Oates 1978).

Mahaney *et al.* (1996b) previously investigated the geochemistry and clay mineralogy of soil ingested from four termite mounds frequently utilized by chimpanzees in the Mahale Mountains National Park in Tanzania. They found that this soil could be a minor source of the nutritionally important elements, mainly iron and potassium. The clay mineralogy revealed a 4 : 1 ratio of metahalloysite/halloysite:smectite, a mineral combination similar to the active ingredients in the pharmaceutical Kaopectate™, which is used to treat minor gastric ailments in humans.

The present study examines the chemical, geochemical, mineralogical and biological properties of termite mound soil ingested by chimpanzees and soil from the forest floor that is not normally eaten to determine whether there is a stimulus or stimuli which might clarify the benefits of geophagy practised by chimpanzees of the Mahale Mountains.

## METHODS AND MATERIALS

### *Study site*

The study area is in the Mahale Mountains National Park in western Tanzania (latitude 6°S, 30°E) (Figure 1). This isolated mountain range extends

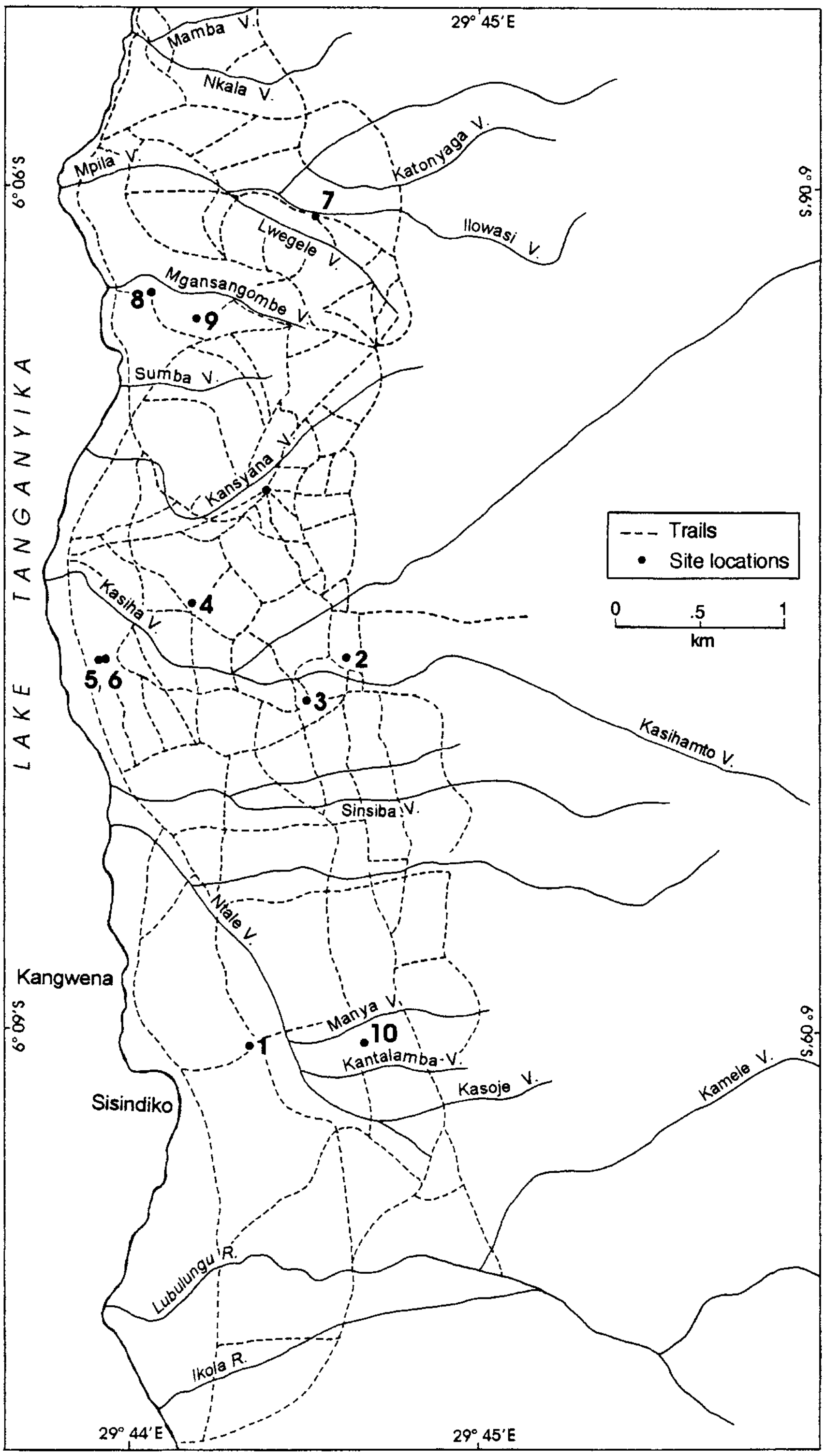

Figure 1. Location of geophagy sites in Mahale Mountains National Park, Tanzania.

north to south along the eastern shore of Lake Tanganyika and is characterized by extensive slopes and valleys, with the highest peak being Mt. Nkungwe at 2462 m asl.

The wet season begins in October and lasts until the beginning of May, with a short dry season from mid-January to February and a longer dry season from June to September (Takasaki *et al.* 1990). The mean annual rainfall is 1874.4 mm, the mean annual daily maximum and minimum temperatures are 29 °C and 18 °C, respectively (data taken from Kansyana camp, which is located within the study area). With high rainfall in the wet season (October–May), there is abundant moisture for soil weathering to occur.

The vegetation of the study site is characterized by semi-deciduous gallery forests which range from 780–1300 m above sea level. White (1983) has classified the vegetation zone as 'wetter Zambezian miombo woodland', dominated by *Brachystegia, Julbernardia* and *Isoberlinea* which extend over western Tanzania.

The Mahale Mountains lie within Ufipa terrane which contains basement rock consisting of coarse, crystalline metamorphic rock of sedimentary and volcanic origin. These include gneisses and schists, with biotite, but also contain kyanite, garnet, hornblende, graphite and chlorite; quartzites, crystalline marbles; amphibolites; pyroxenites, and charnockite rocks (Anon 1976). These may also provide minerals and/or release chemical elements to termite mounds.

### *Soils*

The composition of the soil in the Mahale Mountains consists mainly of sandy clay loam with good drainage (Hathout 1972) and is of granitic–gneissic origin (Baker 1970). Because of the steepness of the terrain, most places in the Mahale Mountains appear to have relatively immature and stony soils (Collins & McGrew 1988). The organic horizons, where present, range between 0–2 cm (Collins & McGrew 1988); complete soil descriptions are not available but generalized horizon sequences indicate they are Inceptisols with A/B/C horizons in profile (Soil Survey Staff 1975).

In the first set of samples the termite mound soil colours range from yellowish brown (10YR 5/4, 6/6) to bright brown (7.5YR 5/6) and the control samples range from brown (10YR 4/4, 4/3) to dark brown (10YR 3/4, 3/3) (assessed using colour chips of Oyama & Takehara 1970). The second set of control sample colours are slightly darker; the termite mound soil colours range from brown (7.5YR 4/4) to dark brown (10YR 3/3, 3/4) and the control samples range from dark brown (10YR 3/3) to brownish black (10YR 2/2) (Oyama & Takehara 1970). The soil colours suggest chimpanzees are selecting soils with light brown colours and avoiding dark soils with higher organic matter content.

Within the study site area, termite mounds mainly *Macrotermes* and *Pseudocanthotermes* are ubiquitous. All members of a chimpanzee group, at any time of the day and throughout the year, can be observed ingesting clumps of termite mound soil *c.* 3 $cm^3$ in volume.

*Analysis*

The soils were collected in pairs with each pair consisting of a sample from a termite mound known to be frequently used by chimpanzees and a control sample taken from surrounding uneaten topsoil *c.* 5 m away from the termite mound. Neighbouring termite mound samples 5 and 6 share the same control sample. In data set 2, all of the samples were re-collected from the same termite mounds and forest floor from the first data set were used; when analysed the second sample set appeared to be different from the first set. Therefore, the two sample sets will be regarded separately and distinctly. The paired samples will be referred to below as 'tm' (termite mound) and 'c' (control) samples.

Particle size distributions were determined by a combination of sedimentation and wet and dry sieving (Day 1965). The sand fraction (63–2000 μm) was determined by wet sieving, with silt (2–63 μm) and clay (<2 μm) determined by hydrometer. An expanded description of this method is given in Mahaney (1990).

X-ray diffraction (XRD) was employed to identify and measure the relative abundance of primary and secondary minerals in the clay fraction. The clay fraction was agitated, centrifuged onto a ceramic tile, and then X-rayed on a Toshiba ADG-301H diffractometer with Ni-filtered CuKα radiation following methods outlined by Whittig (1965).

The fine fraction of the sand grains from 10 ingested samples (63–250 μm) was analysed to determine weathering states and composition of clay mineral coatings on the sands. This was accomplished using a JEOL JSM-840 scanning electron microscope (SEM) along with energy dispersive spectrometry (EDS).

Electron microprobe analysis was used to determine the elemental composition of the following soil samples: 5 and 6 c, 5 tm, 6 tm and 10 tm. For the purpose of this study the wavelength dispersive mode was used. The probe beam diameter was set to 5 μm and the probe current was 10 nA. The minimum detectability limits are shown on the top of Table 1.

The pH was determined by glass electrode, total soluble salt content by electrical conductivity (Bower & Wilcox 1965), and organic content by the Walkley-Black (1934) method. The concentrations of extractable cations ($Na^+$, $Mg^{2+}$, $K^+$ and $Ca^{2+}$) were measured using atomic absorption spectrophotometry (AAS) (McKeague 1976) and total Kjeldahl nitrogen by auto-analyser (AA) (Schuman *et al.* 1973).

The toxin adsorption capacities of soils in the first sample set were determined by capillary gas liquid chromatography using the alkaloids lupanine, sparteine, quinine and atropine. A mass of 100 mg of soil was dissolved in 5 ml distilled water; then 1000 or 5000 μg of alkaloids were added, the vials regularly shaken, and left for 30 min. After that time the flasks were centrifuged at 10,000 **g**, to pellet all soil particles. Then the supernatant was taken, alkaloids were extracted by solid phase extraction, and analysed quantitatively by

Table 1. Electron microprobe data from control samples 5 and 6, and termite mound samples 6, 10 and 5, from Mahale Mountains, Tanzania. Data are in percentages. Detection limits for each element are given on line 2. – means value below detectable limits.

| Point | $Na_2O$ | Mg0 | $Al_2O_3$ | $SiO_2$ | $P_2O_5$ | $SO_3$ | $K_2O$ | CaO | $TiO_2$ | MnO | $Fe_2O_3$ | BaO | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Minimum limit to detection | 0.013 | 0.01 | 0.014 | 0.014 | 0.032 | 0.027 | 0.016 | 0.018 | 0.036 | 0.062 | 0.06 | 0.086 | |
| Transect 3–4, control sample 5 and 6; image 305, 190× | | | | | | | | | | | | | |
| | 0.04 | – | 0.02 | 94.17 | – | – | – | – | – | – | 0.2 | – | 94.43 |
| | 0.18 | 0.18 | 15.1 | 35.02 | 0.25 | 0.07 | 5.76 | 0.11 | 0.2 | – | 1.76 | 0.12 | 58.75 |
| | – | 0.36 | 7.22 | 11.7 | 0.09 | 0.07 | 0.58 | 0.13 | 0.27 | – | 1.66 | 0.1 | 22.18 |
| | 0.05 | 0.05 | 13.91 | 41.1 | – | – | 0.61 | 0.06 | 0.2 | – | 1.4 | – | 57.38 |
| | | 0.6 | 23.96 | 31.75 | – | 0.07 | 1.08 | 0.11 | 0.45 | – | 5.28 | 0.09 | 63.46 |
| | 0.08 | 0.4 | 23.09 | 28.35 | 0.14 | – | 0.78 | 0.11 | 0.37 | – | 4.66 | – | 57.98 |
| | – | 0.3 | 24.94 | 34.66 | 0.14 | – | 0.52 | 0.04 | 0.2 | – | 4.15 | – | 64.95 |
| | 0.05 | 0.43 | 22.98 | 27.98 | 0.27 | – | 0.81 | 0.07 | 0.67 | – | 5.93 | 0.1 | 59.19 |
| | 0.08 | 0.86 | 19.01 | 29.18 | – | – | 2 | 0.06 | 0.43 | – | 5.5 | – | 57.12 |
| | 0.13 | 0.73 | 22.41 | 29.1 | 0.05 | 0.05 | 1.11 | 0.03 | 0.4 | – | 4.65 | 0.17 | 58.83 |
| Transect 5–6, mound sample 6; image 305, 190× | | | | | | | | | | | | | |
| | 0.03 | – | 0.04 | 96.42 | – | – | 0.04 | – | – | – | – | – | 96.53 |
| | 0.24 | 0.78 | 18.54 | 25.46 | 0.05 | – | 0.63 | – | 0.32 | 0.26 | 15.1 | – | 61.38 |
| | 0.04 | 0.58 | 23.62 | 30.66 | – | – | 1.05 | 0.08 | 0.55 | 1.37 | 6.68 | – | 64.63 |
| | – | 0.65 | 19.44 | 23.9 | 0.21 | – | 0.83 | 0.06 | 0.5 | 0.87 | 14.7 | – | 61.16 |
| | 0.05 | 0.46 | 26 | 33.84 | 0.07 | 0.07 | 1.98 | 0.06 | 0.55 | 0.3 | 5.83 | – | 69.21 |
| | 0.07 | 0.71 | 28.55 | 35.79 | 0.11 | – | 1.31 | 0.1 | 0.57 | 0.1 | 7.72 | – | 75.03 |
| | 0.24 | – | 18.67 | 62.17 | – | – | 14.29 | – | 0.07 | – | 0.56 | 059 | 96.59 |
| | 0.53 | – | 12.55 | 37.55 | – | – | 5.18 | – | | – | 0.46 | 022 | 56.49 |
| | 0.09 | 1.18 | 24.58 | 33.4 | – | – | 1.96 | 0.08 | 0.63 | 0.13 | 7.72 | – | 69.77 |
| | 0.42 | – | 16.61 | 61.49 | – | – | 13.55 | – | – | – | 0.24 | 0.5 | 92.81 |
| Transect 7–8, mound sample 10; image 305, 300× | | | | | | | | | | | | | |
| | 0.03 | 0.18 | 4.76 | 8.04 | – | – | 5.88 | – | 0.08 | – | 4.7 | 0.71 | 24.38 |
| | 0.11 | 0.75 | 32.48 | 28.07 | – | – | 6.02 | – | 0.07 | – | 4.03 | 0.58 | 72.11 |
| | – | 0.45 | 29.04 | 39.54 | 0.09 | 0.1 | 0.63 | 0.08 | 0.72 | – | 8.49 | – | 79.14 |
| | 0.07 | 0.32 | 29.7 | 34.19 | – | – | 0.54 | 0.11 | 0.92 | – | 8.62 | 0.1 | 74.57 |
| | – | 0.18 | 24.71 | 30.46 | 0.21 | 0.07 | 0.42 | 0.07 | 0.65 | – | 10.42 | – | 67.20 |
| | 0.18 | 0.3 | 29.17 | 37.4 | 0.25 | – | 0.65 | 0.2 | 0.8 | – | 8.39 | – | 77.34 |
| | – | 0.36 | 30.5 | 40.73 | 0.05 | – | 0.69 | 0.13 | 10.3 | – | 8.15 | – | 81.64 |
| | 0.03 | 0.25 | 31.37 | 39.86 | 0.25 | 0.07 | 0.6 | 0.1 | 0.83 | – | 7.19 | – | 80.55 |
| | – | 0.17 | 28.53 | 36.54 | 0.14 | 0.05 | 0.42 | 0.07 | 0.65 | – | 5.3 | – | 71.87 |
| | 0.07 | 0.33 | 24.36 | 30.68 | – | – | 0.67 | 0.1 | 0.75 | – | 13.2 | – | 70.16 |

Table 1. (*cont.*)

| Point | $Na_2O$ | Mg0 | $Al_2O_3$ | $SiO_2$ | $P_2O_5$ | $SO_3$ | $K_2O$ | CaO | $TiO_2$ | MnO | $Fe_2O_3$ | BaO | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Minimum limit detection | 0.013 | 0.01 | 0.014 | 0.014 | 0.032 | 0.027 | 0.016 | 0.018 | 0.036 | 0.062 | 0.06 | 0.086 | |
| Transect 9–10, mound sample 10; image 305, 750× | | | | | | | | | | | | | |
| | 4.25 | 0.08 | 14.1 | 26.12 | – | 0.15 | 6.42 | 0.28 | 0.43 | – | 6.65 | – | 58.48 |
| | 2.44 | 0.05 | 16.36 | 25.65 | 0.41 | 0.07 | 8.7 | 0.14 | 0.45 | – | 7.09 | – | 61.09 |
| | 1.15 | 0.15 | 18.35 | 30.49 | 0.11 | – | 1.47 | 0.1 | 0.6 | – | 6.66 | – | 59.08 |
| | 2.4 | 0.03 | 15.74 | 23.45 | – | 0.15 | 12.66 | 0.14 | 0.45 | 0.09 | 5.88 | – | 60.99 |
| | 4.04 | 0.2 | 17.06 | 29.25 | 0.09 | 0.2 | 2.48 | 0.27 | 0.47 | – | 5.73 | – | 59.79 |
| | 0.39 | 0.22 | 22.58 | 34.02 | 0.05 | – | 0.53 | 0.06 | 0.83 | – | 7.56 | – | 66.24 |
| | 0.05 | 0.27 | 20.95 | 34.17 | 0.16 | – | 0.57 | 0.07 | 0.68 | – | 8.21 | – | 65.13 |
| | 0.04 | 0.27 | 22.9 | 35.86 | 0.05 | – | 0.63 | 0.07 | 0.55 | – | 7.89 | – | 68.26 |
| | 0.08 | 0.27 | 21.37 | 34.87 | 0.11 | – | 0.59 | 0.06 | 0.85 | – | 6.98 | – | 65.18 |
| | 0.04 | 0.23 | 21.56 | 32.82 | – | – | 0.65 | – | 0.67 | – | 8.46 | – | 64.43 |
| Transect 11–12, mound sample 5; image 305, 370× | | | | | | | | | | | | | |
| | – | 0.81 | 16.76 | 31.17 | 0.07 | – | 1.14 | 0.18 | 0.48 | – | 5.46 | – | 56.07 |
| | 0.09 | 3.07 | 20.09 | 33.76 | – | – | 3.59 | 0.11 | 1.08 | – | 12.84 | – | 74.63 |
| | – | 0.46 | 26.55 | 36.95 | 0.07 | – | 1.02 | 0.2 | 0.85 | – | 7.55 | – | 73.65 |
| | 0.08 | 0.5 | 28.81 | 36.73 | é | 0.05 | 0.99 | 0.14 | 0.8 | – | 8.46 | – | 76.56 |
| | – | 0.23 | 8.65 | 83.65 | 0.14 | – | 0.69 | 0.04 | 0.23 | 0.1 | 2.1 | – | 95.83 |
| | 0.07 | 0.55 | 27.89 | 36.86 | – | – | 0.92 | 0.13 | 1.2 | – | 9.85 | – | 77.47 |
| | 0.07 | 0.63 | 24.64 | 45.1 | – | – | 1.24 | 0.11 | 1.22 | 0.14 | 6.76 | – | 79.91 |
| | 0.09 | 0.76 | 27.7 | 37.05 | – | – | 1.16 | 0.2 | 0.75 | – | 8.49 | 0.09 | 76.29 |
| | – | 0.32 | 21.88 | 55.07 | – | – | 0.87 | 0.1 | 0.32 | – | 4.53 | – | 83.00 |
| | – | 0.55 | 24.51 | 32.24 | – | 0.07 | 1.14 | 0.18 | 1.1 | – | 6.53 | – | 66.32 |

capillary gas liquid chromatography using authentic alkaloids as external standards (Wink 1993, Wink *et al.* 1995).

The geochemistry of the soils was accomplished using Instrumental Neutron Activation Analysis (INAA) at the SLOWPOKE Reactor Facility, University of Toronto. The concentration of the macro-, micro- and trace elements of the samples were measured using procedures established by Hancock (1984).

Dilution plating for microorganisms was carried out using a two-culture medium: modified Leonian's medium for fungi and nutrient agar for bacteria. One g of each sample was diluted serially to obtain dilutions of 1 : 10, 1 : 100, 1 : 1000, 1 : 10000 and 1 : 1000000. One ml of each dilution was pipetted into three Petri dishes containing cooled molten Leonian's and nutrient agar. The media were allowed to solidify and were incubated at 21 °C. After 7–10 d the colonies in each plate were counted and identified. The colony counts were multiplied by the dilution factor to calculate colony forming units (CFUs) per g of soil.

Standard $\chi^2$ and t-test methods were used to establish the statistical significance of the termite mound vs. control soil data sets.

## RESULTS

### *Particle size analysis*

Particle size analysis was used to determine the relative proportion of sand, silt and clay for each soil sample. The majority of termite mound samples have a clay texture while the control samples are predominantly sandy clay loam as indicated by the ternary diagrams (Figures 2a, b). The data from the particle size curves for all termite mound samples show mean clay values of 45.8 ± 11.5%, sand values of 34.8 ± 8.6% and silt values of 19.4 ± 5.2%. The control samples show clay values of 28.5 ± 8.4%, sand values of 52.9 ± 8.4% and silt values of 18.6 ± 2.7%. The control samples fit well with the soil description given by Hathout (1972) for the area. However, the termite mound soil has a relatively greater clay content which arises from mound building activity.

### *Clay mineralogy*

The clay material (<2 μm) was analysed and the results (Figure 3) show the presence of metahalloysite/halloysite, the latter a hydrated aluminosilicate ($Al_2Si_2O_4{\cdot}nH_2O$), present in the majority of the termite mound and control samples. The first order reflection for metahalloysite, at 12.2° 2θ, disappears after heating to 500 °C (Brindley & Brown 1980), revealing that this clay is not kaolinite. Metahalloysite, an analog of purified kaolin clay, is the principal ingredient found in the pharmaceutical Kaopectate™, along with smectite, although at smaller concentrations. Smaller proportions of halloysite at different hydration states were also found in the samples. Approximately 60% of all samples contain illite/smectite. Other clay minerals identified were illite and kaolinite. Other primary minerals include quartz and orthoclase.

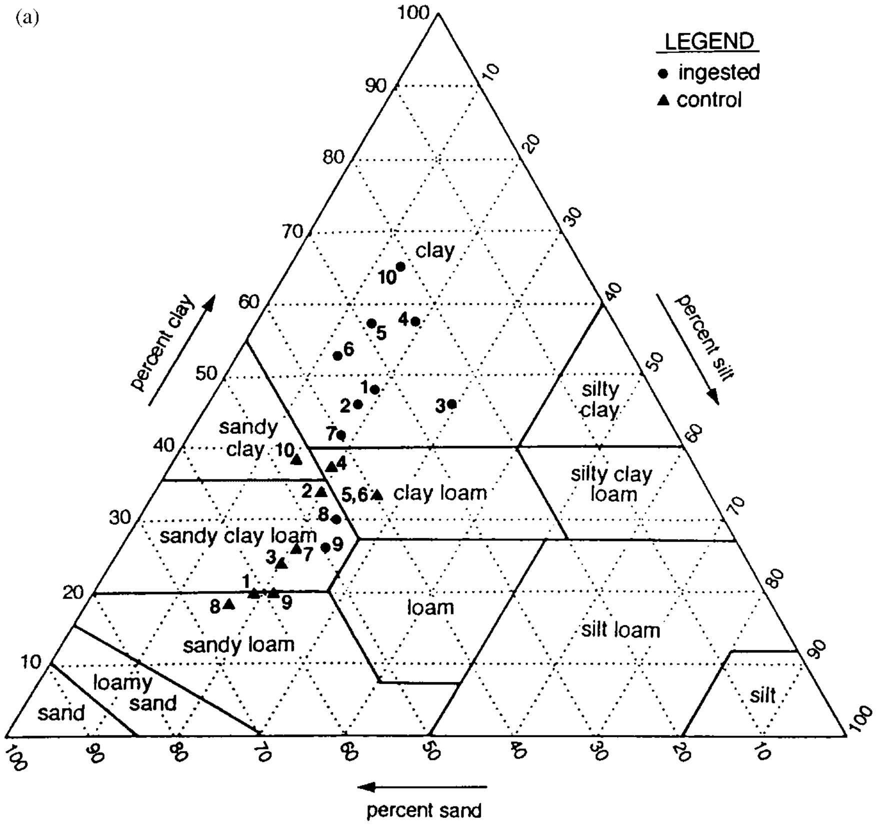

Figure 2. Soil textural classifications for sample sets (a) 1 and (b) 2. Ingested: termite mound soil.

As indicated by the reflections, there is very little difference in relative abundance of kaolinite and metahalloysite between the control samples and the ingested samples. This may be due to the fact that the uneaten samples are located close to the termite mounds resulting in some slope wash into the control samples.

### *Scanning electron microscopy*

A representative cross-section of light and heavy minerals, examined by scanning electron microscope (SEM), from ingested samples 5, 6 and 9 and control samples 5 and 6 are shown in Figure 4. Hematite, an iron oxide, with a textured surface can be seen in Figure 4A. Epidote is shown to be highly weathered (Figure 4B) as well as having an etched surface (Figure 4C). A clay coating is evident on the centre of a quartz grain (Figure 4D). Figure 4E shows an orthoclase grain (left) surrounded by euhedral quartz grains possibly originating from a tuff. Minor etching and wear on the surface of an orthoclase grain is shown in Figure 4F. A phlogopite grain with platy structure and strong basal cleavage is shown in Figure 4G. A highly weathered iron oxide grain with a secondary iron coating is shown in Figure 4H.

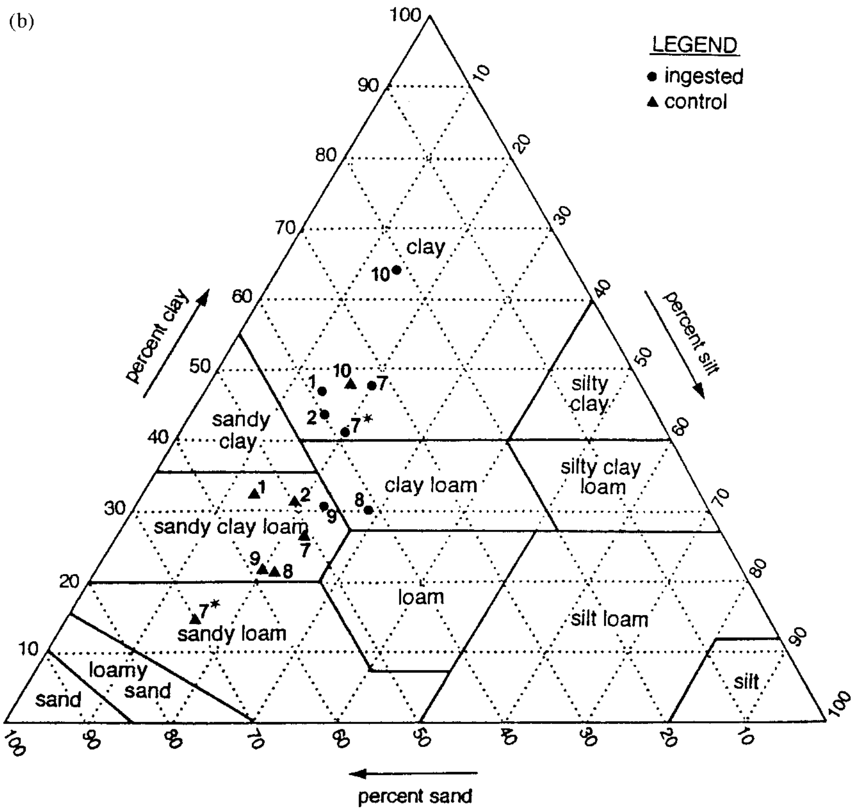

Figure 2 *continued.*

The cross-section of minerals examined by SEM illustrates that a great deal of weathering has taken place within the termite mound group of samples. Weathering may result in partial or full alteration of the primary mineral structure followed by release of nutritionally useful chemical elements such as K, Fe and Ca.

### *Electron microprobe*

Electron microprobe combined with backscatter imagery was used to analyse samples 5 and 6 c, 5 tm, 6 tm and 10 tm. The transects from Table 1 are shown as black lines on the backscatter photographs (Figure 5). Nutritionally important elements that could potentially stimulate the practice of geophagy, such as Na, Ca, P, S, Mn and Mg, are quite low. The silica/aluminum ratio, is close to, but not consistently 1 : 1, which supports the 1 : 1 clay minerals reported herein. Iron (II), the element suspected as a possible stimulus by Mahaney *et al.* (1996a, b), does have concentrations that average 7.2% for 5 tm, 6.5% for 6 tm, and 7.8% for 10 tm. While the data overlap somewhat with the geochemistry reported below, the microprobe provides important information on P, S and Si, which are not obtainable with routine INAA.

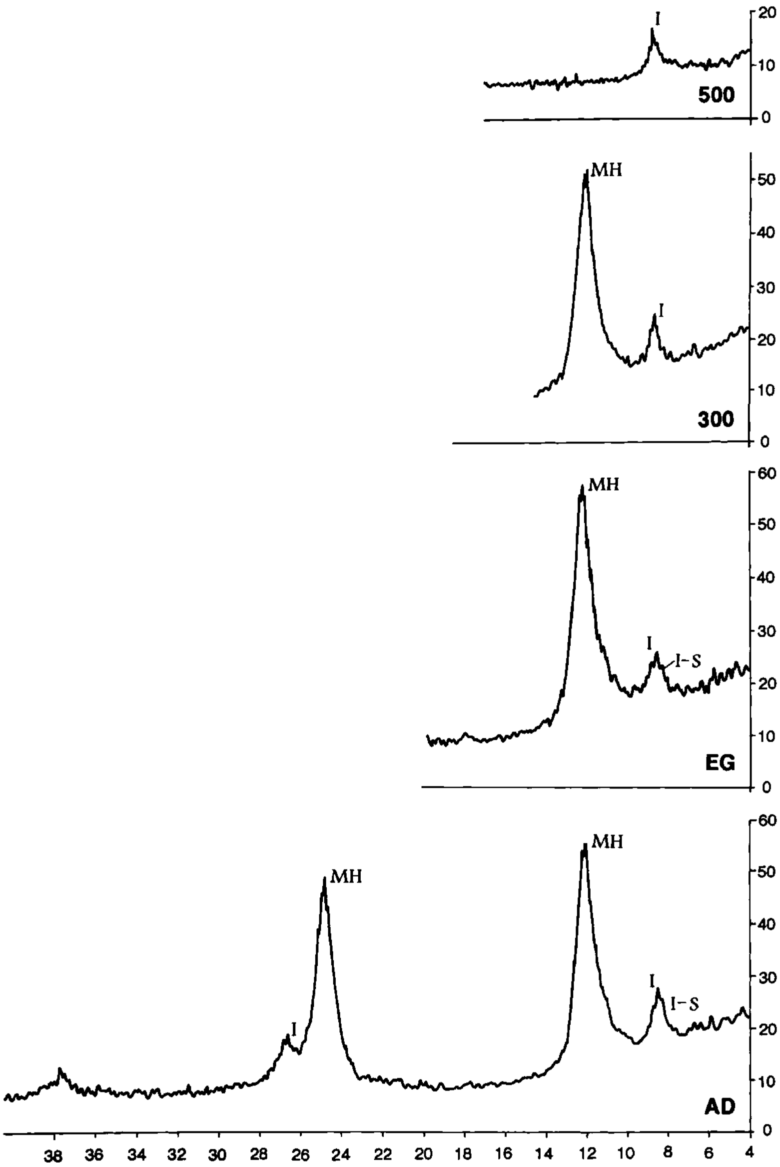

Figure 3. X-ray diffraction pattern of ingested sample 3 from Mahale Mtn. Minerals are identified as: Metahalloysite (MH); Illite-smectite (I-S); Illite (I); Orthoclase (O); Quartz (Q).

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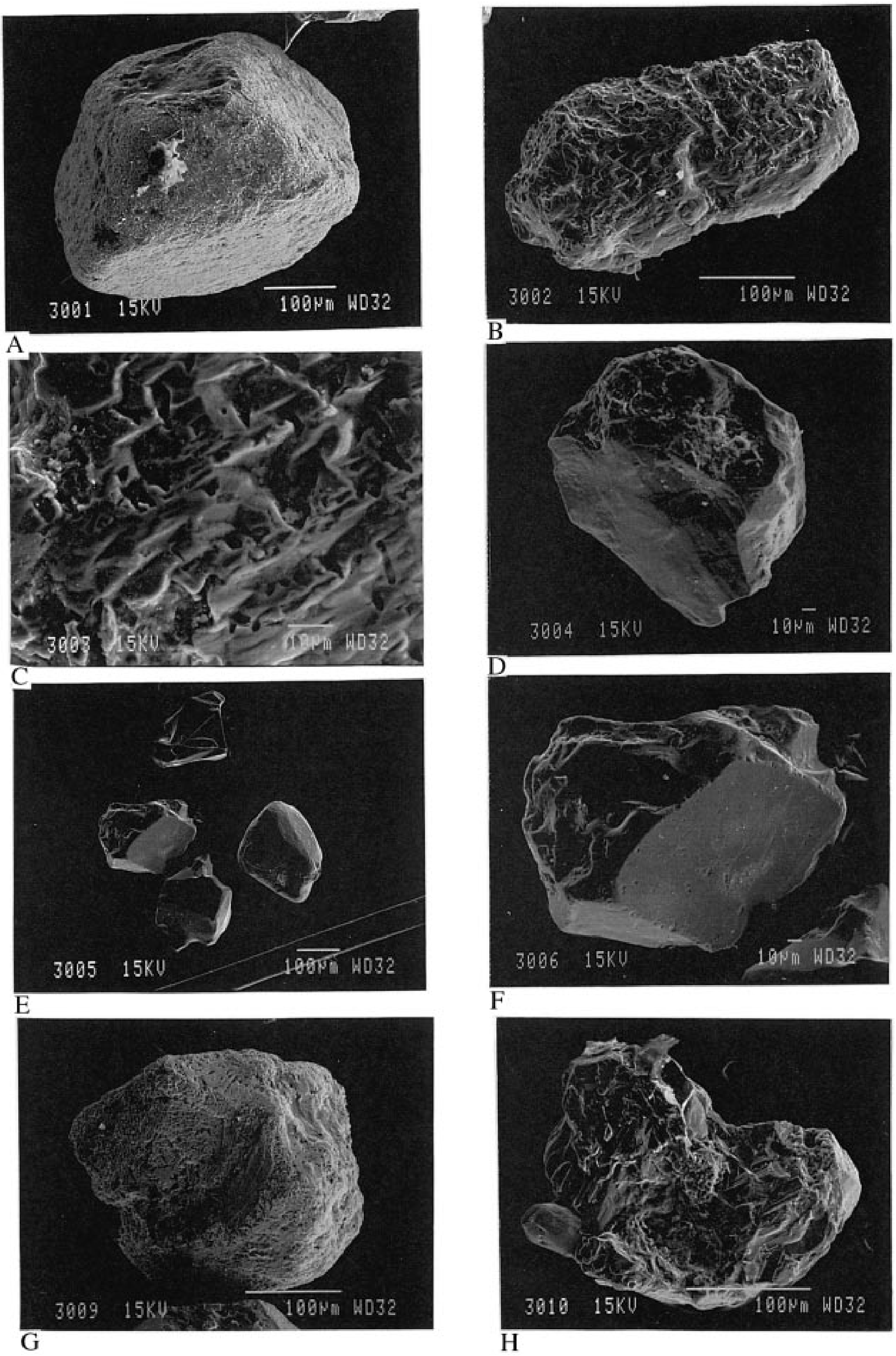
Figure 4. A, hematite with a textured surface; B, highly weathered epidote grain; C, etched surface of an epidote grain; D, precipitation of silica on top right of the grain and a clay coating in the centre of the grain; E, two quartz grains on the right and two orthoclase grains on the left; F, minor etching on the surface of an orthoclase grain; G, iron deposits on an intensely weathered quartz grain; H, intensely pitted surface with an iron coat.


3001 15KV 100µm WD32
A
3002 15KV 100µm WD32
B
3003 15KV 10µm WD32
C
3004 15KV 10µm WD32
D
3005 15KV 100µm WD32
E
3006 15KV 10µm WD32
F
3009 15KV 100µm WD32
G
3010 15KV 100µm WD32
H

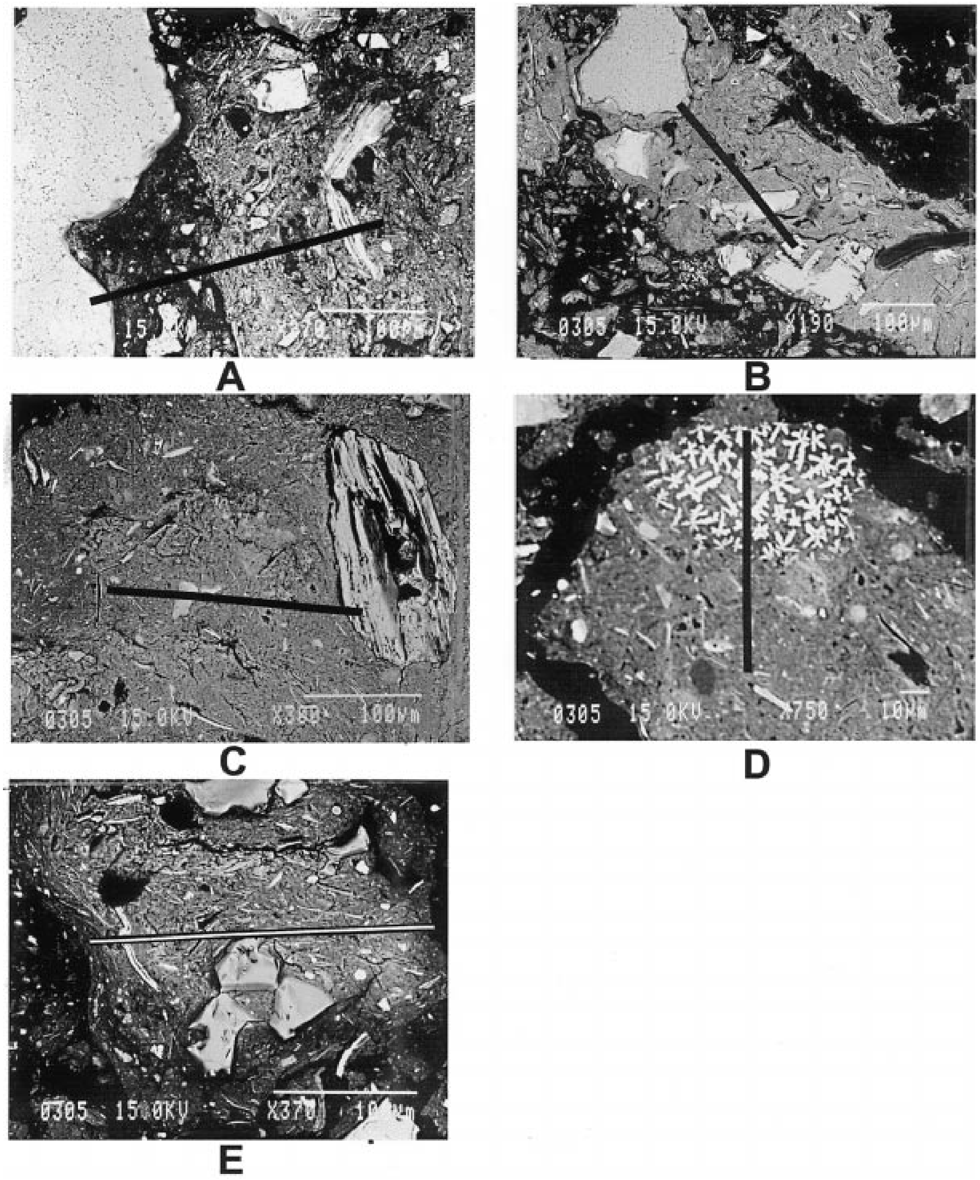


Figure 5 Backscatter imagery for control sample 5 and 6 (A), ingested 6 (B), ingested 10 (C, D), ingested 5 (E). A. The line corresponds with the probe transect 3–4 in Table 1. The microprobe transect runs from left quartz grain to the right. Void spaces show up as black areas in the micrograph. Voids in the matrix material could be from sample preparation or from the nature of the matrix. Voids in the mineral grains are *in situ*. B. The line corresponds with the probe transect 5–6 in Table 1. The transect starts at the upper left quartz grain and finishes at an orthoclase mineral in the lower right. The detrital nature of the clay particles can be clearly recognized. C. The line corresponds with the probe transect 7–8 in Table 1. The transect proceeds from right to left starting in a mica grain that is weathering by hydration. D. The line corresponds with the probe transect 9–10 in Table 1. The top end of the transect bifurcates star shaped crystals that are rich in K and Na compared with the adjacent material. E. The line corresponds with the probe transect 11–12 in Table 1. The transect goes from left to right and the large grains under the transect are quartz. The detrital nature of the clay particles are noticeable in the micrograph.

*Chemistry*

The results of pH, electrical conductivity, the extractable cations ($Na^+$, $K^+$, $Mg^{2+}$, $Ca^{2+}$), organic carbon and total nitrogen are outlined in Tables 2a and 2b. The pH of every termite mound soil is greater than its matching control sample. In addition, over half of the termite mound samples are moderately basic with pH values between 7.2 and 8.6. The electrical conductivity, which is

Table 2. Chemical properties of sample sets (a) 1 and (b) 2 as pairs of control (c) and termite mound (tm) soils.

(a)

| | | | | Extractable cations (Cmol kg$^{-1}$) | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sample | Set 1 | pH (1 : 5) | Soluble salt (S/cm$^{-1}$) | Ca | Mg | K | Na | %$C_{org}$ | %$N_{tk}$ | $C_{org}/N_{tk}$ |
| 1 | tm | 8.09 | 102 | 4.86 | 1.19 | 0.38 | 0.14 | 1.3 | 0.12 | 10.83 |
| | c | 6.15 | 73 | 3.36 | 1.02 | 0.81 | 0.04 | 4.18 | 0.31 | 13.48 |
| 2 | tm | 7.16 | 166 | 2.71 | 0.70 | 0.37 | 0.04 | 0.89 | 0.12 | 7.42 |
| | c | 6.07 | 80.7 | 2.94 | 0.53 | 0.73 | 0.03 | 3.55 | 0.23 | 15.43 |
| 3 | tm | 7.67 | 101 | 2.99 | 0.45 | 0.22 | 0.05 | 1.04 | 0.11 | 9.45 |
| | c | 5.71 | 84.5 | 2.97 | 1.25 | 0.59 | 0.04 | 4.04 | 0.33 | 12.24 |
| 4 | tm | 6.10 | 60.0 | 1.34 | 0.98 | 0.22 | 0.04 | 1.14 | 0.11 | 10.36 |
| | c | 5.55 | 54.2 | 2.31 | 0.98 | 0.54 | 0.03 | 3.46 | 0.29 | 11.93 |
| 5 | tm | 8.11 | 91.5 | 2.91 | 1.07 | 0.36 | 0.03 | 0.82 | 0.11 | 7.45 |
| | c | 5.45 | 105 | 2.18 | 1.55 | 0.68 | 0.03 | 4.16 | 0.37 | 11.24 |
| 6 | tm | 6.90 | 37.1 | 1.79 | 1.15 | 0.55 | 0.00 | 0.67 | 0.10 | 6.70 |
| | c | 5.45 | 105 | 2.18 | 1.55 | 0.68 | 0.03 | 4.16 | 0.37 | 11.24 |
| 7 | tm | 7.21 | 95.5 | 3.17 | 0.78 | 0.28 | 0.01 | 0.92 | 0.11 | 8.36 |
| | c | 5.13 | 258 | 2.96 | 1.27 | 2.2 | 0.01 | 3.46 | 0.45 | 7.69 |
| 8 | tm | 8.57 | 89.1 | 3.81 | 0.70 | 0.19 | 0.06 | 0.68 | 0.08 | 8.50 |
| | c | 5.65 | 192 | 2.84 | 1.68 | 1.14 | 0.04 | 0.94 | 0.36 | 2.61 |
| 9 | tm | 8.37 | 115 | 4.39 | 1.15 | 0.25 | 0.03 | 0.68 | 0.04 | 17.00 |
| | c | 5.44 | 53.6 | 2.01 | 0.49 | 0.59 | 0.01 | 2.13 | 0.19 | 11.21 |
| 10 | tm | 6.88 | 85 | 2.21 | 1.03 | 0.54 | 0.01 | 1.48 | 0.13 | 11.38 |
| | c | 5.02 | 78.1 | 2.06 | 1.02 | 0.63 | 0.04 | 3.65 | 0.35 | 10.43 |

(b)

| | | | | Extractable cations | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sample | Set 1 | pH (1 : 5) | Soluble salt (S/cm$^{-1}$) | Ca | Mg | K | Na | %$C_{org}$ | %$N_{tk}$ | $C_{org}/N_{tk}$ |
| 1 | tm | 7 | 36.3 | 5.01 | 0.86 | 0.42 | 0.02 | 1.09 | 0.10 | 10.9 |
| | c | 5.49 | 26.68 | 1.99 | 0.9 | 0.94 | 0.004 | 1.26 | 0.15 | 8.4 |
| 2 | tm | 6.97 | 16.96 | 1.94 | 57 | 0.43 | 0.00 | 1.12 | 0.08 | 14.0 |
| | c | 6.56 | 59.54 | 3.78 | 2.09 | 1.19 | 0.00 | 4.23 | 0.33 | 12.82 |
| 7a | tm | 7.48 | 21.05 | 3.48 | 0.9 | 0.3 | 0.009 | 1.50 | 0.12 | 12.5 |
| | c | 5.41 | 56.21 | 3.66 | 1.56 | 0.44 | 0.007 | 3.66 | 0.33 | 11.09 |
| 7b | tm | 6.58 | 20.48 | 3.01 | 0.9 | 0.31 | 0.03 | 1.04 | 0.10 | 10.4 |
| | c | 5.3 | 20.2 | 1.46 | 0.61 | 0.42 | 0.01 | 3.12 | 0.11 | 28.36 |
| 8 | tm | 7.82 | 65.64 | 4.64 | 1.44 | 0.59 | 0.03 | 1.02 | 0.09 | 11.33 |
| | c | 6 | 59.73 | 3.61 | 1.19 | 0.77 | 0.01 | 4.17 | 0.37 | 11.27 |
| 9 | tm | 7.98 | 23.53 | 5.01 | 0.98 | 0.25 | 0.02 | 0.72 | 0.07 | 10.29 |
| | c | 5.28 | 43.63 | 3.21 | 1.6 | 1.05 | 0.02 | 4.90 | 0.40 | 12.25 |
| 10 | tm | 6.02 | 42.8 | 2.39 | 1.23 | 0.66 | 0.01 | 1.32 | 0.12 | 11.00 |
| | c | 5.01 | 13.05 | 1.61 | 0.98 | 0.86 | 0.01 | 2.22 | 0.23 | 9.65 |

an estimate of the soluble salt concentration ($NO_3^-$, $Cl^-$, $SO_4^{2-}$), does not reveal any distinct patterns in the data.

The values for $Na^+$ are extremely low and chlorine is nil. The $Ca^{2+}$ values are quite high and therefore may be available for absorption by the chimpanzee gastrointestinal tract.

The control samples all have a significantly greater amount of organic carbon than the termite mound samples. The termite mound samples have an organic carbon concentration ranging between 0.68 and 1.3% while the control samples range between 1.3 to 4.9%.

An attempt to use t-tests on this data set proved partially conclusive. The pH values are on a log scale and are not subject to analysis by t-test; the ordinal scale numbers for the remainder of the data have a high variability around the mean for each variable; thus, there is low probability that the treatment and control groups come from different populations. However, the t-test results for the ingested samples (estimated P value $<0.05$) in the tm group show that K, Na and organic carbon are statistically significantly different from the controls. In the recollected set, K, Na, organic carbon and nitrogen are also statistically different from the controls ($P < 0.05$).

### *Toxin adsorption for sample set 1*

Toxin adsorption measurements were carried out to determine the binding properties of the soils to certain alkaloids. Table 3 shows the binding capacities of the soils from data set 1 for four alkaloids. Both control and ingested samples have similar binding capacities and do not differ significantly ($\chi^2$ test, $P > 0.1$).

Table 3. Toxin adsorption analysis of sample set 1, of control (c) and termite mound (tm) soils.

| Sample | | Adsorption (%) | | | |
|---|---|---|---|---|---|
| | | Lupanine | Quinine | Sparteine | Atropine |
| 1 | tm | 94 | 98 | 95 | 92 |
| | c | 94 | 93 | 92 | – |
| 2 | tm | 83 | 88 | 94 | 87 |
| | c | 91 | 84 | 91 | 87 |
| 3 | tm | 90 | 96 | 96 | 75 |
| | c | 85 | 94 | 88 | 27 |
| 4 | tm | 81 | 82 | 94 | 78 |
| | c | 80 | 87 | 86 | 85 |
| 5 | tm | 80 | 93 | 96 | 68 |
| | c | 84 | 79 | 90 | 72 |
| 6 | tm | 87 | 92 | 93 | 68 |
| | c | 84 | 79 | 90 | 72 |
| 7 | tm | 83 | 91 | 98 | 68 |
| | c | 81 | 94 | 93 | – |
| 8 | tm | 90 | 94 | 98 | 62 |
| | c | 87 | 92 | 96 | 50 |
| 9 | tm | 74 | 94 | 94 | 62 |
| | c | 76 | 93 | 95 | 88 |
| 10 | tm | 54 | 89 | 94 | – |
| | c | 58 | 84 | 91 | 78 |

A slight difference can be seen between the four individual alkaloids which have differing physiochemical properties: mean binding was 73.8 ± 10.1 (SD)% for atropine, 81.6 ± 11.3% for lupanine, 91.7 ± 45.4% for sparteine, and 95. ± 1.75 for quinine; all means except those between atropine and lupanine differ significantly (t-test, $P < 0.05$). An equivalent amount of charcoal would bind 100% of the alkaloids (Wink *et al.* 1993).

### *Geochemistry*

Geochemical analyses, performed on 10 termite mounds and nine control soil samples, allowed determination of the concentrations of major, minor and trace elements. The mean concentrations for 36 elements are displayed in Table 4, along with standard deviations and the mean elemental concentration ratios of ingested to control soils.

Both sets of samples, especially the termite mound group, are relatively high in Al and relatively low in many of the other elements, supporting the finding (above) of a metahalloysite/halloysite mineralogy, with the ingested soils tending to be more Al-rich than the controls. The lower levels of Hf in the ingested samples, relative to the controls, may indicate that the controls are more silica-rich, if Hf proves to be correlatable with zircon.

The ratios of termite mound to control soils also illustrate the differences in elemental concentrations between the two groups of sample material. Approximately 73% of the measurable elements (22/30 elements) have termite mound to control ratios greater than 1, reinforcing the possibility that chimpanzees may be selecting a more enriched material to supplement their diet. While we do not yet fully understand the importance of all of the chemical elements reported here, in terms of nutrition, diet and zoopharmacognosy, the fact that the soils of which they are part are comestible may mean that some, or many, of them have some physiological significance.

### *Microbiology*

The number of microorganisms obtained by dilution plating sample set two (Table 5) varied greatly from sample to sample. Overall, the following patterns were seen in the recollected samples:
(1) unicellular bacteria were more abundant in the control samples than in the termite mound samples in all but samples 2a and 7a; (2) filamentous bacteria were more abundant in the termite mound samples than in control samples except for sample 7a where numbers were equal; and (3) fungi were more abundant in the control samples, except in sample 10.

The control soils contained greater numbers of unicellular bacteria and fungi than termite mound soils. Although the variances were high, there was some indication that unicellular bacteria numbers were not closely correlated with soil type but that filamentous bacteria and fungi could have been.

Table 4. Geochemistry of sample set 1 of control (c) and termite mound (tm) soils. Concentrations in ppm unless otherwise indicated. ⩽: Detection limit at a 68% level of confidence.

| Element | tm samples Mean (n = 10 ) | tm samples SD | c samples Mean (n = 9 ) | c samples SD | tm : c Mean | tm : c SD |
|---|---|---|---|---|---|---|
| Aluminium (%) | 11.2 | 1.1 | 8.4 | 0.5 | 1.3 | 0.3 |
| Calcium (%) | 0.9 | 0.8 | 1.0 | 0.9 | 0.9 | 3.1 |
| Iron (%) | 2.8 | 1.2 | 2.3 | 0.5 | 1.2 | 1.2 |
| Potassium (%) | 2.1 | 0.5 | 2.1 | 0.5 | 1.0 | 1.6 |
| Magnesium (%) | 0.99 | 0.21 | 0.82 | 0.17 | 1.2 | 0.6 |
| Sodium (%) | 0.59 | 0.66 | 0.68 | 0.65 | 0.9 | 3.5 |
| Arsenic | ⩽0.9 | 0.4 | ⩽0.88 | 0.4 | ⩽1.1 | 1.5 |
| Barium | 1150 | 150 | 1190 | 200 | 1.0 | 0.3 |
| Bromine | ⩽3.4 | 0.8 | ⩽3.0 | 0.8 | ⩽1.1 | 0.7 |
| Cerium | 115 | 24 | 74 | 13 | 1.6 | 0.7 |
| Chlorine | ⩽93 | 42 | ⩽100 | 64 | ⩽0.9 | 1.6 |
| Cobalt | 8.8 | 2.4 | 6.2 | 1.6 | 1.4 | 1.0 |
| Chromium | ⩽16.0 | 2.4 | ⩽12.0 | 2.0 | ⩽1.3 | 0.5 |
| Cesium | 2.0 | 0.5 | 1.4 | 0.3 | 1.4 | 0.8 |
| Dysprosium | 5.0 | 1.4 | 3.0 | 0.9 | 1.7 | 1.2 |
| Europium | 2.2 | 0.4 | 1.3 | 0.4 | 1.7 | 0.9 |
| Iodine | 9.5 | 5.5 | ⩽8.0 | 3.6 | ⩽1.2 | 1.9 |
| Gallium | 31 | 14 | ⩽29.6 | 22 | ⩽1.1 | 2.2 |
| Hafnium | ⩽8.8 | 1.1 | ⩽10.7 | 2.3 | ⩽0.8 | 0.3 |
| Lanthanum | ⩽67 | 13 | ⩽39 | 5.1 | ⩽1.7 | 0.7 |
| Lutetium | 0.50 | 0.13 | 0.29 | 0.07 | 1.7 | 0.9 |
| Manganese | 624 | 203 | 528 | 232 | 1.2 | 1.2 |
| Neodymium | 34 | 8 | 18.0 | 3.5 | 1.8 | 1.0 |
| Nickel | ⩽22.0 | 3 | ⩽18.3 | 2.2 | ⩽1.2 | 0.4 |
| Rubidium | 116 | 23 | 100 | 19 | 1.2 | 0.5 |
| Antimony | ⩽0.14 | 0.04 | ⩽0.10 | 0.02 | ⩽1.4 | 0.9 |
| Scandium | 13.2 | 2.7 | 10.8 | 3.6 | 1.2 | 0.8 |
| Samarium | ⩽8.1 | 1.6 | ⩽4.8 | 0.9 | ⩽1.7 | 0.8 |
| Strontium | 200 | 90 | 200 | 90 | 1.0 | 1.3 |
| Tantalum | 0.89 | 0.22 | 0.86 | 0.23 | 1.0 | 0.7 |
| Terbium | 1.1 | 0.2 | 0.6 | 0.1 | 1.8 | 0.8 |
| Thorium | 17.5 | 3.9 | 11.6 | 1.9 | 1.5 | 0.8 |
| Titanium | 4750 | 650 | 3200 | 890 | 1.5 | 0.6 |
| Uranium | 2.9 | 0.5 | 2.1 | 0.3 | 1.4 | 0.6 |
| Vanadium | 89 | 21 | 64 | 16 | 1.4 | 0.8 |
| Ytterbium | 3.8 | 0.7 | 2.2 | 0.4 | 1.7 | 0.8 |

## DISCUSSION

Both humans (Hunter 1993, Vermeer & Ferrell, 1985) and other animals (Mahaney *et al.* 1996a, Ruggiero & Fay 1994) have been observed ingesting soil from termite mounds. In these studies, the investigators reported that termite mound soil specifically, not the surrounding topsoil, was always selected. In a previous study from the Mahale Mountains by Mahaney *et al.* (1996b) parasitological and behavioural evidence suggested a possible use for the ingestion of termite mound soil for obtaining temporary relief from gastric irritation and/or diarrhoea in chimpanzees. A similar study of geophagy, ingesting exposed clayey substrates, in rhesus monkeys also suggested the antidiarrhoeal properties of the behaviour (Knezevich 1995, Mahaney *et al.* 1995a). In this group of highly parasitized monkeys, geophagy was a frequent occurrence among a large

Table 5. Mean colony forming units (CFUs) × $10^{-3}$ $g^{-1}$ of soil of unicellular (UB) and filamentous bacteria (FB) and filamentous fungi (FF) for the re-collected soils of sample set 2.

| Sample | | c | tm | c : tm |
|---|---|---|---|---|
| 1 | UB | 21600 | 23200 | 0.93 |
| | FB | 70 | 120 | 0.58 |
| | FF | 170 | 65 | 2.62 |
| 2 | UB | 72400 | 6500 | 11.14 |
| | FB | 0 | 140 | 0 |
| | FF | 2400 | 13 | 184.62 |
| 7a | UB | 5800 | 2400 | 2.42 |
| | FB | 70 | 70 | 1 |
| | FF | 10 | 1.80 | 5.56 |
| 7b | UB | 1880 | 3100 | 0.61 |
| | FB | 0 | 90 | 0 |
| | FF | 46 | 3.30 | 13.94 |
| 8 | UB | 15000 | 38800 | 0.39 |
| | FB | 50 | 1000 | 0.05 |
| | FF | 2400 | 190 | 12.63 |
| 9 | UB | 21600 | 72000 | 0.30 |
| | FB | 0 | 1600 | 0 |
| | FF | 920 | 80 | 11.50 |
| 10 | UB | 2400 | 4000 | 0.60 |
| | FB | 40 | 150 | 0.27 |
| | FF | 5.20 | 15 | 0.35 |

proportion of its members. Observations of chimpanzees at other sites across Africa show too that at times all members of a group may engage in geophagy on a daily basis (e.g. Goodall 1986). Trends appear to vary from group to group and may be related to seasonal or regional differences in diet as well.

This suggests to us the possibility that geophagy can be a part of their normal foraging routine and supports the fact that mild gastro-intestinal upsets, due to a secondary-plant-rich diet, may also benefit from the properties of ingested termite mound soil. We maintain that regardless of the cause, geophagy has a physiological basis. It is not coincidental that chimpanzees select termite mound soil for consumption even when there is no termite population resident in the mound. The chimpanzees of the Mahale Mountain group have not been observed to habitually feed on termites in the 35-plus y of research. They fish for carpenter ants in trees but not termites in mounds. Furthermore, at sites where termite mounds are not present or obvious, animals select the clayey soils, brought up to the surface by fallen trees or from areas of exposed hillside. Subsurface soil brought to the surface and used to build the mound is the subject of this investigation. Therefore an understanding of the physical and chemical properties of termite mound soil is relevant.

The higher Hf concentrations reported for the control soils may correlate with higher amounts of zircon in them, a relationship resulting from a selective avoidance of heavy minerals by the termites in mound construction. This relationship should be explored in depth with a larger population of samples.

The concentrations of the majority of chemical elements detected in our analyses were greater in the termite mound samples than in the control group.

The effect of termite mound-building in East Africa on soil properties have been studied extensively in the past (Arshad 1981, Hesse 1955, Lee & Wood 1971, Pomeroy 1976). One of the predominant features of termite activity is their influence on the structure of their ecosystem. For example, termites will chemically and physically alter the soil from its original composition when constructing their mounds. This alteration may form a soil with a clay and mineral-rich composition often derived from considerable depth beneath the surface, possibly producing a soil matrix more desirable for ingestion.

Results from experiments performed on termite mound soil from East Africa have shown increased concentrations of major elements such as calcium (Arshad 1981, Hesse 1955, Watson 1975), magnesium (Lee & Wood 1971, Woods & Sands 1978) and potassium (Lee & Wood 1971, Woods & Sands 1978). Ore-forming elements, such as chromium (Prasad & Saradhi 1984), vanadium (Prasad & Saradhi 1984) and uranium (Le Roux & Hambleton-Jones 1991) have also been found to be more concentrated in termite mound soil. With respect to the medical implications of geochemically enriched soil, it can act as protection against diseases caused by nutritional deficiencies. The consistent difference between the termite mounds and nearby control soils suggests that the chimpanzees may be critically selecting a chemically enriched clayey natural earth to supplement their diet. The well-weathered minerals in the termite mound soil undoubtedly provide a great range of chemical elements to the foraging chimpanzees. As shown by SEM analysis, the prevalence of altered hematite and epidote provide Fe and Ca. Indeed, the prevalence of Fe coatings on orthoclase and quartz sands, which prevail in the termite soils reported here, strongly support the interpretations of a previous study in the same area (Mahaney *et al.* 1996b). This relationship is also supported by the electron microprobe data that show higher Fe in the termite mound samples relative to the control group.

Mahaney *et al.* (1996b) suggested that K and Fe, if in a form available for absorption by the gastro-intestinal tract, could have nutritional importance. Iron levels found here in the termite mound soil average 3.3%, which is high enough to provide a chemical benefit when ingested. The high levels of Fe, as indicated from the soil colours, and verified by INAA in both groups of soil, may be important to chimpanzee health. However, the control group soils are suspected to contain undesirable properties (e.g. bacterial contamination) as indicated by darker colours, and higher organic carbon content.

In this study total K is most likely not a highly important benefit of geophagy. Data set 1 has a ratio of <1 and data set 2 (not reported here) has a termite mound over control ratio equal to 1. Exchangeable K, however, as reported in Tables 2a and 2b shows that termite mound soil is statistically different from the control group. Overall, the greater concentrations of all chemical elements seen in the termite mound soils, compared to the topsoils, suggest that chimpanzees can obtain adequate amounts of them by ingesting termite mound soil. Moreover, the higher pH of these soils, commonly observed in tropical soils (Sanchez 1976), may increase nutrient availability. The higher pH also indicates that termite mound soils could have an antacid action in the gut.

The soil chemistry shows little statistical difference of total salts, exchangeable Ca and Mg, and C/N ratios between the termite mound and control soils, which eliminates them as possible stimuli in this case.

The most important characteristic of soils used for mound construction is the proportion of sand, silt and clay (Lee & Wood 1971). Studies have shown that the mounds are generally richer in clay than the surrounding soil (Hesse 1955, Lee & Wood 1971). This may be because the mounds are built from subsoil that is richer in clay than the surrounding topsoil (Hesse 1955). Termite mounds are generally not found on sands where there is inadequate binding material, i.e. clay (Goudie 1988).

In this study, particle size analysis shows that all termite mound samples contain *c.* 20% more clay than the surrounding soil. Finer grained soils offer a greater surface area for acid extraction of nutrients at gastric pHs and increase the uptake of toxins by clay mineral surfaces. Finer grained material also offer a safer alternative to forest floor soil as they are likely to contain lower levels of harmful soil-inhabiting-stage parasite larvae and ova. Moreover, the hardness of the mound material is no doubt related to alternating wet and dry climatic cycles throughout the year with the dry part of the cycle creating an armouring effect that preserves the mound once constructed.

In most studies of geophagy in animals, the soils contain clay minerals which are 1 : 1 layer silicates (Mahaney *et al.* 1995a,b, 1996a, 1997). Humans also prefer to ingest 1 : 1 clay minerals and the reason suggested for this has been that 2 : 1 minerals may absorb required nutrients, such as Fe and Zn, unlike the 1 : 1 clays that are not as effective (Vermeer & Ferrell 1985).

The 1 : 1 clay minerals play an important role as a base for pharmaceutical preparations aimed at remedying gastro-intestinal problems. Specifically, kaolinite forms a protective cover on the mucous membrane of the digestive tract and adsorbs bacteria and toxins (Vermeer & Ferrell 1985). Kaolinite is considered quite safe for internal use, as it is a chemically pure mineral (Vermeer & Ferrell 1985). Metahalloysite, the 1 : 1 clay mineral found in most of the ingested samples, may adsorb tannins and toxins that the chimpanzees would otherwise not be able to detoxify (Hladik 1977, Oates 1978). Since chimpanzees eat large amounts of leaf material, along with fruits in various stages of ripeness, they cannot avoid contact with dietary toxins or antinutrients that most plants produce in defence of herbivores and other plant predators (Wink 1993b). In general, the controls and termite mound soils were found to effectively bind alkaloids considered to be typical animal toxins in plants (Wink 1993b). In many leaves, alkaloid concentrations range from 100 to 500 $\mu g\ g^{-1}$ fresh weight. According to Table 3, 100 mg of soil would be adequate to bind most of the alkaloids present in 1–10 g of leaves.

The chimpanzees of the Mahale Mountains have been closely observed since 1965 (Nishida *et al.* 1983, Nishida 1990). As part of this work, the plant food available to the chimpanzees has been well documented (Nishida & Uehara 1983). Chimpanzees forage on the leaves, bark and pith of a variety of different plant species and the levels of condensed tannins in many of these wild tropical plants are quite high (Gartlan *et al.* 1980). Condensed tannins, which are plant secondary metabolites, may have detrimental effects in many mammals by reducing protein digestibility (Mole & Waterman 1987). Since the concentrations of these chemicals are sometimes high enough to be toxic, animals without specialized guts may adopt methods of detoxification in order to tolerate the tannin levels in their diet. In veterinary medicine, it is common practice to use kaolin as an antacid (Daykin 1960). The clays in termite mound soil could also function as an antacid in response to dietary imbalances. Over half of the samples had pH values between 7.2 and 8.6. The termite mound soils might act as a buffering agent to counteract the effects of acidic foods. It is assumed that chimpanzees would benefit from the antacid effects of termite mound soil the same way humans obtain relief from the pharmaceutical Kaopectate™.

Detoxification is a likely benefit of geophagy, as all termite mound soils displayed superior alkaloid-binding capacities. It was shown that the alkaloid adsorption capacities of both the termite mound and control samples were comparable. However, micro-organisms found in forest floor soils (control samples) are directly related to the organic matter content so that areas rich in organic matter have the largest bacterial numbers. Some microbes found on the forest floor can cause disease or in extreme cases death if ingested.

It is particularly interesting that fungi are usually higher in control soils while filamentous bacteria are higher in the ingested termite mound soils. With respect to geophagy, it would appear that chimpanzees are selecting soils relatively high in filamentous bacteria, except for sample 7a. However, it may not be a matter of this sample being low in filamentous bacteria, but of the control sample being somewhat high. Similarly, the other example where fungi are higher in the ingested sample (sample 10), is because fungi are low in the control sample, not high in the termite mound sample.

The filamentous bacteria are probably all members of the genus *Streptomyces*, which are the most prolific micro-organisms known in the production of medically useful secondary products such as antibiotics. Fungi, while producing some antibiotics, such as penicillin, are also notorious for producing extremely toxic metabolites (Miller 1995). By consuming the soil of termite mounds, instead of top soil, chimpanzees may be avoiding toxic fungi, or obtaining higher than normal doses of *Streptomyces* products. As these speculations are highly premature intensive microbiological investigations of soils consumed by chimpanzees are presently being conducted.

In conclusion, geophagy in chimps appears to be a multifunctional behaviour ranging from dietary (e.g. mineral supplementation) and medical benefits (antacid and antidiarrhoeal properties) to the detoxification of dietary secondary metabolites (such as alkaloids). Because of these many-sided benefits, it is not surprising that geophagy has a wide distribution in animals and humans.

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