MEDICINAL PROPERTIES IN THE DIET OF GORILLAS: AN ETHNO-PHARMACOLOGICAL EVALUATION

Don COUSINS
Michael A. HUFFMAN
Primate Research Institute, Kyoto University

ABSTRACT A growing body of literature in the behavioral, ecological and pharmacological sciences suggests that animals use certain plants for the control of parasite infection and related illnesses. It has also become increasingly apparent that chimpanzees in Africa and their human counterparts share strong similarities in the plants they use for the treatment of similar diseases. Little is yet known, however, of the other closest living ape relative in Africa, the gorilla. Here we review the ethnopharmacological literature to evaluate the possible role of plant secondary compounds in the diet of gorillas in the wild. A total of 118 medicinal plant species from 59 families are listed from an extensive review of the literature on gorilla diet in the wild. The major pharmacological activities of those plant foods, which are also used in traditional medicine include antiparasitic, antifungal, antibacterial, antiviral, cardiotonic, hallucinogenic, stimulatory and respiratory activities. A greater understanding of the role of such plants in the primate diet and how these plants can be used for health maintenance is a promising new avenue for expanding our understanding of the biological basis and origins of traditional human medicinal practices and for developing novel applications of ethnopharmacological knowledge for humans.

Key Words: Gorilla diet; Self-medication; Novel drug search; Ethnoveterinary medicine.

INTRODUCTION

In recent years a growing body of evidence has accumulated regarding the phenomena of self-medication in animals (see Huffman, 1997). A product of biological evolution, selective pressures have acted upon hosts and their pathogens in such a way that animals have adopted behavioral strategies to counteract the deleterious effects of these pathogens. One of the ultimate goals of research in animal self-medication is to shed light upon the evolution of medicinal practices in early humans and the ecological and biological forces that helped shape them. A comparative study of great ape self-medicative behavior and an understanding of the overall medicinal effects of the diet are important steps in understanding this process. The field of ethnopharmacology has much to offer and gain from this research.

A variety of non-nutritional plant secondary compounds are found in the great ape diet, but little is known about the possible medicinal consequences of their ingestion. One of the challenges of interpreting self-medication in animals is to distinguish between possible indirect medicinal benefits derived from secondary compound rich plants that are assumed to be ingested for their nutritional value versus limited and situation specific ingestion of items that are processed solely for their curative value or other physiological effects. In traditional human societies too, the boundary between 'food' and 'medicine' is not always clear. Among the Hausa of Nigeria, over 80% of the plants used for the treatment of malaria and other dehabilitating ailments are also used as food (Etkin, 1996; Etkin & Ross, 1983). Over the last decade or more science has entered a renaissance in its view of food as evidenced by the increase in research and development of so called 'functional foods' or 'neutraceuticals' (e.g. Mazza, 1998; Ohigashi *et al.*, 1997). Many of the traditional spices, condiments and vegetables used around the world are also important sources of anti-tumour agents or possess antioxidant, antibacterial, antiviral and antiparasitic activity (Billing & Sherman, 1998; Murakami *et al.*, 1994; Sherman & Billing, 1999). Ethnopharmacology has played a leading role in documenting and evaluating many of these plants.

Parasites can cause a variety of diseases that affect the overall behavior and reproductive fitness of an individual making the need to counteract such pressures great. Among the recent advances in the study of primate self-medication is research into the behavioral adaptations for parasite control in wild chimpanzees (e.g. Huffman & Seifu, 1989; Huffman *et al.*, 1993, 1997; Huffman, Page *et al.*, 1996; Messer & Wrangham, 1995; Page *et al.*, 1997; Wrangham, 1995). Two such proposed types of self-medicative behavior, bitter pith chewing and leaf-swallowing have been investigated in the most detail from an antiparasitic perspective (e.g. Huffman, 1997; Huffman, Page *et al.*, 1996; Huffman & Caton, 2001). The likelihood of similar 'medicinal foods' in the diet of other great apes is quite high and warrants further extensive research.

It has become increasingly apparent that there are strong similarities in the plants used ethnomedicinally by humans and those exploited by chimpanzees for self-medication (Huffman, Koshimizu & Ohigashi, 1996). With respect to the medicinal properties of the African great ape diet, perhaps the least is known about gorillas. It is the purpose of this paper therefor to discuss some of the ethnomedical plants that form part of the natural diet of western lowland gorillas (*Gorilla gorilla gorilla*), eastern lowland gorillas (*Gorilla g. graueri*), and the mountain gorillas (*Gorilla g. beringei*). A greater understanding of the role of such plants in the primate diet and how these plants may be used for health maintenance is a promising new avenue for expanding our understanding of the biological basis and origins of traditional human medicinal practices and for developing novel applications of ethnopharmacological knowledge (e.g. Huffman, Koshimizu & Ohigashi, 1996; Huffman *et al.*, 1998; Huffman, 2001).

PRIMATOLOGICAL AND ETHNOPHARMACOLOGICAL LITERATURE SURVEY

I. Central Nervous System (CNS) Stimulants, Cardiotonics and Hallucinogens

Appendices 1 and 2 list some particular ethnomedicinal plants found in the diet of lowland and mountain gorillas respectively. The wide variety of medicative properties listed within is a testament to the potential pharmacological diversity of their diet.

The African apes exploit a number of Kola (*Cola*) trees (Sterculiaceae), some species utilised by gorillas being *Cola gabonensis* (fruits), *C. nitida* (seeds), *C. pachycarpa* (seeds) and *C. rostrata* (seeds). It is interesting that in many of these species the gorillas prefer the seeds. Indeed, Raponda-Walker & Sillans (1961) state that the local people emphasize the preference gorillas show for seeds of *C. pachycarpa*, and even name the plant "cola of the gorillas". These seeds usually contain caffeine (between 2-2.5%) and theobromine. The amino acid content of Kola 'nuts' suggests that protein levels are weak (Outuga, 1975), and this in turn may indicate that gorillas eat the fruits and seeds primarily for their caffeine value.

Cola nuts are highly esteemed by people throughout tropical West Africa as charms and remedies, as amulets and as aphrodisiacs. White or light-coloured nuts effect love magic, while red has the opposite effect. Dried *Cola* fruits have also been used as currency and are given as tokens of friendship (Rätsch, 1992). Their reputation for suppressing fatigue and promoting endurance is legendary, and Russell (1995) claimed that the British Consul at Bahia, Brazil wrote a letter in 1890 suggesting that this powerful commodity should be brought to the attention of Her Majesty's War Office.

A curious relationship exists between a *Cola* species, *C. lizae* and gorillas in the Lopé region of Central Gabon. The plant itself is remarkable in that it was described just over a decade ago (Hallé, 1987) despite being the most dominant tree in the area, where its distribution is localised. The fruits of this plant are a major food source for gorillas for a part of each year, and the apes are the primary seed dispersers of the species. When gorillas build their nests in open areas of the forest and deposit their faeces near these nests, the seeds are provided with optimum conditions for germination (Tutin *et al.*, 1991). The other seed disperser is the chimpanzee, but they are only a minor agent.

Although *C. lizae* is obviously an important food source for gorillas, it is not an exceptionally nutritious one. The mature fruits have high sugar content, but gorillas also consume unripe green fruits. The large seeds are swallowed individually and pass through the gastrointestinal (GI) tract unharmed.

Partnerships of this kind are usually to the benefit of both parties. It is clear what the plant gains, but less illuminating from the point of view of the gorilla: analysis showed no measurable alkaloids in the seeds or seed coating (Tutin *et al.*, 1991). Yet one could expect a chemical benefit for the apes, particularly as gorillas seem to be attracted to caffeine and theobromine bearing plants. In Equatorial Guinea they eat the leaves of *Caffea liberica* (Rubiaceae) and the fruits of *Theobroma cacoa* (Sterculiaceae) (Sabater Pi, 1977).

Strophanthus spp. (Apocynaceae) are best known for the arrow poisons extracted from the crushed seeds, but this group of plants are extremely important ethnomedically throughout their distribution. The seeds contain a glucoside called strophanthin, which is a cardio-active agent. In some species the ground seeds are used for cardiac insufficiency, while the roots or leaves of other types (e.g. *S. hispidus, S. kombe, S. gratus, S. welwischii, S. preussii*, etc.) are utilised in preparations for venereal diseases, intestinal parasites and serious skin diseases such as scabies

(Burkill, 1985). In Gabon, gorillas are catalogued as eating the fruits of an unidentified species of *Strophanthus* (Tutin & Fernandez, 1985), and it will be interesting to see if future research reveals a greater exploitation of this species by gorilla and chimpanzee populations in other areas.

In Africa, hallucinogenic plants are either poorly represented or poorly recognised. The best documented is *Tabernanthe iboga*, (Apocynaceae), a shrub first described in 1889. The active principle in iboga is ibogaine, the highest concentration being found in the root. Ibogaine affects the CNS and cardiovascular system, along with tabernanthine and iboluteine, other active constituents in the plant. The stimulating effects are similar to caffeine, i.e. increasing stamina. The plant is employed in traditional African medicine, along with *Tabernaemontana* species, for manic depression, leprosy and as an aphrodisiac. In the former Belgian Congo (Democratic Republic of Congo) the sap is used in the treatment of pox, and the leaves for gum and tooth diseases (Dubois, 1955).

Ibogaine was the first indole to come into vogue in Europe, the extract being initially marketed in 1939 under the name 'Lambarene'. It stayed on the market until at least the mid-1960s, and was promoted as a cure for everything from neurasthenia to syphilis, but above all as an aphrodisiac. The tablets consisted of a dry pharmaceutical extract of the root of *Tabernanthe manii*, a related species to *T. iboga*, with a drug content of 0.20 g of extract per tablet (about 8 mg of ibogaine). Currently ibogaine is being heralded rather extravagantly as an interrupter for drug addiction, without withdrawal symptoms, and the University of Miami is to conduct human trials to demonstrate its properties. For a thorough overview of the discovery of ibogaine, its chemical structure, laboratory investigations and research into its therapeutic qualities and toxicity see De Rienzo & Beal (1997).

T. iboga is an essential component in African religious cults and rites, particularly in Bwiti. The Metsogho-Massango and Bapinzi peoples of southern Gabon practice Bwiti in its original form. The cult is male-orientated and initiation indispensable for social promotion within the tribe; any male unable to join is an outcast and considered feminine (Goutarel, 1997). The use of iboga is controlled in ceremonies, but when the Fang people adopted the cult they adulterated it, allowing women to join and being more reckless in the use of iboga, which they call 'eboka'. Initiates have been given massive doses of iboga to "open their heads" in order to effect contact with the ancestors through collapse and hallucination. One to three baskets full of the material would be consumed over an 8-24 hour period, representing an ingestion of 300-1,000 grams, or some forty to sixty times the threshold dose and close to toxicity. It is not surprising that some of these initiates died, and in a forty-year period a dozen cases of murder or manslaughter were brought against Bwiti cult leaders. The Fang also use the drug casually and regularly outside of Bwiti rituals (Fernandez, 1972, 1982).

In Bwiti legends the pygmies are said to have found iboga, but it is possible that the pygmies themselves discovered the properties of the plant by watching wild boars digging up and eating the roots, only to go into a wild frenzy, jumping around and fleeing from perhaps frightening images. Similar behaviour has been reported by indigenous peoples for porcupines and gorillas who are said to be fond of the roots (Pope, 1969; Raponda-Walker & Sillans, 1961). In south-eastern Cameroon

gorillas eat the flowers and branches of iboga (Bützler, 1980), while in Gabon they eat the fruits, stem and root of the plant (Valker, 1931). There is ample evidence that man globally has discovered the effects of drug plants by observing the behavior of animals (Siegel, 1979; Huffman, 2001).

Pharmacological tests have been carried out on animals by early French scientists (see Pope, 1969). Phisalix (1901) injected dogs with ibogaine, and the animals acted as if they were seeing frightening things; they would suddenly begin to bark loudly at nothing, leap backwards, or desperately try to hide in a corner. In 1905 Landrin (1905) experimented with frogs, guinea pigs and dogs. The effects were similar to a large dose of caffeine in all three species. Toxic doses sometimes produced convulsions, almost invariably paralysis, and finally an arrest of respiration. Fifty years later Schneider & Sigg (1957) did similar research on cats and dogs, confirming Landrin's findings. In these studies the animals exhibited ataxia, peculiar position of the legs, partial pilo-erection, pupil dilation, alertness, outstretched tails, and increased respiration—a picture of fear or rage (Pope, 1969).

The likelihood is that the exploitation of *Tabernanthe iboga* by gorillas is very localised. Valker (1931) made his observations within the environs of Sindara on the Ngounie river, south of Lambarene. Raponda-Walker lived at Sindara for five years, so it is conceivable that he also heard reports of gorillas eating iboga roots in this region. Bützler (1980) found his single piece of evidence in one small area of the Dja Reserve in the vicinity of Djoandjla, but never heard of the apes utilising the plant in any other area of Cameroon that he visited.

These accounts came not only from inland areas, however, but also from coastal regions. Pierre Henri Chanjon, a professional hunter and guide, and former official guardian of the Petit Loango Reserve in south-western Gabon for over a decade, is familiar with the root-eating of iboga by gorillas, but he believes that the apes are intelligent enough to be discriminatory in their consumption, possibly using the plant as a tonic (P.H. Chanjon, personal communication). This would make sense. The apparent "cultural" and infrequent employment of the plant by the pongids suggests a purely medicinal function. Although the fruit is said to be very palatable, and probably contains no active constituents (unlike the rest of the plant), it has not been identified as a food item in any of the diets of gorillas and chimpanzees so far recorded.

The local human inhabitants of the Peti Loango region use *T. iboga* in their secret society Bouiti, and it is noteworthy that they share other medicinal plants with gorillas, including the fruit of the rubber liana *Landalphia mannii* (Aponcynaceae) to combat intestinal parasites, and the bark of *Annodium manni* (Annonaceae) for diarrhoea (P.H. Chanjon, personal communication)

Two other hallucinogenic plants ingested by gorillas and chimpanzees are *Alchornea floribunda* and *A. cordifolia* (Euphorbiaceae). Both contain the alkaloids alchornine and alchornidine. Gorillas have been documented to eat the fruits of both species in Equatorial Guinea (Sabater Pi, 1977), while chimpanzees consume the pith and fruit of *A. cordifolia* in the Republic of Guinea. Local human inhabitants in Guinea use the pith and leaf of this plant as an antiseptic and anti-cough agent (Sugiyama & Koman, 1992).

A. floribunda is used in the same manner as *T. iboga* in Gabonese cults. The root has a reputation as an intoxicant and as an aphrodisiac. After reducing it to powder it is mixed in palm wine and left for several days before being consumed to provide energy for tribal festivities or warfare. It is said to provide a state of intense excitement followed by a deep, sometimes fatal depression (Rätsch, 1992).

The highest percentage of alkaloids in *A. cordifolia* is concentrated in the roots and in the bark, although the leaves are used medicinally for coughs, colds, pneumonia, bronchitis and tachycardia. Perera *et al.* (1991) pharmacologically screened the leaves of plants collected in Cameroon and found good results with jaundice, but a rather weak toxicity that would not be significant for traditional medical uses. However, a screening of leaves, stem and roots of specimens collected in former Zaire showed a broad spectrum of antibacterial activity (Muanza *et al.*, 1993).

These indole drug plants, together with others (such as *Rauwolfia* spp.) suggest that Africa may not be so impoverished in psychotropic plants as is widely believed. It is a tantalising thought too that gorillas might be directly affected by these same properties.

II. Respiratory Ailments, High Altitude Living and the Virunga Mountain Gorilla Diet

The cold, wet and windy slopes of the Virunga volcano range is a unique and inhospitable environment for gorillas. Not surprisingly, the apes commonly suffer from coughs, colds, pleurisy, pneumonia and bronchitis. This habitat lacks the diversity of flora found in the humid lowland forests and consequently has a narrower range of medicinal plants. One important source of food for gorillas is *Vernonia adolfi-frederici* (Compositae), the gorillas eat the flowers, pith and rotten wood of the plants (Schaller, 1963; Fossey, 1983). This genus is very significant ethnomedically in many areas of Africa. At least seven species–*V. ambigua, V. amygdalina, V. cinerea, V. cistifolia, V. conferta, V. nigritiana* and *V. poskeana*–are used in the treatment of naso-pharyngeal illnesses, and at least two others (*V. adoensis* and *V. colorata*) are considered as cures for pulmonary infections (Burkill, 1985; Iwu, 1993).

One of the behavioral puzzles of the Virunga gorillas are their periodic migrations to the upper slopes 1,100-3,200 meters above sea level, to the giant senecio zone. Schaller (1963) followed a group of gorillas to an altitude of 4,100 meters on Mt. Mikeno. Here the animals fed infrequently on *Senecio alticola* (Compositae) and *S. erici-rosenii*, preferring to eat the pith. Senecio are also important in ethnomedicine. For example, *S. biafrae* is used in the treatment of pulmonary complaints, *S. petitianus* for head colds, *S. abyssinicus* for liver conditions, *S. baberka* and *S. manni* for venereal diseases, and *S. lyratipartus* as an emetic (Burkill, 1985; Iwu, 1993). Also at these high altitudes are the giant lobelias (Campanlaceae). All members of this genus contain a number of alkaloids (iobeline, iobelanidine and norlobelanidine), which have stimulating effects upon the entire body lasting a quarter of an hour. Higher doses may have narcotic effects, and New World Indians use many species of *Lobelia* as remedies and inebriates (Rätsch, 1992). It is also of interest that lobeline is a respiratory stimulant. Gorillas feed on *L. giberroa* and *L. wallastonii*. Schaller (1963) found *L. giberroa* to be very abundant at Kabara, but observed only five gorillas that briefly fed on these plants. Injured plants exude a sticky white

fluid that adheres to the skin, is extremely bitter to the taste, and is painful in the eyes. With *L. wollastonii*, the gorillas snapped the heads off young plants to eat the soft pulp at the base of the leaves. They also pulled up the root, which they peeled by biting off the bark (Schaller, 1963). Watts (1984) noted that they ate the ephelium from the roots of *S. johnstonii* and *L. wollastonii* in small quantities.

That these gorillas travel to the high escarpments rarely, expending a great deal of energy in the process, only to spend a few days in a zone presumably lacking in an abundance of nutritional food requires an explanation. The current evidence suggests that gorillas have a tendency to ingest some plants abundant in caffeine and other heart stimulating alkaloids. It is interesting to speculate as to why this should be. Gorillas, especially adult males, are large primates that lead fairly active lifestyles. In mountain forests, particularly the Virunga Volcanoes, gorillas traverse steep slopes in oxygen-thin atmospheres, so it is not difficult to surmise that under both these environmental conditions, that like humans, cardiac stimulants would not only be desirable, but highly adaptive.

The highland gorillas are apparently also fond of medicinal mushrooms. Fossey (1983: 52) wrote: "Still another special food is bracket fungus (*Ganoderma applanatum*), a parasitic tree growth resembling a large solidified mushroom. The shelf-like projection is difficult to break free from the tree; so younger animals often wrap their arms and legs awkwardly around a trunk and content themselves by only gnawing at the delicacy. Older animals who succeed in breaking the fungus loose have been observed carrying it several hundred feet from its source, all the while guarding it possessively from more dominant individuals' attempts to take it away. Both the scarcity of the fungus and the gorillas' liking of it cause many intragroup squabbles, a number of which are settled by the silverback, who simply takes the item of contention for himself."

Ganoderma applanatum (Polyporaceae), also known as "Artist's Conk" and "Red Mother Fungus", grows on a variety of hosts around the world. It has been found to contain various steroidal compounds, such as ergosterol, ergosta, fungisterol, alnusenone, friedelin and other triterpenes. The fungus has demonstrated immunostimulating properties in animal studies (Hobbs, 1995). Doses of nucleic acid isolated from the mycelium conferred protection against tick-borne encephalitis virus in mice, while polysaccharides (from 10-50 mg/kg) from the mushroom have been found to increase spleen cell proliferation in vitro and stimulate antitumour activity against sarcoma 180 in mice, as well as increase spleen cell primary antibody responses to sheep red blood cells. Single doses of polysaccharides (from 10-50 mg/kg) have produced a 100% tumour inhibition ratio (Hobbs, 1995). In China, *G. applanatom* is believed to be useful for rheumatic tuberculosis and oesophageal cancer. It also exhibits antibiotic properties and shows activity against other types of cancer (Hobbs, 1995). In neighbouring Bwindi's Impenetrable Forest *G. australe* is used medicinally by local people, and also ingested by gorillas (J. Berry, personal communication). Although no medicinal properties have yet been scientifically recorded for this species, the genus *Ganoderma* generally includes a number of species that have been used medicinally, or may prove useful in the future, such as *G. lucidum, G. capense, G. japonicum, G. sinense* and *G. tsugae* (Hobbs, 1995).

III. Antiparasitic, Antifungal, Antibacterial, and Antiviral Properties of *Aframomum* spp. (Zingiberaceae)

Several species from the genus *Aframomum* are major food plants for gorillas and chimpanzees throughout the lowland rainforests and in many montane areas (Appendix 3). There appears to be regional preferences. In the coastal forests of southern Cameroon and Equatorial Guinea *A. hanburyi* and *A. subsericeum* are heavily utilised by gorillas, while *A. giganteum* is rarely eaten (Bullock, 1981). Gorillas in south-eastern Cameroon favour *A. danielli*, and it is part of their stable diet (Merfield, 1954). Bioassays of the extract of *A. danielli* have been made by Adegoke and Skura (1994), revealing active growth inhibitors of *Salmonella enteriditis, Pseudomonas fragi, P. flourescens, Proteus vulgaris, Streptococcus pyogens, Staphylococcus aureus, Aspergillus flavus, A. parasiticus, A. ochraceus* and *A. niger*.

In other parts of Equatorial Guinea and in parts of Gabon *A. giganteum* takes precedence as favourite with gorilla populations. The Eschira people of Gabon use the seeds of the fruit as an anthelmintic, the fruit pulp as a light laxative and the macerated roots for treatment against dental decay (Raponda-Walker & Sillans, 1961). Also in Gabon, the Basango pound the stem in water and the liquid is then consumed to counteract intestinal worms.

A. giganteum has been shown to contain quercetin and kaempferol, both possessing antibacterial activities which inhibits the growth of fungi and yeast. They also display potent antiviral responses and are anti-inflammatory. Another agent is syringic acid which has been shown to be a significant local anaesthetic and to have specific anti-Parkinson action (Neuwinger, 1996).

Gorillas living in the Mamfe region of West Cameroon eat the fruits of *A. melegueta* (Migeod, 1925). Bioassays on the fruit and seeds have been tested against several bacterial and fungal strains (Oloke *et al.*, 1988). The crude extracts revealed potent bactericidal activities against *Escheria coli, Pseudomonas aeruginosa, Yersinia entercolitica, Bacillus subtilis, Proteus vulgaris, Klebsiella pneumoniae* and *Serratia marcescens*. Fungicidal activities inhibited *Candida albicans, Trichophyton mentagrophytes, Aspergillus niger, Botryodiplodis theobromae* and species of *Cladasporium* cladosporiodes. Ethnic groups use different parts of the plants for the preparation of folk remedies. In southern Nigeria the fresh fruit is used as an aphrodisiac, the leaf for measles and externally for leprosy, and the root decoction is taken by nursing mothers to reduce excessive lactation (Iwu, 1993).

There are some fifty species of *Aframomum* in Africa, about half of them in the Cameroon-Gabon region. They are closely allied to the *Amomum* of Asia, and indeed some species of *Amomum* are used ethnomedicinally in south-east Asia (Perry, 1980). During low fruiting seasons orangutans (*Pongo pygmaeus pygmaeus*) living in the Gunung Palung National Park, Borneo eat the stems of *Amomum* (Knott, 1998).

A full list of all *Aframomum* spp. exploited by the African apes has yet to be catalogued; present knowledge suggests that *A. sanguineum* is the most popular with gorillas in at least 5 distinct regions spanning Cameroon, Gabon, Congo-Brazzaville, Central African Republic, Congo-Kinshasa, and Uganda (e.g. Calvert, 1985; Tutin & Fernandez, 1985; Sabater Pi, 1977; Yamagiwa *et al.*, 1994; Goodall, 1979; Schaller, 1963). Dr. J.M. Lock, an authority on the taxonomy of the genus *Aframomum* regards *A. sanguineum* as a synonym of *A. angustifolium* (J.M. Lock, personal communication). It is used as an anthelmintic in East Africa, where the seeds are ground with finger millet to make a paste that is stirred in water, making gruel. It is also considered to be a reliable remedy for stomach-ache, while a decoction of the root is taken for dysentery (Kokwaro, 1976).

Bioassays of *A. sanguineum* conducted by John Berry of Cornell University (unpublished data) demonstrated that the flesh and seeds of the fruits contained powerful inhibitors of bacterial growth, acting against *Bacillus cereus, Staphylococcus aureus, Escherichia coli* and *Pseudomonas aeruginosa*. The fruits of *A. milbraedii*, a species sympatric with *A. sanguineum*, revealed no similar antibacterial agents. It is possible that toxins in this species could be sited in other parts of the plant.

Owing to the fact that a number of *Aframomum* species exploited by the great apes demonstrate a wide range of antibacterial and antifungal activities, it is possible that the herbs are as much a source of preventative medicine as they are considered an important source of food (Wrangham *et al.*, 1991; Kuroda *et al.*, 1996). In fact, some species may be so strongly antibiotic that young apes have to regulate their intake. Blancou (1955) observed that captive infant gorillas avidly ate the plants on certain days, but stubbornly refused them on others. Even a captured adult male suffered from diarrhoea when it ate more than five or six *Aframomum* fruits at a time (Schaller, 1963).

THE ACQUISITION OF MEDICINAL PLANT USE IN APES AND HUMANS

Primates acquire knowledge of food plants early on in life, and at a few years of age are already confident at selecting favoured items. Each day confiscated gorilla infants at the Brazzaville orphanage were allowed to forage in a remnant patch of forest nearby. They deliberately choose certain plants, with the youngest animals following the example of the senior ones. Abel M'Passi, a Congolese botany student from Brazzaville University, collected samples of everything the gorillas consumed, eventually identifying 57 plant foods. He suggested that the young gorillas were eating certain plants appropriately when suffering from diarrhoea and/or parasitosis by utilising plant species known locally for their medicinal properties. Among the plants listed were *Alloyphyllus africanas, Caloncoba welwitschii, Costus afer, Elaeis guineensis, Musa sapientum, Palisota hirsuta* and *Solanum torvum* (Attwater, 1999; Mark Attwater, personal communication)

Bitter taste is a reliable signal for toxicity and a number of secondary compounds ubiquitous in nature taste bitter (e.g. saponins, alkaloids, terpenoids, steroid glycosides and some sesquiterpenoids). Many also possess important pharmacological activity. Selective association between taste and gastrointestinal illness is a widely accepted principal of taste aversion learning among mammals (cf. Revusky, 1984) and the learning mechanism of food aversion in response to induced sickness has been well documented in a number of animal species (see Zahorik & Houpt, 1977).

While the highly adaptive significance of the reversed process, i.e., being able to associate improved health with the ingestion of novel plants having medicinal properties, seems self-evident, such learning mechanisms have received little attention (cf. Zahorik, 1977) and is an area greatly in need of further research.

In non-human primates, important benefits also come from social learning, which allow naive individuals to acquire information through the experience of others, and over time to perfect the behavior themselves. Although infant apes almost certainly learn about medicinal plants, just as they do about food plants, from their elders, the question remains as to how this knowledge was acquired in the first place. It is not simply a question of which plant to use, but the exact part of the plant and how to ingest it, at the same time avoiding the dangers of toxicity. What is almost certain is that if great apes can overcome such complexities, then surely the ancestors of man must have had the same capacity (Huffman, 2001). It is most likely that many plant foods of the early hominids, like those of modern apes, contained secondary compounds that were inhibitory agents to pathogens, thus aiding to preserve the health of the ingestor.

Our earliest hominid ancestors can be predicted to have exhibited some similarities in plant selection criteria with both extant apes and modern humans. The fossil record provides no direct evidence for the finer subtleties of feeding behavior and diet, but it seems reasonable to hypothesize that early hominids would have displayed at least the range of extant ape self-medicative behaviours. A major turn of events in the evolution of medicine is likely to have come about in early humans with the advent of language to share and pass on detailed experiences about plant properties and their effect against disease.

It is also likely that humans watching the behaviour of sick animals discovered the medicinal properties of many plants early on in our history (Huffman, 2001). Hallucinatory-type behavior has also been demonstrated in mammals and birds under controlled laboratory conditions, while erratic behaviour has been observed in various species in the field after they had been affected by drug plants (Siegel & Jarvik, 1975). As early as 1888, it was postulated that medicinal plants have outstanding peculiarities of taste, usually bitter, pungent, aromatic, astringent or acidic, (which effectively covers most plants), and frequently a peculiar smell as well (Smith, 1888). He suggested that by these notable qualities two to three hundred species could be selected from the nine thousand South African plants, thus greatly narrowing the field of experiment by trial and error.

The strong similarities in plant selection criteria among the African great apes in response to parasite infection and gastrointestinal upset and the common use of some plants by chimpanzees and humans for treating such illnesses is tantalising evidence for the evolution of medicine and the impact made by parasite infection. The survey presented in this paper also points to several possibilities among the gorillas.

FUTURE PROSPECTS FOR MULTIDISCIPLINARY RESEARCH IN ETHNOPHARMACOLOGY AND ANIMAL BEHAVIOR

It is possible that some *Aframomum* species could be a key factor in modulating parasite loads via chemical action, particularly the nematode *O. stephanostomum*. In the past, wild-caught infant gorillas have suffered massive infections, although free-living animals have not appeared to suffer unduly from the worms. At the Ikunde Centre, a former arm of the Barcelona Zoo situated at Bata, Rio Muni (now Equatorial Guinea), all gorillas that were taking milk were infected with this strongyle nematode. The celebrated white gorilla, "Copito de Nieve", showed an abundance of *Oesophagostomum* eggs when he arrived at the centre (Sabater Pi, 1967). During this time 80% of all captured infant gorillas succumbed to *oesophagostomiasis*. Rousselot & Pellissier (1952) describe *O. stephanostomum* in nine wild-caught gorillas (ages ranged from 18 months to 3 years) in the Brazzaville Zoo. Symptoms began 30 to 40 days (equal to the parasites' prepatent period) after capture, and at autopsy all exhibited intestinal nodules ranging in number from 7 to 60.

Oesophagostomum spp. infections are common in non-human primates, pigs, sheep, cattle and occasionally humans, and are considered significant pathogens (cf. Polderman *et al.*, 1991). *O. stephanostomum* has been identified as a major parasite linked to and effectively controlled by self-medicative behavior in chimpanzees in the Mahale Mountains of western Tanzania (Huffman *et al.*, 1993, 1997; Huffman, Page *et al.*, 1996; Huffman & Caton, 2001).

While a number of broad spectrum anthelmintics are currently available for the treatment of livestock, growing chemoresistance to these anthelmintics and the prohibitive costs of such drugs to developing African nations make their use impractical if not at times impossible (Jackson, 1993; Mathias *et al.*, 1996; Roepstorff *et al.*, 1987). Recently, great interest has been taken in ethnoveterinary research and development, a fast growing field which is looking for new ways of treatment using natural plant products derived from ethnomedicine (cf. Mathias *et al.*, 1996). Combined, ethnopharmacology and the emerging field of animal self-medication have the potential to evaluate evolutionary strategies of health maintenance and contribute to the development of biologically sound health care strategies in the 21st Century (Huffman *et al.*, 1998). We hope that this paper will stimulate such research by others in this ripe new field.

REFERENCES

Adegoke, G.O. & B.J. Skura 1994. Nutritional profile and antimicrobial spectrum of the spice. *Aframomum danielli. Plant Foods for Human Nutrition*, 45 (2): 175-182.

Attwater, H. 1999. *My Gorilla Journey*. Sidgwick & Jackson, London.

Billing, J. & P.W. Sherman 1998. Antimicrobial functions of spices: Why some like it hot. *Quarterly Review of Biology*, 73: 3-49.

Blancou, L. 1955. The lowland gorilla. *Animal Kingdom*, 58: 162-169.

Bouquet, A., A. Cave & R. Paris 1971. Plantes medicinales du Congo-Brazzaville (III)

plantes medicinales et phytotherapie. *Tome*, V (2): 154-158.
Bullock, S.H. 1981. Dynamics of vegetative shoots of three species of *Afromonum* (Zingiberaceae) in Cameroon. *Adansonia*, 20 (4): 388-392.
Burkill, H.M. 1985. *The Useful Plants of West Tropical Africa 2nd ed. Vol 1.* Royal Botanical Gardens, Kew. London.
Bützler, W. 1980. Presence et repartition des gorilles, *Gorilla gorilla gorilla* (Savage & Wyämn, 1847), au Cameroun. *Saugetier. Mitteil*, 28: 68-79.
Calvert, J.J. 1985. Food selection by western gorillas (*G. g. gorilla*) in relation to food chemistry. *Oecologia*, 65: 236-246.
Carroll, R.W. 1986. Status of the lowland gorilla and other wildlife in the Dzangah-Sangha region of south-western Central African Republic. *Primate Conservation*, 7: 38-41.
De Rienzo, P. & D. Beal 1997. *The Ibogaine Story*. Autonomedia, Brooklyn, New York.
Dubois, L. 1955. *Tabernanthe iboga* Baillon. *Bulliten Agricole du Congo Belgium*, XLVI (4): 805-829.
Etkin, N.L. 1996. Medicinal cuisine: Diet and ethnopharmacology. *International Journal of Pharmacology*, 34 (5): 313-326.
Etkin, N.L. & P.J. Ross 1983. Malaria, medicine, and meals: Plant use among the Hausa and its impact on disease. In (L. Romanucci-Ross, D.E. Moerman & L.R. Tancredi, eds.) *The Anthropology of Medicine: From Culture to Method*, pp. 231-259. Praeger, New York & Washington.
Fay, J.M.M., J. Agnagna, J. Moore & R. Okoko 1989. Gorillas (*Gorilla gorilla gorilla*) in the Likoula swamp forests of North Central Congo: Preliminary data on populations and ecology. *International Journal of Primatology*, 10 (5): 477-486.
Fernandez, J.W. 1972. *Tabernanthe iboga*: Narcotic ecstasies and the work of the ancestors. In (P.T. Furst, ed.) *Flesh of the Gods*, pp. 237-260. Praeger, New York & Washington.
——— 1982. *Bwiti: An Ethnography of the Religious Imagination in Africa.* Princeton University Press, Princeton.
Fossey, D. 1983. *Gorillas in the Mist*. Hodder & Stoughton, London.
Goodall, A. 1979. *The Wandering Gorillas*, Collins, Lndon.
Goutarel, R. 1997. Pharmacodynamics and therapeutic applications of iboga and ibogaine. In (De P. Rienzo & D. Beal, eds.) *The Ibogaine Story*, pp. 229-243. Autonomedia, Brooklyn, New York.
Hallé, N. 1987. *Cola lizae* N. Halle (Sterculiaceae) nouvelle espece du Moyan Ogooue (Gabon). *Adansonia*, 3: 229-237.
Hobbs, C. 1995. *Medicinal Mushrooms*. Botanica Press, Santa Cruzica.
Huffman, M.A. 1997. Current evidence of self-medication in primates: A multidisciplinary perspective. *Yearbook of Physical Anthropology*, 40: 171-200.
——— 2001. Self-medicative behavior in the African great apes: An evolutionary perspective into the origins of human traditional medicine. *BioScience*, 51 (8): 1-11.
Huffman, M.A. & M. Seifu 1989. Observations on the illness and consumption of a possibly medicinal plant *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park. *Primates*, 30 (1): 51-63.
Huffman, M.A. & J.M. Caton 2001. Self-induced increase of gut motility and the control of parasite infections in wild chimpanzees. *International Journal of Primatology*, 22 (3): 329-346.
Huffman, M.A., S. Gotoh, D. Izutsu, K. Koshimizu & M.S. Kalunde 1993. Further observations on the use of *Vernonia amygdalina* by a wild chimpanzee, its possible effect on parasite load, and its phytochemistry. *African Study Monographs*, 14 (4): 227-240.
Huffman, M.A., K. Koshimizu & H. Ohigashi 1996. Ethnobotany and zoopharmacognosy of *Vernonia amygdalina*: A medicinal plant used by humans and chimpanzees. In (P. Caligari & D.J.N. Hind, eds.) *Compositae: Biology and Utilisation Vol. 2*, pp. 351-360. The Royal Botanical Gardens, Kew. London.
Huffman, M.A., J.E. Page, M.V.K. Sukhdeo, S. Gotoh, M.S. Kalunde, T. Chandrasiri & G.H.N. Towers 1996. Leaf-swallowing by chimpanzees: A behavioral adaptation for the control of strongyle nematode infections. *International Journal of Primatology*, 72 (4): 475-503.
Huffman, M.A., S. Gotoh, L.A. Turner, M. Hamai & K. Yoshida 1997. Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania. *Primates*, 38 (2): 111-125.
Huffman, M.A., H. Ohigashi, M. Kawanka, J.E. Page, G.C. Kirby, M. Gasquet, A. Murakami & K. Koshimizu 1998. African great ape self-medication, a new paradigm for treating parasite disease with natural medicines? In (H. Ageta, N. Aimi, Y. Ebizuka, T. Fujija & G. Honda, eds.) *Towards Natural Medicine Research in the 21st Century*, pp. 113-122. Elsevier Science B.V. Amsterdam.
Iwu, M.M. 1993. *Handbook of African Medicinal Plants*. CRC Press, London.
Jackson, F. 1993. Anthelmintic resistance. The state of play. *British Veterinary Journal*, 149: 1233-1235.
Knott, C. 1998. Orangutans in the wild. *National Geographic Magazine*, 194 (2): 30-57.
Kokwaro, J.O. 1976. *Medicinal Plants of East Africa*. East African Literature Bureau, Nairobi.
Kuroda, S., T. Nishihara, S. Suzuki & R.A. Oko 1996. Sympatric chimpanzees and gorillas in the Ndoki Forest, Congo. In (W.C. McGrew, L.F. Marchant & T. Nishida, eds.) *Great Ape Societies*, pp. 71-81. Cambridge University Press, Cambridge.
Landrin, A. 1905. Etude botanique, pharmacologue, et chimique (*Tabernanthe iboga*). *Bulletin Science Pharmacologue*, 11: 319.
Mathias, E., C.M. McCorkle & T.W. Schillhorn van Veen 1996. Introduction: Ethnoveterinary research and development. In (C.M. McCorkle, E. Mathias & T.W. Schillhorn van Veen, eds.) *Ethnoveterinary Research and Development*, pp. 1-24. Intermediate Technology Publications, London.
Mazza, G. 1998. *Functional Foods, Biochemical & Processing Aspects*. Technomic Publication, Lancaster.
Merfield, F.G. 1954. The gorilla of the french Cameroon. *Zoo Life*, 9 (3): 84-94.
Messer E.J. & R.W. Wrangham 1995. *In vitro* testing of the biological activity of *Rubia cordifolia* leaves on primate Strongyloide species. *Primates*, 37: 105-108.
Migeod, F.W.H. 1925. *Through British Cameroon*. Heath Cranton, London.
Muanza, D.K., N.L. Dangala & O. Mpay 1993. Zairean medicinal plants as diarrhea remedies and their antibacterial activities. *African Study Monographs*, 14 (1): 53-63.
Murakami, A., H. Ohigashi & K. Koshimizu 1994. Possible anti-tumour promoting properties of traditional Thai foods and some of their active constituents. *Asia Pacific Journal of Clinical Nutrition*, 3: 185-191.
Neuwinger, H.D. 1996. *African Ethnobotany: Poisons and Drugs*. Chapman & Hall, London.
Nishihara, T. 1995. Feeding ecology of western lowland gorillas in the Nouabale-Ndoki National Park, Congo. *Primates*, 36 (2): 151-168.
Ohigashi, H., T. Osawa, J. Terao & S. Watanabe 1997. *Food Factors for Cancer Prevention.* Springer-Verlag, Tokyo.
Oliver-Bever, B.E.P. 1986. *Medicinal Plants in Tropical West Africa*. Cambridge University Press, Cambridge.
Oloke, J.K., D.O. Kolawole & W.O. Erhun 1988. The antibacterial and antifungal activities of certain components of *Afromomum melegueta* fruits. *Fitoterapia*, LIX (5): 384-388.
Outuga, D.B.A. 1975. Chemical composition and potential commercial use of Kola nut,

Cola nitida, Vent. (Schott & Erndlicher). *Ghana Journal of Agricultural Science*, 8: 121-125.
Page, J.E., M.A. Huffman, V. Smith & G.H.N. Towers 1997. Chemical basis for medicinal consumption of *Aspilia* (Asteraceae) leaves by chimpanzees: A re-analysis. *Journal of Chemical Ecology*, 23: 2211-2226.
Perera, P., E. Kumlin, F. Sandberg, H. Dutschweska, V. Christov & S. Philipov 1991. Pharmacological screening of some medicinal plants from Cameroon. *Fitoterapia*, LXII (2): 139-143.
Perry, L.M. 1980. *Medicinal Plants of East and South East Asia*. MIT Press, Cambridge, Mass.
Phisalix, M.C. 1901. Action physciologique de l'ibogaine. *Contes Rendu Societe Biologue*, 53: 1077.
Pope, H.G. 1969. *Tabernanthe iboga*, an African narcotic plant of social importance. *Economic Botany*, 23: 174-184.
Polderman, A.M., S. Krepel, S. Baeta, J. Blotkamp & P. Gigase 1991. Oesophagtostomiasis, a common infection of man in northern Togo and Ghana. *American Journal of Tropical Medicine and Hygiene*, 44: 336-344.
Raponda-Walker, A. & R. Sillans 1961. *Les Plantes Utiles du Gabon*. Pail Lechevalier, Paris.
Rätsch, C. 1992. *The Dictionary of Sacred and Magical Plants*. Prism Press, Dorset.
Revusky, S. 1984. Associative predispositions. In (P. Marler & H.S. Terrace, eds.) *The Biology Learning*, pp. 447-460. Springer-Verlag, Berlin.
Roepstorff, A., H. Bjørn & P. Nansen 1987. Resistence of *Oesophagostomum* spp. in pigs to pyrantel citrate. *Veterinary Parasitology*, 24: 229-239.
Rogers, M.E., F. Maisels, E.A. Williamson, M. Fernandez & C.E.G. Tutin 1990. The diet of gorillas in the Lope Reserve, Gabon: A nutritional analysis. *Oecologia*, 84: 326-339.
Rousselelot, R. & A. Pellissier 1952. Pathologie du Gorille (2e note) III–Oesophogostomose Nodulaire a *Oesophagostomum stephanostomum* du Gorille et du Chimpanze. *Bull. Soc. Path. Exot.*, 45 (4): 568-574.
Russell, T.A. 1995. The Kola of Nigeria and the Cameroons. *Tropical Agriculture, Trin.*, 32 (3): 210-240.
Sabater Pi, J. 1967. An albino lowland gorilla from Rio Muni, West Africa, and notes on its adaptation to captivity. *Folia Primatologica*, 7: 155-160.
Sabater Pi, J. 1977. Contribution to the study of alimentation of lowland gorillas in the natural state in Rio Muni, Republic of Equatorial Guinea (West Africa). *Primates*, 18: 183-204.
Schaller, G.B. 1963. *The Mountain Gorilla: Ecology and Behaviour*. University of Chicago Press, Chicago.
Schneider, J. & E. Sigg 1957. Neuropharmacological studies on ibobaine. *Annals of the New York Academy of Sciences*, 66: 765.
Sherman, P.W. & J. Billing 1999. Darwinian gastronomy: Why we use spices. Spices taste good because they are good for us. *BioScience*, 48 (6): 453-463.
Siegel, R.K. & M.E. Jarvik 1975. Drug-induced hallucinations in animals and man. In (R.K. Siegel & L.J. West, eds.) *Hallucinations*, pp. 81-161. John Wiley & Sons, New York.
Siegel, R.K. 1979. Natural animal addictions: An ethnological perspective. In (J.D. Keehn, ed.) *Psychopathology in Animals*, pp. 29-60. Academic Press, New York.
Smith, A. 1888. *A Contribution to South African Materia Medica*. Lovedale, South Africa.
Sugiyama, Y. & J. Koman 1992. The Flora of Bossou; Its utilization by chimpanzees and humans. *African Study Monographs*, 13 (3): 127-169.
Tutin, C.E.G. & M. Fernandez 1985. Foods consumed by sympatric populations of *Gorilla g. gorilla* and *Pan t. troglodytes* in Gabon: Some preliminary data. *International Journal of Primatology*, 6 (1): 27-43.
Tutin, C.E.G., E.A. Williamson, M.E. Rogers & M. Fernandez 1991. A case study of a plant-animal relationship, *Cola lizae* and lowland gorillas in the Lope Reserve, Gabon. *Journal of Tropical Ecology*, 7: 181-199.
Valker, A. 1931. La vie du gorille au Gabon. *Bulliten Museum Natural d'Historia Naturale*, 3: 393-398.
Watt, J.M & M.G. Breyer-Brandwijk 1962. *Medicinal and Poisonous Plants of Southern and Eastern Africa*. E & S Livingstone, Edingburgh & London.
Watts, D.P. 1984. Composition and variability of mountain gorilla diets in the central Virungas. *American Journal of Primatology*, 7: 323-356.
Wrangham, R.W. 1995. Relationship of chimpanzee leaf-swallowing to a tapeworm infection. *American Journal of Primatology*, 37: 297-303.
Wrangham, R.W., N.L. Conklin, C.A. Chapman & K.D. Hunt 1991. The significance of fibrous foods for Kibale forest chimpanzees. *Philosophical Transactions of the Royal Society of London, Series B*, 334: 171-178.
Yamagiwa, J., N. Mwanza, T. Yumoto & T. Maruhashi 1994. Seasonal change in the composition of the diet of eastern lowland gorillas. *Primates*, 35: 1-14.
Zahorik, D.M. 1977. Associative and non-associative factors in learned food preferences. In (L.M. Barker, M.R. Best & M. Domjan, eds.) *Learning Mechanisms in Food Selection*, pp. 181-199. Baylor University Press, Baylor.
Zahorik, D.M. & K.A. Houpt 1977. The concept of nutritional wisdom: Applicability of laboratory learning models to large herbivores. In (L.M. Barker, M.R. Best & M. Domjan, eds.) *Learning Mechanisms in Food Selection*, pp. 45-67. Baylor University Press, Baylor.

——— Accepted *February 27, 2002*

Author's Name and Address: Michael A. HUFFMAN, *Primate Research Institute, Kyoto University, 41-2 Kanrin, Inuyama, Aichi 484-8506, JAPAN.*
E-mail: huffman@pri.kyoto-u.ac.jp

Appendix 1. Some Ethnomedical Plants in the Diets of *Gorilla g. gorilla* and *Gorilla g. graueri*.

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
Acanthaceae	*Crossandra guineensis*	Leaves used for diarrhoea and skin diseases. [1]	Leaves [2]
	Thomandersia laurifolia	Leaves and roots used for coughs, fevers, asthma, dysentery, fatigue, vaginal infection and anthelmintic. [1]	Leaves [2]
Aniosophylleaceae	*Poga oleosa*	Kernel and leaves used as emollient, laxative and for skin diseases. [3]	Fruits [4]
Annonaceae	*Annodium manni*	Bark used as sedative and dysentery and gastro-enteritis. [1]	Fruits, Bark [5,6]
	Polyalthia suaveolens	Fruits, roots and leaves used as aphrodisiac, deparasitant, rheumatism, and toothache and as an anti-inflammatory. [1]	Fruits [2,5,6]
	Xylopia aethiopica	Fruits and whole plant used as carmanative and analgesic. [3,7,8]	Leaves [9]
Araceae	*Anchomanes difformis*	Roots and leaves used for constipation and coughs. [1,3,7,10]	Leaves [9,11]
	Colocasia esculenta	Tubers and leaves used for whitlow and potherb. [3,7,10]	Roots [4]
	Cyrtosperma senegalense	Roots used as sedative, analgesic and purgative. [1]	Roots [2]
Apocynaceae	*Landolphia owariensis*	Twigs, leaves and stem used for colic, venereal diseases. [1,3,7,10]	Leaves, Bark [6]
	Pycnobotrya nitida	Leaves and fruits used for bronchopneumonia, dysentery [1]	Pith [6]
	Rauwolfia macrophylla	Intestinal complaints, syphilis. [12]	Fruits [4]
	Saba comorensis (var. florida)	Flowers used for jaundice, haemoglobin. [1]	Fruits [2]
	Tabernaemontana crassa	Bark used as anthelmintic, skin diseases, leprosy. [1,8,10]	Fruits [2]
	Tabernanthe iboga	Roots, stem and bark used for debilitating illness of unknown origin, aphrodisiac, hallucinogen and tonic. [1,10,12]	Fruits, Leaves, Roots [12,13,14]
Asclepiadaceae	*Tylophora syvatica*	Dermatitis, ovarian problems and coughs. [1]	Leaves, Bark [4]
Bromeliaceae	*Ananas comosus*	Fruits and leaves used for arthritis, venereal diseases and skin eruptions, laxative. [1,3,7]	Fruits, Bark [4]
Burseraceae	*Canarium schweinfurthii*	Fruits, stems and barks used for coughs, venereal diseases and as exudate. [1,3,10]	Fruits [6]

Appendix 1. (continued)

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
Caesalpiniaceae	*Anthonotha gilletii*	Diuretic, oedema [8]	Fruits [6]
	Brachystegia eurycoma	Seeds and leaves used as anthelmintic. [3]	Leaves [9]
	Detarium macrocarpum	Fruits and leaves used for dysentery and syphilis. [3]	Fruits [2,9]
	Dialium dinklagei	Fruits and leaves used as anti-tussle, anti-infective. [6]	Fruits [3]
	Dialium pachyphyllum	Leaves and bark used for pain relief and coughs. [1]	Fruits [2]
	Gilbertiodendron dewevrei	Used for dysentery. [1]	Seeds [2]
Capparidaceae	*Bucholzia coriacea*	Fruit and seed used for purgative and anthelmintic. [7,10,12]	Fruit [12]
Caricaceae	*Carica papaya*	Leaves and fruits used for fever malaria. Roots used for yaws. [3,7,8]	Trunk [4]
Cecropriaceae	*Myrianthus arboreus*	Leaves, roots and stem used for dysentery, skin infections and as anthelmintic. [7]	Fruits [6]
Chrysobalanaceae	*Parinari excelsa*	Fruit and stem used for diarrhoea, dysentery and as tonic. [3]	Fruits [2]
Combretaceae	*Quisqualis latiolata*	Used for diarrhoea, dysentery and haemorrhoids. [1,7]	Bark [4]
Commelinaceae	*Palisota hirsuta*	Stems and leaves used for sore throat, coughs, and toothache. Sap used as anthelmintic. [3,10]	Fruits [4,5,6]
Compositae	*Gynura scandens*	Crushed leaves used for fevers. [15]	Bark [16]
	Vernonia conferta	Leaves, stems and roots used for coughs, stomach ache and yaws and as anthelmintic. [1,3,7]	Fruit, Pith [4]
Cucurbitaceae	*Cucumeropsis edulis*	Seeds used as vermifuge and purgative. [3]	Buds, Pith [4]
Ebenaceae	*Diospyros crassiflora*	Used for ovarian problems and eye complaints. [1]	Fruits [2]
Euphorbiaceae	*Alchornia cordfolia*	Leaves, stem, bark and roots used for malaria, urinary, respiratory and gastrointestinal disorders, skin infections and as a purgative. [1,3]	Fruits [4,6]
	Alchornia floribunda	Roots and fruits as hallucinogen aphrodisiac and for urinary, respiratory and intestinal disorders. [1]	Fruits, Bark [4,6]

Appendix 1. (continued)

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
	Macaranga kilimandscharica	Root extract used for bilharzia. Decoction of roots and leaves for stomach problems. [15]	Bark [16]
	Manihot esculenta	Leaves and tubers used for diabetes. [3,8]	Tubers [5]
	Manniophytum fulvum	Stem, bark and twigs used for dental caries, leprosy, venereal diseases, and skin infections and as anthelmintic. [1,3]	Leaves [4]
Flacourtiaceae	*Caloncoba glauca*	Seeds used for migraine, leprosy and as aphrodisiac. [1,8,10]	Fruits [2]
	Caloncoba welwitschii	Used for bronchitis, rheumatism and headache and as anthelmintic. [1,8]	Fruits, Bark [2]
	Oncoba spinosa	Fruits and leaves used for colds, fevers and female infertility. [1,3]	Leaves [9]
Gentianaceae	*Gentium africanum*	Leaves and stems used as purgative and tonic. [3]	Leaves [2]
Gramineae	*Pennisetum purpureum*	Leaves used for mouth infections, gingivitis, and thrush. Mild laxative. [3,12]	Leaves [16]
	Saccharum officinarum	Stem and leaves used as laxative. [3]	Fruits [4]
	Zea mays	Diuretic and for urinary infections. [12]	Roots [4,16]
Guttiferae	*Garcinia kola*	Seeds, stems, roots and bark used for coughs, inflammation of respiratory tract, poison, antidote and as an aphrodisiac. [1,3]	Fruits [2]
	Mammea africana	Fruits, leaves and bark used for fevers, skin infections, diarrhoea and bronchitis. [1,3]	Fruits [2,4,9]
Humiraceae	*Saccoglottis gabonensis*	Fruits, leaves and stems used for fevers and emetic. [1,3]	Fruits [4]
Icacinaceae	*Iodes africana*	Leaves used as decongestant for respiratory complaints, sinusitis, bronchitis and diarrhoea. [1]	Leaves [6]
Irvingiaceae	*Irvingia gabonensis*	Fruit rind, roots and bark used for fevers. [1,3]	Fruits [2,5,9]
Leguminosae	*Albizia gummifera*	Crushed pods taken for stomach pains. Pounded roots in water for skin conditions, bark decoction for malaria. [15]	Roots, Bark [6]

Appendix 1. (continued)

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
Loganiaceae	*Anthocleista vogelli*	Stem, bark and leaves used as anti-inflammatory, anti-diabetes and for venereal diseases. [1,3]	Leaves [9]
Marantaceae	*Haumania danckelmaniana*	Roots used as anthelmintic. [1]	Shoots [2,4,11]
	Marantochloa congensis	Roots used as purgative. [1]	Pith [2]
	Thaumatococcus danielli	Fruit and leaves used for liver disorder and as laxative. [1,3]	Fruits, Pith [6]
Meliaceae	*Trichilia heudelottii*	Stem, roots and leaves used as anthelmintic, diuretic and aphrodisiac. [1,3]	Flowers [2]
Menispermaceae	*Triclisia dictyophylla*	Roots used for malaria and anticonvulsant. [1,8]	Fruits [2]
	Triclisia patens	Roots used for oedema, rheumatism and arthritis. [1,8]	Fruits [2]
Mimosoideae	*Parkia filicoldea*	Fruits and leaves used for inflammation. [3]	Fruit, Pulp [9]
	Pentaclethra macrophylla	Bark, fruits and leaves used as anthelmintic and as analgesic. [1,3]	Leaves [9]
	Tetrapleura tetraptera	Fruits and whole plant used for flatulence, jaundice, fevers and convulsions. [1]	Fruits, Seeds [2,11]
	Piptadeniastrum africanum	Stem, bark and roots used for oedema, constipation, dropsy and as anthelmintic. [1,10]	Leaves, Bark [9]
Moraceae	*Chlorophora excelsa*	Roots, leaves and fruits used as tonic and for inflammation. [1,3]	Leaves [2,4,6,9]
	Ficus exasperata	Leaves used for coughs and venereal diseases. [1,3]	Fruits [2]
	Ficus mucuso	Used for bronchitis, otitis, convulsions and as analgesic. [1]	Leaves, Pulp [4]
	Ficus natalensis	Fruits and leaves used for pains and venereal diseases. [15]	Leaves, Fruits [6]
	Ficus thonningii	Leaves and fruits used for bronchitis and urinary tract infection. [1,3]	Fruit, Pulp [9]
	Musanga cecropioides	Leaves and stem used for fevers and as emmenagogue. [3]	Roots [2]

Appendix 1. (continued)

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
	Musanga smithii	Fruits, leaves, bark and sap used for broncho-pneumonia, leprosy, gonorrhoea, rheumatism and as an anthelmintic. [1]	Fruits [17]
	Treculia africana	Fruits and leaves used for chronic coughs, skin infections and as anthelmintic. [1,3]	Fruits [2,3,6,9]
Musaceae	*Musa paradisiaca*	Fruits and leaves used as potent astringent, hemostatic and for indolent ulcers. [3]	Leaves, Fruit [3,11]
	Musa sapientium	Fruit rind and leaves used as anthelmintic aphrodisiac and for high blood pressure. [3]	Fruits [4]
Myrisinaceae	*Maesa lanceolata*	Fruits used as anthelmintic and purgative and for sore throat. [1]	Bark [16]
	Pycnanthus angolensis	Seeds and stem bark used for skin diseases, mouth sores, fevers, asthma and whooping cough. [1,3]	Leaves, Fruit [2,4,5,6]
Ochnaceae	*Lophira alata*	Bark used for visceral pains, toothache, convulsions, and epilepsy. [7]	Leaves [9]
Olacaceae	*Strombosiopsis tetandra*	Fruits, roots and leaves used for ovulation problems, rheumatism and epilepsy. [1]	Fruits [2]
Palmae	*Ancistrophyllum secudiflorum*	Shoots and sap used as vermifuge, tonic and for fever and dysentery. [3]	Pith [5]
	Elaeis guineensis	Leaves, fruit and roots used as analgesic, antibacterial and poison antidote. [1,3]	Fruits, Pith [6]
	Eremospatha haubevilleana	Leaves and roots used for hernia, otitis and as anthelmintic. [1]	Pith [6]
Papilionoideae	*Pterocarpus soyauxi*	Leaves, stem, bark used for fever. [3]	Bark, Leaves, Seeds, Buds [4,8]
Passifloraceae	*Adenia cissampeloides*	Roots and stem used as anthelmintic and poison antidote. [15]	Bark [16]
	Barteria nigritiana	Fruits and leaves used for fevers, aches and stomach disorders. [1,3]	Fruits [2]
	Passiflora foetida	Leaves used for anxiety and sleeplessness. [1,3]	Fruits [3]
Rubiaceae	*Nauclea didrichii*	Roots and stem used for malaria and as febrifuge. [3]	Fruits [9]
	Porterandia cladantha	Leaves used as aphrodisiac and for eczema, diarrhoea and local pain relief. [1,3]	Leaves [2]

Appendix 1. (continued)

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
Sapotaceae	*Baillonella toxisperma*	Fruits, medullas and leaves used for vaginal infections, epilepsy, rheumatism and gingivitis. [1]	Medullas, Fruit [5]
	Gambeya lacourtiana	Fruits used for vaginal infections, rheumatism and uterine haemorrhage. [1]	Fruits [2]
Sapindaceae	*Allophyllus africanus*	Fruits, leaves and roots used for diarrhoea, arthritis, headache, nasal congestion, colic and as anthelmintic. [3]	Fruits [2]
	Lecaniodiscus cupanoides	Stem, bark and leaves used for abdominal swelling caused by liver abscess and for fevers. [1,3]	Fruits [9]
Selaginellaceae	*Selaginella myosurus*	Used for asthma, fever and defatigant. [1]	Leaves [4]
Smilacaceae	*Smilax kraussiana*	Roots used for venereal diseases, fevers and as tonic. [3,10]	Leaves, Flowers, Pith [4,16]
Solanaceae	*Solanum torvum*	Leaves used for epilepsy. [1,3,10]	Leaves, Pith [4,16]
Sterculiaceae	*Cola gabonensis*	Roots, fruits and leaves used for migraine, scabies and as aphrodisiac. [1]	Fruits [2]
	Cola nitida	Fruits used as stimulant and in healing rituals. [3,8,12]	Seeds [2]
	Cola pachycarpa	Fruits and leaves used for coughs internal heat. [3]	Seeds [12]
	Theobroma cacao	Fruit pods and leaves used for lactation and as stimulant and emollient. [12]	Fruits [4]
Tiliaceae	*Duboscia macrocarpa*	Fruits used for tuberculosis and dental problems. [1]	Fruits [2,8]
Ulmaceae	*Celtis adlofi-friderici*	Fruits used for tuberculosis. [1]	Fruits [2]
	Celtis brieyi	Leaves, fruits and roots used for dysentery, rheumatism and as antianaemic. [1]	Leaves, Fruit, Bark [6]
Urticaceae	*Urera hypselodendron*	Leaves in water given to sick children. Decoction of stems mixed with milk for abdominal pains in pregnant women. [15]	Bark [6,16]
Verbenaceae	*Vitex doniana*	Roots and leaves used for nausea, colic and epilepsy. [1,3]	Leaves [2,9]
Zingiberaceae	*Costus afer*	Stem and rhizomes used for coughs, hypertension, arthritis, skin diseases and as an aphrodisiac. [3,8,12]	Leaves [6,9]
	Costus lucanusianus	Used to control filarial worms, ulcers and bronchitis. [12]	Fruit, Stem [4]

Appendix 1. (continued)

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
	Renealmia africana	Leaves and fruit used for medicinal purposes. [1),12)]	Fruit [4)]

[1)] Bouquet *et al.*, 1971; [2)] Nishihara, 1995; [3)] Iwu, 1993; [4)] Sabater Pi, 1977; [5)] Tutin & Fernandez, 1985; [6)] Yamagiwa *et al.*, 1994; [7)] Burkill, 1985; [8)] Oliver-Bever, 1986; [9)] Rogers *et al.*, 1990; [10)] Neuwinger, 1996; [11)] Calvert, 1985; [12)] Raponda-Walker & Sillans, 1961; [13)] Bützler, 1980; [14)] Valker, 1931; [15)] Kokwaro, 1976; [16)] Schaller, 1963; [17)] Merfield, 1954

Appendix 2. Some Ethnomedical Plants in the Diets of *Gorilla g. beringei* in the Virunga Volcanoes.

Family	Species	Ethnomedical uses	Plant parts eaten by gorillas
Boraginaceae	*Cynoglossum geometricum*	Crushed leaves inhaled for treatment against fever and influenza. [1),2)]	Roots, Leaves, Part of stem [3),4),5)]
	Cynoglossum lanceolatum	Diaphoretic and expectorant. [6)]	Shoots, Root [5)]
Compositae	*Crassocephalum bojeri*	Crushed leaves and juice drunk for colds and as an antidote for fever and rheumatism. [2)]	Bark [3),4)]
	Mikania cordata	Decoction of leaves used for headaches. [1),2)]	Leaves [3),4)]
	Senecio maraguensis	Leaves used for yaws, syphilis, and gonorrhoea. [6)]	Roots [3),5)]
Gramineae	*Pennisetum purpureum*	Mild laxative, mouth infections, gingivitis, thrush. [1)]	Leaves [3)]
Menispermaceae	*Stephania abyssinica*	Leaves used as purgative, roots used as aphrodisiac and for roundworm, stem juice used as an emetic. [1)]	Fruits [3),4)]
Monimiaceae	*Xymalos monospora*	Softened leaves used for sores, dried roots for cuts and aches. [2)]	Fruits, Bark [3),4)]
Myrsinaceae	*Rapenea pulchra*	Fruits used as anthelmintic. [2)]	Bark [4),5)]
Piperaceae	*Piper capense*	Seeds used as cough medicine, roots used as anthelmintic. [2)]	Bark, Stem [3),4)]
Polygonaceae	*Rumex usambarensis*	Leaves used for liver and stomach conditions for constipation in children and for abdominal pain during pregnancy. [2)]	Stem [4)]
Ranunculaceae	*Clematis simensis*	Leaves chewed and juice swallowed as cure for headache and colds. Root decoction drunk for treatment of malaria and as purgative. [2)]	Bark [4)]
Rosaceae	*Hagenia abyssinica*	Roots used for general illness and malaria. Flowers used for intestinal worms, especially tapeworm. Bark for diarrhoea and stomach-ache. [1),2)]	Pit Bark, Roots [4),5)]
	Pygium (Prunuus) africanum	Leaves inhaled for fever. Bark for stomach-ache. [1)]	Bark, Fruits [3),4),5)]
Urticaceae	*Urera hypselodendron*	Decoction of stems mixed with milk given to pregnant women for abdominal pains. [2)]	Bark [3),4)]

[1)] Iwu, 1993; [2)] Kokwaro, 1976; [3)] Fossey, 1983; [4)] Schaller, 1963; [5)] Watts, 1984; [6)] Watt & Breyer-Brandwijk, 1962

Appendix 3. *Aframomum* spp. Utilised by *Gorilla spp.*

Location	Species	Parts eaten	Reference
S.W. Cameroon			Calvert, 1985
(Campo Reserve)	*A. danielli*	Shoots	
	A. giganteum	Shoots	
	A. hanburyi	Shoots	
	A. subsericeum	Shoots	
S.E. Cameroon			Merfield, 1954
	A. danielli	Pulp, Pith	
	A. albo-violaceum (syn. A. stipulatum)	Fruit	
W. Cameroon			Migeod, 1925
(Mamfe region)	*A. melegueta*	Fruit	
Gabon			Tutin & Fernandez, 1985
	A. danielli	Fruit, Pith	
	A. giganteum	Fruit, Pith	
	A. leptolepsis	Fruit, Pith	
	A. letestuanum	Fruit, Pith	
	A. limbatum	Pith	
	A. polyanthum	Fruit	
	A. subsericeum	Fruit, Pith	
Central Gabon			Rogers *et al.*, 1990
(Lope Reserve)	*A. longipetiolatum*	Pulp, Stem	
	A. leptolepsis	Pulp, Stem	
S.W. Gabon			P.H. Chanjou,
(Petit Loango Reserve)	*A. citratum*	?	(personal
	A. giganteum	?	communication)
Equatorial Guinea			Sabater Pi, 1977
	A. giganteum	Fruits, Medullas, Leaves, Buds	
	A. sanguineum	Leaf Buds	
	A. danielli	Leaf Buds	
	A. subsericeum	Terminal Buds	
	A. limbatum	Fruit	
Northern Congo-Brazzaville			
(Ndoki Forest)	*A. citratum*	Fruit	Nishihara, 1995
(Likouala Basin)	*A. angustifolium*	Leaves, Pith	Fay *et al.*, 1989
S.W. Congo-Brazaville			M.D. Gouya,
(Koulilou Basin	*A. stipulatum*	?	(personal
Conkouti)	*A. sanquineum*	?	communication)
	A. leptolepsis	?	M. Vacher, (personal communication)

Appendix 3. (continued)

Location	Species	Parts eaten	Reference
S.W. Central African			Carroll, 1986
Republic	*A. sulcatum*	Pith	
(Dzanga Sangha)			
Congo-Kinshasa			
(Itebero)			Yamagiwa *et al.*, 1994
	A. laurentii	Fruit, Pith	
	A. sanguineum	Fruit	
(Kahuzi-Biega)			Goodall, 1979
	A. sanguineum	?	
(Mwenga-Fizi)			Schaller, 1963
	A. sanguineum	Pith	
Uganda			Schaller, 1963
(Bwindi Forest)	*A. milbraedii*	Fruit	D. Tukahabwa, (personal
	A. sanguineum	Fruit	communication)

第11章
自己治療行動の学際的研究

マイケル・A・ハフマン
大東　肇
小清水弘一

一　はじめに

最近、野生霊長類の自己治療行動に関する新しい研究分野が開拓されたことにより、動物、植物、寄生虫の三者の複雑な関係に注目が集まってきている。チンパンジーをはじめとする野生霊長類は日常、栄養価に富んだ果実や葉、若い芽などを食べるが、それ以外に、特殊な二次代謝産物を含む種の葉や樹皮、さらには根などの部位を食べることもある。栄養的には乏しいと考えられるこれらの植物の非栄養的な採食の意義に、ここ数年、興味がもたれ、その一つとして薬理的効果が指摘されつつある。しかしながら、これらの種や部位の薬理効果や、その有効成分についてはほとんど知られていなかった。ところが最近、非栄養的なある種の植物を食べると、寄生虫感染症の制御や、その二次的病徴である腹痛の治癒などに有効であるとする仮説が、アフリカの大型類人猿研究により実証されてきている。

すなわち、東アフリカのチンパンジー三集団において、強烈な苦味をもつ茎の汁（髄部液）を摂取したり、葉をそのまま呑み込むといった行動が生態学的・寄生虫学的解析から寄生虫感染症の軽減に役立っていることが指摘されている。

アフリカの大型類人猿についてのこの種の調査・研究は、初期人類の自己治療から現世人類の医療行為への進化の過程を考察する上でのよい手がかりとなるであろう。また、霊長類の自己治療研究には、ヒト、家畜、飼育動物などの寄生虫感染症を効果的に治療することに対する天然物の有効利用や新しい治療方法の提供についての期待を抱かせるものである。

*

右に述べたように、アフリカの大型類人猿の薬用植物利用に関する多くの観察結果が次々と報告されるようになり、動物の自己治療に関する研究に一層拍車がかかってきた[1]。野生動物の自己治療能は、各個体の経験により、また、部分的には本能、食欲を通して、さらには通常の採食行動の副次的産物としてもたらされ、以後の行動においてはこの経験や結果が記憶され定着するものと考えられる。

一部の霊長類研究者は、野生霊長類が日常的に食べる植物に含まれている二次代謝産物をなぜ食するのか、あるいはまた、毒物も含むであろうこれら産物にどのように対処したかに焦点を当てて研究している[2]。自己治療を理解する上で難点であり、また重要な今後の研究課題の一つは、二次代謝産物の豊富な植物を栄養補給の目的で採食し、その結果として間接的に薬効を得ている場合と、直接薬効を期待して意識的に当該植物を採食する場合とを区別することである。ヒトの社会でも食用と薬用植物の区別は、元来あまり明確ではなかった。その顕著な事例として、アジア各地の日常食に見られるスパイス、香辛料、各種ハーブなどを挙げることができる。これらのなかには、抗菌、抗ウイルス、抗酸化

や発がん抑制作用など生体防御や機能調節作用が期待できるものもあることは、よく知られている。[3]

寄生虫は多くの病気を誘発し、個体それ自身の行動や、繁殖能力にも影響を及ぼす。したがって、これらの悪影響を取り除くことは重要である。寄生虫感染症が宿主へ与える影響や、感染した際の宿主への反応は、長い進化の過程で培われてきた産物であることは間違いない。霊長類やその他の哺乳類において、偶然採食した植物二次代謝産物が寄生虫駆除に効果があるかもしれないという可能性は、ジャンセン[4]によって初めて示唆された。しかしながら、アフリカの大型類人猿についての最近の調査結果は、偶然ではなく、薬効を期待してある種の植物を積極的に摂取していることが示唆されている。とくに、自己治療行動の主役は寄生虫感染症の制御（感染に由来する腹痛を和らげる効果も含む）にあるとの仮説が提出されている。アフリカの大型類人猿についてのこの調査結果は、現時点で、哺乳動物一般の自己治療に関する最も決定的な状況証拠を提供しているものと考えることができる。一方、著者らの調査域（マハレ山塊国立公園周辺）では、ヒトとチンパンジーでよく似た病徴を示す疾病に対し、同じ植物を選択することが知られている。この事実はおそらく両者が系統的に最も近縁なためであろう。[5]

ジャンセンらの報告から示唆されているように、自己治療の世界は、類人猿ばかりでなく、類人猿以外の霊長類、さらにはその他の哺乳類にも見られるものと推察される。しかしながら、これまで、自己治療に関する情報はアフリカ大型類人猿からのそれが最も顕著である。自己治療行動の観察から導きだされる研究結果は、一般の哺乳動物から霊長類、さらには大型類人猿から初期人類、現世人類にいたるまでの医療行為の進化を考える上できわめて重要と考えられる。

本稿の目的は、現在得られているアフリカ大型類人猿の間接的、直接的自己治療についての裏づけをレビューし、今後の調査研究の基本的ガイドラインを提供すること、さらには今後この知識をヒトの日常の生活にどう活用していくかを探ることにある。

二　大型類人猿日常食の薬理効果に関する生態化学的考察

1　果実や葉の採食と薬理効果

チンパンジー、ビーリャ（ボノボ）、低地に住むゴリラなどは概して果実食者であるが、同時に葉、髄部、種子、花、樹皮、樹液などの多様な部位を採食している。これら植物各部位からは、これまで、種に特徴的な産物として、多彩な二次代謝産物が分離されてきている。植物側から見れば、自己の含むある種の無機物質や二次代謝産物は草食動物に対する防衛最前線であると考えられている。[6]すなわち、他者に影響を及ぼすこれら二次代謝産物は、採食者（草食動物）にとって有毒であったり、消化力を低下させ食欲を減退させたりすることにより摂取されにくくする物質と捉えることができる（表11-1）。

リチャード・ランガムとイザビリエ-バスタによると西ウガンダのキバレのチンパンジー（カニャワラグループ）は、ヤマゴボウ科のフィトラッカ・ドデカンドラ（*Phytolacca dodecandra*）の果実を多量に高頻度で採食している。[7]（図11-1）その果実は苦味があり、少なくとも四種の毒性トリテルペンサポニンを含んでおり、これらは単独または混合物のわずか二グラムでマウスとラットに対して致死量となる。果実に最も多量に含まれているこれらサポニン類は住血吸虫の中間宿主である巻貝を殺す作用があり、現在アメリカで殺巻貝剤として開発中である。その他の生物活性としては、抗ウイルス、抗菌、避妊、殺精子、胚毒性作用などが挙げられている。

アフラモムム属（野生のショウガ類）の髄部や果実はアフリカ全土のチンパンジー、ビーリャ、ゴリラが採食している。

表 11-1　一般的な植物2次代謝産物とそれらが動物に与える影響

化合物のタイプ	薬理効果（特記事項）
テルペノイド，アルイカロイド	イオンチャンネルの修飾（高毒性）
イソキノリンアルカロイド	DNAに挿入，受容体と相互作用，痙攣作用（毒性があり，苦みを呈する）
キノリジンアルカロイド	ACH受容体に結合（毒性があり，苦みを呈する）
トロパンアルカロイド	ACH受容体の阻害（高毒性）
ヒロリジジンアロカロイド	変異原性，発癌性（肝臓毒）
シアン配糖体	呼吸阻害
アルジアック配糖体	Na＋/K＋－ATPase阻害（高毒性）
テルペン	利尿作用（苦み）
揮発性テルペン	抗菌性，刺激性
揮発性モノテルペン	抗菌性（芳香性）
サポニン，アミン	生体膜に対し界面活性（苦み）
トリテルペン，サポニン	生体膜に対し界面活性（苦み，催吐性）
セスキテルペン，ピロリジジン	変異原性，発癌性，刺激性（細胞毒，肝臓毒）
コンバラトキシン	Na＋/K＋－ATPase阻害（高毒性，苦み）
アントラキノン	便通作用（毒性）
フェノール性物質	収斂（しゅうれん）性，抗消化性
セルロース，ヘミセルロース，リグニン，シリカ	非消化性

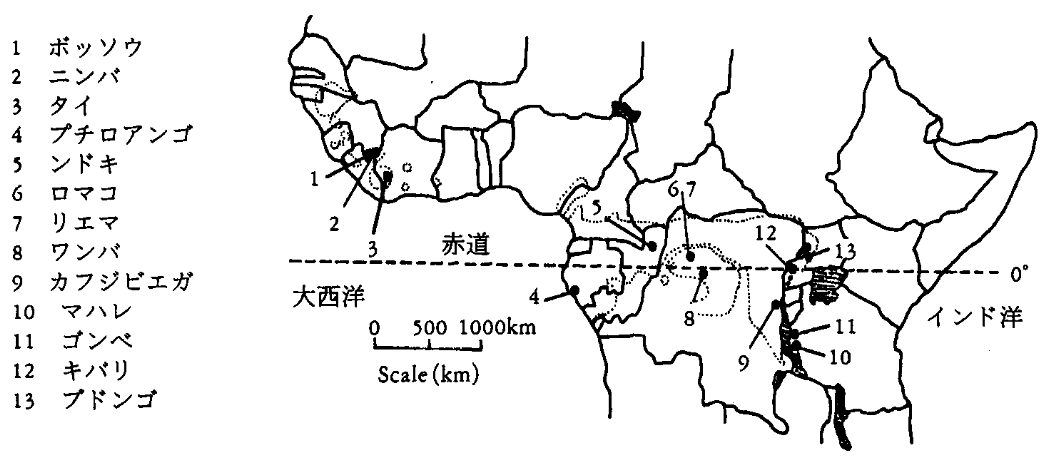


図 11-1　類人猿の葉の呑み込み行動が観察されたアフリカの調査地.

コーネル大学生物学部のジョン・ベリーが南西部ウガンダ、ブウインディにおいて、ゴリラの日常食を生態化学的に研究を進めているが、その一環としてアフラモムム・サングィネウム（*Aframomum sanguineum*）の果肉の生物活性について評価し、本種に強力な抗菌活性物質が含まれていることを明らかにした。また、ベリーによれば、この（実）は、バクテリア感染や真菌感染の治療薬として、さらには駆虫剤としてブウィンディの市場や路端で市販されている。[8]

北部コンゴのンドキの森では、キツネノゴマ科のトマンデルシア・ラウリフォリア（*Thomanderia laurifolia*）の若葉の先端をニシローランドゴリラが噛むことがまれにある。[9] 滋賀県立大学の黒田末寿らによれば、原住民はこの若葉を抗寄生虫薬や解熱剤として利用しているとのことである。この葉の抽出物には、弱いながらも抗住血吸虫作用が認められている。

2　栄養価の乏しい樹皮と木部の採食と薬理効果

樹皮と木部は繊維質や木質に富むが、時には毒性もあり、消化性はよくなく栄養価も低い。[10] チンパンジーやゴリラが多くの種の樹皮や木部を頻繁に採食することはよく知られているが、日常食のなかで樹皮がいったいどのような役割を果たしているのかは、まだほとんど明らかにされていない。アフリカの民俗生薬学の文献によれば、これらの植物樹皮のなかには重要な薬理効果をもつものもあり、今後の類人猿の行動学・植物化学的な調査・研究にとって新しい対象材料となりうるものと考えられる。

マハレのチンパンジーはニクズク科のピクナントゥス・アンゴレンシス（*Pycnanthus angolensis*）の木部を採食するが、西アフリカの人々も、下剤、消化剤、吐剤、歯痛止めなどとして利用している。また、マハレのチンパンジーは現地人が胃痛の治療薬として利用（しがむ）するグレウィア・プラティクラダ（*Grewia platyclada*）の樹皮を剝いで噛んでいることがと

きどき観察されている。同じくマハレのチンパンジーはエリトリナ・アビシニカ（*Erythrina abyssinica*）の樹皮を時に食するが、この種の樹皮の抽出物からは強い殺マラリア原虫および抗住血吸虫活性が認められている。[11] 一方、ゴンベのチンパンジーは、エンタダ・アビシニカ（*Entada abyssinica*）の樹皮をときどき食しているが、ガーナの人々はこれを下痢または吐剤として利用している。ギニア、ボッソウのチンパンジーはきわめて苦い味のするゴングロネマ・ラティフォリウム（*Gongronema latifolium*）の樹皮を食べることが観察されている。西アフリカの人々は、一方、この植物の茎を肛門にさしこみ、痛時の下剤、腹痛、腸内寄生虫感染症の治療に利用している。

3　マハレ・チンパンジーの薬用的植物利用の可能性――寄生虫駆除を目的として

著者の一人ハフマンらは、マハレのチンパンジーが食用とする植物が寄生虫駆除に効果があるかどうかを検討するため、アフリカの民俗生薬文献を参考にし、文献調査を実施した。本分析には、マハレ・チンパンジーの採食種一九二種中、学名まで同定されている非栽培種一七二種を対象とした。[11] ある植物は複数の民間生薬として利用される一方、一七二種の二二パーセントにあたる四三種が寄生虫や胃腸病の治療薬として使用されていることが分かった。チンパンジーはこの四三種すべてをこのような薬理効果を狙って食べているとは限らないが、一六種の植物において、それぞれの採食部位合計六三部位の一六パーセントにあたる二〇部位は、腸内寄生虫症や胃腸病の治療薬としてヒトが利用している部位と一致していた。[12] さらに興味深いことに、このうち一六種の植物のチンパンジーによる採食頻度が雨季に際立って高い傾向を示していた。この事実は、後に述べる野外観察結果と合わせ考え、マハレのチンパンジーがたびたび感染する腸結節虫（*Oesophagostomum stephanostomum*）の制御にこれら植物が何らかの形で関係しているのではないかと考えられる。

4　アフリカ以外の大型類人猿の薬用的植物利用の可能性

東南アジアのオランウータンについては自己治療の全貌がまだ明らかにされていない。しかしながら、彼らも多くの植物の形成層を主とした樹皮を採食することが知られている。多くの場合、樹皮は噛みしがまれるだけで、繊維質は食べられることなく吐き出されることが知られている。このような採食行動は、アフリカの大型類人猿の場合と同様、樹皮の薬的利用を示唆している。

以上の調査の概略から、大型類人猿の日常食に潜在する薬理的効果、とくに寄生虫への対処法としての意義が推察されるであろう。今後、大型類人猿が摂取する食素材の薬理的活性スクリーニングを推し進めることが、潜在する抗寄生虫活性を追求するための効果的な方法の一つである。

三　マハレ・チンパンジーの自己治療行動に関する具体例と展望

これまでアフリカの大型類人猿の自己治療行動に関する具体例として、①枝の髄部から苦い汁をしがみ出して呑み込

む行動、と、②葉の呑み込み行動、の二つのタイプが示されている。[13] 本節では、おもにマハレのチンパンジーに焦点を当て、その自己治療行動の具体例と、今後の展開について解説する。

1　髄部の苦汁摂取行動の生態学・化学・寄生虫学的調査・研究——ヴェルノニアを例として

(1) マハレ・チンパンジーのヴェルノニアの採食行動における特徴

チンパンジーによる髄部の苦汁摂取行動は薬効（寄生虫制御効果）を求めているのではないかとする仮説が提示されたのは、明らかに病気と見られるマハレのチンパンジーによるヴェルノニア・アミグダリナ（*Vernonia amygdalina* Del.（キク科））の採食行動の詳細な観察に端を発している。

一九八七年一一月のある日、著者（ハフマン）と共同研究者のモハメディは、マハレ・チンパンジーの興味ある採食場面に遭遇した。日中の活動時間をほとんど横になって過ごすなど病気と思われる成熟雌（チャウシクと命名）がヴェルノニアの茎の髄部を噛み砕き、滲み出る樹液を呑み下した。ヴェルノニアは樹液も含めて強烈な苦味を呈し、このためマハレ・チンパンジーにとっては日常食とはならないものと考えられていた。事実、一九六五年から一九八三年までの長期間に渡る調査記録によると、その葉および樹皮の採食が観察された回数はそれぞれ一回および二回のみである。この三五年間、ほとんど例外なく髄部のみの採食が記録されている。[14] 採食当日の活力の無さとともに、食欲の減退、排便・排尿の異常も観察され、体調不良は明らかであったが、ヴェルノニアの採食後には除々に回復しているように見え、翌日の午後には通常の活動状態に戻った事が確認されている。[15] ヴェルノニア・アミグダリナは、熱帯アフリカに広く分布している植物であり、周辺の人々には多彩な薬理効果を示す民間薬として広く使われている。ハフマンらは、このよう

な事実をも考え合わせ、この時点で、チャウシクがヴェルノニアを薬として利用したのに違いないと結論づけた。なお、一九八七年の観察と同じような採食行動が一九九一年にもハフマンらによりなされている。[16]

ヴェルノニア属植物の他種の苦汁摂取行動は、タンザニアのゴンベではヴェルノニア・コロラタ（*V. colorata*）、カフジ-ビエガではヴェルノニア・ホクステッテリ（*V. hochstetteri*）やヴェルノニア・キルガエ（*V. kirungae*）など、各地で観察されている。また、象牙海岸のタイ森林では、パリオソタ・ヒルスタ（*Paliosota hirsuta*）、エムレモスパト・マクロカルパ（*Emmenospath macrocarpa*）などの苦汁摂取行動が時に観察されている。[17]

マハレのチンパンジーはヴェルノニア・アミグダリナの若い茎から苦い汁を摂取する際、まず外部の樹皮と葉を取り除き、露出した内部だけをしがみ、そこから抽出する苦い髄液を呑む（写真11-1）。一回に利用する髄部は小片であり、直径一センチメートル、長さ五～一二〇センチメートル位である。量にもよるが、採食時間は一～八分である。[18] また、これまでマハレにおけるヴェルノニア・アミグダリナの苦汁摂取行動は、六月と一〇月（乾季後期）を除くすべての月に観察されている。[19] しかしながら、先に述べたように、その採食全頻度はきわめて少なく、また、その季節も一一月から二月にかけて多いが、雨季の中期から後期にあたる一二月から一月にかけて最も高頻度で観察されている。

(2) ヴェルノニアの抗寄生虫活性成分の化学的研究

行動生態学から提起されたハフマンらによるヴェルノニアの薬的利用仮説は、その後、植物化学的、寄生虫学的分析により補強され、より論拠のある仮説へと進歩してきている。[20]

一九九一年から精力的に実施された小清水・大東らによるヴェルノニアの化学分析的展開には、偶然と言ってもいい背景があった。それは、それ以前に別途に、アフリカ熱帯降雨林産植物を対象として化学的研究を実施していた小清水

は、ヴェルノニアが民間薬としての利用されているばかりでなく、強壮食素材として饗されていること（西アフリカ）に興味を抱き、研究題材の一つとして取り上げようとしていた事実である。この時点で、小清水およびハフマンらの共同研究が始まり、次のような成果を生み出すことになった。

　小清水・大東らは、まずヴェルノニアの有機溶媒抽出物について広範な生物・生理活性を検討し、予想通りその抽出物中に抗菌、抗腫瘍、免疫抑制など多様な生理活性物質が存在することを見出した。[21] 次いで、各活性物質を化学的に明らかにするため粗抽出物の分画操作を行なったところ、面白いことに、各種の活性を示す区分にはヴェルノニアの特徴的性質である苦味が附随していることに気づいた。かねてより苦味は、薬理作用など種々の生理活性を担う物質に広く認められる特性と

写真 11-1　*Vernonia amygdalina* の苦い髄部吸い込み行動（上）と *Aspilia mossambicensis* の葉の呑み込み行動（下）を行なうチンパンジー（写真マイケル・ハフマン）

して知られていた。そこで、その後は、ヴェルノニアの苦味成分の研究へと進展した。種々の化学的操作を経て、二つの型の苦味成分を単離・構造決定した。[22] その一つは、ヴェルノダリン（vernodalin）を主とするセスキテルペンラクトン類四種であり、他方はヴェルノニオサイド（vernonioside）群と命名したステロイド配糖体類である。ヴェルノニオサイド類では、苦味をもつA群（ヴェルノニオサイドA 1〜A 4）とともに、関連する非苦味性B群（ヴェルノニオサイドB 1〜B 3）も附随して明らかにできた。とくに、非苦味性ヴェルノニオサイドB 1はステロイド配糖体のなかで量的に主要となるもので、本化合物が以後の展開に大きく役立つこととなった。図11-2に、それぞれの化合物群の主要物質であるヴェルノダリンおよびヴェルノニオサイドB 1の構造を示す。

　ヴェルノダリンなどのセスキテルペンラクトン類はヴェルノニア属植物に共通した化合物で、抗腫瘍、昆虫摂食阻害活性など多彩な生理活性が知られていた。事実、著者らは、粗抽出物の段階で認めていた抗腫瘍、抗菌、免疫抑制活性等は、これら化合物の存在により理解可能であることを確認している。[23] 一方、ヴェルノニオサイド類は、とくにステロイド環骨格に付く側鎖部の酸化状態に特徴のある、新規な化合物群である。

　さて、先に掲げた化合物がマハレのチンパンジーによるヴェルノニアの薬的利用とどのようにつながったのであろうか。ハフマンらは、後に述べるように種々の病態解析から、ヴェルノニアの樹液を呑み病状を回復したチンパンジーは何らかの寄生虫症であったと推察した。そこで、次はこれら化合物の寄生中への影響を検索することとした。

　ヴェルノニアを採食したチャウシクがいかなる寄生虫に侵されていたか特定できていなかったが、ここで、川中博士（国立感染症研究所）、ライト博士（ロンドン大）、ならびにバランサル博士（マルセーユ大）らの協力を得て、熱帯性をも含む重篤な寄生虫感染症を想定し、試験管内試験による寄生虫活性を検討した。[24] その結果が、以下のようにまとめることができる。

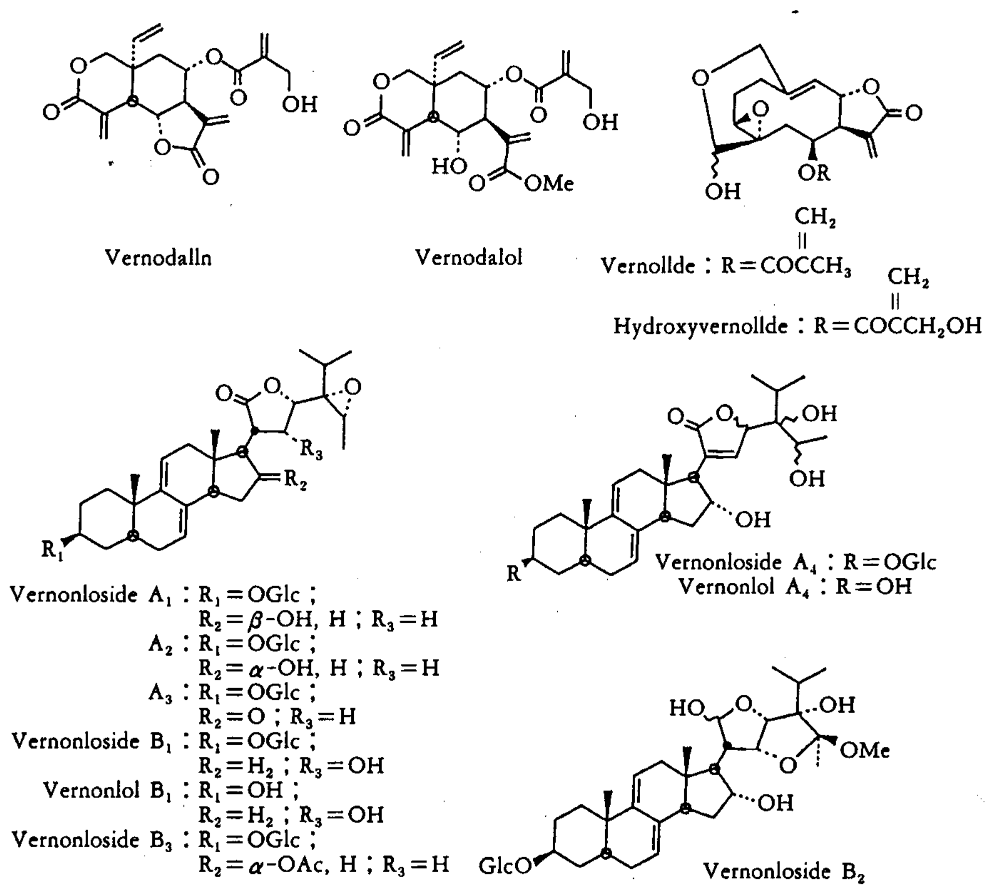


図11-2　ヴェルノニア・アミグダリナから単離されたステロイド配糖体とセスキテルペンラクトン関連化合物の化学構造.

①セスキテルペンラクトン類には住血吸虫（AS：*Schistosoma japonicum*）に対し有意な運動抑制（IM）や産卵抑制（EL）効果が認められる。また、殺マラリア（PL：*Plasmodium falciparum*）、殺リーシュマニア（*Leishmania infantum*）活性も認められ、とくに主要ラクトン、ヴェルノダリンの活性が最も顕著である。

②ステロイド配糖体の抗寄生虫活性は一般に弱いが、主要配糖体、ヴェルノニオサイドB１やA４では二〇ミクログラム／ミリリトルで住血吸虫の産卵抑制活性があり、この活性は二ミクログラム／ミリリトルでも有意である。さらに、酵素的あるいは化学的に誘導したB１やA４の一次および二次アグリコン（脱糖体：ヴェルノニオールB１、ヴェルノニオールA４、イソヴェルノニオールB１など）で

は、住血吸虫の運動抑制が二〇ミクログラム／ミリリットルで観測でき、さらに殺マラリアや赤痢アメーバー（EA：*Entamoeba histolytica*）活性も含め、これらアグリコンの抗寄生虫活性は、元の配糖体のそれらよりも一般的に高まる。

なお、多くの配糖体では対応するアグリコンが天然にも存在し、とくに主要配糖体であるヴェルノニオサイドB１のアグリコン（ヴェルノニオールB１）は、配糖体の一／五量程度存在することが明らかになっている。[24]

前記の試験結果から、ヴェルノダリンがヴェルノニアの抗寄生虫活性を担う中心的化合物と考えられた。しかしながら、住血吸虫感染マウスを用いて実際の活性を検討したところ、ヴェルノダリンは毒性が強く、毒性のないレベルでは無効であることが分かった。[25] つまり、チンパンジーによるヴェルノニアの抗寄生虫的利用は、ヴェルノダリンでは説明できないことが判明したのである。

ところで前述したように、西田らの記録によれば、マハレのチンパンジーのヴェルノニアの採食では、その髄部が唯一の摂取部位とされている。[26] そこで、ヴェルノニアの各部位におけるヴェルノダリンおよびヴェルノニオサイドB１の存在レベルを検討してみた。[27] マハレが雨季になり始める季節（一〇月下旬）のヴェルノニアを対象として定量したところ、毒性の強いヴェルノダリンは葉に多量（二・一八ミリグラム／グラム生葉）含まれ、摂取部位である髄部にはほとんど存在していない（〇・〇三ミリグラム／グラム生髄）ことが判明した。一方、ヴェルノニオサイドB１は全ての部位で評価できる量（例えば髄部では〇・七五ミリグラム／グラム生髄）存在していた。

ここまで、住血吸虫やマラリアなど重篤な病気を招く熱帯性寄生虫に対する活性について述べてきた。これらの寄生虫にチンパンジーが感染することは事実らしいが、[28] 当該チンパンジーが真にこれら寄生虫に侵され、その対処法としてヴェルノニアを利用していたかは疑問である。当然ながら、次節で述べるように、条虫や線虫などより一般的な寄生虫

にも目を向ける必要があろうが、以上の研究から現時点で、マハレのチンパンジーのヴェルノニア利用に関して著者らは次のような仮説を提出している。

①マハレのチンパンジーは何らかの寄生虫を制御するためにヴェルノニアを利用している。

②彼らは、毒性の強いセスキテルペンラクトン類を多量に含む葉の摂取は避け、茎部髄を選択的に利用する。

③おそらくそこに含まれるステロイド関連化合物が薬として働いているのであろう。

(3) ヴェルノニアの寄生虫制御に関するその後の生態学的・寄生虫学的解析

前節で述べた熱帯性寄生虫を対象とした研究はさて置き、その後ハフマンらは、ヴェルノニアの採食と寄生虫制御との関係を、生態学的視点よりさらに深めてきた。過去三年間にわたるマハレチンパンジーの寄生虫感染度の調査によれば、腸結節虫に感染した個体の発症率は雨季に上昇するが、他の線虫類ではそうではない（図11-3）。腸結節虫感染症は、鞭虫（*Strongyloides fulleborni*）、糞線虫（*Trichuris trichiura*）に比べ、苦汁摂取行動との深い関連性が認められる。[29]

本節の（1）で述べたように、苦汁摂取行動の詳細な観察から、ハフマンらが接触した個体は病気（下痢、倦怠感、線虫感染など）であったと推察された。また、病気の二個体を追跡調査した結果、苦い髄部の苦汁摂取行動後、二〇～二四時間以内に病状が回復していることが確認されている。腸結節虫感染の糞便一グラム中の寄生虫卵数（ＥＰＧ）は、苦い髄部樹液の摂取後二〇時間以内に一三〇卵から一五卵へと減少したことが明らかになっている。しかし併発していた鞭虫感染症の糞便では、このような減少は認められなかった。[30] 同じ時期に観察された個体のほとんどに、腸結節虫のＥＰＧが徐々に増加していたことが明らかになっている。雨季初めのＥＰＧ価の増加は、腸結節虫の再感染度の増加を反映し

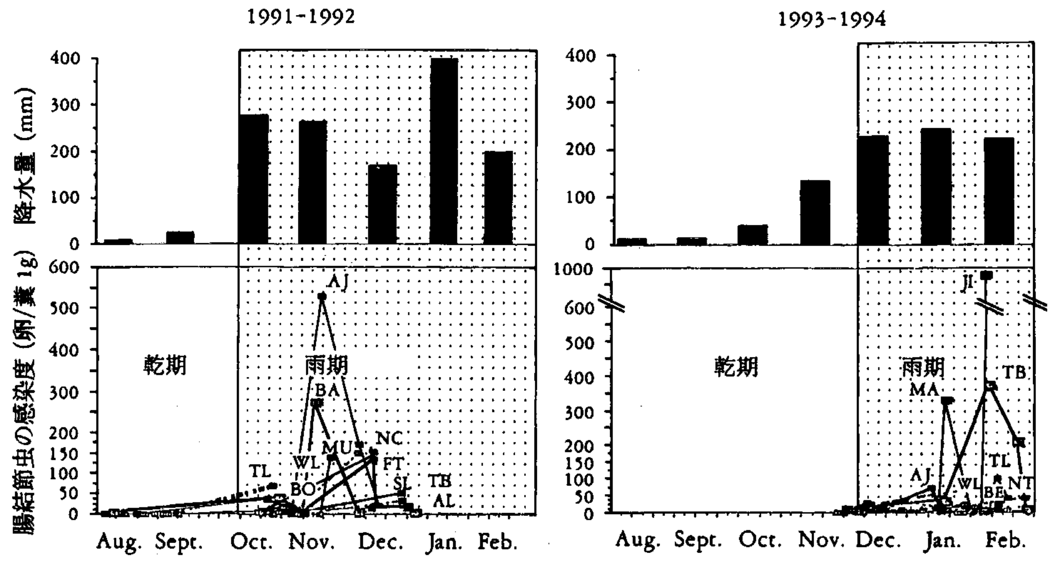


図11-3　マハレで1991～1992年，1993～1994年に追跡調査したチンパンジーの腸結節虫 *Oesophagotomun stephanosotomun* の個体感染度（卵/糞1グラム当り）の季節的変動．

ていると考えられる（図11-3）。

以上のように、ヴェルノニアの採食は、少なくともマハレでは一般的な腸結節虫症の治癒（または軽減）に効果があると期待されている。

2　葉の呑み込み行動の生態学

葉の呑み込み行動は腸内寄生虫の駆除を通して腸結節虫感染症の制御や、条虫感染症による痛みの緩和に効果があると報告されている。これまでに寄生虫駆除について、薬理的および物理的メカニズムが提唱されている。[31]

葉の呑み込み行動は、ゴンベとマハレのチンパンジーでの記録が端緒となっている。[32] ランガムと西田は、キク科のアスピリア・モッサンビケンシス（*Aspilia* (syn. *Wedilia*) *mossambiensis*）、アスピリア・プルリセタ（*A. pluriseta*）、アスピリア・ルディ（*A. rudis*）の葉が未消化のまま糞便中に排泄されていることに気づき、葉の呑み込み行動は栄養補給のためではないことを初めて示唆した。その後、ロドリゲスら[33]は、アスピリアの葉を噛まずに呑み込むという一風

変わった採食方法は、チンパンジーによる高度な薬的利用法であることを示唆するものであると提唱した。その後、他の類人猿にも同様な採食方法が見られるのではないかと、野外研究者たちの関心を集めることになった。また、ロドリゲスらはその化学的分析にも着手し、抗線虫、抗ウイルスなど生物活性に富む含硫化合物、チアルブリンAを単離できたことから、「アスピリア-チアルブリンA殺線虫仮説」を提唱した。[34] しかし、その後の詳細な化学分析の結果から、この仮説は現在では否定されている。[35]

二〇〇一年一月現在、アフリカの一三カ所の調査地で、チンパンジー、ビーリャ、ゴリラによる三四種以上の植物の葉の呑み込み行動が観察されている（図11-1）。呑み込み行動で食される植物は多種多様（草本、つる、低木、樹木など）であるが、これらに共通した特徴としては、葉の表面に毛状突起がありザラザラしていることである。採食する際には、葉の先端の半分を口の中にゆっくりと入れ、舌、くちびるや上あごで丸め、やがて一枚一枚呑み込む。一度の採食で、一～五五枚程度を呑み込む事が報告されている。苦汁摂取行動と同様に、葉の呑み込み行動もきわめてまれな行動である。

アスピリアの葉は、ゴンベやマハレでは一年中採取できるが、チンパンジーによる採食は雨季（一一月～五月）に頻度高く観察されている。マハレのチンパンジーではその採食のピーク時は一月と二月で、その他の月の一〇～一二倍であることが報告されている。[36] マハレKグループのチンパンジーでも、アスピリアの呑み込み行動は乾季より雨季に圧倒的に多く観察され、これはマハレにおける髄部の苦汁摂取行動のパターンと類似している。マハレにおいて、アスピリア以外の九種の植物の葉も類似の方法で呑み込まれ、同様に雨季に頻度高く観察されている。[37]

ハフマンらは一九九三年一二月から一九九四年二月にかけての三ケ月間、チンパンジーの採食行動様式や採食個体の健康状態に関するデータを収集するとともに、葉の呑み込み行動を直接観察した。詳しく観察できた八頭のチンパンジー

のうち、七頭は葉を呑み込んだ日時に下痢をしており、倦怠感や腹痛の徴候が認められた。[38] 直接観察、あるいは葉を含んだ糞便の分析調査などの間接的証拠によって、呑み込み行動をした一二例のうち、八三パーセントの個体に線虫の感染が認められた。[39] 通常、糞便中に寄生虫の成虫が認められることはまれであるが（三パーセント、九／二五四）、この調査では、倦怠感や下痢の症状を示す個体に限られていた。なお、観察できた寄生虫成虫は腸結節虫であった。

葉の呑み込み行動と腸結節虫との間には強い関連性が認められた。一九九三～一九九四年の調査において、九個体の糞便（N＝二五四）のうち六個体からのそれらにアスピリア・モッサンビケンシス、トレマ・オリエンタリス（*Trema orientalis*）またはアネイレマ・エキノクティアレ（*Aneilema aequinoctiale*）の葉が未消化のまま排泄されていることが確認できた。しかも、糞便中の未消化の葉と腸結節虫の出現率には統計的にきわめて高い相関があった。[40] 興味あることに、アネイレマ・エキノクティアレの葉が未消化のまま排泄されていた一個の糞便中には、その表面の毛状突起に二匹の腸結節虫が強固に付着しているのが認められた。残りの腸結節虫のほとんどは丸められた葉の中に入っていた。また、このように糞中に発見された結節虫の全てはまだ生存しており、動いていた。数日間、腸結節虫を糞や葉とともに保管しておいても成虫は変わりなく生き動き続けることが観察された。

以上のことより、著者らは、呑み込み行動に用いられた葉の腸結節虫駆除効果が、化学的な作用ではなく、その物理的作用によるとする、新たなメカニズムである「呑み込み行動による寄生虫駆除仮説」を提唱している。[41]

最近、そのメカニズムをさらに支持する事実が得られている。すなわち、一九九三～一九九四年の調査データの再分析の結果、マハレ・チンパンジーが呑み込む葉は五～六時間で消化器官を通過し、未消化のまま排泄されることがわかった。これは通常の葉の消化時間に比べ四分の一あるいはそれ以下である。ハフマンとジュディス・ケイトン（オーストラリア国立大学、シドニー）は、類人猿の葉の呑み込み行動においては、葉の表面のザラザラとした毛状突起が腸管を刺激

し、その結果、消化時間が短縮され、物理的に腸結節虫を駆除しやすくするのではないかとの仮説を立てている。表面に毛状突起がある葉は、消化しにくく、朝、空腹時に食べることで、腸の粘膜に付着している腸結節虫が極度に刺激され、体外に排泄されやすくなるものと推察される。

これらの寄生虫駆除作用に加えて、葉の呑み込み行動には、摂食した果実などに含まれているタンニン類による口腔内の付着異物を物理的に払拭・清浄化することも目的の一つである可能性もあることから、その検証のために小清水らはチンパンジーが採食している植物部位のタンニン含量について定性試験を試みた。

柿の渋味成分を測定するタンニンプリント法（三パーセント塩化第二鉄水溶液にろ紙を浸漬後、風乾した試験紙に試料断片をまんべんなく押しつけ、タンニンプリントを作成する）を適用し、チンパンジーの採食植物部位について作成したタンニンプリントの発色度を目測によって＋＋＋〜ーの四段階でタンニン含量を評価した（表11-2）。西田[42]の試食により評価されたチンパンジーの植物性食物一二三品目（九五種）のうち、予備的調査（一九九九年一〇月、マハレ）として一五種について定性試験を行なったところ、＋以上の陽性反応を呈した採食植物種は予想以上の七種に及び、陰性の植物種は八種であった。例えばシュードスポンディアス・ミクロカルパ（*Pseudospondias microcarpa*）果実の反応はきわめて強く、＋＋＋と評価されるなど、タンニン含有果実類を採食していることが明らかになった。タンニン定性試験を、さらに広く詳細にチンパンジーの植物性食物について検定すれば、採食行動の解明に新たな知見が得られるものと期待される。

表 11-2　試食による味と塩化第二鉄試験紙による陽性反応との比較

食用植物種（科，現地名）	食べられた部分*	味*	FeCl3 と試験紙反応**	備考*
Ampelocissus cavicaulis (Vitacease, Lukosho)	P	LO	+	pleasant
Canthium crassum (Rubiacease, Lungogolo)	F(U)	SA	NT	formidably astringent
Canthium venosum (Rubiaceae, Luntafwanengwa)	NR, F		++	
Ficus capensis (Moraceae, Ikubila)	F(R)	SS	++	pleasant
Ficus capensis (Moraceae, Ikubila)	F(U)	LA	NT	unpleasant
Ficus vallis-choudae (Moraceae, Ihambwa)	F(R)	SS	++	like Japanese common fig
Landolphia owariensis (Apocynaceae, Mpila)	P	IN	+	pleasant
Leea guineensis (Vitaceae, Lingoga)	NR, F		+++	
Mussaenda aruata (Rubiaceae, Mmpindu)	NR, F		+	
Paullinia pinnata (Sapindaceae, Mpatwe)	NR, F		+	
Pseudospondias microcarpa (Anacardiaceae, Buhono)	F	SA	+++	pleasant
Saba florida (Apocynaceae, Ilombo)	F(U)	OB	NT	very sour,unpleasant
Saba florida (Apocynaceae, Ilombo)	F(R)	SO	+	pleasant
Smilax kraussiana (Similaceaceae, Linselele)	P Sh	LO	++	pleasant
Aframomum mala (Zingiberaceae, Itungulu isigo)	P	IN	−	flabor of ginger, pleasant
Costus after (Zingiberaceae, Omoji)	P	OO	−	pleasant
	F		−	
Ficus urceolasris (Moraceae, Kankolonkombe)	F(R)	VS	−	pleasant
Garcinia huillensis (Guttiferae, Kasolyo)	F	SO	−	pleasant
Mangifera indica (Anacardiaceae, Mango)	F(U)	SO	−	
Pycanthus angolensis (Myristicaceae, Lulumasha)	F	BS/SB	−	unpleasant
Uvaria angolensis (Annonaceae, Lujongololo)	F(R)	VS	−	pleasant, umami

[食べられた部位] F：果実，(R)：完熟，P：枝や茎の髄；[味] VS：たいへん甘い，SO：甘酸っぱい，OO：中程度に酸っぱい，SB：甘苦い，BB：中程度に苦い，IN：無味，+++（強），++（中），+（弱），−（反応せず）＊西田，神経進歩；701-710(5)，43，1999

四　類人猿自己治療植物の民間薬的利用法

1　苦汁摂取行動植物の民間薬的利用法

苦汁摂取行動植物の代表例であるヴェルノニア・アミグダリナはアフリカにおける多くの民族がマラリア、住血吸虫感染症、赤痢アメーバ、さらには腸内寄生虫症や胃痛の治療薬として利用している。すでに述べたように、ヴェルノニアの採食行動が詳しく観察されたマハレMグループの二頭のチンパンジーの病徴は、髄部の苦汁摂取後二〇～二四時間で回復したことが認められた。この回復時間は、面白いことに、現地人トングェがヴェルノニア・アミグダリナの冷たい抽出液を寄生虫感染症、下痢、胃痛などの治療に利用した際に症状が改善される時間と一致している。[43]

ゴンベ、カフジビエガ、タイ（図11-1）でチンパンジーが採食する苦い髄部のあるその他の植物のなかには、民間生薬として薬理的な特徴を多くもっているものもある。なかでも、ゴンベのチンパンジーが時に採食するヴェルノニア・コロラタはヴェルノニア・アミグダリナときわめて近縁種であり、現地の伝統的な民間薬である。この二種は、民間では分類的に区別されておらず、薬効も同じとされている。同様に、これらと近縁にあるヴェルノニア・ホクステッテリも民間薬として著明であり、その髄部にはアルカロイドが含まれている。直接寄生虫とは関連していないが、パリオソタ・ヒルスタやエムレモスパト・マクロカルパは、西アフリカでは腹痛、腸炎、抗菌剤、鎮痛剤、また性病に対する治療薬としても利用されている。

以上のように、苦味を呈する植物の抗寄生虫的利用は広範に認められることが伺い知れる。

2　葉の呑み込み行動植物の抗寄生虫効果

呑み込み行動により採食される植物について、その二次代謝産物が寄生虫駆除に特別な役割を果たしていると提唱できる十分な化学的・薬理学的証拠は、現在のところ得られていない。すでに述べた物理的メカニズムは、呑み込み行動植物の寄生虫駆除における種々の観察結果をうまく説明できる、よいモデルと考えられる。しかしながら、化学的効果による寄生虫駆除もまだ捨てきれない以下のような事実もある。すなわち、最近五ケ所の調査地で類人猿が呑み込んだとされる五属五種[44]の葉の抗住血吸虫と殺マラリア活性を in vitro（生体外）で検討した。[45]その結果、五種のうち四種の抽出物中には一〇〇マイクログラム毎ミリリットルの濃度で住血吸虫の産卵活動に対する阻害活性が認められた。また殺マラリア活性も認めれている。化学的効果の説明として、消化器官を通過する過程で葉に存在する成分が腸粘膜壁への線虫の付着能力を減退させ、ザラザラした表面をもつ葉によりくっつきやすくさせ、効率的に体外へと排出されるのではないかと考えられる。[46]物理的効果と相まった化学的効果仮説の検証には、ヴェルノニアで展開された方法と同様、活性を示す成分の単離・同定を通した今後の研究に待たねばならない。

五　今後の研究の方向性と実際の応用

1　基本的ガイドラインと予見

ここまで述べてきた証拠から、類人猿は腸内を中心に多様な寄生虫を制御する目的で、さまざまな適応行動をとることが示唆された。アフリカ大型類人猿の自己治療行動仮説に関する現在の詳細な証拠のほとんどは、彼らが寄生虫感染度の違いに応じて対処方法を変えていることを示唆しているかもしれない。この仮説モデルは、季節的繁殖をする寄生虫に感染した他の多くの霊長類にも当てはまるものと考えられる。

寄生虫感染度の変動を、集団レベルでなく、個体レベルで体系的に通年追跡調査することは、主要な寄生虫が宿主に与える影響の高まる時期を判定する一つの有力な手がかりとなる。種々の行動（休息時間、歩行様式、食事時間など）を詳細に分析し、集団の健康状態を長期に追跡調査し、健康状態を表す一般的な症状（例：下痢、せき、鼻水など）を体系的に調査することは、発病時の病気判定に必須である。また、この調査は、提起されている自己治療行動の機能と効果の検証にのみ資するだけでなく、問題としている病気の直接の影響を把握するためにも必要であると考えている。これらの調査は、大型類人猿のみではなく他の霊長類においても十分可能である。

また、腸内を初めとする種々の寄生虫が野生霊長類の病気の唯一の原因ではなく、他の原因も検証する必要がある。しかしながら、野外調査で可能な事項には限界がある。自己治療行動の予想される効果を十分把握するためには、動物や植物に関する各研究分野（獣医学、薬理学、天然代謝物化学など）の多彩な研究者の協力が不可欠である。マハレのチン

パンジーに関して実施されてきたＣＨＩＭＰＰ（Chemo-ethology of Hominoid Interaction with Medicinal Plants and Parasites）グループによる学際的研究は、各専門分野での研究がいかに効果的に進められてきたかを示すよい一例である[47]。

自己治療行動に関する野外調査で、最大の制約となるのは、①行動がいつ起こるか予測できないこと、②病気の個体の密着追跡調査を確実に遂行できるとは限らないこと、③自然環境における実験操作上の制限、の三点である。自己治療行動の仮説から得られる考察をより発展的に検証して行くためには、これらの制約を取り払う必要がある。例えば、飼育されているサルに無害の薬用植物を与えるとしよう。そうすることにより、彼らが薬草を選択する際の基準を評価し、個体が自己治療法をどのように獲得し、この経験が集団内にいかに伝えられてゆくのかを明らかにすることができるかもしれない。動物園の霊長類やその他の動物の自己治療行動の潜在能力を探ることにより、野生動物の世界に何が起こってきたか、あるいは将来何が起こるかを、より詳しく把握できるのではないかと期待される。さらにこの試みは、環境エンリッチメントや健康維持の全体論的なアプローチという点において、飼育動物にとっても有益であろう。

2　発展途上国における家畜用治療薬資源としての評価

自己治療行動研究の将来の方向性の一つは、今までに得られた食用・薬用植物についての知識を応用し、それらを医学や獣医学に活用することである。腸結節虫感染症は霊長類とブタ、ヒツジ、ウシなどの家畜に共通して認められる疾病であるが、時にはヒトにも感染が認められる。現在では、家畜用治療薬として各種の市販の駆虫剤を手に入れることのできる時代となっているが、反面、薬剤耐性をもつ寄生虫が一層顕著になってきているのが現状である。発展途上国の貧しい家庭や、小規模の家畜産業あるいは動物園にとっては、経済的に市販駆虫剤を入手するに難しいし、たとえ時

には購入できたとしても持続的には非実用的である。従って、民間生薬から得られる天然化合物を治療に利用するという新しい方法が模索されつつある。大型類人猿における自己治療行動の研究によって、植物それ自体や、それから単離される天然化合物は、ヒト、家畜、飼育動物などの寄生虫駆除にも効果を発揮するものと期待される。アフリカでの調査結果をもとに、著者らは日本、デンマーク、フランス、タンザニア、ウガンダやケニアの共同研究者と、さまざまの寄生虫感染に対する、これらの植物の効果の検証に励んでいる。この研究の一環として、アフリカ固有で、安く手に入るなど自給可能な植物の抗寄生虫物質としての可能性も検証する予定である。

3　今後への期待

類人猿以外の霊長類の自己治療行動についても、野外と実験室の両方で研究を進めることが強く望まれる。本稿で述べたように、疑問に対する答えは必ず次の疑問を生み出す。多くの野外研究者が類似した自己治療行動を探しているので、そうした行動が実際に見出されるのもそう遠くないだろう。その結果、現在提起されている疑問にも一つ一つ答えが出されていくだろう。別の形であっても、自己治療行動は大型類人猿だけでなくサルや原猿類にも見られるものと考えられる。自己治療行動は明らかに適応的に重要であるため、動物界に広く存在していると推察される。ある集団において動物の健康や生存そのものへの直接の脅威はいったい何なのか、そしてその種はその脅威にいかなる方法でどう対処しているのかを明らかにすることが、今後の研究課題である。

アフリカ大型類人猿の間では、自己治療行動に使う植物の選択基準が酷似していること、ヒトとチンパンジーが類似した疾病には共通の植物で治療をすることは、人類の医療行為のルーツの古さを示唆する。この点において、初期人類

は現存の類人猿と現世人類の植物選択基準と類似したものをすでに獲得していたと考えられる。化石からは食事行動と食事内容の微細な点まで裏づける直接の証拠は見出せないが、初期人類は現存の類人猿と同程度までの自己治療行動をすでに獲得していただろうことは容易に想像できる。

霊長類の自己治療研究を行なうことは、自然界の多様性を表す宿主・寄生虫・植物の複雑な相互作用、霊長類の行動生態学、人類の進化過程などさまざまな課題を理解する上で、また一つの斬新な複雑さを提供することになろう。

註

(1) Huffman 1997.
(2) Glander 1982; Waterman 1984.
(3) Murakami, Ohigashi & Koshimizu 1994.
(4) Janzen 1978.
(5) Huffman, *et al.* 1996a.
(6) Howe & Westley 1988.
(7) Wrangham & Isabirye-Basuta 私信。
(8) J. Berry 私信。
(9) Kuroda, Mokumu & Nishida 私信。
(10) Waterman 1984.
(11) Nishida & Uehara 1983.
(12) Huffman *et al.* 1998.
(13) Huffman 1997.
(14) Nishida & Uehara 1983.
(15) Huffman & Seifu 1989.
(16) Huffman *et al.* 1993.
(17) C. Boesch 私信 (Huffman 1997 で引用)。
(18) Huffman 1997.
(19) Nishida & Uehara 1983.
(20) Huffman & Seifu 1989; Ohigashi *et al.* 1994; Huffman *et al.* 1993, 1996b.
(21) Koshimizu *et al.* 1993.
(22) Ohigashi *et al.* 1991; Jisaka *et al.* 1992a, 1993a.
(23) Jisaka *et al.* 1993b.
(24) Ohigashi *et al.* 1994.
(25) Jisaka *et al.* 1992b.
(26) Nishida & Uehara 1993.
(27) Ohigashi *et al.* 1994.
(28) Brack 1987.
(29) Huffman *et al.* 1996.
(30) Huffman *et al.* 1993.
(31) Huffman *et al.* 1996; Wrangham 1995.

(32) Wrangham & Nishida 1983.
(33) Rodriguez 1985.
(34) Rodriguez & Wrangham 1993.
(35) Huffman *et al.* 1996b; Page *et al.* 1997.
(36) Wrangham & Nishida 1983.
(37) Huffman *et al.* 1997.
(38) Huffman *et al.* 1996.
(39) Huffman *et al.* 1996, 1997.
(40) フィッシャーの正確確率検定（両側検定）、P = 0.0001 (Huffman *et al.* 1996b)。
(41) Huffman *et al.* 1996b.
(42) 西田 1999b.
(43) Huffman *et al.* 1993, 1996a.
(44) *Maniophyton fulvum*, *Ipomea involucrata*, *Trema orientalis*, *Lippia plicata*, *Lagenaria abyssinica*.
(45) Huffman *et al.* 1998.
(46) Huffman *et al.* 1996.
(47) Huffman 1993.

(2002) 31-42
(Eds) Jacques Fleurentin
Jean-Marie Pelt
Guy Mazars
IRD Editions

Animal origins of herbal medicine

Michael A. Huffman
Center for Human Evolution Modeling Research, Primate Research Institute, Kyoto University
41-2 Kanrin Inuyama Aichi 484-8506 - Japan Huffman@pri.kyoto-u.ac.jp

Abstract

Parasites and pathogens cause a variety of diseases that affect the behavior and reproductive fitness of all animals. Because the need to counteract such pressure is great, anti-parasitic behaviors are predicted to occur throughout the animal kingdom. Early in the co-evolution of plant – animal relationships, some arthropod species began to utilize the chemical defenses of plants to protect themselves from their own predators and parasites. The origins of herbal medicine have their roots deep within the animal kingdom. From prehistoric times humans have looked to wild and domestic animals for sources of herbal remedies. Both folklore and more recent examples provide accounts of how the use of some medicinal plants are obtained by observing the behavior of animals. Animals too learn about the details of self-medication by watching each other. To date, perhaps the most striking scientific studies of self-medication have been made on the African great apes. The great ape diet is often rich in plants containing secondary compounds of non-nutritional, sometimes toxic, value that suggest medicinal benefit from their ingestion. Chimpanzees and humans co-existing in sub-Saharan Africa are known to use *Vernonia amygdalina* for the control of parasite infections. Phytochemical studies have demonstrated the wide array of biologically active properties in this plant species. In light of the growing resistance of parasites and pathogens to synthetic drugs, the study of animal self-medication offers a new line of investigation to provide ecologically sound methods for the treatment of parasites using plant-based medicines in people and their livestock living in the tropics.

Animals in ethnomedecine

Throughout the history of humankind people have looked to animals for sources of herbal medicines and narcotic stimulation (Brander, 1931; Riesenberg, 1948). Anecdotal reports of the possible use of plants as medicine by wild animals such as the elephant, civet, jackal, and rhinoceros are abundant (Table I).

The Navajo living in the southwestern United States credit the bear for their knowledge of the antifungal, antiviral and antibacterial properties of the Umbelliferae *Ligusticum porteri* (Grasanzio, 1992; Moore, 1979).

Tabernanth iboga (Apocynacea) contains several indole alkaloids, and is used as a powerful stimulant and aphrodisiac in many secret religious societies in Gabon (Harrison, 1968). Harrison speculated that because of the wide spread reports from local people of bush pigs, porcupine and gorilla going into wild frenzies after digging up and ingesting the roots, they probably learned about these peculiar properties of the plant from watching the animals' behavior. The most active principle, found in the root, is called ibogaine and is shown to affect the central nervous system and the cardiovascular system. Two other active known compounds in the plant are tabernanthine and iboluteine. The stimulating effects are similar to caffeine (Dubois, 1955). The sloth bear and local people of central India are noted to become intoxicated from eating the fermented Madhuca flowers (Brander, 1931) and reindeer and the indigenous Lapps consume fly agaric mushrooms known for their intoxicating effects (Phillips, 1981).

One version of the discovery of coffee is that the chance observation by a shepherd of goats becoming stimulated after grazing on the berries of wild coffee plants in the highlands of Ethiopia provided the clue for humans to exploit the plant as a stimulant. Dr. Jaquinto, the trusted physician to Queen Ann, wife of James I in 17th Century England, is said to have made systematic observations of domestic sheep foraging in the marshes of Essex which led to his discovery of a successful cure for consumption (Wilson, 1962).

My Tanzanian collaborator in research since 1987, Mohamedi S. Kalunde, a Tanzanian National Parks wildlife officer comes from a long line of traditional healers. He credits the discovery of at least two medicinal treatments passed down to him by his mother and late grandfather from their observations of animal behavior. One day, Mohamedi's grandfather Babu Kalunde observed a young porcupine ingest the roots of a plant known locally as 'mulengelele' (yet unidentified species). Keeping it captive in the village compound for observation, he observed that it subsequently recovered from a severe case of diarrhea and malaise. Based on these observations, Babu Kalunde later successfully used the plant to treat a dysentery-like epidemic that broke out in his village. Mohamedi's mother, Joha Kasante, discovered an antidote for snake bite by having Mohamedi follow the snake that bit his younger brother and bring back leaves of the plant that the snake subsequently chewed on. The leaves are said to prevent the snake's poison from circulating throughout the body. In the foothills of the Himalayas near Mt. Everest the use of the roots of 'chota-chand' as a potent antidote for snake bite is said to have been learned by observing mongoose feeding on the plant before fighting with cobra (Balick & Cox, 1996). All of these examples suggest the occurrence of self-medication in a variety of animal species and ways that humans may learned about the medicinal value of plants from them.

Why should any of this really surprise us? After all, from an evolutionary standpoint, preservation of health is a basic principle of survival and all species alive today can be expected to have evolved a variety of ways of protecting themselves from other organisms, large and small, in their environment.

Where did this all begin? In the plant world, a common line of defense is to produce a variety of toxic secondary compounds such as sesquiterpenes, alkaloids, and saponins which prevent predation by animals (Howe & Westley, 1988; Swain, 1978). At some point in their co-evolutionary history, likely starting with the arthropods, animals began to take advantage of the plant kingdom's protective chemical arsenal to protect themselves from predators and parasites and to enhance their own reproductive fitness (Blum, 1981). For example, adult danaine butterflies of both sexes utilize pyrrolizidine alkaloids for defense against predators and males have also been shown to depend on it as a precursor for the biosynthesis of a pheromone component needed for courtship (Boppré, 1978; 1984). The monarch butterfly is reported to feed on *Asclepias* species containing cardiac glucosides which makes birds sick, conditioning them not to feed on the species (Brower, 1969). Such three-trophic level interactions are likely to have provided the foundation for the evolution of a more sophisticated level of self-medication seen in the higher vertebrates.

The impact of parasites on the evolution of self-medicative behaviour

Parasitism has played an important role in the evolution of host behavior throughout the animal kingdom (Anderson & May, 1982; Clayton & Moore, 1997; Futuyma & Slatkin, 1983). Co-evolution between host and parasite has resulted in the development of mechanisms by which the host limits parasitic infection and the parasite increases its chance of infecting the host (Toft *et al.*, 1991; Ewald, 1994). At the primary level, the host's immune response (innate & acquired) normally controls infections, however, some parasites invariably establish themselves by undergoing antigenic variation, thus disguising themselves with the hosts antigens, or by interfering directly with the immune response (Cox, 1993; Wakelin, 1996).

Where physiological adaptation is not enough, hosts have developed behavioral responses to avoid or limit contact with parasites and other pathogens. These behaviors, widespread among the vertebrates, include regular changing of sleeping or feeding sites, differential use of drinking sites, use of antiparasitic leaf material to line nests or dens occupied over long periods, and the application of aromatic substances to repel fur and feather infesting parasites (Baker, 1996; Clark, 1991; Freeland, 1980; Gompper & Holyman, 1993; Gresianzio, 1992; Hart, 1990; Hausfater & Meade, 1982; Kummer in Nelson, 1960; Seigstadt in Cowen, 1990; Sengputa, 1981). Learned aversion of foods or tastes associated with illness, parasite infection, and compensatory changes in host dietary preferences induced by parasites have been demonstrated in the laboratory and field for a wide range of vertebrates (Gustavson, 1977; Kyriazakis *et al.*, 1994; Keymer *et al.*, 1983). From what has been discovered about self-medication in the great apes over the last few years, parasites and gastrointestinal upset clearly appears to be a major focus of self-medication in non-human animals (Huffman, 1997).

These learned aversions are another level at which the host avoids prolonged exposure to pathogens. Diet modification has also been proposed as a means of altering or controlling internal parasite load. A causal relationship between a sudden change in diet and reduced tapeworm load has been suggested for black bears (Rausch, 1954; 1961). Another example of this type of behavior involves the ingestion of specific plant parts, which have little or no nutritional value, for their antiparasitic qualities, which may be either pharmacological (Huffman *et al.*, 1993; 1998; Ohigashi *et al.*, 1994) or physical (Huffman *et al.*, 1996).

Food as medicine

From an evolutionary perspective, it seems likely that the use of many medicinal plants may have derived from the ingestion of rarely eaten or fall-back foods (eaten in periods of main food shortage) with supportive medicinal properties. One of the challenges and difficulties of interpreting self-medication is distinguishing between possible indirect medicinal benefits derived from secondary compound rich plants that are assumed to be ingested for their nutritional value versus limited and situation specific ingestion of items that are processed solely for their medicinal properties. In some cases it may not even be necessary to draw the distinction.

When consumed on a fairly regular basis year round in seasons of wide availability, food and medicine may be one in the same. Particularly in traditional human societies, the difference between food and medicine is not always clear. A case in point is the study by Etkin (1996) which found 30% of the plant foods used among the Hausa of Nigeria are also used as medicine. Furthermore, 89% of species used to treat symptoms of malaria were also eaten in a dietary context (Etkin & Ross, 1983). Etkin and Ross propose that many Hausa foods were originally acquired from non-cultivated plants first used as medicine. Similarly, many traditional spices, condiments and vegetables of Asian cuisine used today, such as ginger root, marine algae, and various herbs contain significant sources of anti-tumor agents (Murkami *et al.*, 1994; 1996; Ohigashi *et al.*, 1992) that may also have an active role in the suppression of parasitic and viral infections.

Many of these "food-medicines" are beneficial beyond their nutritional value because of the variety of plant secondary compounds contained within. As discussed above, these compounds are considered to be produced by the plant to deter herbivores from ingesting them (Ehrlich & Raven, 1964; Feney, 1976; Howe & Westley, 1988; Wink *et al.*, 1993), but in small amounts such compounds may be of some benefit to the consumer. A number of plant foods found in the diet of the great apes appear to share these properties and are worth mentioning here.

The berries of *Phytolacca dodecandra* L. Herit (Phytolaccaceae) are an abundant and frequently ingested food item of the Kanyawara group of chimpanzees in Kibale, western Uganda (Wrangham and Isabirye-Basuta, in Huffman and Wrangham, 1994). These bitter tasting berries are a concentrated source of at least 4 toxic triterpenoid saponins (lemmatoxin, lemmatoxin-C, oleanoglycotoxin-A, phytolacca-dodecandra glycoside). Consumption of about 2 grams of the material is fatal in mice and rats. Other known properties of these triterpenoid saponins include antiviral, antibacterial, antifertility, spermicidal and embryotoxic activities (Kloos & Mc Cillough, 1987).

Pith and fruit of *Afromomum* species (wild ginger family) are commonly ingested by chimpanzees, bonobos and gorillas across Africa (Idani *et al.*, 1994; Moutsambоté *et al.*, 1994; Nishida & Uehara, 1983; Sugiyama & Koman, 1992; Tutin *et al.*, 1994; Wrangham *et al.*, 1993; Yumoto *et al.*, 1994). A study in progress of the chemical ecology of Bwindi gorilla (*Gorilla gorilla beringei*) diet by John Berry (Rodriquez Laboratory, Division of Biological Sciences, Cornell University) is investigating the bioactivity of the fruit of one of these wild ginger species, *Afromomum sanguineum* (K. Schum.) K. Schum. (Zingiberaceae). The fruits of this species, in particular, are also known to be ingested by gorillas in the Kahuzi-Biega National Park, Congo-Kinshasa (Yumoto *et al.*, 1994). Assays of homogenized fruit and seed extracts show significant antimicrobial activity (Berry, in prep.). The fruits are sold locally in market stalls and along the road in the Bwindi area for the treatment of bacterial and fungal infection and as an anthelmintic (John Berry, personal communication).

The tips of the young leaves of *Thomandersia laurifolia* (T. Anders. ex Benth.) Baill. (Acanthaceae) are on rare occasion chewed by western lowland gorillas (*G. g. gorilla*) in the Ndoki forest of northern Congo (Kuroda, Mokumu, Nishihara, in prep). According to Kuroda and colleagues, the local human inhabitants use these leaves as a treatment for parasites and fever. Weak anti-schistosomal activity has also been found from crude leaf extracts (Ohigashi, 1995).

Bark and wood are characteristically highly fibrous, heavily lignified, sometimes toxic, relatively indigestible and nutrient poor (Waterman, 1984). Chimpanzees and gorillas are known to infrequently ingest the bark and wood of several plant species (Huffman & Wrangham, 1994).

While the list of plant species whose bark is ingested is long, little is actually known about the contribution of bark to the diet and general health. The literature on African ethnomedicine warrants mention of a few of these species. The bark of *Pycnanthus angolensis* (Welw.) Warb. (*Myristicaceae*) ingested by chimpanzees at Mahale in western Tanzania is used by West Africans as a purgative, laxative, digestive tonic, emetic and reliever of toothaches (ABBIW, 1990). Bark strips of *Grewia platyclada* K. Schum (Tiliaceae) are sometimes chewed for the relief of stomach aches by local residents at Mahale (Huffman, unpublished data, Mohamedi S Kalunde, personal communication about human uses). In 1992 one juvenile male suffering from diarrhea was observed chewing, but not swallowing, the fibers of the bark of this species at Mahale (Huffman, unpublished data). In Tanzania, the chimpanzees of Gombe National Park occasionally eat the bark of *Entada abyssinica* Steud. ex A. Rich. (Mimosaceae). In Ghana, the bark is used by humans for diarrhea and as an emetic (Abbiw, 1990). The bark of *Erythrina abyssinica* DC. (Papilionacea) is occassionally eaten by Mahale chimpanzees. Significant plasmodicidal and antischistosomal activities have been demonstrated from the bark of this species collected at Mahale (Ohigashi, 1995; Wright *et al.*, 1993). The bark of *Gongronema latifolium* Benth. (Asclepiadaceae) occasionally eaten by the chimpanzees of Bossou Guinea is extremely bitter, and the stems are used by humans in West Africa as a purge for colic, stomach pains and symptoms connected with intestinal parasite infection (Burkill, 1985).

The preceeding discussion of peculiar fruit, leaf, bark, and wood items ingested by the apes serve to demonstrate the diversity of secondary compounds or inferred pharmacological activity present in their diet. The total effect of ingesting these items is not clear, but it is unrealistic to assume nutritional gain where little is likely to be obtained.

Use of plants as medicine of plants by chimpanzees in the wild

Perhaps due to our phylogenetic closeness, humans and chimpanzees select some of the same plants when displaying similar symptoms of illness (Huffman *et al.*, 1996a). Recent evidence from the African great apes suggests that certain plants are ingested, not incidentally, but directly for their significant medicinal value. The hypothesis currently being developed is that the behaviors aid in the control of intestinal parasites and / or provide relief from related gastrointestinal upset (Huffman *et al.*, 1996a; Huffman, 1997).

These observations provide the clearest systematic evidence collected thus far for self-medication in animals. Unquestionably, these implications of self-medicative behavior are of extreme interest when considering the early emergence of medicinal habits from the great apes to early hominids and modern humans.

Vernonia amygdalina and bitter pith chewing behavior

The hypothesis that bitter pith chewing has medicinal value for chimpanzees was first proposed from detailed behavioral observations and parasitological and phytochemical analyses of patently ill chimpanzees' ingesting *Vernonia amygdalina* Del. (Compositae) at Mahale (Huffman & Seifu, 1989; Huffman *et al.*, 1993). These are the first reported observations to verify illness and apparent improvement thereafter of an animal ingesting putative medicinal plants.

V. amygdalina occurs throughout tropical sub-Saharan Africa (Watt & Breyer-Brandwijk, 1962). Bitter pith chewing of other *Vernonia* species has been observed at Gombe, Tanzania (*V. colorata* (Willde.) Drake: Huffman & Wrangham, 1994; Hilali, unpublished data as personal communication from J. Wallis) and Kahuzi-Biega, Congo-Kinshasa (*V. hochstetteri* Schi-Bip., *V. kirungae* Rob. E. Fries: Yumoto *et al.*, 1994; A.K. Basabose, personal communication). At Tai, Ivory Coast, the bitter piths of *Paliosota hirsuta* (Thunb.) K. Schum. (Commelinacea) and *Eremospath macrocarpa* (Mann & Wendl.) Wendl. (Palmae) are chewed (C. Boesch, personal communication in Huffman, 1997).

When ingesting the pith from young shoots of *V. amygdalina*, chimpanzees meticulously remove the outer bark and leaves to chew on the exposed pith, from which they extract the extremely bitter juice and residual amounts of fiber. The amount of pith ingested in a single bout is relatively small, ranging from portions of
5 to 120 cm X 1 cm. The entire process, depending on the amount ingested takes anywhere from less that one to 8 minutes. Mature conspecifics in proximity to an individual chewing *Vernonia* bitter pith or leaf swallowing show no interest in ingesting the pith (Huffman & Seifu, 1989; Huffman *et al.*, 1997). Infants of ill mothers, however, have been observed on occasion to taste the pith discarded by their ill mothers. In this way, group individuals are exposed to both the behavior and the extremely bitter taste of the pith at a very young age.

At Mahale, use of *V. amygdalina* has been recorded in all months except June and October (late dry season), demonstrating its year-round availability (Nishida & Uehara, 1983). However, use by chimpanzees is highly seasonal despite its year round availability. It is most often used during the rainy season months of December and January, the time parasite re-infection by nematodes is at their peak in some species (Huffamn *et al.*, 1997).

The ethnomedicine and phytochemistry of bitter pith chewing

V. amygdalina is used by numerous African ethnic groups across the continent as medicine (Table II). A concoction made from this species is prescribed treatment for malarial fever, schistosomiasis, amoebic dysentery, several other intestinal parasites and stomachaches (Burkill, 1985; Dalziel, 1937; Huffman *et al.*, 1996a; Watt & Breyer-Brandwijk, 1962). The Tongwe of Mahale use this plant as a treatment for intestinal parasites, diarrhea and stomach upset.

Phytochemical analysis of *V. amygdalina* samples collected at Mahale from plants known to be used by chimpanzees reveal the presence of two major classes of bioactive compounds. From this work, a total of 4 known sesquiterpene lactones, 7 new stigmastane-type steroid glucosides and 2 freely occurring aglycones of these glucosides have been isolated (Ohigashi *et al.*, 1991; Jisaka *et al.*, 1992a, b; Jisaka *et al.*, 1993 a, b). The sesquiterpene lactones present in *V. amygdalina*, also found in *V. colorata* and a number of other *Vernonia* spp, are well known for their anthelmintic, antiamoebic, antitumor, and antibiotic properties (Asaka *et al.*, 1977; Gasquet *et al.*, 1985; Jisaka *et al.*, 1992a; Jisaka *et al.*, 1993 b; Kupchan *et al.*, 1969; Toubiana & Gaudemer, 1967). From crude methanol extracts of the leaves, Koshimizu *et al.* (1993) also found inhibition of tumor promotion and immunosupressive activities.

In vitro tests on the antischistosomal activity of the pith's most abundant steroid glucoside, vernonioside B1, and sesquiterpene lactone, vernodaline (Figure 1), showed significant inhibition of movement of the adult parasites and adult females' egg-laying capacity (Jisaka *et al.*, 1992b). These findings are consistent with the observed decline in nodular worm (*Oesophagostomum stephanostomum*) EPG level 20 hours after an adult female chimpanzee 1993). The sesquiterpene lactones showed significant *in vivo* plasmodicidal activity, while that of the steroid glucosides was weaker (Ohigashi *et al.*, 1994).

Some of the species with bitter piths ingested by chimpanzees at Gombe, Kahuzi-Biega, and Tai also have a number of ethnomedicinal and pharmacological properties. *V. colorata* and *V. amygdalina* are not distinguished from each other ethnomedicinaly with regard to their medicinal properties and folk classification (Burkill, 1985). Alkaloids occur in the pith, as well as flower and leaf of *V. hochstetteri* (Smolenski *et al.*, 1974). *P. hirsuta* and *E. macrocarpa* are used in west African ethnomedicine for the treatment of upset stomachs, colic, as an antiseptic and analgesic and for venereal disease (Abbiw, 1990; Neuwinger, 1996). Moluscicidal activity has also been reported for *P. hirsuta* (Okunji and Iwu, 1988).

A link between animal self-medication and ethnomedicine

The ethnomedicinal uses of *V. amygdalina* and the conditions under which ill chimpanzees have been observed to ingest this species are similar in many respects. In the two documented cases of use by chimpanzees described above, the rate of recovery (20-24 hr) was comparable to that of local human inhabitants at Mahale, the Watongwe (within 24 hr), who use *V. amygdalina* for the treatment of parasitosis and gastrointestinal upset.

This preparation is typically made by the Watongwe from a cold water decoction of 2-3 crushed fresh leaves (approximately 10-15 g f. w.) in 300-400 ml of water. Due to the plant's toxic effect on the patient, this is usually only a one-dose treatment (M.S. Kalunde, personal communication). An analysis replicating this traditional method (3 trials) yielded 3.3-5.0 mg of vernonioside B1 (Figure 1; Huffman *et al.*, 1993 a). This was directly compared by quantitative analysis of pith collected from the plant used by the adult female chimpanzee that experienced a drop in parasite load 20 hr after its ingestion. The amount of pith she ingested (60 cm, approximately 50-100 g f. w.) was found to contain approximately 3.8-7.6 mg of vernonioside B1, or roughly an equal amount to that normally obtained by a Tongwe patient (Hufman *et al.*, 1993 a).

We are intrigued by this close similarity in use by humans and chimpanzees. Both humans and chimpanzees appear to have recognized the important physiological activity of this plant, and evidence suggests that chimpanzees ingest *V. amygdalina* when they experience some of the same symptoms.

From an ethnobotanical viewpoint, the greater number of different cultures that recognize a single plant species as having some kind of medicinal property, the more likely that species is to contain significant physiological activity. The example of *V. amygdalina* with its widely recognized medicinal value in Africa takes this one step further by bridging the gap between apes and humans (Table II).

Self-medication as a learned behavioral tradition

How do animals learn to medicate themselves? In non-human primates important benefits come from social learning which allow naive individuals to acquire information through the experience of others, and over time to perfect the behavior themselves. Once an effective self-medicative behavior is recognized, it will likely spread through the group, first slowly, but after a time increasingly faster as it is passed onto the youngest members. At Mahale, and presumably elsewhere, initial exposure to self-medicative behaviors take place by individuals at an early age, not when ill themselves, but by observing the behavior and tasting the items used by others that are ill- often their mothers.

In the case of *Vernonia amygdalina*, it is not just what species is used and the context of use, but also the appropriate plant part and in what amounts it is ingested that must be learned for the plant to be used effectively and safely. Avoidance of bitter tasting things has evolved as a means of avoiding toxic substances. This innate tendency must be learned to be ignored if the medicinal benefits of these substances are to be gained. Humans often end up having to put sugar coatings on medicines to convince others to ingest them. For chimpanzees the observational learning process is undoubtedly an important component. Given the high degree of conservatism in chimpanzee feeding habits the random sampling of new plants, especially when ill, does not seem likely to occur very frequently. If so, traditions must have started rarely, perhaps as a result of ill, hungry chimpanzees trying new foods during periods of extreme food scarcity, recovering their health, and associating their improvement with the new item.

Chimpanzees have a strong capacity for empathy and good long-term memory. Any associations made between the change in a sick individual's feeding habits and subsequent recovery are likely to reinforce the learning of both context and the details of plant use. On numerous occasions ill chimpanzees' travel companions have been observed to co-ordinate their activities to be near the ill and thus had ample opportunity to observe their self-medicative behavior in its proper context. This probably worksstrongest on naive dependent offspring who follow closely and mimic the behavior of their mothers. Newly immigrant females have also shown intense interest in individuals while ingesting the bitter pith of this plant.While all of the adults in M group have been observed to self-medicate at some time or another, they rarely if ever show interest in plants used for this simply because they come across them along a trail or because somebody else is using them.

Taste perception and physiological feedback in response to the ingestion of bitter plants are likely to play a supportive role in the learning process. Historically, herbalists have emphasized the importance of taste and smell in the evaluation of plant medicinal properties. In a study of the criteria of medicinal plant selection by the Tzeltal Mayans of Highland Chiapas in Mexico, John Brett noted that taste and smell were consistently used to select or evaluate a plant to treat related illnesse (Brett, 1994). Regardless of taxonomy, bitter tasting plants were selected and predominantly used to treat gastrointestinal upsets, parasites and stomach pains.

This close correspondence between bitter taste and pharmacological activity may also aid chimpanzees in their selection of plants for treating parasite infection and related gastrointestinal illness based on previous experiences. This would be particularly adaptive for immigrating females when they move to new areas where the vegetation is different but similar pharmacologically active bitter plants may be available.

Selective association between taste and gastrointestinal illness is a widely accepted principal of taste aversion learning among mammals and the learning mechanism of food aversion in response to induced sickness has been well documented in a number of animal species. The capacity to associate improved health after eating novel plants having medicinal properties has received less attention but the highly adaptive significance of this process is self-evident. Such biological and psychological processes in conjunction with observational learning are proposed to constitute the core of non-human primate self-medicative behavior and if so are at the roots of the human cultural practice of medicine.

Evolution of medicinal plant use and the future

These strong similarities in plant selection criteria among the African great apes in response to parasite infection and gastrointestinal upset and the common use of some plants by chimpanzees and humans for treating such illnesses is tantalizing evidence for the evolution of medicine and the impact made by parasite infection. Our earliest hominid ancestors can be predicted to have exhibited some similarities in plant selection criteria with both existing apes and modern humans. The early fossil record provides no direct evidence for the finer subtleties of feeding behavior and diet, but it seems reasonable to hypothesize that early hominids would have displayed at least the range of extant ape self-medicative behaviors.

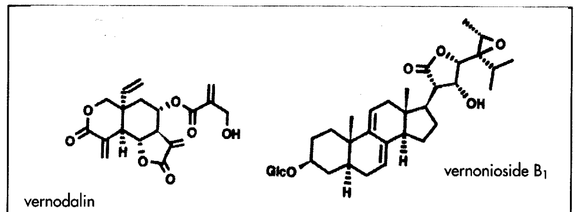
The fundamentals of associating the medicinal properties of a plant by its taste, smell and texture have their roots deep in our primate history. A major turn of events in the evolution of medicine is likely to have come about in early humans with the advent of language to share and pass on detailed experiences about plant properties and their effect against disease. Another major event in human history is considered to have been the attainment of food preparation and detoxification technologies which allowed humans to exploit a wider range of plant life as food. Johns (1990) argues that it was this turning point that may actually have increased our dependence on plant secondary compounds because of their disappearance from the daily diet. In this way, perhaps a greater specialization of plant use specifically as medicine came about. Furthermore, with the skilled use of fire to boil, steam, vaporize, condense or otherwise extract useful secondary plant compounds from plants, a greater variety of uses for these compounds were developed.

The current level of sophisticated medicinal practices in traditional humans societies may be the product of the greater variety of diseases and stress brought about by a subsistence revolution from hunting and gathering to a greater dependence on domestic crops and livestock in a sedentary setting (Johns, 1990). In this light, our early modern human ancestors may have had a smaller pharmacopoeia, but this was not because of any lack of technical sophistication. More likely it was because of less diseases and stress to respond to (Cohen and Armelagos, 1984). Thanks to the technological advancement of modern medicine, the lives of millions of people in the so called civilized world are saved or prolonged every year. Yet, it is also technological advancement that brings about the changes in our diets (preservatives, additives, genetic engineering) and lifestyles responsible for the modern diseases which nations spend fortunes every year trying to find cures for.

We do not have to turn back the clock of time or abandon civilization to regain a piece of that paradise lost. We may have much to re-learn and gain from the "ancient wisdom" of our primate cousins and the wealth of traditional medicine still being practiced today by a large majority of the world's population.

Further field and laboratory research into self-medicative behavior in other animal species is strongly encouraged. As this review has shown, answers to a few questions invariably lead to more questions. As more researchers in the field begin to look for similar types of behavior, they will be found and more answers will be provided. Because of the obvious adaptive significance of self-medication, its existence is predicted to be wide-spread. Self-medicative behaviors are predicted to occur in all animal species.

Figure 1



vernodalin

vernonioside B_1

The most abundant constituents isolated from the pith of *Vernonia amygdalina*, a steroid glucoside (vernonioside b_1) and a sesquiterpene lactone (vernodaline)

References

ABBIW D.K. (1990) *Useful Plants of Ghana*, Kew, Intermediate Technology Publications and Royal Botanic Gardens.

ABEBE D. (1987) Plants in the health care delivery system of Africa. in A.J.M. LEEUWENBURG (Compiler), *Medicinal and poisonous plants of the tropics*, Wageninigen, Pudoc Wageninigen, 79-87.

AKAH P.A., OKAFOR C.L.(1990) Blood sugar lowering effects of *Vernonia amydgalina* in experimental rabbit model, in A. SOFOWORA (ed), *The state of medicinal plant research in Nigeria*, Abstract volume for "Integrative seminar on natural products research and development of plant based drugs", University of Science and Technology, Kumani, Ghana, 23-30 September, 1990, 27.

ANDERSON R.M., MAY R.M. (1982) *Population Biology of Infectious Diseases*, Berlin, Springer-Verlag.

ASAKA Y., KUBOTA T., KULKARNI A.B. (1977) Studies on a bitter principle from *Vernonia anthelmintica*, *Phytochemistry*, 16,1838-1839.

BAER M. (1996) Fur rubbing. Use of medicinal plants by capuchin monkeys (*Cebus capucinus*), *American Journal of Primatology*, 38, 263-270.

BALICK M.J., COX P. A. (1996) *Plants, people, and culture*, New York, Scientific American Library, W. H. Freeman and Company.

BLIM M.S. (1981) *Chemical defenses of arthropods*, New York, Academic Press.

BOPPRE M. (1978) Chemical communication, plant relationships, and mimicry in the evolution of danaid butterflies, *Entomol. Exp. Appl.*, 24, 264-277.

BOPPRE M. (1984) Redifining "Pharmacophagy", *Journal of Chemical Ecology*, 10 (7), 1151-1154.

BRANDER A.A.D. (1931) *Wild Animals in Central India. London*, Edward Arnold.

BRETT J. A. (1994) *Medicinal plant selection criteria among the Tzeltal Maya of Highland Chiapas, Mexico*, PhD Dissertation, San Francisco, University of California.

BROWER L. P. (1969) Ecological chemistry, *Scientific American*, 22 (2), 22-29.

BURKILL H.M. (1985) *The Useful Plants of West Tropical Africa*, 2nd ed., Vol. 1, Kew, Royal Botanical Gardens.

BURTON R.W. (1952) The tiger as fruit eater, *Journal of the Bombay Natural History Society*, 50, 649.

CLAYTON D.H., MOORE J. (1997) Host-Parasite evolution. General Principles & Avian Models, Oxford, Oxford Unviversity Press.

CLARK C.C. (1991) The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings, in LOYE J.E. and ZUK M. (eds.), *Bird-parasite intearctions: ecology, evolution, and behaviour*, Oxford, Oxford Unviersity Press, 205-221.

COHEN M.A, ARMELAGOS G. J. (eds) (1984) *Paleopathology and the origins of agriculture*, Orlando, Florida, Academic Press.

COWEN R. (1990) Medicine on the wild side, *Science News*, 138, 280-282.

COX F.E.G. (1993) *Modern Parasitology*, 2nd edition, Oxford, Blackwell Scientific Press.

DALZIEL J. M. (1937) The Useful Plants of West Tropical Africa in Hutchinson J. & Dalziel J.M. (eds.), *Appendix to Flora of West Tropical Africa*, London, Whitefriars Press.

DHARMAKUMARSINHJI R. S. (1960) Indian wild boar (*Sus scrofa cristatus* Wagner) feeding on *Boerhavia diffusa* Linn., *Journal of the Bombay Natural History Society*, 57, 654-655.

DUBOIS L. (1955) *Tabernanthe iboga* Baillon, *Bull. Agric. Congo Belge*, 46, 805-829.

EHRLICH P., RAVEN P. H. (1964) Butterflies and plants: A study in coevolution, *Evolution*, 18, 586-608.

ETKIN N.L. (1996) Medicinal cuisines: diet and ethnopharmacology, *International Journal of Pharmacology*, 34 (5), 313-326.

ETKIN N.L., ROSS P.J. (1983) Malaria, Medicine, and Meals: Plant use among the Hausa and its impact on disease, in ROMANUCCI-ROSS L., MOERMAN D.E. and TANCREDI L.R. (eds), *The Anthropology of Medicine: From Culture to Method*, New York, Praeger, 231-259

EWALD P.W. (1994) *Evolution of Infectious Disease*, Oxford, Oxford University Press.

FEENY P. (1976) Plant apparency and chemical defense, *Recent advances in phytochemistry*, 10, 1-40.

FREELAND W. F. (1980) Mangoby (*Cercocebus albigena*) movement patterns in relation to food availability and fecal contamination, *Ecology*, 61 (6), 1297-1303.

FUTUYMA D.J., SLATKIN M. (1983) *Coevolution*, Sunderland, MA, Sinauer Associates Inc.

GASQUET M., BAMBA D., BABADJAMIAN A., BALANSARD G., TIMON-DAVID P., METZGER J. (1985) Action amoebicide et anthelminthique du vernolide et de l'hydroxyvernolide isoles des feuilles de *Vernonia colorata* (Willd.) Drake, *European Journal of Medical Chemical Theory*, 2, 111-115.

GOMPPER M.E., HOLYMAN A.M. (1993) Grooming with Trattinnickia resin: possible pharmaceutical plant use by coatis in Panama, *Journal of Tropical Ecolology*, 9, 533-540.

GRISANZIO J.A. (1992) Fur-bearing pharmacists, *Animals*, September/October, 26-30.

GUSTAVSON C.R. (1977) Comparative and field aspects of learned food aversions, in BARKER L.M., BEST M.R. and DOMJAN M. (eds.), *Learning mechanisms in food selection*, Baylor (Texas), Baylor University Press, 23-43.

HARBORNE J.B. (1978) Biochemical aspects of plant and animal coevolution, London. (Academic Press.Phytochemical Society of Europe Symposia, Series No.15)

HARRISON G. P. (1968) *Tabernanthe iboga*: an African narcotic plant of social importance, *Economic Botany*, 23, 174-184.

HART B.L. (1990) Behavioral adaptations to pathogens and parasites. Five strategies, *Neuroscience and Biobehavioral Review*, 14, 273-294.

HAUSFATER G., MEADE B.J. (1982) Alternation of sleeping groves by yellow baboons (*Papio cynocepahalus*) as a strategy for parasite avoidance, *Primates*, 23, 287-297.

HOWE H.F., WESTLEY L.C. (1988) *Ecological relationships of plants and animals*, Oxford, Oxford University Press.

HUBBACK T.B. (1939) The two-horned Asiatic rhinoceros (*Dicerorhinus sumatrensis*), *Journal of the Bombay Natural History Society*, 40, 594-617.

HUBBACK T.B. (1941) The Malay Elephant, *Journal of the Bombay Natural History Society*, 42, 483-509.

HUFFMAN M.A., GOTOH S., IZUTSU D., KOSHIMIZU K., KALUNDE M. S. (1993) Further observations on the use of *Vernonia amygdalina* by a wild chimpanzee, its possible effect on parasite load, and its phytochemistry, *African Study Monographs*, 14 (4), 227-240.

HUFFMAN M.A., GOTOH S., TURNER L.A., HAMAI M. and YOSHIDA K. (1997) Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania, *Primates*, 38 (2), 111-125.

HUFFMAN M.A., KOSHIMIZU K., OHIGASHI H. (1996a) Ethnobotany and zoopharmacognosy of *Vernonia amygdalina*, a medicinal plant used by humans and chimpanzees, in CALIGARI P.D.S., HIND D.J.N. (eds.) *Compositae: Biology & Utilization*, Vol. 2., Kew, The Royal Botanical Gardens, 351-360.

HUFFMAN M.A., & SEIFU M. (1989) Observations on the illness and consumption of a possibly medicinal plant *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park, Tanzania, *Primates*, 30, 51-63.

HUFFMAN M.A., WRANGHAM R.W. (1994) The diversity of medicinal plant use by chimpanzees in the wild, in WRANGHAM R.W., MC GREW W.C., de WAAL F.B., HELTNE P.G. (eds.), *Chimpanzee Cultures*, Cambridge, Harvard University Press, 129-148.

IDANI G., KURODA S., KANO T., ASATO R. (1994) Flora and vegetation of Wamba Forest, Central Zaire with reference to Bonobo (*Pan paniscus*) foods, *Tropics*, 3 (3/4), 309-332.

IRVINE F. R. (1961) *Woody plants of Ghana. London*, Oxford University Fress.

JANZEN D. H. (1978) Complications in interpreting the chemical defenses of tree against tropical arboreal plant-eating vertebrates, in G.G. MONTGOMERY (ed.), *The ecology of arboreal folivores*, Washington D.C., Smithsonian Institute Press, 73-84.

JISAKA M., KAWANAKA M., SUGIYAMA H., TAKEGAWA K., HUFFMAN M.A., OHIGASHI H., KOSHIMIZU K. (1992a) Antischistosomal activities of sesquiterpene lactones and steroid glucosides from *Vernonia amygdalina*, possibly used by wild chimpanzees against parasite-related diseases, *Bioscience, Biotechnology and Biochemistry*, 56 (5), 845-846.

JISAKA M., OHIGASHI H., TAKAGAKI T., NOZAKI H., TADA T., HIROTA M., IRIE R., HUFFMAN M.A., NISHIDA T., KAJI M., KOSHIMIZU K. (1992b) Bitter steroid glucosides, vernoniosides A1, A2, and A3 and related B1 from a possible medicinal plant *Vernonia amygdalina*, used by wild chimpanzees, *Tetrahedron*, 48, 625-632.

JISAKA M., OHIGASHI H., TAKEGAWA K., HIROTA M., IRIE R., HUFFMAN M.A., KOSHIMIZU K. (1993a) Steroid glucosides from *Vernonia amygdalina*, a possible chimpanzee medicinal plant, *Phytochemistry*, 34, 409-413.

JISAKA M., OHIGASHI H., TAKEGAWA K., HUFFMAN M.A., KOSHIMIZU K. (1993b) Antitumor and antimicrobial activities of bitter sesquiterpene lactones of *Vernonia amygdalina*, a possible medicinal plant used by wild chimpanzees, *Bioscience, Biotechnology, Biochemistry*, 57 (5), 833-834.

JOHNS T. (1990) *With bitter herbs they shall eat it*, Tucson, The University of Arizona Press.

JOHNS T. (1994) Ambivalence to the palatability factors in wild food plants, in ETKINS N.L., *Eating on the Wild Side*, Tucson, The University of Arizona Press , 46-61.

KEYMER A., CROMPTON D.W.T., SAHAKIAN B.J. (1983) Parasite induced learned aversion involving Nippostrongylus in rats, *Parasitology*, 86, 455-460.

KLOOS H., MC CULLOUGH F.S. (1987) Plants with recognized molluscicidal activity, in MOTT K.E. (ed.), *Plant Molluscicides*, New York, John Wiley & Sons Ltd., 45-108.

KOKWARO J.O. (1976) *Medicinal Plants of East Africa*, Nairobi, General Printers Ltd.

KOSHIMIZU K., OHIGASHI H., HUFFMAN M.A., NISIHDA T., TAKASAKI H. (1993) Physiological activities and the active constituents of potentially medicinal plants used by wild chimpanzees of the Mahale Mountains, Tanzania, *International Journal of Primatology*, 14 (2), 345-356.

KUPCHAN S.M., HEMINGWAY R.J., KARIM A., WERNER D. (1969) Tumor Inhibitors XLVII. vernodalin and vernomygdin, two new cytotoxic sesquiterpene lactones from *Vernonia amygdalina* Del., *Journal of Organic Chemistry*, 34, 3908-3911.

KYRIAZAKIS I., OLDHAM J. D., COOP R.L., JACKSON F. (1994) The effect of subclinical intestinal nematode infection on the diet selection of growing sheep, British Journal of Nutrition, 72, 665-677.

McCANN C. (1932) A cure for tapeworm, *Journal of the Bombay Natural History Society*, 36, 282-284.

MOORE M. (1979) *Medicinal plants of the mountain west*, Santa Fe, Museum of New Mexico Press.

MOUTSAMBOTÉ J., YUMOTO T., MITANI M., NISHIHARA T., SUZUKI S., KURODA S. (1994) Vegetation and list of plant species identified in the Nouabalé-Ndoki Forest, Congo, *Tropics*, 3 (3/4), 277-293.

MUANZA D.N., DANGALA N.L., MPAY O. (1993) Zairean medicinal plants as diarrhea remedies and their antibacterial activities, African Study Monographs, 14 (1), 53-63.

MURAKAMI A., OHIGASHI H., KOSHIMIZU K. (1994) Possible anti-tumor promoting properties of traditional Thai foods and some of their active constituents, *Asia Pacific Journal of Clinical Nutrition*, 3, 185-191.

MURAKAMI A., OHIGASHI H., KOSHIMIZU K. (1996) Anti-tumor promotion with food phytochemicals. A strategy for cancer chemoprevention, *Bioscience, Biotechnology Biochemistry*, 60 (1), 1-8.

NELSON G.S. (1960) Schistosome infections as zoonoses in Africa, *Tanscripts of the Royal Society of Tropical Medicine and Hygiene*, 54, 301-314.

NEUWINGER H.D. (1996) *African Ethnobotany. Chemistry, pharmacology, toxicology*, London, Chapman & Hill.

NISHIDA T., UEHARA S. (1983) Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*). Long term record from the Mahale Mountains, Tanzania, *African Study Monographs*, 3, 109-130.

NYAZEMA N.Z. (1987) Medicinal plants of wide use in Zimbabwe, in A.J.M. LEEUWENBURG (Compiler), *Medicinal and poisonous plants of the tropics*, Wageningen, Pudoc Wageningen, pp. 36-43.

OGILVIE G.H. (1929) Bison eating bark, *Journal of the Bombay Natural History Society*, 33, 706-707.

OHIGASHI H. (1995) *Plants used medicinaly by primates in the wild and their physiologically active constituents*, Report to the Minestry of Science, Education and Culture for 1994 Grant-in-Aid for Scientitific Research (n° 06303012).

OHIGASHI H., HUFFMAN M.A., IZUTSU D., KOSHIMIZU K., KAWANAKA M., SUGIYAMA H., KIRBY G.C., WARHURST D.C., ALLEN D., WRIGHT C.W., PHILLIPSON J.D., TIMMON-DAVID P., DELNAS F., ELIAS R., BALANSARD G. (1994) Toward the chemical ecology of medicinal plant-use in chimpanzees. The case of *Vernonia amygdalina* Del.. A plant used by wild chimpanzees possibly for parasite-related diseases, *Journal of Chemical Ecology*, 20, 541-553.

OHIGASHI H., JISAKA M., TAKAGAKI T., NOZAKI H., TADA T., HUFFMAN M.A., NISHIDA T., KAJI M., KOSHIMIZU K. (1991) Bitter principle and a related steroid glucoside from *Vernonia amygdalina*, a possible medicinal plant for wild chimpanzees, *Agricultural and Biological Chemistry*, 55, 1201-1203.

OHIGASHI H., SAKAI Y., YAMAGUCHI K., UMEZAKI I., KOSHIMIZU K. (1992) Possible anti-tumor promoting properties of marine algae and in vitro activity of wakame seaweed extract, Bioscience Biotechnology and Biochemistry, 56 (6), 994-995.

OKUNJI C. O., IWU M. M. (1988) Control of schistosomiasis using Nigerian medicinal molluscicides, *International J. Crude Drug Research*, 26 (4), 246-252.

PALGRAVE K.C. (1983) *Trees of Southern Africa*, 2nd revised edition, Cape Town, Struik Publisher.

PHILLIPS R. (1981) Mushrooms and other fungi of great britain and Europe, London, Pan.

RAUCH R. (1954) Studies on the helminth fauna of Alaska. XXI. Taxonomy, morphological variation, and ecology of *Diphyllobothirium ursi* n. sp. *provis.* on Kodiak Island, *Journal of Parasitology*, 40, 540-563.

RAUCH R. (1961) Notes on the black bear, *Ursus americanus Pallas*, in Alaska with particular reference to dentition and growth, *Z. Saugetierk*, 26, 77-107.

RIESENBERG S.H. (1948) Magic and medicine in Ponape, Southwest, *Journal of Anthropology*, 4, 406-429.

SENGPUTA S. (1981) Adaptive significance of the use of margosa leaves in nests of house sparrows Passer domesticus, *Emu*, 81, 114-115.

SMOLENSKI S.J., SILINIS H., FARNSWORTH N. R. (1974) Alkaloid screening. V, *Lloydia*, 37 (3), 506-536.

SUGIYAMA Y., KOMAN J. (1992) The flora of Bossou: Its utilization by chimpanzees and humans. African Studies Monographs 13(3): 127-169.

TOFT, C.A., AESCHLIMANN, A., BOLIS, L. (1991) Parasite-Host Associations; Coexistence or Conflict? Oxford, Oxford Science Publications.

TOUBIANA, R., GAUDEMER, A. (1967) Structure du vernolide, nouvel ester sesquiterpique isole de *Vernonia colorata*, *Tetrahedron Letters*, 14, 1333-1336.

TUTIN C.E.G., WHITE L.J.T., WILLIAMSON E.A., FERNANDEZ M., Mc PHERSON. G. (1994) *List of plant species identified in the northern part of the Lopé Reserve*, Gabon, Tropics, 3 (3/4), 249-276.

WAKELIN D. (1996) Immunity to parasites - How parasitic infections are controlled, 2nd edition, Cambridge, Cambridge University Press.

WATERMAN P.G. (1984) Food acquisition and processing as a function of plant chemistry. in CHIVERS D. J., WOOD BN. A., BILSBOROUGH A (eds.), Food Acquisition and Processing in Primates, New York, Plenum Press, 177-211.

WATT J. M., BREYER-BRANDWINJK M.G. (1962) *The Medicinal and Poisonous Plants of Southern and East Africa*, Edinburgh, E. and S. Livingstone Ltd.

WILSON E. (1962) Aubrey's brief lives edited edition by O.L. Dick, Ann Arbor, Ann Arbor Paperbacks, p. xix.

WINK M., HOFER A., BILFINGER M., ENGLERT E., MARTIN M., SCHNEIDER D. (1993) Geese and dietary allelochemicals- food palatability and geophag,. Chemoecology, 4, 93-107.

WRANGHAM R.W., ROGERS M.E., ISABIRYE-BASUTA G. (1993) Ape food density in the ground layer in Kibale Forest, Uganda, *African Journal of Ecology*, 31, 49-57.

WRIGHT C., PHILLIPSON C., KIRBY D.V., HUFFMAN M.A., OHIGASHI H. (1993) *Do chimpanzees know how to treat protozoal diseases?* Paper presentation at the 5th British Society for Parasitology Malaria Meeting, September, 1993: Oxford.

YUMOTO T., YAMAGIWA J., MWANZA N., MARUHASHI T. (1994) *List of plant species identified in Kahuzi-Biega National Park*, Zaire, Tropics, 3 (3/4), 295-308.

Table I: Some anecdotal evidence for self-medication in animals

Species	Plant (chemical evidence)	References
Malay elephant	*Entada schefferi* (Leguminosae): for stamina before long walk, possible pain killer?	Hubback, 1941, Janzen, 1978
African elephant	Boraginaceae sp.: induce labor; used by Kenyan ethnic group to induce labor and abortion. Similar story related to Huffman about observations made in Tanzania	Cowen, 1990 M.S. Kalunde, pers. comm.
Indian bison	*Holarrhena antidysenterica* (Apocynaceae): bark regularly consumed. Species name suggests antidysentaric action.	Oglivie, 1929
Wild Indian boar	*Boerhavia diffusa* (Nyctaginaceae): called pig weed. Roots are selectively eaten by boar and is a traditional Indian antihelmintic.	Janzen,1978, Dharmkumarsinhji, 1960
Pigs	*Punicum granatum* (Punicaceae) pomegranate: root sought after by pigs in Mexico. Alkaloid in roots toxic to tapeworms.	Janzen, 1978, McCann, 1932 Caius, 1940
Indian tigers wild dogs, bears civets, jackals	*Careya arborea* (Barringtonaeaceae), *Dalbergia latifolia* (Leguminosae) etc.: fruits of various species eaten by large carnivores. Possibly helps in elimination of parasites ingested along with contents of intestines of herbivore prey	McCann, 1958, Burton, 1952 Janzen, 1978
S. American wolf	*Solanum lycocarpon* (Solanaceae): rotting fruit said to be eaten to cure stomach or intestinal upset	D.A.O. Courtnay, G.C. Kirby pers. comm.
Asiatic two-horned Rhinoceros	*Ceriops candoleana* (Rhizophoraceae): tannin rich bark eaten in large amounts enough to turn urine bright orange. Possible use in control of bladder and urinary tract parasites.	Hubback, 1939
Black howler monkey Spider monkey	Indigenous peoples living in primate habitats of the Neotropics claim that some monkey species are parasite-free because of the plants they eat.	S. Vitazkova, M. Pavelka pers.. Comm.

Table II: Ethnomedicinal uses of *Vernonia amygdalina* in Africa

Application	Plant part used	Region used, comments
General intestinal upsets		
enteritis	root, seeds	Nigeria
constipation	leaves, sap	Nigeria, Tanzania, Ethiopia: as a laxative
diarrhoea	stem, root-bark, leaves	W. Africa, Zaire
stomach upset	stem, root-bark, leaves	Angola, Ethiopia
Parasitosis		
schistosomiasis	root, bark, fruit	Zimbabwe, Mozambique, Nigeria: sometimes mixed with *Vigna sinensis*
malaria	root, stem-bark, leaves	E. Africa, Angola, Guinea, Nigeria, Ethiopia: a quinine substitute
trematode infection	root, leaves	E. Africa: treatment for children used as a suppository
amoebic dysentory	root-bark	S. Africa
ringworm	leaves	Nigeria: ringworm and other unidentified epidermal infections
unspecified	leaves	Nigeria: prophylactic treatment for nursing infants, passed through mother's milk
	root, seeds	Nigeria: worms
	leaves	W. Africa: crushed in water and given to horses as a vermifuge, livestock fodder supplement for treating worms
	leaves	Ghana: purgative
Tonic food	leaves	Cameroon, Nigeria: boiled or soaked in cold water prepared as soup or as a vegetable fried with meat ; "n'dole", "fatefate", "mayemaye", leaves sold in markets and cultivated in home gardens
Other ailments		
amenorrhoea	root	Zimbabwe
coughing	leaf	Ghana, Nigeria, Tanzania
diabetes	all bitter parts	Nigeria
fever	leaves	Tanzania, Kenya, Uganda, Congo-Kinshasa: leaves squeezed and juice taken
gonorrhoea	roots	Ivory Coast: taken with *Rauwolfa vomitoria*
"heart weakness"	root	W. Africa: vernonine is a cardiotonic glycoside comparable to digitalin
lack of appetite	leaf	W. Africa: leaves soaked in cold water to remove bitter and then boiled in soup
pneumonia	leaf	Ivory Coast: taken with Argemone maxicana or used in a bath
rheumatism	stem, root-bark	Nigeria
scurvy	leaves	Sierra Leone, Nigeria, W. Cameroon: leaves sold in markets and cultivated in home gardens
General hygiene		
dentrifice	twig, stick	Nigeria: chew stick for cleansing and dental caries
disinfectant	not given	Ethiopia
soap	stems	Uganda

Sources: Abebe, 1987; Akah and Okafor, 1990; Burkill, 1985; Dalziel, 1937; Irvine, 1961, Kokwaro, 1976; Muanza, *et al.*, 1993; Nyazema, 1987; Palgrave. 1983; Watt and Breyer-Branwijk, 1962; Huffman, personal unpublished data from interviews in Uganda and Tanzania.

M.A. Huffman

Aspilia massambicensis (Oliv.) Asteracea
Mahale National Park (Tanzania) 1996

Adult male Linda swallowing leaf of *Aspilia massambicensis* (Oliv.) Asteracea
Mahale National Park (Tanzania) 1993

M.A. Huffman

Adult male Jilba chewing bitter pith of *Vernonia amygdalina* (Compositae)
Mahale National Park (Tanzania) 1993

M.A. Huffman

Vernonia amygdalina Del.
Compositae
Mahale National Park (Tanzania) 1996

M.A. Huffman

Origines animales de la médecine par les plantes

Michael A. Huffman

Center for Human Evolution Modeling Research, Primate Research Institute, Kyoto University
41-2 Kanrin Inuyama Aichi 484-8506 - Japan Huffman@pri.kyoto-u.ac.jp

Résumé

Les parasites et les agents pathogènes sont à l'origine de toute une série de maladies qui affectent le comportement et les capacités reproductives de tous les animaux. Considérant que le besoin de réagir face à une telle pression est grand, on pouvait s'attendre à ce que le règne animal mette en place des comportements antiparasitaires. A un stade précoce de la co-évolution animal-végétal, certaines espèces d'arthropodes ont commencé à appliquer les moyens de défense chimiques de certaines plantes pour se protéger de leurs propres prédateurs et parasites. Les plantes médicinales sont donc profondément enracinées dans le règne animal. Depuis la préhistoire, les hommes ont considéré les animaux sauvages et domestiques comme des sources de remèdes à base de plantes. Le folklore, de même que des exemples plus récents, montrent la façon dont on a appris à utiliser certaines plantes médicinales à partir de l'observation du comportement animal. Les animaux aussi collectent également des informations sur l'automédication en s'observant mutuellement. Les études scientifiques les plus étonnantes concernant l'automédication qui ont été faites à ce jour sont celles menées sur les grands primates d'Afrique. Le régime alimentaire des grands singes est souvent riche en plantes contenant des composés secondaires, sans valeur nutritive, parfois toxiques, ce qui donne à penser que leur ingestion a un certain pouvoir thérapeutique. On sait que les chimpanzés et les hommes co-habitant en Afrique sub-saharienne utilisent la *Vernonia amygdalina* pour lutter contre les infections parasitaires. Des études phytochimiques ont démontré la gamme très large des propriétés biologiquement actives que cette espèce contient. A la lumière de la résistance croissante que les parasites et agents pathogènes opposent aux médicaments de synthèse, l'étude de l'automédication chez les animaux ouvre de nouvelles perspectives de recherche vers des méthodes écologiquement viables pour le traitement des parasites en utilisant des médicaments à base de plantes pour les hommes et leur bétail vivant sous les tropiques.

Les animaux en ethnomédecine

Tout au long de l'histoire de l'humanité, les hommes se sont tournés vers les animaux pour identifier des plantes médicinales et des produits stupéfiants (Brander, 1931 ; Riesenberg, 1948). Les textes comportent de nombreux récits anecdotiques sur l'utilisation possible de plantes en tant que médicaments par des animaux sauvages tels que l'éléphant, la civette, le chacal, le rhinocéros. (Tableau I).

Les Navajos vivant dans le sud-ouest des États-Unis attribuent aux ours leurs connaissances sur les propriétés antifongiques, antivirales et antibactériennes de l'ombellifère *Ligusticum porteri* (Grasanzio, 1992 ; Moore, 1979)

La *Tabernanth iboga* (Apocynacea) contient plusieurs alcaloïdes indoles; elle est utilisée comme stimulant et aphrodisiaque puissant par de nombreuses sociétés secrètes du Gabon (Harrison, 1968). Harrison a avancé l'hypothèse selon laquelle, ces sociétés ont appris à connaître les propriétés particulières de la plante en observant le comportement des porcs sauvages, porcs-épics et gorilles pris de frénésie après en avoir déterré et ingéré les racines. Le principe le plus actif que l'on trouve dans la racine est l'ibogaïne, connue pour affecter le système nerveux central et le système cardiovasculaire.

Deux autres composés sont connus pour leur action : ce sont la tabernanthine et l'ibolutéine. Leur effet stimulant est comparable à celui de la caféine (Dubois, 1955). On sait aussi que le paresseux et les peuples vivant au centre de l'Inde s'enivrent en mangeant des fleurs fermentées de Madhuca (Brander, 1931) et que les rennes et les Lapons consomment des amanites tue-mouche connues pour l'intoxication qu'elles provoquent (Phillips, 1981).

L'une des versions de la découverte du café parle d'un berger qui aurait remarqué par hasard que ses chèvres changeaient de comportement après avoir ingéré des baies de plants de café sauvage sur les plateaux d'Éthiopie, ce qui a donné aux hommes l'idée d'exploiter la plante en tant que stimulant. On raconte que, au 17e siècle, en Angleterre, le docteur Jaquinto, médecin attiré de la reine Anne, épouse de Jacques Ier, a procédé à l'observation systématique de moutons occupés à brouter dans les zones marécageuses de l'Essex, ce qui lui a permis de découvrir un remède efficace contre la phtisie (Wilson, 1962).

Mohamedi S. Kalunde, mon collaborateur tanzanien pour mes recherches depuis 1987, responsable de la faune dans les Parcs Nationaux de Tanzanie, est le descendant d'une longue lignée de guérisseurs. Il attribue le mérite de la découverte d'au moins deux traitements médicaux à sa mère et son arrière grand-père, lesquels avaient observé le comportement des animaux. Un jour, le grand père de Mohamedi, Babu Kalunde, avait remarqué un jeune porc-épic ingérant les racines d'une plante connue localement sous le nom de mulengelele (une espèce non encore identifiée). Ayant gardé l'animal en captivité au village afin de l'observer, il pu le voir se remettre d'un crise grave de diarrhée et d'une grande faiblesse. Sur la base de ces observations, Babu Kalunde utilisa la plante pour soigner avec succès une épidémie d'une maladie rappelant la dysenterie et qui s'était répandue dans le village. La mère de Mohamedi, Joha Kasante, avait découvert, elle, un antidote contre les morsures de serpent, en demandant à Mohamedi de suivre le reptile qui avait mordu son plus jeune frère et de ramener des feuilles de la plante que le serpent était allé ensuite manger. On rapporte que ces feuilles empêchent le venin du serpent de se disséminer dans le corps. Dans les collines de l'Himalaya, près du Mont Everest, l'utilisation des racines de chota-chand, en tant que puissant antidote contre les morsures de serpent, a été mise en évidence en observant les mangoustes qui se nourrissent de cette plante avant de se battre contre les cobras (Balick & Cox, 1996). Tous ces exemples sont autant de cas d'automédication chez de nombreuses espèces animales et des façons dont les humains ont pu saisir la valeur thérapeutique des plantes en les observant.

Ceci devrait-il vraiment nous surprendre ? Après tout, du point de vue de l'évolution, la conservation de la santé est un principe de base de la survie et on pouvait s'attendre à ce que toutes les espèces en vie aujourd'hui aient évolué de différentes façons pour se protéger contre d'autres organismes, petits et grands, faisant partie de leur environnement.

Comment tout cela a-t-il commencé ? Dans le monde végétal, un moyen commun de se défendre consiste à produire une variété de composés secondaires toxiques tels que sesquiterpènes, alcaloïdes et saponines, lesquelles permettent aux plantes de ne pas être ingérées par les animaux (Howe & Westley, 1988 ; Swain, 1978). A un certain stade de l'histoire de leur co-évolution, probablement à l'époque des arthropodes, les animaux ont tiré profit de l'arsenal chimique défensif du règne végétal pour se protéger des prédateurs et des parasites, et renforcer leurs capacités reproductives (Blum, 1981). Par exemple, les papillons danaïs adultes des deux sexes utilisent les alcaloïdes de pyrrolizidine pour se défendre contre les prédateurs et il a également été prouvé que les mâles en dépendent pour la biosynthèse de la phéromone qu'ils utilisent dans la parade nuptiale (Boppre, 1978 ; 1984). On sait que le machaon se nourrit de l'*Asclepias*, laquelle contient des glucosides cardiaques qui rendent les oiseaux malades et qui se conditionnent pour ne pas en manger (Brower, 1969). De telles interactions à un triple niveau trophique ont probablement été à l'origine de la mise en place de formes plus élaborées d'auto-médication observées chez les vertébrés supérieurs.

L'impact des parasites sur l'évolution du comportement d'automédication

Le parasitisme a joué un rôle important dans l'évolution du comportement des hôtes dans le règne animal (e.g. Anderson & May, 1982 ; Clayton & Moore, 1997; Futuyma & Slatkin, 1983). La co-évolution parasite – hôte a conduit à la mise en place de mécanismes par lesquels l'hôte limite les infections parasitaires et le parasite augmente la probabilité d'infecter l'hôte (Toft *et al.*, 1991; Ewald, 1994). Au niveau primaire, la réaction immunitaire de l'hôte (innée et acquise), normalement, contrôle les infections. Cependant, certains parasites parviennent à s'implanter en développant des formes antigènes nouvelles, en devenant les sosies des antigènes de l'hôte ou en interférant directement avec la réaction immunitaire (Cox, 1993 ; Wakelin, 1996).

Là où l'adaptation physiologique ne suffit pas, les hôtes ont développé des réactions comportementales pour éviter ou limiter le contact avec les parasites ou d'autres agents pathogènes. Ces comportements, largement répandus chez les vertébrés, comportent des changements concernant les endroits où l'animal dort et se nourrit, une utilisation différente des lieux où il s'abreuve, l'utilisation de la substance anti-parasitaire des feuilles pour remplir les nids ou les tanières occupés pendant de longues périodes et l'application de substances aromatiques pour repousser les parasites qui infestent le pelage ou les plumes (Baer, 1996 ; Clark, 1991 ; Freeland, 1980 ; Gompper & Holyman, 1993 ; Gresianzio, 1992 ; Hart, 1990 ; Hausfater & Meade, 1982 ; Kummer in Nelson, 1960 ; Seigstadt In Cowen, 1990 ; Sengputa, 1981). L'aversion apprise envers certains aliments ou saveurs associés à la maladie, l'infection parasitaire, et les changements compensatoires dans le régime alimentaire de l'hôte induits par le parasite ont été démontrés en laboratoire et testés sur un large éventail de vertébrés (Gustavson, 1977 ; Kyriazakis *et al.*, 1994 ; Keymer *et al.*, 1983). A partir de ce qui a été découvert concernant l'automédication chez les primates au cours des dernières années les parasites et les troubles gastro-intestinaux apparaissent clairement comme l'une des préoccupations principales de l'automédication chez les animaux non humains (Huffman *et al.*, 1997).

Ces aversions se situant à un autre niveau permettent aux hôtes d'éviter un exposition prolongée aux agents pathogènes. Une modification du régime alimentaire a également été proposée en tant que moyen d'altération ou de contrôle des parasites internes. Une relation de cause à effet entre un changement soudain dans le régime alimentaire et la diminution du ténia a été suggérée chez l'ours brun (Rausch, 1954 ; 1961).

Un autre exemple de ce type de comportement concerne l'ingestion de parties spécifiques de plantes, ayant peu ou pas de valeur nutritionnelle, mais des qualités anti-parasitaires, d'ordre soit pharmacologiques (Huffman *et al.*, 1993 ; 1998 ; Ohigashi *et al.*, 1994), soit physiques (Huffman *et al.*, 1996).

La nourriture comme remède

Du point de vue de l'évolution, il semble fort probable que l'utilisation de nombreuses plantes médicinales soit dérivée de l'ingestion d'aliments rarement mangés ou d'aliments ingérés par défaut (c'est-à-dire lorsque la nourriture principale manque) ayant des propriétés thérapeutiques importantes. Le problème et la difficulté lorsqu'il s'agit d'interpréter l'automédication est de faire la distinction entre les bienfaits médicaux tirés indirectement des plantes riches en composé secondaire censées être ingérées à cause de leur valeur nutritionnelle, par opposition à l'ingestion en quantité limitée et l'ingestion en situation de produits utilisés uniquement pour leurs propriétés thérapeutiques. Dans certains cas, il n'est pas nécessaire de faire la distinction. La nourriture et les remèdes peuvent ne faire qu'un lorsqu'ils sont consommés régulièrement et toute l'année, alors qu'on en trouve en abondance. La différence entre nourriture et remède n'est pas toujours claire, particulièrement dans les sociétés humaines traditionnelles. On en trouve un cas précis dans l'étude de Etkin (1996), laquelle a trouvé que 30 % des aliments végétaux utilisés chez les Hausa du Nigeria étaient également utilisés comme remèdes. De plus, 89 % des espèces employées pour traiter les symptômes de la malaria sont également mangées dans des situations de diète particulière (Etkin & Ross, 1983). Etkin et Ross pensent que beaucoup d'aliments propres aux Hausa proviennent à l'origine de plantes non cultivées et qui étaient utilisées autrefois comme remèdes. De même, de nombreuses épices, condiments et légumes traditionnels de la cuisine asiatique, largement utilisés aujourd'hui, tels que la racine de gingembre, l'algue marine et plusieurs herbes aromatiques, constituent des sources importantes d'agents anti-tumoraux (Murakami *et al.*, 1994 ; 1996 ; Ohigashi *et al.*, 1992) jouant également un rôle actif dans la lutte contre les infections parasitaires et virales.

Bon nombre de ces "alicaments" ont des qualités au-delà de leur valeur nutritive, par leur teneur en composés végétaux secondaires. Comme on l'a dit plus haut, ces composés sont produits pour dissuader les herbivores de les ingérer (Ehrlich & Raven, 1964 ; Feney, 1976 ; Howe & Westley, 1988 ; Wink *et al.*, 1993), alors que, s'ils sont en petite quantité, ces composés peuvent être bénéfiques pour le consommateur. Un certain nombre d'alicaments trouvés dans le régime alimentaire de grands singes semblent partager ces propriétés et il est opportun de les mentionner ici.

Les baies de *Phytolacca dodecandra* L'Herit. (Phytolaccaceae) représentent un aliment fréquemment ingéré et abondant pour le groupe de chimpanzés de Kanyawara à Kibale, à l'ouest de l'Ouganda (Wrangham et Isabirye-Basuta, in Huffman & Wrangham, 1994). Ces baies, au goût amer, constituent une source concentrée, composée d'au moins 4 saponines triterpénoides toxiques (lemmatoxine, lemmatoxine-C, oléanoglycotoxine-A, glucoside phytolacca-dodecandra). La consommation d'environ 2 grammes de cette substance est fatale chez les souris et les rats. Parmi les autres propriétés connues de ces saponines triterpénoides, on citera des activités antivirales, antibactériennes, contraceptives, spermicides et embryotoxiques (Kloos & Mc Cullough, 1987).

La moelle et le fruit des espèces *Afromonum* (de la famille du gingembre sauvage) sont couramment ingérés par les chimpanzés, les bonobos et les gorilles dans toute l'Afrique (Idani *et al.*, 1994 ; Moutsamboté *et al.*, 1994 ; Nishida & Uehara, 1983 ; Sugiyama & Koman, 1992 ; Tutin *et al.*, 1994 ; Wrangham *et al.*, 1993 ; Yumoto *et al.*, 1994). Une étude en cours sur l'écologie chimique du régime alimentaire du gorille de la région de Bwindi, conduite par John Berry (Rodriquez Laboratory, Division of Biological Sciences, Cornell University) porte sur la bio-activité du fruit de l'une de ces espèces de gingembre sauvage, *Afromomum sanguineum* (K. Schum.) K. Schum. (Zingiberaceae). On sait que les fruits de ces espèces sont ingérés par les gorilles dans le Parc National de Kahuzi-Biega, Congo-Kinshasa) (Yumoto *et al.*, 1994). Des essais portant sur des fruits homogénéisés et des extraits de graines démontrent qu'il existe une activité antimicrobienne considérable (Berry, sous presse). Les fruits sont vendus sur les marchés traditionnels et le long des routes dans la région de Bwindi, pour le traitement des infections bactériennes et fongiques, et comme médicament anthelmintique (John Berry, information personnelle).

Les gorilles des plaines de l'ouest (G. g. gorilla) dans la forêt de Ndoki, au nord du Congo (Kuroda, Mokumu, Nishihara, sous presse) se gardent de manger l'extrémité des jeunes feuilles de *Thomandersia laurifolia* (T. Anders. ex Benth.) Baill. (Acanthaceae). Selon Kuroda et ses collègues, les hommes habitant la région utilisent ces feuilles pour des traitements contre les parasites et la fièvre. On a relevé une faible activité antischistosomale dans des extraits de feuille brute (Ohigashi, 1995).

L'écorce et le bois ont pour caractéristique d'être hautement fibreux, fortement lignifiés, relativement indigestes et pauvres en aliments (Waterman, 1984). Il est bien connu que les chimpanzés et les gorilles ingèrent assez rarement l'écorce et le bois de plusieurs espèces de plantes (Huffman & Wrangham, 1994).

Alors qu'il existe une longue liste d'espèces de plantes dont l'écorce est ingérée, on connaît très peu de choses sur la façon dont elle entre dans le régime alimentaire et sur son impact sur la santé. La littérature en ethnomédecine n'a pas manqué de mentionner quelques unes de ces espèces. L'écorce de *Pycnanthus angolensis*

(Welw.) Warb. (Myristicaceae), ingérée par les chimpanzés à Mahale, dans l'ouest de la Tanzanie, est utilisée par les Africains de l'ouest comme purgatif, laxatif, digestif tonique, émétique et comme antalgique contre les maux de dents. Les habitants de la région de Mahale (Huffman, données non publiées, Mohamedi S Kalunde, communication personnelle à propos des utilisations faites par les hommes) mâchent quelquefois les fibres de l'écorce de *Grewia platyclada* K. Schum (Tiliaceae) pour soulager les maux d'estomac. En 1992, on a observé à Mahale qu'un jeune homme atteint de diarrhée, mâchait, sans cependant les avaler, les fibres de l'écorce de cette espèce (Huffman, données non publiées). En Tanzanie, les chimpanzés du Parc National de Gombe mangent de temps à autre de l'écorce d'*Entada abyssinica* Steud. ex A. Rich. (Mimosaceae). Au Ghana, l'écorce est utilisée par les hommes pour lutter contre la diarrhée et comme émétique (Abbiw, 1990). Il arrive que les chimpanzés de Mahale mangent l'écorce de l'*Erythrina abyssinica* DC. (Papilionaceae). L'étude de cette dernière, prélevée dans la région de Mahale, a démontré qu'elle avait d'importantes activités plasmodicide et antischistosomale (Ohigashi, 1995 ; Wright *et al.*, 1993). L'écorce de *Gongronema latifolium* Benth. (Asclepiadaceae), parfois consommée par les chimpanzés en Guinée-Bissau, est extrêmement amère. Les tiges sont utilisées par les hommes en Afrique de l'ouest comme purgatif contre la colique, les maux d'estomac et les symptômes liés à une infection intestinale due à un parasite (Burkill, 1985).

La discussion qui précède sur les composants spécifiques issus des fruits, feuilles et écorces ingérés par les singes sert à démontrer la diversité des composés secondaires ou l'activité pharmacologique déduite présente dans leur régime alimentaire. L'effet global dû à l'ingestion de ces éléments n'est pas clair, mais il n'est pas réaliste de supposer qu'il y a un gain nutritionnel alors que celui-ci est peu probable.

Utilisation des plantes comme remède par les chimpanzés en liberté

La raison pour laquelle les hommes et les chimpanzés sélectionnent en partie les mêmes plantes lorsqu'ils présentent des symptômes identiques est peut-être due à notre proximité phylogénétique (Huffmann *et al.*, 1996a). Certains éléments recueillis par la recherche sur les primates vivant en Afrique donnent à penser que certaines plantes sont ingérées, non pas par hasard, mais bien en raison de leur grand pouvoir médicinal. Selon une hypothèse développée actuellement, ces comportements contribueraient à contrôler certains parasites intestinaux et /ou à soulager les troubles gastro-intestinaux qui y sont liés (Huffmann *et al.*, 1996a ; Huffmann, 1997).

Ces observations sont les meilleures preuves que l'on ait pu rassembler jusqu'ici en matière d'automédication chez les animaux.

Vernonia amygdalina et la mastication de la moelle amère

L'hypothèse selon laquelle la mastication de la moelle amère ait des vertus thérapeutiques chez les chimpanzés a été avancée sur la base d'observations comportementales approfondies et d'analyses parasitologiques et phytochimiques de chimpanzés manifestement malades, ayant ingéré de la *Vernonia amygdalina* Del. (compositae), dans la région de Mahale (Huffmann & Seifu, 1989 ; Huffman *et al.*, 1993). Ce sont là les premières observations ayant fait l'objet d'un rapport, constatant la maladie et l'apparente amélioration de l'état de santé d'un animal ayant ingéré des plantes médicinales purgatives.

V. amygdalina est présente à travers l'Afrique tropicale sub-saharienne (Watt & Breyer-Brandwijk, 1962). La mastication de la moelle amère d'autres espèces de *Vernonia* a été observée dans la région de Gombe en Tanzanie (*V. colorata* (Willde.). Drake : Huffman & Wrangham, 1994 ; Hilali, données non publiées sous forme de communication personnelle de J. Wallis) et Kahuzi-Biega, Congo-Kinshasa (*V. hochstetteri* Schi-Bip., *V. kirungae* Rob. E. Fries : Yumoto *et al.*, 1994 ; A.K. Basabose, communication personnelle). A Taien, Côte d'Ivoire, on mâche la moelle amère de *Paliosota hirsuta* (Thunb.) K. Schum. (Commelinacea) et d'*Eremospath macrocarpa* (Mann et Wendl.) Wendl. (Palmae) (C. Boesch, communication personnelle in Huffman, 1997).

En ingérant la moelle de jeunes pousses de *V. amygdalina*, les chimpanzés enlèvent méticuleusement l'écorce externe et les feuilles pour mieux mastiquer la moelle mise à nu dont ils extraient un jus extrêmement amer et des résidus de fibre. La quantité de moelle ingérée en cas de simple crise est relativement petite, allant de 5 à 120 centimètres x 1 centimètre. L'ensemble du processus, selon la quantité ingérée, varie en temps, allant de moins d'une minute jusqu'à 8 minutes. On a observé qu'un sujet mûr, se trouvant à proximité d'un individu occupé à mastiquer de la moelle ou à avaler des feuilles de *Vernonia,* ne semble pas désireux d'ingérer de la moelle (Huffman et Seifu, 1989 ; Huffman *et al.*, 1997). En revanche, on a vu des jeunes de mères malades goûtant à l'occasion la moelle jetée par leur mère malade. De cette façon, des individus du groupe sont exposés au comportement et au goût extrêmement amer de la moelle et ceci dès leur plus jeune âge.

A Mahale, on a fait état de l'utilisation de *V. amygdalina* sur tous les mois de l'année, sauf juin et octobre (fin de la saison sèche), ce qui démontre que la plante est disponible toute l'année (Nishida et Uehara, 1983). Cependant, l'utilisation par les chimpanzés est très saisonnière, en dépit du fait qu'elle soit disponible toute l'année. Ils l'emploient le plus souvent pendant les mois de la saison des pluies, en décembre et en janvier, moment où la réinfection parasitaire par les nématodes atteint sa crête chez certaines espèces (Huffman *et al.*, 1997).

L'ethnomédecine et la phytochimie de la mastication de la moelle amère

V. amygdalina est utilisée comme médicament par de nombreux groupes ethniques africains, sur tout le continent (Tableau II). La décoction préparée à partir de cette espèce constitue un traitement prescrit en cas de paludisme, schistosomiase, dysenterie amibienne, de nombreux autres parasitoses intestinales et de maux d'estomac (Burkill, 1985 ; Dalziel, 1937 ; Huffman *et al.*, 1996 a ; Watt & Breyer-Brandwijk, 1962). Les Tongwe de Mahale utilisent cette plante pour le traitement des parasites intestinaux, de la diarrhée et le dérangement d'estomac.

L'analyse phytochimique d'échantillons de *V. amygdalina*, prélevés à Mahale à partir de plantes dont se servent les chimpanzés, révèle la présence de deux classes importantes de composés bio-actifs. Ces recherches ont permis d'isoler au total 4 lactones sesquiterpèniques, 7 glucosides stéroïdes nouveaux de type stigmastane et 2 aglycones libres (Ohigashi *et al.*, 1991; Jisaka *et al.*, 1992a, b; Jisaka *et al.*, 1993 a, b). Les lactones sesquiterpèniques, qui sont présents dans la *V. amygdalina* et que l'on retrouve également dans la *V. colorata* ainsi que dans un certain nombre d'autres espèces de *Vernonia*, sont réputés pour leurs propriétés anthelmintique, antiamibienne, antibiotique et anti-tumoral (Asaka *et al.*, 1977; Gasquet *et al.*, 1985; Jisaka *et al.*, 1992a; Jisaka *et al.*, 1993 b; Kupchan *et al.*, 1969; Toubiana & Gaudemer, 1967). A partir d'extraits de méthanol brut de feuilles, Koshimizu *et al.* (1993) ont également mis en évidence une inhibition de l'évolution de la tumeur et des activités immunodépressives.

Des tests *in vitro* sur l'activité antischistosomiale du glucoside stéroïde, de la vernonioside B1, de la lactone sesquiterpénique, et de la vernodaline (Figure 1), lesquels sont abondants dans la moëlle de la plante, ont montré que ces substances ont un important pouvoir inhibiteur du mouvement chez les parasites adultes et de la quantité des œufs pondus par les femelles adultes (Jisaka *et al.*, 1992b). Ces découvertes correspondent à la baisse du niveau EPG observé chez le ver nodulaire (*Oesophagostomum stephanostomum*) 20 heures après qu'un chimpanzé femelle adulte a ingéré de la moelle de *V. amygdalina* (Huffman *et al.*, 1993). Les lactones sesquiterpèniques ont mis en évidence une activité plasmodicide *in vivo* considérable, alors que celle des glucosides stéroïdes serait moindre (Ohigashi *et al.*, 1994).

Quelques-unes des espèces comportant de la moelle amère, ingérée par les chimpanzés à Gombe, Kahuzi-Biega et à Tai, possèdent également un certain nombre de propriétés phytothérapeutiques et pharmacologiques. Du point de vue ethnothérapeutique, *V. colorata* et *V. amygdalina* ne se distinguent pas l'une de l'autre en ce qui concerne leurs propriétés thérapeuthiques et la classification populaire (Burkill, 1985). Des alcaloïdes sont présents dans la moelle, de même que dans la fleur et dans la feuille de la *V. hochstetteri* (Smolenski *et al.*, 1974). L'ethnomédecine en Afrique de l'ouest fait appel à la *P. hirsuta* et la *E. macrocarpa* en tant qu'antiseptique et analgésique pour traiter les maux d'estomac, les coliques et pour lutter contre les maladies vénériennes (Abbiw, 1990 ; Neuwinger, 1996). On a également fait état d'une activité molluscicidale de la part de *P. hirsuta* (Okunji and Iwu, 1988).

Un lien entre l'automédication chez les animaux et l'ethnomédecine

Les utilisations thérapeutiques de la *V. amygdalina*, ainsi que les conditions dans lesquelles on a observé les chimpanzés ingérer ces espèces sont similaires à bien des égards. Dans les deux cas d'utilisation faite par les chimpanzés rapportés ci-dessus, le taux de guérison (20-24 heures) était comparable à celui observé chez les hommes habitant dans la région de Mahale, les Watongwe (dans un délai de 24 heures), lesquels utilisent la *V. amygdalina* pour traiter les parasitoses et les troubles gastro-intestinaux.

Cette préparation est propre aux Watongwe, qui la réalisent à partir d'une décoction en eau froide de feuilles fraîches écrasées (environ 10-15 g poids frais) dans 300-400 ml d'eau. En raison de l'effet toxique de la plante sur le patient, ce traitement est habituellement pris en une seule dose (M.S. Kalunde, communication personnelle). Une analyse reprenant cette méthode (3 essais) a produit 3.3-5.0 mg de vernonioside B1 (Figure 1 ; Huffmann *et al.*, 1993 a). Ceci a été directement comparé par une analyse quantitative de moelle recueillie sur la plante utilisée par la femelle chimpanzé adulte qui avait présenté une baisse de la charge parasitaire 20 heures après l'ingestion. On s'est aperçu que la quantité de moelle qu'elle avait ingérée (60 cm, environ 50-100 g poids frais), contenait environ 3,8 - 7,6 mg de vernioside B1, ou à peu près une quantité équivalente à celle que l'on obtient chez un patient Tongwe (Huffmann *et al.*, 1993 a).

Nous sommes intrigués par cette forte similitude entre l'utilisation faite par les humains et celle faite des chimpanzés. Il semble que les humains, tout comme les chimpanzés, aient reconnu l'importante activité physiologique de cette plante et nous avons des raisons de penser que les chimpanzés ingèrent la *V. amygdalina* lorsqu'ils présentent des symptômes comparables.

D'un point de vue ethnobotanique, plus grand est le nombre de cultures différentes reconnaissant une espèce de plante ayant certaines propriétés thérapeutiques, et plus il est probable que cette espèce présente une activité physiologique considérable. L'exemple de la *V. amygdalina*, avec ses qualités thérapeutiques largement reconnues en Afrique, nous permet même de faire un pas de plus pour faire le lien entre les primates et les humains (Tableau II).

L'automédication en tant que tradition comportementale acquise

Comment les animaux apprennent-ils à se soigner ? Chez les primates non-humains, d'importants bienfaits proviennent de l'apprentissage social qui permet aux individus naïfs d'obtenir des renseignements au travers de l'expérience des autres et, avec le temps, de perfectionner leur propre comportement. Une fois qu'un comportement d'automédication efficace est reconnu, il pourra s'étendre au groupe, tout d'abord lentement, mais ensuite de plus en plus rapidement, à mesure qu'il se transmet aux membres les plus jeunes. A Mahale, et probablement ailleurs, il se produit pour des individus d'un très jeune âge, une mise en contact initiale avec des comportements d'automédication, non pas lorsqu'ils sont eux-mêmes malades, mais en observant le comportement et en goûtant les aliments utilisés par d'autres individus malades, le plus souvent leurs mères.

Dans le cas de *Vernonia amygdalina*, ce n'est pas seulement l'espèce et le contexte d'utilisation qui importent, mais aussi la partie de la plante et la quantité nécessaire à ingérer pour obtenir à la fois efficacité et innocuité. Le fait d'éviter les produits au goût amer s'est transformé en un moyen d'éviter les substances toxiques. Il faut apprendre à surmonter cette tendance innée si l'on veut profiter des bienfaits de ces substances. Très souvent, l'homme enrobe de sucre les médicaments pour convaincre les autres de les ingérer. Pour les chimpanzés, le processus d'apprentissage basé sur l'observation constitue indubitablement une procédure essentielle. Étant donné le degré élevé de conservatisme en matière d'habitudes alimentaires chez les chimpanzés, surtout lorsqu'ils sont malades, il semble peu probable qu'ils choisissent une nouvelle plante au hasard. Si tel est le cas, ces pratiques ont dû se mettre en place de manière isolée, éventuellement par le biais de chimpanzés affamés et malades qui ont testé de nouveaux aliments pendant des périodes de pénurie extrême de nourriture, leur permettant de se rétablir et associant ce rétablissement à ce nouvel aliment.

Les chimpanzés ont une forte capacité d'empathie et aussi une bonne mémoire à long terme. Il est probable que le lien établi entre les changements dans les habitudes alimentaires d'un individu malade et un rétablissement consécutif renforce la connaissance acquise à la fois du contexte et des conditions entourant la consommation de la plante. On a pu observer à maintes reprises que les compagnons de voyage des chimpanzés malades coordonnaient leurs activités afin de se retrouver à proximité du malade, ce qui leur offrait l'opportunité d'observer le comportement d'automédication en contexte. Le cas le plus probant est sans doute celui des jeunes, dépendants et inexpérimentés, encore très proches de leur mère et qui en imitent le comportement. Des femelles récemment arrivées ont également manifesté un très vif intérêt pour les individus ingérant la moelle amère de cette plante.

Alors qu'on a observé que tous les adultes appartenant au groupe M avaient eu recours à l'automédication à un moment ou un autre, ces mêmes adultes ne montrent que rarement ou même jamais d'intérêt pour les plantes utilisées à cette fin, simplement parce qu'ils ne les trouvent que par hasard au détour d'un sentier ou parce que quelqu'un d'autre les utilise.

Il est probable que le sens du goût et le retour d'information physiologique suite à l'ingestion de plantes amères viennent renforcer le processus d'apprentissage. Historiquement, les herboristes ont souligné l'importance du goût et de l'odorat dans l'évaluation des propriétés thérapeutiques des plantes. Dans le cadre d'une étude sur les critères de sélection de plantes thérapeutiques réalisée par les Mayas de Tzeltal habitant les Plateaux du Chiapas au Mexique, John Brett a remarqué que le goût et l'odorat étaient constamment utilisés afin de sélectionner et d'évaluer les plantes destinées à traiter une maladie (Brett, 1994). Indépendamment de leur taxinomie, les plantes au goût amer étaient choisies et utilisées essentiellement pour le traitement des troubles gastro-intestinaux, les parasitoses et les maux d'estomac. Ce lien étroit entre le goût amer et l'activité pharmacologique peut également aider le chimpanzé à sélectionner les plantes pour soigner les infections parasitaires et les maladies gastro-intestinales qui y sont liées, et ceci sur la base d'expérience acquise. Cette pratique permettra aux femelles de mieux s'adapter lorsqu'elles arrivent dans des régions nouvelles où la végétation est différente tout en ayant des plantes amères et actives similaires du point de vue pharmacologique.

Le fait d'associer de façon sélective le goût et la maladie gastro-intestinale est un principe largement accepté dans l'apprentissage de l'aversion par le goût parmi les mammifères. L'acquisition du mécanisme d'aversion en réaction à une maladie a été observée chez bon nombre d'espèces animales. La capacité à associer un meilleur état de santé et l'ingestion de plantes nouvelles ayant des propriétés thérapeutiques n'a pas fait l'objet d'autant d'attention, mais il est évident que ce processus contribue énormément au développement d'un sens de l'adaptation. On pense que de tels processus biologiques et psychologiques pour l'apprentissage par observation sont au cœur des comportements d'automédication chez les primates et les non-humains. Si tel est le cas, ils constituent également les fondements de la pratique culturelle de la médecine par les hommes.

Evolution de l'utilisation des plantes médicinales et l'avenir

Ces fortes ressemblances concernant les critères de sélection des plantes chez les grands singes africains, en réaction à une infection parasitaire et à des troubles gastro-intestinaux, et l'utilisation commune de certaines plantes par les chimpanzés et les humains pour soigner ces maladies sont des références essentielles pour l'étude de

l'évolution de la médecine et de l'impact sur l'infection parasitaire. On peut dire que nos ancêtres hominidés les plus lointains ont présenté des similarités dans les critères de sélection des plantes, de même que les singes existants et les hommes modernes. Les fossiles les plus anciens ne donnent aucun renseignement sur le détail des comportements et des régimes alimentaires, mais il y a de bonnes raisons de penser que les premiers hominidés ont eu des comportements comparables aux pratiques d'automédication observées chez les primates.

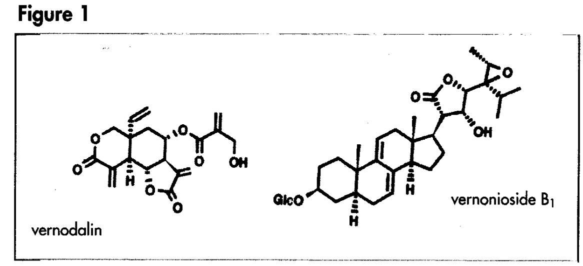
Les fondements de cette association entre les propriétés thérapeutiques d'une plante et son goût, son odeur et sa texture, sont à chercher au plus profond de l'histoire des primates. Il y a probablement eu un changement majeur dans l'évolution de la médecine à l'époque des premiers hommes avec l'avènement du langage, qui permettait de partager des connaissances acquises quant aux propriétés des plantes et à leurs effets contre la maladie. Il est probable qu'un autre événement majeur dans l'histoire de l'homme ait été le fait que l'on a préparé sa nourriture et appliqué des techniques de désintoxication, ce qui a permis aux hommes d'exploiter une gamme plus large de plantes comme aliments. Johns (1990) pense que c'est ce bouleversement qui a pu renforcer notre dépendance face aux composés secondaires de plantes, en raison de leur disparition du régime alimentaire quotidien. C'est peut être de cette façon qu'est apparue une plus grande spécialisation dans l'usage des plantes comme remèdes. De plus, grâce à l'utilisation habile du feu pour faire bouillir, fumer, cuire à la vapeur, condenser ou bien extraire des composés secondaires de plantes utiles, on a pu développer une gamme plus large d'utilisations de ces composés.

Le niveau actuel des pratiques médicinales sophistiquées dans les sociétés humaines traditionnelles est peut-être le produit d'une plus grande variété de maladies et de la tension due à un bouleversement de l'économie de subsistance, en passant de la chasse et la cueillette à une plus grande dépendance envers l'agriculture et l'élevage lors de la sédentarisation (Johns, 1990). Dans cette optique, il est possible que nos premiers ancêtres humains modernes aient eu une pharmacopée moins importante, mais ce n'était pas en raison d'un sous-développement du point de vue technique. La vraie raison a plutôt été le fait qu'il existait moins de maladies et de tensions face auxquelles il fallait réagir (Cohen & Armelagos, 1984). Grâce au progrès technologique de la médecine moderne, la vie de millions de personnes dans le monde dit civilisé est sauvée et prolongée chaque année. Cependant, c'est également le progrès technologique qui apporte les changements dans notre régime alimentaire (conservateurs, additifs, manipulations génétiques) et de notre style de vie, lesquels sont responsables des maladies modernes pour lesquelles les pays dépensent chaque année des fortunes dans l'espoir de trouver des remèdes.

Nous n'avons pas à remonter dans le temps ou à tourner le dos à la civilisation pour retrouver un peu de ce paradis perdu. Nous avons peut être beaucoup de choses à réapprendre et à gagner de "l'ancienne sagesse" de nos cousins primates et de la richesse de la médecine traditionnelle encore pratiquée aujourd'hui par la majorité de la population mondiale.

Il faut appeler de nouvelles recherches en laboratoire et sur le terrain sur les comportements d'automédication chez d'autres espèces animales. Comme l'a démontré ce bilan, les réponses à quelques questions soulèvent invariablement d'autres questions. Puisque plusieurs scientifiques commencent à chercher des types de comportement similaires, on peut penser qu'on en identifiera un certain nombre et que des réponses seront trouvées. Il est clair que l'automédication se fonde sur une certaine adaptation ; on peut donc penser que ce comportement est très répandu. On peut même penser que les comportements d'auto-médication ont cours chez toutes les espèces animales.

Figure 1



The most abundant constituents isolated from the pith of *Vernonia amygdalina*, a steroid glucoside (vernonioside b_1) and a sesquiterpene lactone (vernodaline)

Références

ABBIW D.K. (1990) *Useful Plants of Ghana*, Kew, Intermediate Technology Publications and Royal Botanic Gardens.

ABEBE D. (1987) Plants in the health care delivery system of Africa. in A.J.M. LEEUWENBURG (Compiler), *Medicinal and poisonous plants of the tropics*, Wageningen, Pudoc Wageningen, 79-87.

AKAH P.A., OKAFOR C.L. (1990) Blood sugar lowering effects of *Vernonia amydgalina* in experimental rabbit model, in A. SOFOWORA (ed), *The state of medicinal plant research in Nigeria*, Abstract volume for "Integrative seminar on natural products research and development of plant based drugs", University of Science and Technology, Kumani, Ghana, 23-30 September, 27.

ANDERSON R.M., MAY R.M. (1982) *Population Biology of Infectious Diseases*, Berlin, Springer-Verlag.

ASAKA Y., KUBOTA T., KULKARNI A.B. (1977) Studies on a bitter principle from *Vernonia anthelmintica*, *Phytochemistry*, 16,1838-1839.

BAER M. (1996) Fur rubbing. Use of medicinal plants by capuchin monkeys (*Cebus capucinus*), *American Journal of Primatology*, 38, 263-270.

BALICK M.J., COX P. A. (1996) *Plants, people, and culture*, New York, Scientific American Library, W. H. Freeman and Company.

BLIM M.S. (1981) *Chemical defenses of arthropods*, New York, Academic Press.

BOPPRE M. (1978) Chemical communication, plant relationships, and mimicry in the evolution of danaid butterflies, *Entomol. Exp. Appl.*, 24, 264-277.

BOPPRE M. (1984) Redifining "Pharmacophagy", *Journal of Chemical Ecology*, 10 (7), 1151-1154.

BRANDER A.A.D. (1931) *Wild Animals in Central India. London*, Edward Arnold.

BRETT J. A. (1994) *Medicinal plant selection criteria among the Tzeltal Maya of Highland Chiapas, Mexico*, PhD Dissertation, San Francisco, University of California.

BROWER L. P. (1969) Ecological chemistry, *Scientific American*, 22 (2), 22-29.

BURKILL H.M. (1985) *The Useful Plants of West Tropical Africa*, 2nd ed., Vol. 1, Kew, Royal Botanical Gardens.

BURTON R.W. (1952) The tiger as fruit eater, *Journal of the Bombay Natural History Society*, 50, 649.

CLAYTON D.H., MOORE J. (1997) *Host-Parasite evolution. General Principles & Avian Models*, Oxford, Oxford Unviversity Press.

CLARK C.C. (1991) The nest protection hypothesis: the adaptive use of plant secondary compounds by European starlings, in LOYE J.E. and ZUK M. (eds.), *Bird-parasite intearctions: ecology, evolution, and behaviour*, Oxford, Oxford Unviersity Press, 205-221.

COHEN M.A, ARMELAGOS G. J. (eds) (1984) *Paleopathology and the origins of agriculture*, Orlando, Florida, Academic Press.

COWEN R. (1990) Medicine on the wild side, *Science News*, 138, 280-282.

COX F.E.G. (1993) *Modern Parasitology*, 2nd edition, Oxford, Blackwell Scientific Press.

DALZIEL J. M. (1937) The Useful Plants of West Tropical Africa in Hutchinson J. & Dalziel J.M. (eds.), *Appendix to Flora of West Tropical Africa*, London, Whitefriars Press.

DHARMAKUMARSINHJI R. S. (1960) Indian wild boar (*Sus scrofa cristatus* Wagner) feeding on *Boerhavia diffusa* Linn., *Journal of the Bombay Natural History Society*, 57, 654-655.

DUBOIS L. (1955) *Tabernanthe iboga* Baillon, *Bull. Agric. Congo Belge*, 46, 805-829.

EHRLICH P., RAVEN P. H. (1964) Butterflies and plants: A study in coevolution, *Evolution*, 18, 586-608.

ETKIN N.L. (1996) Medicinal cuisines: diet and ethnopharmacology, *International Journal of Pharmacology*, 34 (5), 313-326.

ETKIN N.L., ROSS P.J. (1983) Malaria, Medicine, and Meals: Plant use among the Hausa and its impact on disease, in ROMANUCCI-ROSS L., MOERMAN D.E. and TANCREDI L.R. (eds), *The Anthropology of Medicine: From Culture to Method*, New York, Praeger, 231-259

EWALD P.W. (1994) *Evolution of Infectious Disease*, Oxford, Oxford University Press.

FEENY P. (1976) Plant apparency and chemical defense, *Recent advances in phytochemistry*, 10, 1-40.

FREELAND W. F. (1980) Mangaby (*Cercocebus albigena*) movement patterns in relation to food availability and fecal contamination, *Ecology*, 61 (6), 1297-1303.

FUTUYMA D.J., SLATKIN M. (1983) *Coevolution*, Sunderland, MA, Sinauer Associates Inc.

GASQUET M., BAMBA D., BABADJAMIAN A., BALANSARD G., TIMON-DAVID P., METZGER J. (1985) Action amoebicide et anthelminthique du vernolide et de l'hydroxyvernolide isoles des feuilles de *Vernonia colorata* (Willd.) Drake, *European Journal of Medical Chemical Theory*, 2, 111-115.

GOMPPER M.E., HOLYMAN A.M. (1993) Grooming with Trattinnickia resin: possible pharmaceutical plant use by coatis in Panama, *Journal of Tropical Ecolology*, 9, 533-540.

GRISANZIO J.A. (1992) Fur-bearing pharmacists, *Animals*, September/October, 26-30.

GUSTAVSON C.R. (1977) Comparative and field aspects of learned food aversions, in BARKER L.M., BEST M.R. and DOMJAN M. (eds.), *Learning mechanisms in food selection*, Baylor (Texas), Baylor University Press, 23-43.

HARBORNE J.B. (1978) Biochemical aspects of plant and animal coevolution, London. (Academic Press.Phytochemical Society of Europe Symposia, Series No.15)

HARRISON G. P. (1968) *Tabernanthe iboga*: an African narcotic plant of social importance, *Economic Botany*, 23, 174-184.

HART B.L. (1990) Behavioral adaptations to pathogens and parasites. Five strategies, *Neuroscience and Biobehavioral Review*, 14, 273-294.

HAUSFATER G., MEADE B.J. (1982) Alternation of sleeping groves by yellow baboons (*Papio cynocepahalus*) as a strategy for parasite avoidance, *Primates*, 23, 287-297.

HOWE H.F., WESTLEY L.C. (1988) *Ecological relationships of plants and animals*, Oxford, Oxford University Press.

HUBBACK T.B. (1939) The two-horned Asiatic rhinoceros (*Dicerorhinus sumatrensis*), *Journal of the Bombay Natural History Society*, 40, 594-617.

HUBBACK T.B. (1941) The Malay Elephant, *Journal of the Bombay Natural History Society*, 42, 483-509.

HUFFMAN M.A., GOTOH S., IZUTSU D., KOSHIMIZU K., KALUNDE M. S. (1993) Further observations on the use of *Vernonia amygdalina* by a wild chimpanzee, its possible effect on parasite load, and its phytochemistry, *African Study Monographs*, 14 (4), 227-240.

HUFFMAN M.A., GOTOH S., TURNER L.A., HAMAI M., YOSHIDA K. (1997) Seasonal trends in intestinal nematode infection and medicinal plant use among chimpanzees in the Mahale Mountains, Tanzania, *Primates*, 38 (2), 111-125.

HUFFMAN M.A., KOSHIMIZU K., OHIGASHI H. (1996a) Ethnobotany and zoopharmacognosy of *Vernonia amygdalina*, a medicinal plant used by humans and chimpanzees, in CALIGARI P.D.S., HIND D.J.N. (eds.) *Compositae: Biology & Utilization*, Vol. 2., Kew, The Royal Botanical Gardens, 351-360.

HUFFMAN M.A., SEIFU M. (1989) Observations on the illness and consumption of a possibly medicinal plant *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park, Tanzania, *Primates*, 30, 51-63.

HUFFMAN M.A., WRANGHAM R.W. (1994) The diversity of medicinal plant use by chimpanzees in the wild, in WRANGHAM R.W., MC GREW W.C., de WAAL F.B., HELTNE P.G. (eds.), *Chimpanzee Cultures*, Cambridge, Harvard University Press, 129-148.

IDANI G., KURODA S., KANO T., ASATO R. (1994) Flora and vegetation of Wamba Forest, Central Zaire with reference to Bonobo (*Pan paniscus*) foods, *Tropics*, 3 (3/4), 309-332.

IRVINE F. R. (1961) *Woody plants of Ghana. London*, Oxford University Press.

JANZEN D. H. (1978) Complications in interpreting the chemical defenses of tree against tropical arboreal plant-eating vertebrates, in G.G. MONTGOMERY (ed.), *The ecology of arboreal folivores*, Washington D.C., Smithosonian Institute Press, 73-84.

JISAKA M., KAWANAKA M., SUGIYAMA H., TAKEGAWA K., HUFFMAN M.A., OHIGASHI H., KOSHIMIZU K. (1992a) Antischistosomal activities of sesquiterpene lactones and steroid glucosides from *Vernonia amygdalina*, possibly used by wild chimpanzees against parasite-related diseases, *Bioscience, Biotechnology and Biochemistry*, 56 (5), 845-846.

JISAKA M., OHIGASHI H., TAKAGAKI T., NOZAKI H., TADA T., HIROTA M., IRIE R., HUFFMAN M.A., NISHIDA T., KAJI M., KOSHIMIZU K. (1992b) Bitter steroid glucosides, vernoniosides A1, A2, and A3 and related B1 from a possible medicinal plant *Vernonia amygdalina*, used by wild chimpanzees, *Tetrahedron*, 48, 625-632.

JISAKA M., OHIGASHI H., TAKEGAWA K., HIROTA M., IRIE R., HUFFMAN M.A., KOSHIMIZU K. (1993a) Steroid glucosides from *Vernonia amygdalina*, a possible chimpanzee medicinal plant, *Phytochemistry*, 34, 409-413.

JISAKA M., OHIGASHI H., TAKEGAWA K., HUFFMAN M.A., KOSHIMIZU K. (1993b) Antitumor and antimicrobial activities of bitter sesquiterpene lactones of *Vernonia amygdalina*, a possible medicinal plant used by wild chimpanzees, *Bioscience, Biotechnology, Biochemistry*, 57 (5), 833-834.

JOHNS T. (1990) *With bitter herbs they shall eat it*, Tucson, The University of Arizona Press.

JOHNS T. (1994) Ambivalence to the palatability factors in wild food plants, in ETKINS N.L., *Eating on the Wild Side*, Tucson, The University of Arizona Press , 46-61.

KEYMER A., CROMPTON D.W.T., SAHAKIAN B.J. (1983) Parasite induced learned aversion involving Nippostrongylus in rats, *Parasitology*, 86, 455-460.

KLOOS H., MC CULLOUGH F.S. (1987) Plants with recognized molluscicidal activity, in MOTT K.E. (ed.), *Plant Molluscicides*, New York, John Wiley & Sons Ltd., 45-108.

KOKWARO J.O. (1976) *Medicinal Plants of East Africa*, Nairobi, General Printers Ltd.

KOSHIMIZU K., OHIGASHI H., HUFFMAN M.A., NISIHDA T., TAKASAKI H. (1993) Physiological activities and the active constituents of potentially medicinal plants used by wild chimpanzees of the Mahale Mountains, Tanzania, *International Journal of Primatology*, 14 (2), 345-356.

KUPCHAN S.M., HEMINGWAY R.J., KARIM A., WERNER D. (1969) Tumor Inhibitors XLVII. vernodalin and vernomygdin, two new cytotoxic sesquiterpene lactones from *Vernonia amygdalina* Del., *Journal of Organic Chemistry*, 34, 3908-3911.

KYRIAZAKIS I., OLDHAM J. D., COOP R.L., JACKSON F. (1994) The effect of subclinical intestinal nematode infection on the diet selection of growing sheep, British Journal of Nutrition, 72, 665-677.

McCANN C. (1932) A cure for tapeworm, *Journal of the Bombay Natural History Society*, 36, 282-284.

MOORE M. (1979) *Medicinal plants of the mountain west*, Santa Fe, Museum of New Mexico Press.

MOUTSAMBOTÉ J., YUMOTO T., MITANI M., NISHIHARA T., SUZUKI S., KURODA S. (1994) Vegetation and list of plant species identified in the Nouabalé-Ndoki Forest, Congo, *Tropics*, 3 (3/4), 277-293.

MUANZA D.N., DANGALA N.L., MPAY O. (1993) Zairean medicinal plants as diarrhea remedies and their antibacterial activities, African Study Monographs, 14 (1), 53-63.

MURAKAMI A., OHIGASHI H., KOSHIMIZU K. (1994) Possible anti-tumor promoting properties of traditional Thai foods and some of their active constituents, *Asia Pacific Journal of Clinical Nutrition*, 3, 185-191.

MURAKAMI A., OHIGASHI H., KOSHIMIZU K. (1996) Anti-tumor promotion with food phytochemicals. A strategy for cancer chemoprevention, *Bioscience, Biotechnology Biochemistry*, 60 (1), 1-8.

NELSON G.S. (1960) Schistosome infections as zoonoses in Africa, *Tanscripts of the Royal Society of Tropical Medicine and Hygiene*, 54, 301-314.

NEUWINGER H.D. (1996) *African Ethnobotany. Chemistry, pharmacology, toxicology*, London, Chapman & Hill.

NISHIDA T., UEHARA S. (1983) Natural diet of chimpanzees (*Pan troglodytes schweinfurthii*). Long term record from the Mahale Mountains, Tanzania, *African Study Monographs*, 3, 109-130.

NYAZEMA N.Z. (1987) Medicinal plants of wide use in Zimbabwe, in A.J.M. LEEUWENBURG (Compiler), *Medicinal and poisonous plants of the tropics*, Wageningen, Pudoc Wageningen, 36-43.

OGILVIE G.H. (1929) Bison eating bark, *Journal of the Bombay Natural History Society*, 33, 706-707.

OHIGASHI H. (1995) *Plants used medicinaly by primates in the wild and their physiologically active constituents*, Report to the Minestry of Science, Education and Culture for 1994 Grant-in-Aid for Scientitific Research (n° 06303012).

OHIGASHI H., HUFFMAN M.A., IZUTSU D., KOSHIMIZU K., KAWANAKA M., SUGIYAMA H., KIRBY G.C., WARHURST D.C., ALLEN D., WRIGHT C.W., PHILLIPSON J.D., TIMMON-DAVID P., DELNAS F., ELIAS R., BALANSARD G. (1994) Toward the chemical ecology of medicinal plant-use in chimpanzees. The case of *Vernonia amygdalina* Del.. A plant used by wild chimpanzees possibly for parasite-related diseases, *Journal of Chemical Ecology*, 20, 541-553.

OHIGASHI H., JISAKA M., TAKAGAKI T., NOZAKI H., TADA T., HUFFMAN M.A., NISHIDA T., KAJI M., KOSHIMIZU K. (1991) Bitter principle and a related steroid glucoside from *Vernonia amygdalina*, a possible medicinal plant for wild chimpanzees, *Agricultural and Biological Chemistry*, 55, 1201-1203.

OHIGASHI H., SAKAI Y., YAMAGUCHI K., UMEZAKI I., KOSHIMIZU K. (1992) Possible anti-tumor promoting properties of marine algae and in vitro activity of wakame seaweed extract, *Bioscience Biotechnology and Biochemistry*, 56 (6), 994-995.

OKUNJI C. O., IWU M. M. (1988) Control of schistosomiasis using Nigerian medicinal molluscicides, *International J. Crude Drug Research*, 26 (4), 246-252.

PALGRAVE K.C. (1983) *Trees of Southern Africa*, 2nd revised edition, Cape Town, Struik Publisher.

PHILLIPS R. (1981) *Mushrooms and other fungi of great britain and Europe*, London, Pan.

RAUCH R. (1954) Studies on the helminth fauna of Alaska. XXI. Taxonomy, morphological variation, and ecology of *Diphyllobothirium ursi* n. sp. *provis* on Kodiak Island, *Journal of Parasitology*, 40, 540-563.

RAUCH R. (1961) Notes on the black bear, *Ursus americanus Pallas*, in Alaska with particular reference to dentition and growth, *Z. Saugetierk*, 26, 77-107.

RIESENBERG S.H. (1948) Magic and medicine in Ponape. Southwest, *Journal of Anthropology*, 4, 406-429.

SENGPUTA S. (1981) Adaptive significance of the use of margosa leaves in nests of house sparrows Passer domesticus, *Emu*, 81, 114-115.

SMOLENSKI S.J., SILINIS H., FARNSWORTH N. R. (1974) Alkaloid screening. V, *Lloydia*, 37 (3), 506-536.

SUGIYAMA Y., KOMAN J. (1992) The flora of Bossou: Its utilization by chimpanzees and humans, *African Studies Monographs*, 13(3): 127-169.

TOFT, C.A., AESCHLIMANN, A., BOLIS, L. (1991) *Parasite-Host Associations; Coexistence or Conflict?* Oxford, Oxford Science Publications.

TOUBIANA, R., GAUDEMER, A. (1967) Structure du vernolide, nouvel ester sesquiterpique isole de *Vernonia colorata*, *Tetrahedron Letters*, 14, 1333-1336.

TUTIN C.E.G., WHITE L.J.T., WILLIAMSON E.A., FERNANDEZ M., Mc PHERSON. G. (1994) *List of plant species identified in the northern part of the Lopé Reserve*, Gabon, Tropics, 3 (3/4), 249-276.

WAKELIN D. (1996) Immunity to parasites - How parasitic infections are controlled, 2nd edition, Cambridge, Cambridge University Press.

WATERMAN P.G. (1984) Food acquisition and processing as a function of plant chemistry. in CHIVERS D. J., WOOD BN. A., BILSBOROUGH A (eds.), *Food Acquisition and Processing in Primates*, New York, Plenum Press, 177-211.

WATT J. M., BREYER-BRANDWINJK M.G. (1962) *The Medicinal and Poisonous Plants of Southern and East Africa*, Edinburgh, E. and S. Livingstone Ltd.

WILSON E. (1962) *Aubrey's brief lives edited edition by O.L. Dick*, Ann Arbor, Ann Arbor Paperbacks, p. xix.

WINK M., HOFER A., BILFINGER M., ENGLERT E., MARTIN M., SCHNEIDER D. (1993) Geese and dietary allelochemicals- food palatability and geophag, *Chemoecology*, 4, 93-107.

WRANGHAM R.W., ROGERS M.E., ISABIRYE-BASUTA G. (1993) Ape food density in the ground layer in Kibale Forest, Uganda, *African Journal of Ecology*, 31, 49-57.

WRIGHT C., PHILLIPSON C., KIRBY D.V., HUFFMAN M.A., OHIGASHI H. (1993) *Do chimpanzees know how to treat protozoal diseases?* Paper presentation at the 5th British Society for Parasitology Malaria Meeting, September, 1993: Oxford.

YUMOTO T., YAMAGIWA J., MWANZA N., MARUHASHI T. (1994) *List of plant species identified in Kahuzi-Biega National Park*, Zaire, Tropics, 3 (3/4), 295-308.

Tableau I. Preuves anecdotiques de l'automédication chez les animaux

Espèces	Plante (preuve chimique)	Références
Eléphant de Malaysie	*Entada schefferi* (Leguminosae) : pour la résistance avant une longue marche, éventuellement antalgique ?	Hubback, 1941, Janzen, 1978
Eléphant d'Afrique	Boraginaceae sp. : accélère l'accouchement ; utilisée par une communauté ethnique du Kenya pour engager le travail de l'accouchement et amener un avortement. Récit identique rapporté par Huffman après des observations faites en Tanzanie	Cowen, 1990 M.S. Kalunde, comm. pers.
Buffle indien	*Holarrhena antidysenterica* (Apocynaceae) : écorce consommée régulièrement. Le nom de l'espèce suggère qu'elle a un effet anti-dysenterie	Oglivie, 1929
Sanglier sauvage des Indes	*Boerhavia diffusa* (Nyctaginaceae) : appelée herbe aux porcs. Les racines sont consommées sélectivement par les sangliers ; c'est aussi un antihelminthique traditionnel chez les Indiens	Janzen,1978, Dharmkumarsinhji, 1960
Porc	*Punicum granatum* (Punicaceae) pomegranate : racine de la grenade recherchée par les porcs au Mexique. Alcaloïde dans les racines, toxique pour les ténias	Janzen, 1978, McCann, 1932 Caius, 1940
Tigre indien, chien sauvage, ours, civette, chacal	*Careya arborea* (Barringtonaeaceae), *Dalbergia latifolia* (Leguminosae) etc : les fruits de diverses espèces sont mangés par des grands carnivores. Il est possible qu'elles contribuent à l'élimination des parasites ingérés en même temps que le contenu des intestins des proies herbivores	McCann, 1958, Burton, 1952 Janzen, 1978
Loup d'Amérique du S.	*Solanum lycocarpon* (Solanaceae) : on dit du fruit blette qu'on le consomme pour traiter des dérangements gastriques ou intestinaux	D.A.O. Courtnay, G.C. Kirby pers. comm.
Rhinocéros d'Asie bicorne	*Ceriops candoleana* (Rhizophoraceae) : écorce riche en tannin mangée en grande quantité suffisamment pour faire virer l'urine à l'orange clair. Utilisation possible pour traiter les parasites dans les conduits vésicaux et urinaires	Hubback, 1939
Singe hurleur noir, Spider monkey	Les peuples indigènes vivant dans des habitats de primates des Neotropiques prétendent que certaines espèces de singes sont exemptes de parasites à cause des plantes qu'ils mangent	S. Vitazkova, M. Pavelka pers.. Comm.

Tableau II. Utilisations ethnomédicinales de *Vernonia amygdalina* en Afrique

Application	Partie utilisée	Région étudiée, commentaires
Dérangements intestinaux généraux		
entérite	racine, graines	Nigeria
constipation	feuilles, sève	Nigeria, Tanzanie, Ethiopie : comme laxatif
diarrhée	tige, écorce de racine, feuilles	Afrique de l'ouest, Zaïre
dérangement de l'estomac	tige, écorce de racine, feuilles	Angola, Ethiopie
Parasitoses		
schistosomiase	racine, écorce, fruit	Zimbabwé, Mozambique, Nigeria : parfois mélangé avec *Vigna sinensis*
malaria	racine, écorce, feuilles	Afrique de l'est, Angola, Guinée, Nigeria, Ethiopie : un substitut de la quinine
infection à la trématode	racine, feuilles	Afrique de l'est : traitement pour enfants comme suppositoire
dysenterie amibienne	écorce de racine	Afrique du Sud
teigne	feuilles	Nigeria : contre les teignes et autres infections non identifiées
non précisé	feuilles	Nigeria : traitement prophylactique pour nourrissons transmis par le lait de la mère
	racines, graines	Nigeria : contre les vers
	feuilles	Afrique de l'ouest : pilé dans l'eau et donné aux chevaux comme vermifuge, supplément alimentaire pour le traitement des vers
	feuilles	Ghana : purgatif
Alimentation tonique		
	feuilles	Cameroun, Nigeria : bouilli ou trempé dans de l'eau froide, préparé comme une soupe ou un légume frit avec de la viande ; "n'dole", "fatefate", "mayemaye", feuilles vendues sur les marchés et cultivées dans les jardins domestiques
Autres affections		
aménorrhée	racine	Zimbabwé
toux	feuilles	Ghana, Nigeria, Tanzanie
diabete	toutes parties amères	Nigeria
fièvre	feuilles	Tanzanie, Kenya, Uganda, Congo-Kinshasa : feuilles pressées et jus extrait
gonorrhée	racine	Côte d'Ivoire : pris avec *Rauwolfa vomitoria*
"faiblesse du coeur"	racine	Afrique de l'ouest : la vernonine est un glycoside cardiotonique comparable à la digitaline
manque d'appétit	feuilles	Afrique de l'ouest : feuilles trempées dans l'eau froide pour enlever l'amertume et bouillies dans la soupe
pneumonie	feuilles	Côte d'Ivoire : prises avec *Argemone maxicana* ou utilisées en bain
rhumatisme	tige, écorce de racine	Nigeria
scorbut	feuilles	Sierra Leone, Nigeria, ouest du Cameroun : feuilles vendues sur les marchés et cultivées dans les jardins domestiques
Hygiène générale		
dentifrice	rameau, baguette	Nigeria : bâton mâché pour le lavage des dents et contre les caries
désinfectant	non communiqué	Ethiopie
savon	tige	Uganda

Sources : Abebe, 1987 ; Akah and Okafor, 1990 ; Burkill, 1985 ; Dalziel, 1937 ; Irvine, 1961, Kokwaro, 1976 ; Muanza, *et al.*, 1993 ; Nyazema, 1987 ; Palgrave, 1983 ; Watt and Breyer-Branwijk, 1962 ; Huffman, données personnelles non publiées, recueillies à partir d'interview en Uganda et en Tanzanie.

Primates (2003) 44: 61–66
DOI 10.1007/s10329-002-0008-6

ORIGINAL ARTICLE

**Valentina Carrai · Silvana M. Borgognini-Tarli
Michael A. Huffman · Massimo Bardi**

Increase in tannin consumption by sifaka (*Propithecus verreauxi verreauxi*) females during the birth season: a case for self-medication in prosimians?

Received: 1 May 2002 / Accepted: 10 September 2002 / Published online: 20 November 2002

Abstract In this study we report preliminary data on the consumption of tannin-rich plants by sifakas (*Propithecus verreauxi verreauxi*) living in the Kirindy forest, western Madagascar. Sifakas spent most of their time feeding on only a few plant species. The tannin intake during the period between the pregnancy and birth season was significantly higher in pregnant females or females with lactating infants than in non-reproductive females and males. These periparturient females secured a larger proportion of condensed tannins by short feeding bouts on plants not included in the group's limited preferred food species. The measured increase in tannin intake is puzzling in light of the fact that tannins are commonly known for their protein-binding properties. Since protein demands are highest in pregnant and lactating females, possible medicinal benefits of tannin ingestion are considered. Tannin consumption is associated with an increase in body weight and stimulation of milk secretion. Veterinarians administer tannins as an astringent, anti-hemorrhagic and anti-abortive. Their high potential as an alternative anthelminthic has also recently been recognized. Thus, when viewed as self-medicating behavior, controlled increase in tannin intake could have multiple prophylactic advantages for females during the periparturient period. The high selectivity in their plant choice, and the presence of unusual feeding habits by a particular group of individuals (females with infants) limited in time (birth season), suggests that an increase in tannin ingestion may be a self-medicating behavior with multiple directly adaptive benefits to female reproduction.

V. Carrai · S.M. Borgognini-Tarli · M. Bardi
Department of Ethology, Ecology, Evolution, University of Pisa, Pisa, Italy

M.A. Huffman ( )
Section of Ecology, Primate Research Center, Kyoto University, Kanrin 2–41, Inuyama 484–8506, Japan
E-mail: huffman@pri.kyoto-u.ac.jp
Tel.: +81-568-630538
Fax: +81-568-630358

Keywords Self-medication · Condensed tannins · Sifaka females · Reproductive benefits

Introduction

The study of self-medication, or zoopharmacognosy, is a relatively new field in the discipline of animal behavior (see Huffman 2001; Engel 2002). Research on primate self-medication was first inspired by Janzen (1978) and gained momentum with the observation of chimpanzees in western Tanzania (Wrangham and Nishida 1983; Huffman and Seifu 1989) and baboons in Ethiopia (Philips-Conroy 1986) consuming plants of known medicinal value. Further detailed studies pointed to the control of internal parasite infection and/or relief from the related discomfort as a principle function of such behavior in the African great apes (e.g., Huffman et al. 1993, 1996; Wrangham 1995; Huffman and Caton 2001). Geophagy and charcoal ingestion, two variations of the same form of self-medication, are widely reported among apes and monkeys (Krishnamani and Mahaney 2000). Based on the excellent absorptive capacity of charcoal and clay, self-medication is proposed as a means of relieving gastric distress brought on by the ingestion of too much toxic plant material, intestinal parasite infection or a restricted diet etc. (e.g., Cooney and Struhsaker 1997; Wakibara et al. 2001). It has been proposed, for black lemurs and capuchins, that rubbing volatile insect or plant matter into the fur, controls infestation by ectoparasites (Baker 1996; Birkinshaw 1999; Valderrama et al. 2000). All of these behaviors are considered to enhance, in one way or another, the user's immediate wellbeing and thus increasing the user's chances of survival.

Little is known to date about the possibility of self-medication directly altering reproductive fitness. It has been suggested that secondary compounds in the primate diet can enhance or inhibit reproductive outcome. For example, although tentative, intriguing evidence has been presented to suggest that feeding on seasonally available plants with known phytoestrogens may mediate conception and estrous in chimpanzees, muriquis and vervets (Whitten 1983; Garey et al. 1992; Strier 1993; Wallis 1997). It has also been speculated that other secondary plant compounds present in commonly consumed foods induce facultative birth spacing and influence the sex of offspring in mantled howler monkeys (Glander 1980, 1994). The line between instances of a primarily nutritional and of a medicinal function can be difficult to draw from field observations alone. Pharmacological evidence and direct analyses suggest that a medicinal component does exist, particularly in highly seasonally ingested items of demonstrated pharmacological value (e.g., Huffman et al. 1998; Cousins and Huffman 2002).

From this brief overview, it seems likely that there is a reproduction-modulating component in the primate diet, but at present little is known about the possible effects of such a diet on reproduction and even less about the potential for self-medication in prosimians. The periparturition period is a critical time for females, and the alleviation of related problems via behavioral and biological adaptations are considered to be a high priority for reproduction and survival. From a dietary perspective, females are in need of increased amounts of protein for the maintenance of reproductive function, such as development of the uterus and mammary glands (e.g., Houdijk et al. 2001). The physiological prioritizing of protein and other nutrient resources to reproduction comes at a price, resulting in a drop in immunity to parasite infection during pregnancy and lactation (see Coop and Holmes 1996; Coop and Kryiazakis 1999; Houdijk et al. 2001).

When faced with such biologically mediated challenges at critical times, flexible behavioral adaptations are likely to play an increasingly important role (e.g., Huffman and Caton 2001). From the perspective of self-medication, we are interested in the possible role of plant secondary compounds in directly and indirectly overcoming the challenges of reproduction by females. Focusing on peculiar dietary changes offers an interesting area of investigation.

In this paper we take advantage of preliminary data on tannin content in the plant-food diet of a population of sifaka (*Propithecus verreauxi verreauxi*) living in the Kirindy forest, western Madagascar, to test the hypothesis that tannin consumption has a self-medicating function beneficial to pregnant and lactating females.

Methods

Study area

Kirindy is a primary dry deciduous forest of about 100,000 km^2 in the central-western part of Madagascar. The field camp is located at roughly 44 ±9 E, 20 3 S, at an altitude of 30 m above sea level. The research area, CS7, is a locality in the southern part of Conoco road, 7 km from the main road. The surface area is about 40 ha, 2 km east of the main camp. The climate is characterized by a long dry season (April–November) and a short wet season (December–March). The mean annual rainfall is 800 mm, mostly in the rainy season. The temperature shows contrasting daily highs and lows (7–25 C) during the dry season, but is relatively stable (25–30 C) during the wet season.

Study groups

Since the beginning of 1995, we have placed color-fabric collars on all members of eight sifaka study groups living in CS7. We followed four neighboring groups during 8 months, from May 1995 to August 1998. Environmental changes (e.g., river flooding) and variations in group composition (e.g., death of an individual) took place during the study period, causing some modification of the study groups.

Three adults (3 years or older) from each group were observed 3 days per month, from dawn to dusk, using focal animal sampling. One of the females, Alice, was technically a sub-adult, but she gave birth to her first infant at the age of 2.5 and is included in the analyses. Hourly turnover of the focal animal allowed us to have, at the end of every monthly cycle, a full day of observation per individual. In total, 27 subjects, belonging to three categories (males, reproductively active females, and reproductively inactive females), were observed. The monthly observations were grouped into four periods corresponding to a female's reproductive state: the mating season; the pregnancy period; the birth season; and the lactation period. The number of individuals observed per period is given in Table 1.

Plant samples and chemical analyses

During behavioral observations, plants eaten by sifakas were marked and every part not eaten was collected immediately after the animal left the spot or within 1–2 days later, depending on circumstances. Plant identification was performed by a Malagasy plant expert at the Centre de Formation Professionelle Forestale, Morondava. Each sample was sun- or oven-dried and stored in a closed plastic bag until chemical analysis could be performed in the laboratory. Plant food specimens were analyzed in two different test runs at the following institutions and times: Deutsches Primatenzentrum (DPZ), Gottingen, Germany, July 1996; Zoology Department, University of Hamburg (ZDU), Germany, October 1998. The extraction technique used was the same at both laboratories, but the dilution of suspension was different.

Each plant sample was first pulverized in a grinder, then kept overnight in an oven at +60 C to dry. An aliquot from each dried sample (50 mg) was suspended in 50% methanol/water (at DPZ) or 100% methanol (at ZDU). After 24 h, 0.5 ml of the suspension was diluted with 4.5 ml of 50% or 100% methanol. An aliquot (2.5 ml) of the suspension was mixed with 2.5 ml of the reagent and kept in a boiling water bath for 2 h.

From this aliquot, condensed-tannin content was photometrically evaluated by measuring light absorption at 540 nm, using the following formula: % tannin = (absorbency 4,500)/milligrams of dried sample. The amount of plant material ingested by each sifaka was evaluated by multiplying the percentage of each item ingested (dry-weight unit) by the time spent (seconds) feeding on any given plant/plant part. The data were pooled by month in order to smooth out random fluctuations.

Statistical analysis

In comparing average levels of condensed tannins consumed in the three categories (males, pregnant/lactating females, and reproductively inactive females), we used the non-parametric Kruskal–Wallis analysis of variance. Owing to the small sample size, we selected the level of significance of =0.1 (see Hays 1991, p. 1029).

Results

Sifakas spent more than 97% of their feeding time concentrated on a few plant species. The Malagasy

Table 1 Distribution of observations (*x*) made on study subjects, by month and sex over reproductive class of individuals between 1995 and 1998 in the Kirindy forest, western Madagascar. *F+I* Reproductively active females, *F–I* reproductively inactive females, *M* males, – not observed. Total observation time 2,592 h (27 individuals 12 h/month 8 months)

Subject	Class	Mating season		Pregnancy		Birth season		Lactation	
		Feb	Mar	May	Jun	Jul	Aug	Oct	Nov
Vienna	F–I	x	x	x	x	x	x	x	x
Linz	M	x	x	x	x	x	x	x	x
Bregenz	M	x	x	x	x	x	x	x	x
Bonn	M	x	x	–	–	–	–	–	–
Colonia	F+I	x	x	–	–	–	–	x	x
Fulda	F+I	x	x	–	–	–	–	x	x
Jever	M	–	–	–	–	–	–	x	x
Tamatave	F–I	x	–	–	–	–	–	–	–
Tana	F+I	x	–	–	–	–	–	–	–
Tulear	M	x	–	–	–	–	–	–	–
Milano	M	–	–	x	x	x	x	–	–
Napoli	M	–	–	x	x	x	x	–	–
Roma	F+I	–	–	x	x	x	x	–	–
Alice [a]	F+I	x	x	x	x	x	x	x	x
Darwin	M	x	x	–	–	–	x	–	–
Adelaide	F–I	x	x	–	–	–	x	–	–
Canberra	F–I	–	–	x	x	x	–	–	–
Sydney	M	–	–	x	x	x	–	x	x
Berlin	M	–	–	–	–	–	–	x	x
Atlanta [b]	F+I	–	–	x	x	x	–	x	–
Boston	M	–	–	x	x	x	–	–	–
Dallas [c]	F–I	–	–	x	x	x	–	x	x
Juneau	M	–	–	–	–	–	–	x	x
Philadel	F+I	–	–	–	–	–	–	–	x
Geneva	F+I	–	–	–	–	–	x	–	–
Pisa	F–I	–	–	–	–	–	x	–	–
Pinky	M	–	–	–	–	–	x	–	–

[a] Alice belongs to F+I in August only
[b] Atlanta belongs to F+I in October
[c] Dallas belongs to F+I in October and November

names, species, family, and percentage tannin ingested from these plants are given in Table 2.

The yearly intake of tannins by females with infants did not differ significantly from that of females without infants and that of males (Kruskal–Wallis test: $H_2=0.82$, $n=27$, $P=0.66$). However, the increase in tannin intake from the pregnancy season to the birth season was significantly higher in females with infants than in the other two categories (Kruskal–Wallis test: $H_2=4.74$, $n=12$, $P=0.09$).

Monthly variation in the plant's percentage of condensed tannin explains the overall increase in tannin consumption for all three categories, since the peak in concentration is in the birth season (Fig. 1). Nevertheless, females with infants secured a larger proportion of condensed tannins by short feeding bouts on plants not included in the preferred species list of the group (Table 2). The peculiar choice of plant by females in this category was confirmed by the overall significantly lower number of plants consumed during the birth season in comparison with females without infants and males (Kruskal–Wallis test: $H_2=6.7$, $n=17$, $P=0.05$).

Discussion

During pregnancy and lactation, energy and protein requirements may increase between two- and ten-fold (Blaxter 1989; Jessops 1997). Protein requirements are expected to be considerably higher at this time than any other period of a female's life. Ideally therefore, periparturient females should adapt their dietary habits to meet the increased demand for metabolizable proteins in order to maintain reproductive function. This is supported by the findings of Sauther (1994) for female ringtailed lemur at Beza Mahafaly and by Vasey (2000, 2002) for female ruffed lemur and brown lemur at Andranobe, Madagascar. Pregnant and lactating females minimized foraging costs and ate more young leaves high in protein and low in fiber than non-lactating females and adult males in the group.

At Kirindy, sifaka are highly selective in their plant-food choice, both in the sense of positive (feeding on rare plants) and negative (excluding abundant plants) selection (Carrai 1999). A significant trend of increased ingestion of tannins by periparturient females, compared to other adult females and males, was demonstrated in the present study. One of the plants with relatively high tannin content was eaten exclusively by periparturient females (fihamy, scientific name unknown), and a second one (kily, *Tamarindus indica*) was eaten by periparturient females, but not by non-pregnant females, whereas males consumed it in significantly lower amounts (Table 2). Furthermore, in the birth season, fihamy leaves were found to have very little nutritional content. Fats and carbohydrates were below the analytical sensitivity of the technique applied, and proteins were present in an extremely low amount (Carrai 1999).

Taken in large amounts, tannins are known to affect plant palatability and to bind with important nutrients, such as protein and polysaccharides, and are typically considered to have a negative effect on food intake and

Table 2 Percentage of condensed tannins present in the plants eaten by males and females in the birth season (July and August). *F+I* Reproductive females, *F–I* non-reproductive females, *M* males; – not observed

Malagasy name	Species name	Family name	Mean % tannins ingested in the birth season		
			F+I	F–I	M
Alimboro	*Albizia bernieri* [b]	Mimosaceae	–	0.003	0.002
Alimboromalao	*Albizia* sp.	Mimosaceae	0.010	–	–
Amaninomby	*Terminalia bovini*	Combretaceae	–	0.024	0.005
Anakaraka [a]	*Cordyla madagascariensis*	Cesalpinaceae	0.029	0.086	0.314
Anatsiko	*Securinega seyrigii*	Euphorbiaceae	–	0.006	0.003
Arofy	*Commiphora guillaumini*	Burseraceae	–	0.003	0.001
Fihamy	Unknown	Unknown	0.138	–	–
Hazomboenga [a]	*Diospyros tropophylla*	Ebenaceae	–	0.328	0.243
Hompy	*Quivisianthe papinae*	Meliaceae	–	0.022	0.002
Kily	*Tamarindus indica*	Cesalpinaceae	0.606	–	0.254
Kironono [a]	*Capurodendron rubrocostatum*	Sapotaceae	–	–	0.027
Liana	Unknown	Unknown	0.442	0.215	0.142
Lopingo	*Diospyros perrieri* [b]	Ebenaceae	–	0.001	0.001
	Diospyros greveana [b]		–	–	–
Maintifototra	*Diospyros* sp.	Ebenaceae	–	0.030	0.015
Mamiaho [a]	*Baseonema acuminatum*	Asclepiadaceae	–	–	–
Manary	*Dalbergia* sp.	Fabaceae	–	–	0.027
Mandravasarotra [a]	*Desmodium ramosissimum*	Leguminosae	–	–	–
Manjakabenitany [a]	*Baudonia fluggeiformis*	Cesalpinaceae	0.056	0.053	0.035
Mapandry	*Cedrelopsis* sp.	Meliaceae	–	–	0.006
Mapilazy	Unknown	Unknown	0.015	–	–
Menambaho	*Foetidia asymetrica*	Lecythidaceae	–	0.006	–
Menavahitsy [a]	Unknown	Unknown	–	–	0.021
Namologna [a]	Foetidia retusa	Lecythidaceae	0.266	–	0.153
Nato	*Capurodendron perrieri*	Sapotaceae	–	–	0.002
Piropitsokala	*Rothmannia tropophylla*	Rubiaceae	–	0.022	0.076
Sarigoavy	*Bivinia jalberti*	Flacourtiaceae	–	–	0.020
Sarinato	*Foetidia* sp.	Lecythidaceae	–	0.005	–
Talinala	*Terminalia calcicola*	Combretaceae	–	–	0.001
Tanjaka	*Anakolosa pervillana*	Oleaceae	–	0.086	0.075
Tratramborondreo	*Colubrina decipiens*	Rhamnaceae	0.025	0.044	0.009
Tsingena	*Doratoxylon stipulatum*	Sapinaceae	–	0.007	–
Tsitake	*Rhus perrieri*	Anacardiaceae	0.001	–	–
Vahipindy [a]	*Alafia intermedia*	Apocynaceae	–	–	–
Vahipisaka	Unknown	Unknown	–	0.004	–
Valotsy	*Breonia perrieri*	Rubiaceae	0.001	–	–
Vohamea	*Dyospyros sakalavarum*	Ebenaceae	0.008	0.004	0.004

[a] Plants listed here accounted for more than 97% of sifaka feeding time
[b] Uncertain identification

Fig. 1 Mean amount and SD of tannins ingested (mean tannin concentration mean feeding time) over the four reproductive periods (mating, pregnancy, birth season, lactation) for the study subjects, by sex and reproductive state (*bars*, refer to left vertical axis) and the mean tannin concentration present in plants available in each period (*continuous line*, refer to right vertical axis). *F+I* Reproductively active females, *F–I* reproductively inactive females, *M* males. Values, based on all ingested plant species analyzed, are combined

digestibility (Glander 1982). While the level of tolerance to condensed tannins is not known in depth for lemurs, and particularly for *Propithecus v. verreauxi,* some data on avoidance by lemur species are available. According to Ganzhorn (1989) the tolerance of *P. v. coquereli* to condensed tannins should be relatively high, at least in terms of a lack of avoidance. The significant increased ingestion of tannins by periparturient sifakas is puzzling and led us to explore self-medication explanations for the selective ingestion of tannins by pregnant and lactating females and the role this foraging decision may play in overall health maintenance at this critical period.

Although it is difficult to obtain direct evidence for prophylactic effects of tannin consumption from field studies alone, a survey of the chemo-ecological, veterinary and pharmacological literature reveals a number of potentially beneficial and relevant properties that help to explain the observed increased intake of tannins by periparturient females. Tannin consumption is associated with increase in weight and the stimulation of milk secretion (e.g., Aerts et al. 1999; Barry and McNabb 1999). In veterinary practice, tannins are used for their astringent, anti-hemorrhagic and anti-abortive effects (Biagi and Speroni 1988). Recent work has also shown their high potential as an alternative anthelminthic (Athanasiadou et al. 2001). An increase in tannin intake therefore could have multiple prophylactic advantages during the periparturient period.

These properties of moderated tannin ingestion are consistent with the needs of pregnant and lactating females. Furthermore, the possible positive effect on reproductive fitness of this behavior for Kirindy sifaka females is supported by the fact that, in general, females here successfully give birth yearly, compared to every 2 years as noted in other sites (Richard et al. 1991). The benefit of increased tannin consumption by periparturient females at Kirindy is a hitherto unreported possible new form of self-medication enhancing female reproductive fitness. In the future, cross-site ecological and diet comparison should prove enlightening. The self-medication hypothesis advanced in this paper needs to be confirmed by further studies on this and other lemur species, as well as in other primate species. If confirmed by analogous or similar findings, our results will support the prediction that self-medication is widespread in primates (Huffman 2001) and furthermore that there are direct consequences of self-medication for increased reproductive fitness in females.

Acknowledgements Thanks are due to J. Ganzhorn and P. Kappeler for logistic facilities in Kirindy, laboratory use in Germany, useful suggestions in the set-up of the research project and stimulating discussions on sifaka socioecology. We are also grateful to A. Lunardini for significant contributions to the set-up of the research project on sifaka socioecology; R. Ralisoamalala for contribution to data collection; C. Rakotondrasoa, E. Rakotovao, R. Randriamarosoa for plant identification (Malagasy names); P. Meletti for plant taxonomy; A. Pagni and E. Bernardini for useful information on tannin effects; and E. Martinotti for valuable comments on a previous version of this manuscript. We wish to thank Drs. I. Kyriazakis and S. Athanasiadou for thoughtful discussions and information on tannins and to Dr. J. Caton for comments relating to the digestive tracts of sifakas.

References

Aerts RJ, Barry TN, McNabb WC (1999) Polyphenols and agriculture: beneficial effects of proanthocyanidins in forages. Agric Ecosyst Environ 75:1–12

Athanasiadou S, Kyriazakis I, Jackson F, Coop RL (2001) Direct anthelminthic effects of condensed tannins towards different gastrointestinal nematodes of sheep: in vitro and in vivo studies. Vet Parasitol 99:205–219

Baker M (1996) Fur rubbing: use of medicinal plants by capuchin monkeys (*Cebus capucinus*). Am J Primatol 38:263–270

Barry TN, McNabb WC (1999) The implications of condensed tannins on the nutritive value of temperate forages fed to ruminants. Br J Nutr 81:263–272

Biagi GL, Speroni E (1988) Farmacognosia. Patron, Bologna

Birkinshaw CR (1999) Use of millipedes by black lemurs to anoint their bodies. Folia Primatol 70:170–171

Blaxter KL (1989) Energy metabolism in animals and man. Cambridge University Press, Cambridge

Carrai V (1999) Eco-etologia di *Propithecus verreauxi verreauxi*, lemure della famiglia Indriidae. Dissertation, University of Pisa, Pisa (Italy) Available from Biblioteca Nazionale Centrale, Rome and Florence

Cooney DO, Struhsaker TT (1997) Absorptive capacity of charcoals eaten by Zanzibar red colobus monkeys: implications for reducing dietary toxins. Int J Primatol 18:235–246

Coop RL, Holmes PH (1996) Nutrition and parasite interaction. Int J Parasitol 26:951–962

Coop RL, Kryiazakis I (1999) Nutrition-parasite interaction. Vet Parasitol 84:187–204

Cousins D, Huffman MA (2002) Medicinal properties in the diet of gorillas – an ethnopharmacological evaluation. Afr Stud Monogr 23:65–89

Engel C (2002) Wild health. Houghton and Mifflin, New York

Ganzhorn JU (1989) Primate species separation in relation to secondary plant chemicals. J Hum Evol 4:125–132

Garey J, Markiewicz L, Gurpide E (1992) Estrogenic flowers, a stimulus for mating activity in female vervet monkeys. In: Proceedings of the XIVth Congress of the International Primatological Society (Abstracts). Strasbourg, p 210

Glander EK (1980) Reproduction and population growth in free-ranging mantled howling monkeys. Am J Phys Anthropol 53:25–36

Glander EK (1982) The impact of plant secondary compounds on primate feeding behavior. Yearb Phys Anthropol 25:1–18

Glander EK (1994) Nonhuman primate self-medication with wild plant foods. In: Etkin NL (ed) Eating on the wild side: the pharmacologic, ecologic and social implications of using non-cultigens. University of Arizona Press, Tucson, pp 239–256

Hays WL (1991) Statistics. Harcourt Brace, Orlando, Fla.

Houdijk JGM, Jessop NS, Kyriazakis I (2001) Nutrient partitioning between reproductive and immune functions in animals. Proc Nutr Soc 60:515–525

Huffman MA (2001) Self-medicative behavior in the African great apes: an evolutionary perspective into the origins of human traditional medicine. Bioscience 51:651–661

Huffman MA, Caton JM (2001) Self-induced increase of gut motility and the control of parasite infections in wild chimpanzees. Int J Primatol 22:329–346

Huffman MA, Seifu M (1989) Observation on the illness and consumption of a possibly medicinal plant *Vernonia amygdalina* (Del.), by a wild chimpanzee in the Mahale Mountains National Park, Tanzania. Primates 30:51–63

Huffman MA, Gotoh S, Izutsu D, Koshimizu K, Kalunde MS (1993) Further observations on the use of the medicinal plant, *Vernonia amygdalina* (Del) by a wild chimpanzee, its possible effect on parasite load, and its phytochemistry. Afr Stud Monogr 14:227–240

Huffman MA, Page JE, Sukhdeo MVK, Gotoh S, Kalunde MS, Chandrasiri T, Towers GHN (1996) Leaf-swallowing by chimpanzees, a behavioral adaptation for the control of strongyle nematode infections. Int J Primatol 72:475–503

Huffman MA, Ohigashi H, Kawanaka, Page JE, Kirby GC, Gasquet M, Murakami A, Koshimizu K (1998) African great ape self-medication: a new paradigm for treating parasite disease with natural medicines. In: Ageta A, Aimi N, Ebizuka Y, Fujita T, Honda G (eds) Towards natural medicine research in the 21st century. Elsevier, Excerpta Medica, Amsterdam, pp 113–122

Janzen DH (1978) Complications in interpreting the chemical defenses of trees against tropical arboreal plant-eating vertebrates. In: Montgomery GG (ed) The ecology of arboreal folivores. Smithsonian Institution Press, Washington, D.C., pp 73–84

Jessops NS (1997) Protein metabolism during lactation. Proc Nutr Soc 56:169–175

Krishnamani R, Mahaney WC (2000) Geophagy among primates: adaptive significance and ecological consequences. Anim Behav 59:899–915

Phillips-Conroy JE (1986) Baboons, diet, and disease: food plant selection and schistosomiasis. In: Taub D, King F (eds) Current perspectives in primate social dynamics. Van Nostrand Reinhold, New York, pp 287–304

Richard AF, Rakotomanga P, Schwartz M (1991) Demography of *Propithecus verreauxi* at Beza Mahafali, Madagascar: sex ratio, survival, and fertility, 1984–1988. Am J Phys Anthropol 84:307–322

Sauther ML (1994) Wild plant use by pregnant and lactating ringtailed lemurs with implications for early hominid foraging. In: Etkin LN (ed) Eating on the wild side. The University of Arizona Press, Tucson, pp 240–256

Strier KB (1993) Menu for a monkey. Nat Hist 102:34–43

Valderrama X, Robinson JG, Attygale AB, Eisner T (2000) Seasonal anointment with millipedes in a wild primate: a chemical defense against insects? J Chem Ecol 26:2781–2790

Vasey N (2000) Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*. I. Interspecific patterns. Am J Phys Anthropol 112:411–431

Vasey N (2002) Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*. II. Intraspecific patterns. Am J Phys Anthropol 118:169–183

Wakibara J, Huffman MA, Wink M, Reich S, Aufreiter RGV, Hancock R, Mahaney Russ S (2001) The adaptive significance of geophagy for Japanese macaques (*Macaca fuscata*) at Arashiyama, Japan. Int J Primatol 22:495–520

Wallis J (1997) A survey of reproductive parameters in the free-ranging chimpanzees of Gombe National Park. J Reprod Fertil 109:297–307

Whitten PL (1983) Flowers, fertility and females (abstract). Am J Phys Anthropol 60:269–270

Wrangham RW (1995) Relationship of chimpanzee leaf-swallowing to a tapeworm infection. Am J Primatol 37:297–303

Wrangham RW, Nishida T (1983) *Aspilia* spp. leaves: a puzzle in the feeding behavior of wild chimpanzees. Primates 24: 276–282