

Geophagy in the golden-faced saki monkey (*Pithecia pithecia chrysocephala*) in the Central Amazon

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Abstract

The golden-faced saki monkey *Pithecia pithecia chrysocephala* (Cebidae, Primates) was observed eating soil from termite nests during a long-term study of a family group in a Central Amazonian forest fragment. In this paper we describe the behaviour involved in the geophagy in these monkeys, and the results of geochemical and physical analyses of the termite nest material, as well as root mat and topsoil samples below the trees, in order to clarify the possible reasons for it. The sakis ate soil from nine arboreal termite nests on 26 soil feeding-bouts (in 853 observation hours); 25 soil feeding-bouts occurred in March 1987 (rainy season), during 19 days or 132 observation hours, and occupied 0.7% of the feeding time. Geophagy frequencies did not differ between sexes (17 feeding-bouts of four females and 8 for two males). Mineral composition was higher in arboreal termitaria than in the topsoil. Kaolinite was the major clay component. Tannin adsorptive capacity, tested through a modified radial diffusion method of Hagerman, was around 10–20%, similar to a control with kaolin (10–20%), but lower than bentonite or celite (30–45%). The observations reported here, although inconclusive as to the function of geophagy in this species, indicate that it is not a mineral supplement during times of scarcity or high consumption of leaves, as has been reported for other primates, nor that it is related to fruit consumption (redressing possible mineral imbalance), as has been suggested for some other frugivorous mammals. Our results do not rule out tannin adsorptive hypothesis for the ingestion of clays, but, being an irregular habit, we argue that it is most likely related to rare and occasional dietary components.

Key words: arboreal termitaria, Central Amazon, geophagy, *Pithecia*, rain forest, tannin adsorption, *Trichilia*

INTRODUCTION

The consumption of soil, geophagy or pedophagy, has been reported for reptiles (Marlow & Tollestrup, 1982), birds (Emmons & Stark, 1979; Mayer & Brand, 1982; Izawa, 1993), and mammals (Weeks & Kirkpatrick, 1976, 1978; Oates, 1978; Mayer & Brand, 1982; Izawa, 1993). The principal functions have been attributed to (1) mineral supplementation (Mayer & Brand, 1982; Vermeer & Ferrell, 1985; Davies & Baillie, 1988; Mahaney, Watts & Hancock, 1990; Heymann & Hartmann, 1991; John & Duquette, 1991 in Mahaney, Aufreiter & Hancock, 1995); (2) adsorption of plant tannins and toxins (Hladik, 1977*a, b*; Oates, 1978) and/or counteraction of gastric upsets or diarrhoea (Said, Shibel & Abdullah, 1980; Vermeer & Ferrell 1985; John & Duquette, 1991 in Mahaney *et al.*, 1995;

Mahaney *et al.*, 1993, 1995; Knezevich, 1998); (3) antacid action of clays (Morris, 1927 in Poirier, 1970) or adjustment of pH in the stomach forechamber (Oates, 1978); (4) tactile sensations in the mouth (Hladik & Gueguen, 1974); (5) tradition (Mahaney *et al.*, 1990). In humans, geophagy is also related to certain parasitic infestations, as a source of iron to counteract anaemia caused by ancylostomiasis (Neves, 1991).

However, the function of this behaviour is still not known, and may vary from species to species, and even within a species it may serve different functions at different times (Davies & Baillie, 1988; Heymann & Hartmann, 1991; Izawa, 1993).

Mineral supplementation may be related to diets with high foliage content year-round or at times of food scarcity. Sodium is most frequently suggested as the target element (see Weir, 1972; Mayer & Brand, 1982).

At times of fruit abundance, however, potassium/sodium ratios can reach excessive values because of the high potassium content in fruits. In this situation, sodium would also be needed (Weeks & Kirkpatrick, 1976, 1978; but see Hladik, 1977*b*, and Sick, 1949). In the tortoise, calcium appears to be the target for long-term geophagy (Marlow & Tollestrup, 1982); while in parrots and macaws sodium and magnesium are also implicated (Emmons & Stark, 1979). At high altitudes, iron is considered the main candidate for African buffalo (Mahaney, 1987), and iron and sodium are considered the key elements for the mountain gorilla (Mahaney, Watts *et al.*, 1990). Iron is also the main available element for chimpanzee in Kibale (Mahaney, Milner *et al.* 1997). For macaques *Macaca mulatta*, however, the iron content of leaves and fruits is believed to cover their physiological requirements, and clay ingestion may be important as an adsorbent of plant tannins (Lindburg, 1977).

The tannin adsorption hypothesis originated from observations on the consumption of clay with acorns and potatoes in human populations (Hladik, 1978; Johns, 1986). Both adsorption of plant tannins and toxins and/or counteraction of gastric upsets or diarrhoea are related to kaolinite (Vermeer & Ferrell, 1985) or halloysite, a hydrated form of kaolinite clay (see Mahaney, Aufreiter *et al.*, 1995). The lattice structure of kaolinite is believed to function as an adsorbent for toxins and bacteria (Said *et al.*, 1980) and has been reported to form a protective coat on the mucous membrane of the digestive tract (Swinyard, 1965 in Vermeer & Ferrell, 1985). Smectite (montmorillonite) swells when wet, and halloysite may have a similar effect because of its capacity to adsorb molecular water (Mahaney, Aufreiter *et al.*, 1995).

The antacid function of ingested soil may derive from both the adsorptive properties of clay minerals and the buffering capacity of the clay fraction's exchange capacity, and from a higher pH of the soil. In some primates with sacculated stomachs, the adsorption of fatty acids from rapid anaerobic fermentation can prevent fatal 'acidosis' (Goltenboth, 1976, in Davies & Baillie, 1988). Also, a higher pH from the ingested earth helps maintain a higher pH in the stomach forechamber, where fermentation occurs (Oates, 1978; see also Morris, 1927, in Poirier, 1970). This higher pH also can enhance nutrient availability (Sanchez, 1976, in Davies & Baillie, 1988).

Tactile sensation in the mouth was suggested by Hladik & Gueguen (1974) after investigating thoroughly either the soil or the diet for all mineral contents.

The hypothesis of tradition appeared to explain the use of soil by one group of mountain gorillas (Mahaney, Watts *et al.*, 1990). No other gorilla group studied ate soil at all.

Geophagy correlation with endoparasitism is rooted in Brazilian (Afro-Brazilian?) folklore. People say that if someone eats soil, it is a sign that he has worms, but we could find nothing in the literature besides Vermeer & Frate's (1979) study in rural Mississippi. In this case, geophagy could be a therapeutic mediator supple-

menting minerals (Neves, 1991) and counteracting diarrhoea and intestinal problems (Knezewich, 1998). Therapeutic behaviour in non-human primates appears also as charcoal consumption to reduce dietary toxins by red colobus monkeys (Struhsaker, Cooney & Siex, 1997) and as medicinal plant use against a strongyle nematode by chimpanzees (Huffman *et al.*, 1997).

New World primates (*Saguinus mystax*, *Alouatta seniculus*, *A. caraya*, *Ateles belzebuth*, *Chiropotes albinasus*, *Callicebus personatus melanochir*) eat soil (Izawa, 1975, 1993; Heymann & Hartmann, 1991, Bicca-Marques & Calegario-Marques, 1994; Ferrari, 1995; Müller, Ahl & Hartmann, 1997). Heymann & Hartmann (1991) suggest that mineral supplementation is the important factor, while Izawa (1993) arrived at no decisive conclusion and Müller *et al.*, (1997) support adsorption of plant toxins.

Here we report on geophagy by the golden-faced saki monkey *Pithecia pithecia chrysocephala*. We describe this behaviour and investigate its possible mineral supplementation and tannin adsorption functions with regard to the monkeys' feeding ecology and life in a forest fragment. We compare geochemistry and mineralogy of two termite nests and nearby surface soil samples, and test their tannin adsorptive capacity. Our aim is to determine if potential chemical or mineral stimuli are present in the samples studied, which can explain this aspect of the sakis' feeding behaviour.

METHODS

Study site

The study was conducted in a 10 ha elongate forest fragment known as 'Colosso', along a creek ravine (2°25'S, 59°50'W) of the Biological Dynamics of Forest Fragments Project of the Smithsonian Institution and the National Institute for Amazon Research (INPA), 80 km north of Manaus, Amazonas, Brazil (see Lovejoy & Bierregaard, 1990).

Soils from the region are clayish, and classified as Red Yellow and Alic Yellow Podzolic with high clay content and poor in nutrients (Ranzani, 1980; Chauvel, 1982). The dominant clay fraction is comprised of kaolinite (80%), gibbsite (10%) and goethite (Chauvel, 1982).

The vegetation is lowland *terra firme* tropical rain forest. Mean annual rainfall is 2500 mm and mean temperature is 24.8°C. The rainy season extends from November to May, with a dry period from June to October. Flowering peaks in October–November and fruiting in January. Both flowers and fruits are scarce for the rest of the year (Setz, 1993).

Subjects

The study group of golden-faced saki monkeys *P. p. chrysocephala* consisted of 6 or 7 individuals. Most were habituated to the presence of human observers in 1985, when a long-term study on their ecology was begun

Table 1. Hours of observation on the ecology of golden-faced sakis in a forest fragment in Central Amazon

	1985	1986	1987	1988	1989	1990	Total
Jan				45			45
Feb	X		2			4	6
Mar			132			4	136
Apr			15			15	30
May			4				4
Jun			4		4	1	9
Jul		133	14		2		149
Aug	2 ^a		55				57
Sep	1 ^a		55		3	16	75
Oct	6 ^a		28		37	33	104
Nov	9		33		34	59	135
Dec	27		66		10		103
Total	45	133	408	45	90	132	853

^a Saki habituation.

(Setz, 1993). In 1987, the group consisted of 1 adult male, 2 adult females, 1 young female and 2 one-year-old juveniles (a female and a male). Since golden-faced sakis are sexually dichromatic from birth (Hershkovitz, 1987), sex was easily recognized.

Data collection

We followed the group throughout the day (from 06:00 to 16:00; Setz, 1993). Systematic data on activity budgets and the diet were collected by scan sampling at 10 min intervals. All occurrences of geophagy were also recorded as soil feeding-bouts (sfb) or the length of time a single animal was recorded eating soil from a single termite nest (definition adapted from Klein & Klein, 1974), including the identity of the individual, time, and location of the termite nest. Total sampling time from 1985 to 1991 was 853 h (Table 1). Information on diet, time budgets and use of space by the golden-faced sakis, as well as vegetation analyses of the forest fragment, are presented elsewhere (Setz, 1993).

We collected 2 earth samples from each of 2 arboreal termite nests (Nos 9A and 16AE; Fig. 3) where the sakis had been feeding, one from the upper part and the other from the lower part of the nest. A sample was also collected from the root mat in the surface (0–5 cm depth) and another from the topsoil (5–15 cm) near the base of the tree with the nest. The samples were air-dried in the field, and oven-dried (<40 °C) in the laboratory, ground up in a mortar and sieved (2 mm mesh). Termites were identified by Eliana M. Cancellato, and the ants by Carlos Roberto Brandão, at the Zoology Museum of the University of São Paulo (MZUSP – col. no. 9550).

Geochemical and physical analyses

Ammonium acetate-extractable cations (Na, K, Ca, Mg) were determined as in Stark (1970), Emmons & Stark

(1979), Ranzani (1980), Chauvel (1982), Davies & Baillie (1988), Izawa (1993). 5 cm³ of soil were leached with 50 ml of ammonium acetate at pH 7. P was extracted by ion exchange resin (Amberlite IRA-400 and IR-120, 0.4 mm mesh; Raij & Quaggio, 1983), and organic matter was determined by the colorimetric method.

Two sample preparations were used for metal determinations. In one set, samples were dried for 2 h at 110 °C then digested with 50 ml 2 M HCl at 30 °C. After 4 h, samples were centrifuged and solutions were made up to a final volume of 50 ml with distilled and deionized water. Another sample was ignited at 800 °C for 3 h. A portion of the sample was digested by heating on a hotplate in 10 ml of concentrated HNO₃. After centrifugation samples were brought to 50 ml final volume. Na, K, Mg, Zn, Cu, Co and Ni were determined by atomic absorption spectrometry using an air-acetylene flame, and Ca and Al using nitrous oxide-acetylene. Ionization of Na, K, Ca and Al was suppressed by diluting samples and adding an excess of caesium chloride (final concentration 1000 µg ml⁻¹). A Varian AA 1475 atomic absorption spectrometer was used for all determinations.

For X-ray diffractometry, samples were prepared according to a modified procedure after Jackson (1969; Appendix).

Tannin adsorption analysis

The adsorptive capacity of tannins by earth samples was determined by comparing tannic acid (Ecibra 0180) solutions with the same solutions added to earth, using the radial diffusion method of Hagerman (1987). In this assay, a visible precipitation ring develops as tannin from the solution being tested diffuses from a well into a protein-containing agar slab. The amount of tannin in the solution is proportional to the area of the precipitation ring. 1 ml of tannic acid solution (0.05 M, 0.1 M and 0.2 M) was added to 625 mg of each sample. For comparative purposes, the procedure was repeated using kaolin (Reagen 10317), bentonite (Sigma B3378) and celite (Merck 365). For bentonite and celite, a sample of 39 mg with diluted tannic solutions (400 µl tannic acid solution and 6 ml water) was used, because of the great liquid adsorption of these compounds. The same procedure was used for kaolin as for the earth samples. After 48 h, 300 µl of the supernatant was diluted with 700 µl of acetone. After 3 h the solution was applied to the plate wells (3 successive 8 µl aliquots). Petri dishes were covered, sealed with Parafilm and incubated at 30 °C. Precipitation ring diameters were measured after 48 h.

RESULTS

Frequency and seasonality of geophagy

Soil intake from nine arboreal termite nests was

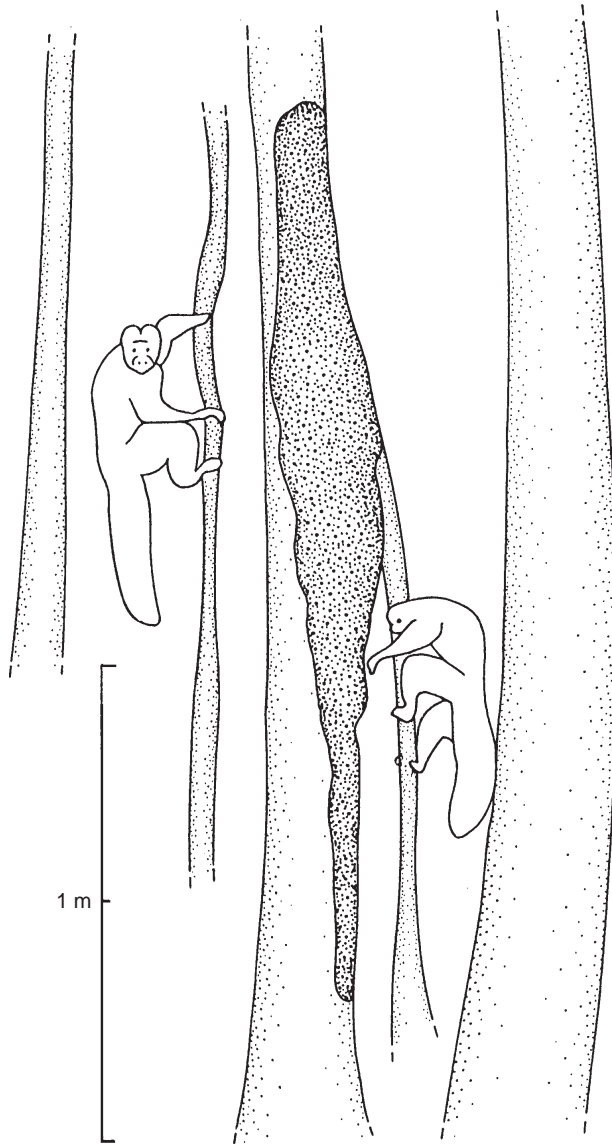


Fig. 1. Arboreal termite nest used by golden-faced sakis (drawn from photographs).

observed during 26 soil feeding-bouts (Fig. 1) during 853 observation hours (0.03 sfb/obs. h). Twenty-five soil feeding-bouts occurred in March 1987 (Fig. 2), comprising 0.7% of the feeding time (six scan records), estimated by scan sampling during 132 observation hours (0.19 sfb/obs. h) in nine (47%) from 19 obs. days. Nine soil feeding-bouts took place from 08:00 to 09:00 (36%) and nine others, from 11:00 to noon (36%). In November 1990, another soil feeding-bout was observed (D. A. Gaspar, pers. comm).

March is in the late wet season when fruit is abundant (10.9% of the species bearing fruits vs 5.6% in the dry season: Setz, 1993). Soil feeding was not observed in July 1986 (dry season, $n = 133$ obs. h, 19 days), when the sakis occasionally ate mature leaves (only 2% of the diet), nor during another 10-month observation period at the same site in 1987 ($n = 408$ obs. h, Table 1), nor later during periodic observations in 1989 and 1990 ($n = 222$ obs. h: Table 1).

Behaviour during geophagy

In all soil feeding-bouts observed, the saki descended to about 2 m from the ground, and using a tree or a liana near the nest, broke a bit off the termite nest and ate it (Fig. 1). Eighty per cent of the soil feeding-bouts lasted less than 3 min, and the longest took 6 min. On one soil feeding-bout, a female saki took two bits from the same termite nest (11 March, nest No. 2.5C: Figs 2 & 3). Only once (12 March, Fig. 2) did all six sakis eat soil in a 5-minute span, but on this occasion from two different termite nests (Nos. 16AE – 4 sfb and W – 2 sfb: Fig. 3). On 22 March six soil feeding-bouts occurred on four different occasions, over 3 h on three different termite nests (Fig. 2).

Gender differences

There were no gender differences in the frequency of geophagy. The four female sakis (66% of the six sakis) were responsible for 17 soil feeding-bouts (68% from 25). The average frequency of soil intake was 0.03 soil feeding-bouts per individual per observation hour, during March 1987 ($n = 132$ obs. h: Fig. 2). Although the young male was recorded more than the adult (6 vs 2 sfb), age considerations are problematic because of records of unrecognized females (11 sfb).

Association of geophagy with other foods

Fifteen (60%) soil feeding-bouts were preceded by fruit ingestion (pulp or seeds were the last things they had fed on, 1–17 min earlier), from six different plant species: *Trichilia* cf. *quadrijuga* (Meliaceae–8 sfb), *Inga* sp. (Mimosaceae–2 sfb), *Hevea guianensis* (Euphorbiaceae–2 sfb), *Licania apetala* (Chrysobalanaceae–1 sfb), *Duguetia latifolia* (Annonaceae–1 sfb), *Vitex* sp. (Verbenaceae–1 sfb). The saki which ate a fruit of *Vitex* sp. 2 min before soil, had eaten *Trichilia* cf. *quadrijuga* 5 min earlier. Apart from *Duguetia*, which also appeared in the diet of the sakis in April 1987, these fruit species were used only in March 1987.

Ten (40%) soil feeding-bouts occurred after ingesting new leaves from at least three different species: *Clarisia ilicifolia* and *Sorocea muriculata* (both Moraceae, each 1 sfb) and *Eschweilera tessmannii* (Lecythidaceae, 1 sfb). The leaves of both Moraceae species were used by the sakis in other months (December 1987 and July 1986, respectively), but they were not followed by geophagy.

Trichilia fruit pulp was one of the seven most consumed items in the rainy season (49 scan records or 5.5% of the feeding-time, about 80 fruit feeding-bouts: Setz, 1993). On the *Trichilia* trees, three of the six sakis would feed at the same time and alternate with the others, giving a considerably higher number of *Trichilia* fruit feeding-bouts than scan records. The high frequency (36%, 9 from 25 sfb) of soil ingestion after *Trichilia* is probably also related to the fact that the

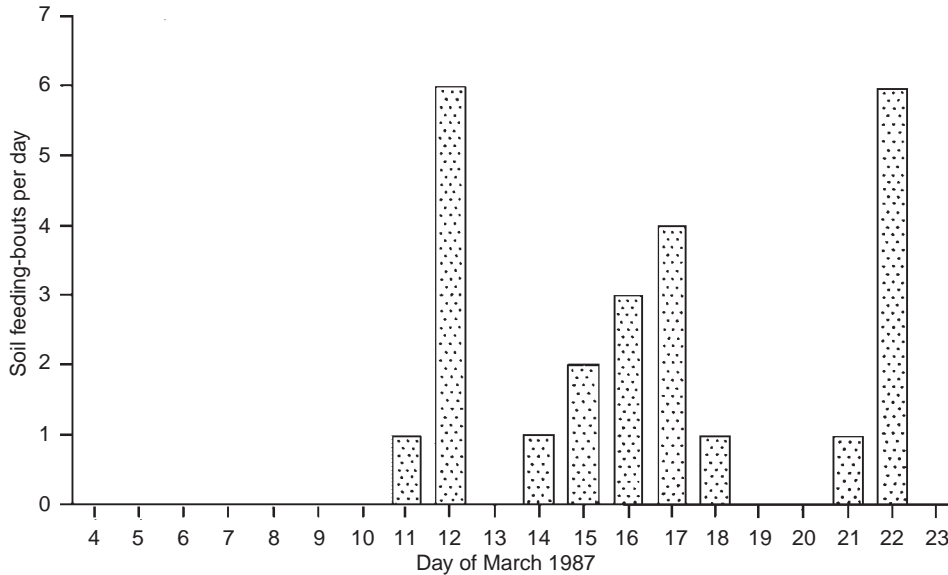


Fig. 2. Relation between soil feeding-bouts and sampling day for a habituated group of golden-faced saki monkeys near Manaus, Brazil. Apart from 13 March, when the sakis were not observed, 19 days summed 131.7 hours of observation.

three *Trichilia* cf. *quadrijuga* trees used were near the four most visited termite nests (Nos. 9A, 2.5C, 16AE and 16AW; Fig. 3).

We compared days with and without ingestion of termite soil to days where each of the six most-consumed plant species (*Helicostylis tomentosa*, Moraceae – pulp and immature seeds; *Theobroma subincanum*, Sterculiaceae – pulp only; *Inga alba*, Mimosaceae – pulp only; *Fusaea longifolia*, Annonaceae – seeds only; *Trichilia* cf. *quadrijuga* – pulp and seeds; *Passiflora nitida*, Passifloraceae – pulp; seeds were observed in faecal samples) were eaten or not through a chi-square test. Only *Trichilia* gave a significant value ($\chi^2 = 4.23$, $P < 0.05$, d.f. = 1), showing a positive daily co-occurrence. Fruit from another *Trichilia* species (*T. micrantha*) was eaten by the sakis in October 1990.

Faecal samples

Faecal samples collected opportunistically early in the morning in March 1987 ($n = 9$ from 5 days), as well as during other observation periods ($n = 7$ from 4 days, July 1986; $n = 10$ from many days, April–July 1987), showed no signs of diarrhoea (E. Setz, unpubl. data). No parasite investigation was performed.

Termite nests

The nine termite nests visited were on tree trunks at a height of 2 m. They were oval-shaped (about 40 cm width \times 100 cm length and with the long axis aligned to the tree trunk; Fig. 1) and dark brown, almost black in colour. The termite-nest soils were hard and dry, and judging by the washed-out look of their surface and the absence of recently deposited soft soil, the termitaria

were old. No termites were found when removing pieces up to a depth of 3 cm. Termites were found only in the area of direct nest/trunk contact.

Termite species

One termite nest (No. 9A) was occupied by *Nasutitermes* sp. (Termitidae, Nasutiterminae) and the ant *Dolichoderus laminata* (Mayr) (Formicidae, Dolichoderinae), and the other (No. 16AE), by an undescribed species of *Cavitermes* (Termitidae, Termitinae). *Nasutitermes* builds its nests on or inside tree trunks, in the subsoil or at the soil surface, while *Cavitermes* occurs in nests built by other species, where they feed on the organic soil of the nest (Mathews, 1977).

Topsoil

In the study area, there were exposed soils at the bases of trees uprooted by wind, and creek banks, which, although as accessible as the termite mounds, were never exploited by the sakis during the long-term study period. Digging samples of soil near the trees with the termitaria was difficult because of the dense, at least 5-cm-thick root mat under the leaf litter and above the soil surface.

Geochemistry of termitaria, root mat and topsoil

All the earth samples were acid, with pH values (in water) between 4.0 and 4.8. Termite nest soils presented a total extractable cation and a cation exchange capacity (CEC) considerably higher than the topsoil, and the root mat presented intermediate results (Table 2). The

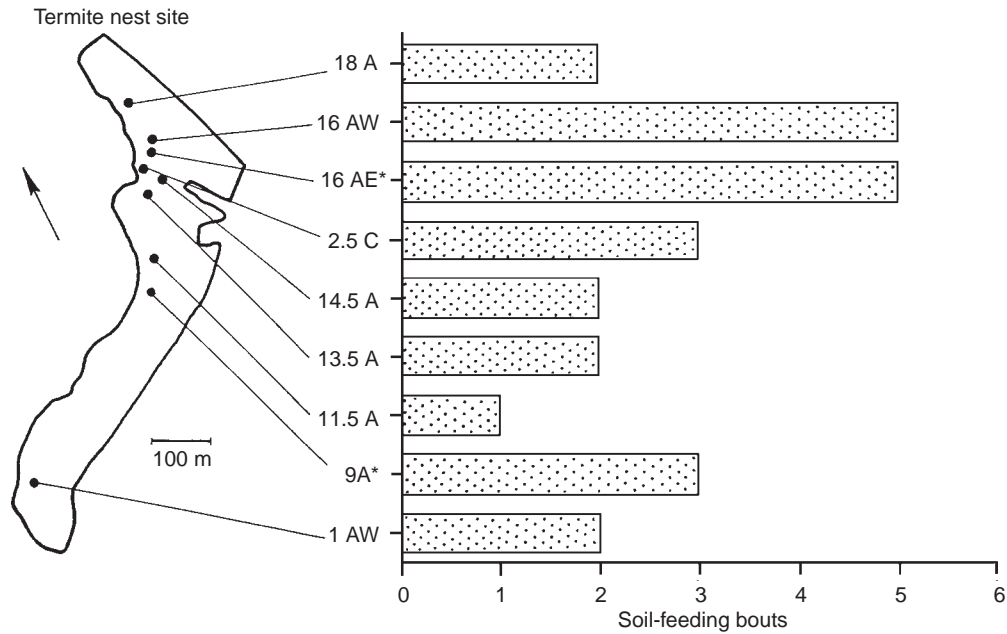


Fig. 3. Relation between saki soil feeding-bouts and termite nest, showing also the geographical distribution of the nests in the forest fragment.

Table 2. pH, extractable cations and cation exchange capacity of earth from arboreal termite nests consumed by *Pithecia pithecia chrysocephala*, and of root mat and topsoil samples under the termite nest trees. *n*, number of samples analysed (see text)

	Earth sample		
	Termite nests (<i>n</i> = 4)	Root mat (<i>n</i> = 2)	Topsoil (<i>n</i> = 2)
pH, H ₂ O	4.3 ± 0.3	4.1 ± 0.0	4.1 ± 0.1
pH, CaCl ₂	3.5 ± 0.4	3.2 ± 0.0	3.6 ± 0.1
P mg/cm ^{3a}	38 ± 12	19 ± 3	12 ± 2
Na meq/100 cm ^{3b}	0.05 ± 0.04	0.03 ± 0.01	0.02 ± 0.01
K meq/100 cm ^{3b}	0.26 ± 0.06	0.13 ± 0.06	0.004 ± 0.003
Ca meq/100 cm ^{3b}	0.55 ± 0.13	0.07 ± 0.04	0.03 ± 0.03
Mg meq/100 cm ^{3b}	0.54 ± 0.19	0.20 ± 0.0	0.05 ± 0.0
Total extractable cations	1.7 ± 0.2	0.7 ± 0.3	0.2 ± 0.0
H + Al meq/100 cm ³	37.1 ± 6.3	20.7 ± 3.0	10.5 ± 2.3
CEC	38.72 ± 6.3	21.3 ± 3.3	8.0 ± 2.3
Base saturation %	4.2 ± 1.1	2.6 ± 0.1	3.2 ± 3.1

^a By ion exchange resin (Amberlite IRA-400 and IR-120; Raij & Quaggio, 1983).

^b By leaching 5 cm³ of soil with 50 ml ammonium acetate at pH 7.

Table 3. Organic matter (colorimetric method; meq/100 cm³) of earth from two arboreal termite nests, consumed by *Pithecia pithecia chrysocephala*, and of root mat and topsoil samples under the respective termite nest trees

Nest No.	Earth sample		
	Termite nests	Root mat	Topsoil
9A	Superior	18.5	6.0
	Inferior	18.5	
16.5A E	Superior	8.4	3.8
	Inferior	8.4	

termitaria pH was equally acid. Termite nest No. 9A had more organic matter than both root mats, which in turn had more than topsoil (Tables 2 & 3). Termite nest No. 16.5AE had an organic matter content similar to the root mat (Table 3). On average, termite nest samples presented higher concentrations of P, K, Ca, Mg, Mn and Fe, besides Al and H⁺, compared with topsoil (Tables 2 & 4). Na, Co, Zn, Cu and Ni contents were similar between termitaria and topsoil (Table 4). Analyses with prior ignition showed similarly equal results between the three substrates (Table 4), with the exception of Mg and Ca for the termite nest samples (Table 4).

Table 4. Mineral composition of earth from arboreal termite nests consumed by *Pithecia pithecia chrysocephala*, and of root mat and topsoil samples under the termite nest trees. *n*, number of samples analysed (see text). Analysis by flame atomic absorption spectrophotometer (Intralab AA12/1475) after digestion in HCl/HNO₃. Numbers in parenthesis included previous ignition at 800 °C for 3 h

Element	Earth sample		
	Termite nests (<i>n</i> = 4)	Root mat (<i>n</i> = 2)	Topsoil (<i>n</i> = 2)
	µg/g	µg/g	µg/g
Na	48 ± 33 (93 ± 28)	43 ± 18 (70 ± 17)	16 ± 5 (80 ± 21)
Mg	90 ± 41 (56 ± 16)	45 ± 8 (46 ± 6)	18 ± 3 (33 ± 3)
Al	916 ± 197 (18158 ± 13950)	487 ± 62 (18399 ± 4544)	447 ± 54 (20677 ± 6930)
K	136 ± 27 (156 ± 35)	84 ± 54 (129 ± 38)	31 ± 16 (103 ± 10)
Ca	221 ± 41 (60 ± 14)	61 ± 52 (33 ± 34)	18 ± 4 (7 ± 1)
Mn	9 ± 3 (13 ± 2)	5 ± 1 (9 ± 1)	1 ± 0 (7 ± 2)
Fe	1094 ± 90 (4257 ± 419)	565 ± 112 (2679 ± 497)	499 ± 75 (3336 ± 906)
Co	3 ± 1 (10 ± 2)	3 ± 0 (8 ± 3)	3 ± 1 (8 ± 1)
Zn	26 ± 15 (17 ± 4)	24 ± 25 (12 ± 3)	18 ± 10 (17 ± 14)
Cu	0.3 ± 0.3 (6 ± 1)	0.8 ± 1.0 (4 ± 1)	0.4 ± 0.5 (6 ± 4)
Ni	5 ± 1 (11 ± 1)	5 ± 1 (10 ± 0)	4 ± 1 (10 ± 1)
Cr	< 4 (< 4)	< 4 (< 4)	< 4 (< 4)

Mineralogical contents and tannin adsorbent properties

X-ray diffractograms showed that the clay mineral fraction is composed mainly of kaolinite, with traces of gibbsite, feldspar, plagioclase and quartz.

Ring diameter measures from the termite nest, the topsoil and root mat samples indicated an adsorptive capacity around 10–20% (Table 5), similar to control with kaolin (10–20%), but lower than bentonite or celite (30 to 45%). In comparisons using ANOVA and Tukey (Wilkinson, 1991), with tannin concentration as a co-variable, ring measures among samples ($F=102.31$, $P<0.0001$) and tannin concentrations ($F=958.10$, $P<0.0001$) differed significantly. Termite nest No. 16.5A E samples adsorbed significantly less than samples from termite nest No. 9A (pairwise mean difference = -0.391 , $P=0.01$), but neither differed significantly from the topsoil and root mat samples or kaolin. Rings from both termite nest samples were significantly smaller than the tannin control (difference = 1.11 to 1.30, $P<0.0001$), showing tannin adsorptive capacity, but significantly larger than those for bentonite and celite (difference = 1.41 to 2.08, $P<0.0001$). Bentonite and celite were better tannin adsorbents.

DISCUSSION

Whereas some primates consume soil exposed by up-turned trunks (*Indri indri* – Pollock, 1977), stream banks (*Colobus guereza* – Oates, 1978), subsoil sediments (*Gorilla gorilla beringei* – Mahaney, Watts *et al.*, 1990;

Table 5. Average precipitation ring diameter, standard deviation and percentage of ring reduction (red) for arboreal termite nests, topsoil and root mat (*n* = number of samples × number of replications), in relation to the precipitation ring observed for tannin control samples, for each tannic acid concentration used

	Tannic acid concentration (M)					
	0.05		0.1		0.2	
	Precipitation ring		precipitation ring		precipitation ring	
	Diameter (mm)	Red (%)	Diameter (mm)	Red (%)	Diameter (mm)	Red (%)
Tannin	6.6 ± 0.24 (<i>n</i> = 24)	–	7.6 ± 0.33 (<i>n</i> = 24)	–	9.7 ± 0.55 (<i>n</i> = 20)	–
Termite nests	5.8 ± 0.35 (<i>n</i> = 2 × 8)	12	6.5 ± 0.51 (<i>n</i> = 2 × 8)	14	8.2 ± 0.80 (<i>n</i> = 2 × 8)	15
	5.3 ± 0.24 (<i>n</i> = 2 × 8)	20	6.2 ± 0.43 (<i>n</i> = 2 × 8)	18	7.9 ± 0.59 (<i>n</i> = 2 × 8)	19
Topsoil	5.6 ± 0.42 (<i>n</i> = 2 × 8)	15	6.5 ± 0.30 (<i>n</i> = 2 × 8)	14	8.2 ± 0.36 (<i>n</i> = 2 × 8)	15
Root mat	5.6 ± 0.55 (<i>n</i> = 8)	15	6.0 ± 0.76 (<i>n</i> = 7)	21	8.2 ± 0.55 (<i>n</i> = 8)	14
Kaolin	5.8 ± 0.49 (<i>n</i> = 12)	12	6.9 ± 0.32 (<i>n</i> = 4)	9	7.6 ± 1.37 (<i>n</i> = 4)	22
Celite	4.6 ± 0.25 (<i>n</i> = 4)	30	4.9 ± 0.25 (<i>n</i> = 4)	35	5.4 ± 0.32 (<i>n</i> = 8)	44
Bentonite	4.8 ± 0.29 (<i>n</i> = 4)	27	4.9 ± 0.25 (<i>n</i> = 8)	35	5.3 ± 0.20 (<i>n</i> = 4)	45

Pan troglodytes – Mahaney, Milner *et al.*, 1997), natural salt licks (*Alouatta seniculus* and *Ateles belzebuth* – Izawa 1993), and plastic clayish soil after rains (*Pan troglodytes* – Hladik, 1973), *Pithecia* used soil from termite nests, as has been reported for a number of primates (*Pan troglodytes* – Hladik, 1973 and Wrangham, 1977, *Macaca mulatta* – Lindburg, 1977, *Alouatta seniculus* and *Ateles belzebuth* – Izawa, 1993). Other animals have also been seen to eat other types of insect constructions such as homopteran larval ‘chimneys’ (*Pan troglodytes* – Hladik, 1973) and leaf-cutter ant mounds (Chacoan peccary *Catagonus wagneri* – Mayer & Brand, 1982, *Saguinus mystax* – Heymann & Hartmann, 1991, *Callicebus personatus melanochir* – Müller *et al.*, 1997). The ‘earth that has been moulded by insects’ (Hladik, 1973) usually has a higher mineral content than topsoil (Salick, Herrera & Jordan, 1983), as was observed here.

As pointed out by Müller *et al.* (1997), even if soils did not differ markedly in quality, it would be advantageous for monkeys to obtain soil from an ant mound (or termite nest) rather from the forest floor, because of the lower risk of predation and the soil’s clod structure (cemented together by insects).

Unlike termitaria used by spider monkeys and howlers, which were built by *Constrictotermes* (Izawa, 1993), sakis consumed soil from *Nasutitermes* nests, indicating that these nests are not unpalatable, as has been proposed for *Labiatermes* (Izawa, 1993). Lower organic matter of nest No. 16.5AE is probably related to *Cavitermes* feeding on the organic soil of the host mound (Mathews, 1977).

As was found for the lemurs *Indri indri*, where Pollock (1977) recorded between five and ten such earth-feeding sites in each group (2–6 individuals) territory, sakis from our study group ate soil from nine termitaria. A rhesus macaque *Macaca mulatta* group (141 monkeys) used ten mine sites (Knezevich, 1998). Unlike chimpanzees and indris, however, saki group members did not usually feed sequentially at a specific spot or termitaria that they would return to several days later (Pollock, 1977; Hladik, 1977b).

The spatial association of geophagy and food (like the three most used termite nests and *Trichilia* trees observed here) was also observed for rhesus macaques (preferred mines and monkey chow corrals: Knezevich, 1998). However, temporal association, like alternate consumption of chow and soil in rhesus macaques (Knezevich, 1998), was not observed in sakis.

Topsoil geochemistry

Typically in the Central Amazon, soil floor samples are poor in soluble nutrients (Stark, 1970; Ranzani, 1980; Chauvel, 1982). Compared with other surface soil samples (0–20 cm) in the same region (30 km from our site), our soil samples had a lower (Stark, 1970), similar (Ranzani, 1980) or higher pH in water (Chauvel, 1982). Our soil also had a lower to almost lower cation

exchange capacity and a lower total extractable content than samples from 0 to 10 cm depth analysed by Chauvel (1982), average values for A horizon samples analysed by Ranzani (1980), or 0–3 cm depth podzol sands analysed by Stark (1970). Cation content (Na, K, Ca, Mg) was lower (Ranzani, 1980; Chauvel, 1982) or similar, except for potassium which is lower than in podzol sands (Stark, 1970). Our samples were similar to the 10–20 cm depth samples of Chauvel (1982), except for total extractable cations and Ca content (both lower in our samples).

Evidence for geophagy as mineral supplement

There was a consistent pattern of mineral concentration, with termitaria having the highest values, followed by the root mat, and the soil surface (Salick, Herrera & Jordan, 1983; Table 3). The relative cation concentration in termite nests tends to be greater on poor soils (Pomeroy, 1983 in Davies & Baillie, 1988; see also Izawa, 1993) and this clearly applies to ‘Colosso’. Both termite nests examined, although arboreal, presented localized mineral concentrations in an intensely leached environment, as was also found by Salick *et al.* (1983). Termite or ant nest soil consumption in these circumstances provides a concentrated source of scarce minerals (Emmons & Stark, 1979) in a generally oligotrophic environment (but see Mayer & Brand, 1982). High iron (Ripley, 1970 in Hladik, 1977a; Lindburg, 1977; Mahaney *et al.*, 1990, 1993, 1997), sodium and bromine content (Mahaney, Watts *et al.*, 1990) may be important in primate geophagy. Calcium, potassium and magnesium are all better supplied by the mound soils, although there is no information on whether any of these minerals were deficient in the sakis’ highly diverse diet (Setz, 1993).

In three primate studies, analysis of soil samples failed to show high concentrations of specific minerals (Pollock, 1977; Izawa, 1993; Müller *et al.*, 1997). The elements, which might have some nutritive value for chimpanzee, langur or gorilla, occur at lower levels in the earth samples than in many common food plants (Hladik, 1977a, b; Mahaney, Watts *et al.*, 1990). Soils ingested by other primates had higher or much higher concentrations of Na, K, Ca or Mg (Davies & Baillie, 1988) and Mn, Fe, Zn or Cu (Hladik, 1977a, b; Oates, 1978; Davies & Baillie, 1988). Besides this, higher cation exchange capacities (not observed here) can interfere with the absorption of iron (Minnich *et al.*, 1968 in Vermeer & Ferrell, 1985; but see Mahaney, Aufreiter *et al.*, 1995), even contributing to the development of anaemia (Minnich *et al.*, 1968 in Underwood, 1977).

Contrary to observations by Davies & Baillie (1988), termitaria eaten by the sakis also had higher concentrations of aluminum than adjacent soil samples. Clay ingested by the South Indian elephant and the Nilgiri langur also showed a high concentration of aluminum (see Poirier, 1970). Such high aluminum levels are

Table 6. Reported geophagy frequency for primates and peccaries. Fo, folivores; Fr, frugivores; See, seed eaters; Om, omnivores.

Common name	Main diet	Event frequency	No. of study months	Reference
Nilgiri langur	Fo	5	12	Poirier, 1970
Black colobus	Fo	Occasional	9	Harrison & Hladik, 1986
Red leaf monkey	Fo See	9	13	Davies & Baillie, 1988
Moustached tamarin	Fr	3 (dry season)	3 (345 h)	Heymann & Hartmann, 1991
Titi monkey	Fr	14 times (warm season)	11 (1030 h)	Müller <i>et al.</i> , 1997
Saki monkey	Fr	26 times (rainy season)	>15 (853 h)	This study
Howler monkey	Fo	40% of obs. days	203 days	Izawa, 1993
Spider monkey	Fr	—	—	Izawa, 1993
Indri lemur	Fo Fr	75% of obs. days		Pollock, 1977
Rhesus macaque	Fr Fo	Once a month (dry season)	12	Lindburg, 1977
	Chow	Common Routinely	3	Sultana & Marriot, 1982 Knezewich, 1998
Japanese macaque		Considerable time		Inoue, 1987 in Izawa, 1993; Mahaney, Hancock <i>et al.</i> , 1993
Mandrill	Fr	Rare (incidental?)		Lahm, 1986
Chimpanzee	Om	Once a day Twice a day		Wrangham, 1977 Hladik, 1977b
Mountain gorilla	Fo	5 to 6 times/year Once a day (dry season)		Watts, 1984 Mahaney <i>et al.</i> , 1990, 1993, 1995
Chacoan peccary	Fr	43% of obs. days (winter)		Mayer & Brand, 1982

poorly absorbed (Underwood, 1977) and may be immobilized by the clay structure (Mahaney, Aufreiter *et al.*, 1995).

Unlike mountain goats, where females use natural salt licks during postpartum stress (Hebert & Cowan, 1971), saki geophagy did not show any gender difference in frequency or relation to reproductive cycle (see Setz & Gaspar, 1997). This was expected since New World primates do not have menstrual cycles (Flowerdew, 1987). Besides, adult females were not pregnant or lactating for dependent infants in March 1987 (feeding juveniles was observed sporadically: E. Setz, pers. obs.), when most soil feeding-bouts (96%) were observed.

Monotonous diets or species-poor diets might be expected to be deficient or unbalanced for some nutrients (Hladik, 1977a; Oates, 1978), but geophagy is reported for primates with diverse diets (Davies & Baillie, 1988). Sakis with their highly diverse diet (190 spp. eaten: Setz, 1993) are no exception. Although geophagy is usually related to nutrient-poor and highly folivorous diets, sakis, along with tamarins (Heymann & Hartman, 1991), spider monkeys (Izawa, 1993), bearded sakis (Ferrari, 1995), and masked titis (Müller *et al.*, 1997) are predominantly frugivorous (Setz, 1993; see Table 6).

Seasonal folivory or mature leaf consumption (Harrison & Hladik, 1986) could favour geophagy in the dry season (Table 6) when fruits are scarce, either as a mineral supplement, or as a secondary compound adsorbent (see Mahaney, Aufreiter *et al.*, 1995). However, in our study sakis ate soil in the rainy season, when fruits are abundant and leaves are least prevalent in their diet (4% vs. 18%: Setz, 1993). As in deer, woodchuck, and fox squirrels (Weeks & Kirkpatrick, 1976, 1978), the correlation between geophagy and the

fruiting season in *P. p. chrysocephala* could point to excess potassium, but potassium content was higher than sodium in the termite nest earth (Table 3). Sodium content was lower in our samples than in soil ingested by other primates (Hladik, 1977a, 1977b, Mahaney, Watts *et al.*, 1990) and soil samples from salt licks (Weeks & Kirkpatrick, 1976; Emmons & Stark, 1979). Soil samples ingested by chimpanzees in the wet season in Gabon had higher quantities of potassium (and calcium) than their diet (Hladik, 1977b; Uehara, 1982).

Evidence for geophagy as antacid

As for regolith analysed and discussed by Mahaney, Aufreiter *et al.* (1995), termite soil had 10% Al and 1% Mg, an elemental composition comparable to commercial antacid preparations (10% Al, 1.1% Mg), its effectiveness depending on the chemical form of the elements.

Since sakis do not have sacculate stomachs and the termitaria pH was low (acid), we do not discuss here the soil function as pH buffer of the forestomach, as suggested for *Colobus guereza* (Oates, 1978).

Evidence for geophagy as an adsorbent for tannins and toxins

Immature fruits or seeds were consumed equally by the sakis in both the dry (19.6 and 18.4%, respectively) and rainy (23.4 and 21.7%) seasons (Setz, 1993). Fruit consumption (64.2% dry season vs 95.8% wet season) and seed predation (33.3% vs 19.6%), however, were more frequent in the rainy season (Setz, 1993). Our soil

samples showed an adsorptive capacity for tannins (Table 4). If sakis ingest soil because of high levels of tannin in fruits and seeds in general (see Kinzey & Norconk, 1993) they would eat soil more regularly in the fruiting season, which was not the case. In spite of similar sample sizes in October, November and December (Table 1), only one soil feeding-bout was observed then (November, 1990). Abrupt seasonal changes in the diet such as a sudden lack of fibre, or increases in carbohydrates and soluble proteins, may lead to digestive disorders apparently ameliorated by geophagy (Kreulen, 1985; Mahaney, Aufreiter *et al.*, 1995). These would occur in a short period of dietary transition (such as the event observed in November 1990, when fruits start to increase in the sakis' diet), but would regularly also occur.

Since supra-annual fruiting is common, or even predominant in Amazon forests (see Schulz, 1960; Setz, 1993), geophagy related to species-specific detoxification could occur less regularly. The coincidental ingestion of *Trichilia* spp. and soil favours this idea which, however, needs to be verified.

Evidence for geophagy as tactile sensations in the mouth or as tradition

Infrequent geophagy led Mahaney, Watts *et al.* (1990) to suggest that there is a real possibility that it has almost no essential nutritional role (but provides tactile sensations in the mouth, for example), but our data do not rule out a relation to detoxification of items which rarely appear in the diet.

Since we studied only one group of sakis we do not have data to discuss traditional factors.

Evidence for geophagy as a therapeutic mediator of endoparasitism

In spite of heavy infection of enteric parasites, rhesus macaques exhibit low levels of diarrhoea and excellent physical condition, with a high reproductive rate and low mortality (Knezevich, 1998). Although we do not have data on endoparasite prevalence, signs of diarrhoea were not observed in the sakis. Adult female sakis reproduced every second year (see Setz & Gaspar, 1997), as expected for monkeys of their size (Dunbar, 1987; Setz, 1993). Only one saki death was registered for the group in 6 years (a sub-adult male; see Setz & Gaspar, 1997). The young male was recorded eating soil more often than the adult, and this is consistent with a higher prevalence of parasites in younger animals, such as occurs in rhesus macaques (Knezevich, 1998). But unlike Cayo Santiago macaques, which commonly engage in geophagy (Sultana & Marriot, 1982; Knezevich, 1998), saki geophagy was an irregular habit, and too infrequent to consider it further as a therapeutic mediator without evidence of endoparasitism.

The observations reported here on geophagy in the

golden-faced saki, although inconclusive on its function in this species, demonstrate that it does not occur always when food is scarce and is not associated with folivory, as reported for other primates, nor is it consistently related to the fruiting season, as has been found for some other frugivorous mammals. The tannin adsorptive role of the clay cannot be ruled out. Supra-annual observations point to an irregular habit of geophagy, probably related to rare dietary components.

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Appendix. X-ray diffractometry sample preparation procedure modified from Jackson (1969):

A portion of the sample was transferred to a beaker and 60 ml of sodium acetate/acetic acid (pH 5) was added, followed by 20 ml of hydrogen peroxide (30%). This mixture stood at room temperature overnight and was then gently heated on a steam bath. More H_2O_2 was added until reaction ceased completely. The excess of H_2O_2 was removed by boiling. The mixture was centrifuged and the supernatant discarded. The sample was re-suspended with water and passed through a 270 mesh sieve. The fine fraction was transferred to a beaker and 50 ml of a combined sodium citrate/bicarbonate (pH 7.3) mixture was added and the whole was heated to 75 °C on a steam bath. Sodium ditionite (*c.* 1 g) was added, the mixture was homogenized, left reacting, and the second portion of sodium ditionite was added and

the sequence repeated. After cooling the mixture was centrifuged, the supernatant discarded, the material re-suspended and centrifuged again for 2.45 min at 750 rpm to separate the silt fraction from clay minerals. The supernatant was divided in two fractions which were treated with 1 M NaCl solution and 1 M $MgCl_2$ respectively, by suspending the clay fraction in the salt solution, centrifuging and discarding the supernatant. This step was repeated three times. The excess of salt was washed by successive steps of washing with de-ionized water, centrifugation until the supernatant solution was free of chlorides.

Suspended clay fraction was pipetted over a glass and left to dry. The K-saturated clay fraction was run on the diffractometer as derived and after heat treatment at 350 and 550 °C. The Mg-saturated fraction was run as derived and after saturation with ethyleneglycol.