

Bears, Pigs, and Plio-Pleistocene Hominids: A Case for the Exploitation of Belowground Food Resources

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Belowground plant parts were important potential food resources in the habitats associated with Pliocene and early Pleistocene hominids. The food gathering and dental adaptations of three groups of modern mammals – bears, pigs, and humans – testify to the earlier convergence of these animals on this resource. Since belowground food reserves are relatively unaffected by the factors controlling aboveground food supply (fire, drought, and grazing stress), exploitation of this stable nutritional bank had distinct energetic and behavioral advantages for hominids.

KEY WORDS: belowground food resources; convergence; ursids; suids; Plio-Pleistocene hominids.

INTRODUCTION

Past paleoecological interpretations of the behavior and way of life of early hominids have been colored by the status of the sole surviving hominid, *Homo sapiens sapiens*. Our understanding of the early hominid has been hindered by a preoccupation with the process of hominids becoming human, rather than with hominids behaving as mammals in extinct communities.³ Viewing hominids as mammals first and ancestors second allows consideration of the early hominids as full, interacting members of their communities. Further, paleoecological re-

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³This notion was at the heart of discussions in a seminar at Yale, conducted by Alison Richard and David Pilbeam, out of which this paper grew. The best here must be attributed to the comments and proddings of Alison and David and many other generous friends.

constructions too often pay exclusive attention to either the vegetational or faunal component of past communities and are not attentive to the dynamic relationship between the two.

This article traces the convergence of several animals, all subject to similar environmental constraints, on an underestimated resource base: belowground plant storage parts. The interplay of factors within certain habitat types made a hominid diet utilizing these resources both nutritionally and behaviorally advantageous.

ADAPTIVE ZONES

The theory of adaptive zones was developed by Simpson (1944, 1953) in an attempt to explain how organisms become adapted to their environments.⁴ Simpson views the environment as being divided into zones that correspond to discontinuities existing in nature, ranged along a continuum from broad to narrow. The broadest zones include the most general physical divisions of nature (e.g., terrestrial, aerial, aquatic). Narrower zones involve finer environmental subdivisions of the broad zones (e.g., terrestrial, arboreal, leaves). Organisms respond to these subdivisions of the environment by evolving certain adaptations which allow them to exploit the resources of different zones. The resources, then, are a part of the environment and exist independently of the organism. The organism's response to the resources, which can have morphological, functional, or behavioral aspects, is defined as its adaptive type (Simpson, 1953). Simpson recognizes the relationship between the environmental zone and the adaptive type and notes that adaptive types may be defined in terms of their zone. The important point in his discussion of adaptation is the interaction between the environmental zone and the organism. He defines this interaction, or "way of life," as an adaptive zone.

BELOWGROUND FOOD RESOURCES

With the aid of improved sampling techniques in recent years, ecologists are bringing to light the striking preponderance of plant material present below rather than above ground in semiarid and subhumid ecosystem types — i.e.,

⁴ Although the concept of adaptive zone is rarely used in current ecological research, it does appear to be the most serviceable framework for constructing analyses of fossil communities (cf. Andrews and Nesbit Evans, 1979).

grasslands, savannahs, and shrublands (Murphey, 1975; Coupland, 1979). New data underscore both the possible dimensions of underground productivity and its variability between regions. For example, an average range in semiarid shrubland may be 100-600 g/m²/yr aboveground and 250-1000 g/m²/yr belowground (Noy-Meir, 1973). In temperate and tropical grasslands, the ratios of belowground plant biomass to maximum canopy biomass (living and dead tissue) fall between 0.2 and 10.3 (Coupland, 1979). In seasonal climates, the yearly pattern of fluctuation in subterranean biomass involves the banking of surpluses during photosynthetically active periods and the expending of the reserve in recovering from periodic or aperiodic stress, such as drought. The relative proportion of belowground to total plant biomass in a particular vegetation type is thought to be directly related to increasing aridity, though exceptions to this rule are emerging. For instance, some tropical systems undergoing grazing show heightened productivity (Coupland, 1979); similarly, fire has increased the investment in this compartment by plants (Van Rensberg, 1971).

Such biomass figures are useful to describe the contours of variation in production between regions. However, in order to bring the unrefined category of "belowground biomass" into finer resolution as a food source it is necessary to chart the consumer (e.g., large herbivores) and environmental (e.g., moisture) relations affecting particular loci of belowground production. The widespread semiarid shrublands of Africa are, to differing extents, dominated by "drought evaders" – perennial plants (geophytes and hemi-cryptophytes) which maintain a large part of their biomass belowground. In this region the belowground portion of the plant is marked by storage parts that maintain a "pulse reserve" utilized in recovering from the stress of seasonal drought, or to a lesser extent, from fire and grazing (Noy-Meir, 1973; Daubenmire, 1968).

The traditional categories of ecological investigation, for example, "semiarid shrubland," imply a certain uniformity to vegetative and environmental patterns. However, when specific localities are inspected on the ground the homogeneity tends to disappear, replaced by a mosaic of habitats and conditions. A case in point are the seeps, springs, and perennial or intermittent watercourse edges scattered across dryland regions. Seasonal fluctuations in water availability in such sites have created a pattern of belowground vegetative storage much like that of the surrounding subhumid or semiarid areas.

The degree of productivity along lake edges and similar sites is due to the active trading of nutrients between water and land systems (Piecynska, 1975). In addition, in standing waters there is a marked zonation of plant biomass, peaking in the shallow limnosal and littoral regions. Land vegetation adjacent to lakes generally shows declining productivity away from the lakeside groundwater cushion. This productivity, however, varies with the aridity of the surrounding system. Belowground biomass is markedly present in the zone of emergent vegetation, where it can constitute more than 60% of the standing

crop (Dykojová and Kvet, 1975). This preponderance of belowground material necessitates a special kind of marsh plant architecture. Hutchinson (1975) notes "a striking tendency for water plants to develop horizontal creeping axes or rhizomes, often of great size and rich in starch." The presence of this storage capacity seems to be necessitated both by the energy requirements of vegetative reproduction and by the stress resulting either from dry periods when water retreats from shallow zones of lakes and marshes (Hutchinson, 1975), or from fire (Van Rensberg, 1971).

In systems like the aquatic margin and semiarid types discussed above, a similar set of modified plant parts – roots, tubers, rhizomes, stem bases, and bulbs – all serve as vegetative storage sites. Consequently, these specially adapted plant parts constitute rich nutrient lodes. In dryland perennials, "storage organs . . . often contain water reserves as well as a reserve of carbohydrates [largely in the form of sugars – particularly fructosans – and starches] and protein which may be comparable in magnitude to vegetative biomass" (Noy-Meir, 1973; cf. Trlica, 1977). The same pattern is evident in marsh vegetation. For example, the rhizomes of *Cyperus marginatus*, an African sedge, have an unusually high mineral and carbohydrate content compared with other parts of the plant (Hamilton *et al.*, 1978). The nutritional richness of the storage parts of certain groups of plants is suggested by comparison to that of dryland root crops domesticated in West Africa. Recent work indicates that under West African climatic conditions the caloric and protein availability of yams exceeds that of either corn or soybeans by a large margin (Coursey and Booth, 1977). The long process of domestication of root crops underscores the utility of subterranean stems, roots, and tubers as a zone of significant food resources in the landscape in which they occur.

CONVERGENCE

Convergence upon similar adaptive zones by different animals is well documented from fieldwork with living animals, and is inferred from studies of extinct forms. The concept of convergence derives from the idea that a given environmental zone poses certain problems and constraints which are independent of the organism. Solutions to these problems and constraints can result in morphological, functional, and/or behavioral similarities in the different kinds of organisms living within a given adaptive zone. For example, functionally analogous food-gathering structures and similar dentitions are often seen in animals that converge upon the same food source (Cartmill, 1974).

The environmental aspects of an organism's adaptive zone can be divided rather simplistically into what the organism eats (food resources) and what eats the organism (predators). The interplay between body size and food resources

deserves consideration.⁵ This relationship appears to be intimately connected to the difference in energetic requirements between large- and small-bodied animals. Smaller animals have relatively higher metabolic rates than larger animals (Schmidt-Nielson, 1979), so that smaller species need a relatively higher intake of energy. Large animals are able to exploit this lower *relative* requirement by emphasizing low-energy food items within their diets (Jarman, 1974; Bell, 1971). At the same time, however, larger animals do have greater *absolute* energy requirements, a difference reflected in their home range size (McNab, 1963). Larger animals can more easily move greater distances than can smaller animals and, unless their food is superabundant, must do so in order to satisfy their higher absolute energy requirements.

These size-related differences in metabolism are known as the Jarman-Bell principle. This principle suggests that body size is an important factor in resource utilization (see Gaulin, 1979). Convergence upon a given adaptive zone should result in similar feeding strategies among similarly sized animals. An investigation of convergence must include some body-size parameter in order to account for the effects of the Jarman-Bell principle. We are interested here in the convergence of large terrestrial mammals upon the adaptive zone of belowground plant storage parts. A survey of Walker's *Mammals of the World* (1975), with 40 kilograms as an arbitrary lower weight boundary, reveals that the large terrestrial mammals whose diets include a significant portion of roots, tubers, and other belowground plant materials are traditionally called omnivores. These mammals fall within the family Ursidae (Order Carnivora), the family Suidae (Order Artiodactyla) and the family Hominidae (Order Primates).

THE LARGE OMNIVORES

The ursids have a geologic range extending from the early or middle Oligocene to the Recent in Europe, the middle or late Miocene to the Recent in Asia, the middle or late Miocene to the Recent in North America, the Pleistocene to the Recent in South America, and the late Miocene to the Pleistocene in Africa (Walker, 1975; Berggren and Van Couvering, 1974). Ursids appear to have arisen from a canid line (Kurtén, 1968).

⁵The relationship between body size and predators is more difficult to discern. As a rule, the large animals suffer little predation since one way to escape predators is to outgrow them (Stanley, 1973). However, predator evasion may also be accomplished through a wide range of behavioral responses by the individual and/or its social group (Jolly, 1972). These may include avoidance, hiding, swamping the enemy, hiding within the group, ringing younger animals with older animals, etc. Such variable responses render tenuous generalizations about the relationship between a single variable such as body size and predator evasion.

Molar enlargement and the loss of the shearing carnassial are characteristic traits of the ursids and point to a shift from a carnivorous to an omnivorous diet. The loss of the last molar in the ursid ancestor is compensated for by the enlargement of the remaining molars. The bunodont molars are presumably adapted for grinding and crushing. Early forms such as *Hemicyon* and *Dinocyon* show the loss of the shearing carnassial, and later forms such as *Ursavus* and *Agriotherium* show the beginning of molar enlargement (Romer, 1966). The post-cranial anatomy of ursids also reflects the shift to a generalized adaptation. Bears have emphasized power of the limbs at the expense of great cursorial abilities. The strong limbs, with their long, nonretractable claws, are used for digging, rolling rocks, and tearing apart logs (Vaughan, 1972).

Craighead and Craighead (1971), in a study of the grizzly bear (*Ursus arctos*) in Yellowstone National Park, call the animal "an efficient omnivore but a relatively inefficient carnivore." An examination of the bear diet supports this view. Bears emerge from a winter sleep around April or May and pamper their shrunken stomachs with grasses, willows, bulbs, skunk cabbage, roots, tubers, herbs, winter-kill carrion, and small mammals. Summer again shows a wide range of food items including most of the spring diet plus fish (caught with the teeth and claws), garbage (from national parks), wild cherries, blackberries, and acorns. To the fall diet can be added late salmon, beechnuts, apples, and wild grapes (Bennett *et al.*, 1943; Bergman, 1936; Craighead and Craighead, 1971; Elman, 1974; Jonkel and McT. Cowan, 1971; Murie, 1937; Walker, 1975). Digging, "presumably for roots," is one of three major feeding activities (the others being consumption of mammals and carrion) of the Yellowstone National Park population of grizzly bears (Annual Report, Interagency Study Team, 1977).

The plasticity of ursid eating habits is clearly indicated in several studies. Murie (1937) reports a cricket "bloom" in Yellowstone National Park during the summer of 1935. The black bears caught the usually elusive crickets by hunting them during the early hours of the day before the insects could warm up. Bennett *et al.* (1943) showed that in any given season the black bear diet is in close accord with the natural abundance of a popular food crop.

The suids have a geologic range extending from the early Oligocene to the Recent of Europe, the middle Miocene to the Recent of Africa, and the late Miocene to the Recent of Asia (Romer, 1966; Berggren and Van Couvering, 1974; Cooke and Wilkinson, 1978). Swine underwent an extensive radiation in Africa during Plio-Pleistocene time (White and Harris, 1977; Cooke, 1978; Harris and White, 1979). While many of these early African forms show an increase in hypsodonty (an adaptation for grazing), others (such as *Kolpochoerus afarensis*) retain the more simple bunodont and brachyodont dentition that is seen in the living wild boar (*Sus*) and the bushpig (*Potamochoerus*) (Cooke and Wilkinson, 1978).

The suids are the most primitive of the artiodactyls and probably arose from members of the paleodonts. Most suids are characterized by having bunodont and brachyodont molar teeth (hypsodont molars appear in some forms), canine tusks, four-toed feet with separate metapodials, and a simple stomach (Romer, 1966). Enamel thickness can vary in the living (and extinct) forms, with the bushpig (*Potamochoerus*) having thicker enamel than the wild boar (*Sus*) (Cooke and Wilkinson, 1978). Specializations for rooting are present. The suid snout is equipped with a disc-like piece of cartilage at its tip which is strengthened by the addition of a bone found in no other mammal, the prenasal. The cartilage and the prenasal combine with the tusks to make a rather formidable digging tool (Walker, 1975). Leister (1939) reports that *Sus scrofa*'s digging abilities are so well developed that two animals encountered no difficulties in digging up their pen's floor of crushed and flattened rock. In the genus *Babyrousa*, males dig through their habitat, turning up food for the females and young which follow behind (Walker, 1975). The padded knees of the warthog (*Phacochoerus africanus*) allow this animal to graze at ground level, an adaptation presumably suited for the recovery of tiller bases (Walker, 1975; Leister, 1939).

It has been said that the warthog is "an exploratory animal which will investigate almost any potential food source" (Field, 1970). This observation seems to be valid for most suids. The suid diet includes grubs, roots, tubers, tiller bases, acorns, herbs, ferns, small rodents, carrion, leaves, fungi, and truffles (Dorst, 1969; Elman, 1974; Galdikas, 1978; Kurtén, 1968; Leister, 1939; Stegeman, 1938). Field (1970), in a study of the warthog in Uganda, reports that 83% of all roots and tiller bases are taken during the five dry months of the year. Roots and tubers are considered to be of primary importance in the diet of the bushpig (*Potamochoerus porcus*) (Dorst, 1969).

Hominids have a geologic range extending from perhaps the Miocene of Africa, Europe, and Asia, but definitely from the Pliocene of Africa and Java, with a present worldwide distribution (Simons, 1972). The weight estimates of 18-63 kg for Pliocene and early Pleistocene hominids (*Australopithecus* and *Homo*) (Pilbeam, 1972) place these animals in the lower to middle weight range for large omnivores.

The dentition of the early hominids is marked by the enlargement of the molars relative to body size and to the incisors (with molar reduction in more recent species) and the reduction of the canines. The cheek teeth are usually broad, have low, blunt cusps, and are covered with thick enamel (Pilbeam, 1972). While the interpretations of this dentition in relation to food processing are numerous and varied (cf. herbivory, Wolpoff, 1973; carnivory, Szalay, 1975; graminivory, Jolly, 1970; frugivory, Walker, 1979), we feel that the evidence most strongly supports an omnivorous diet (Gregory, 1922; Pilbeam, 1972; Simons, 1972). Kay (1975) suggests that the large postcanines of the australopithecines may indicate that these animals had a diet high in fiber and grit content.

The adaptation of the recent hominid *Homo sapiens sapiens* varies widely through time with respect to seasonality, geography, and technological advancement. A study by Tanaka (1976) of the Central Kalahari ≠Kade San substantiates this view. A breakdown of the ≠Kade San diet by weight shows that vegetables comprise 81.3% and animals 18.7%. The vegetable figure increases to 96.4% if certain foods that are utilized as water sources during the dry season are included (Tanaka, 1976). Out of 79 potential vegetable foods, the ≠Kade San use 13 extensively. Six out of these 13 plants are belowground species (as are 30 of the remaining 66). The great importance of belowground plant parts in the !kū San diet is evidenced by their practice of giving separate names to the aerial and belowground parts of the same plant (Heinz and Maguire, n.d.).

Hominids do not appear to be morphologically suited to the recovery of belowground plant resources. The weak fingernails and well-innervated fingers of *Homo sapiens sapiens* preclude digging in all but the softest of soils. Nevertheless *Homo sapiens sapiens* is able to compensate for its lack of morphological specialization for rooting by substituting a digging stick.

DISCUSSION

Convergence upon a given adaptive zone is manifested in similar morphological, functional, and/or behavioral responses. Molar similarities among ursids, suids, and hominids are well known. *Hesperopithecus*, the molar originally classified as belonging to a hominid, thought by some to be a bear, but later discovered to be a peccary, is one famous example (Gregory and Hellman, 1923a, b). Although the peccary (family Tayassuidae) is not a suid, their families are closely related and the dentitions of *Tayassu* and *Sus* are very similar (Cooke and Wilkinson, 1978). Comparisons of the dentitions of bears and pigs have led Kurtén (1968) to remark that "at first glance it may even be difficult to see any difference between the back teeth of a bear and a pig."

As noted by Dunbar (1976), "Similarities in dental morphology do not necessarily imply exact correspondences in diet, but only that the diets in question require similar kinds of processing prior to ingestion." However, in areas of range overlap between living ursids (*Ursus americanus*) and suids (*Sus scrofa*), fieldwork suggests that these animals are utilizing the same foods (Stegeman, 1938). In this case, as in the case of the ≠Kade and !kū San, belowground plant foods comprise an often significant part of the diet. Wild plant rhizomes require substantial dental preparation prior to ingestion (Dunbar, 1976). We feel that the bunodont dental pattern seen in these three forms — broad cheek teeth with low, blunt cusps — is in part a specialization for processing a plant part that is tough, fibrous, and gritty.

The reduction of the canines in early hominids has been a matter of much debate, and has often been viewed as one result of the replacement of teeth by

tools for defense and offense (see Every, 1970). A more plausible argument is one that involves the function(s) of the entire dental complex, such as postulated by Szalay (1975), where canine reduction is seen as a "response to the need for additional incisivation, and perhaps to the need to reduce projection of canines which interfered with the new functions of either the incisor row or the post-canine dentition." While Szalay believes that the cutting and tearing functions of the incisors are adapted to dealing with a meat diet, we feel that such functions are equally well suited to breaking up tough and fibrous plant rhizomes into chunks that can then be prepared by the cheek teeth. The molars and premolars, with their thick enamel, bunodont surfaces, and heavy musculature, seem to be adapted for processing just such a food.

The earliest recovery of these belowground plant storage organs by hominids was probably accomplished by hand, without the aid of a digging stick, as is seen in some lower terrestrial primates (Coursey, 1973; Dunbar, 1976). But, as noted by Coursey (1973), "Even the crudest form of a digging stick so greatly facilitates the operation that a creature which habitually used such tools would be at a marked evolutionary advantage, in the savanna ecological mix." One other important aspect of the simple digging stick is that it possibly served as the example from which other ideas concerning tool manufacture and use arose (Coursey, 1972, 1973; Mann, 1972; Dunbar, 1976).

The morphological differences in the anterior dentitions of ursids and suids, as compared to hominids, appear to relate to specific methods of food gathering and defense (cf. Crompton and Hiiemäe, 1969). The anterior teeth of hominids appear to have lost any actual food gathering or defensive functions. Food gathering was probably under the control of the hands, either directly or indirectly through the use of tools. The possible methods of predator avoidance used by early hominids have received much attention. Peters (1979), among others, suggests that the gracile hominids may have climbed trees as one method of predator evasion, while the robust forms could have defended themselves in open country "with minimal technological investment." The still-functional large canines of ursids are used to procure the meat portion of their diet in a typically carnivorous fashion. The tusks of the suids can function as a part of the rooting complex, and are also the primary means of defense (Elman, 1974). The incisors of all three forms retain their slicing and cutting functions.

Recent archaeological investigations in East Africa suggest that a certain amount of Plio-Pleistocene hominid activity was centered around a home base. The implications of home base use, and its possible interrelationships with bipedality, food carrying, delayed consumption, and food sharing have been reviewed by Isaac (1976, 1978). The stone artifact and bone concentrations at such sites appear to offer evidence of hunting and/or scavenging (Leakey, 1971; Isaac, 1972, 1976). While artifacts have most often been taken as evidence for meat consumption, it seems equally plausible that stone tools were used in the preparation of vegetable foods (see Peters, 1979). The absence of vegetable

parts at these sites does not necessarily mean that plants were not consumed; rather, this absence is most probably due to the preservational bias against plant remains in these settings (Isaac, 1978). As mentioned previously, the yearly pattern of fluctuation in belowground plant storage parts in seasonal climates involves the banking of surpluses during photosynthetically active periods and the expending of the reserve in recovering from periodic or aperiodic stress. The adaptive strategy of the tuberous plant part is one of spending long periods of time in a state of dormancy in between periods of growth. It seems possible that hominids may have exploited this period of dormancy by storing the plant parts until needed for consumption. In addition, some of the larger plant tubers would lend themselves to group consumption, thus making transportation back to a home base a worthwhile effort.

Fieldwork suggests that the diets of bears, pigs, and humans often contain a significant proportion of plant rhizomes. We believe that the postcanine similarities evident among ursids, suids, and hominids are in part an adaptation for processing this tough, fibrous, and gritty plant part. Bears, pigs, and humans are adapted to exploiting plant roots and tubers, although their methods of food gathering are functionally rather than morphologically analogous. Convergence upon the resource of belowground plant storage parts appears to make the responses of nonretractable claws, cartilaginous snout, and digging stick equivalent.

PALEOECOLOGICAL CONSIDERATIONS

As more complete fossil remains are uncovered, paleoecologists are adding detail to their descriptions of the settings of hominid evolution. However, such reconstructions have tended to be cautiously static. A richer approximation of the dynamics of life in the communities in which hominids occurred can be constructed in light of ecological observations of present-day life in analogous situations. Paleoecological reconstructions of the habitats of Pliocene and early Pleistocene hominids usually place these animals in lake margin or flood plain settings that are components of a larger landscape of semiarid shrubland, savannah, or subhumid grassland (Hay, 1976; Jolly, 1970; Isaac, 1978). Recent taphonomical work demonstrates that such water-connected places were probably often the actual site of life of these forms, rather than accidental sites of burial (Behrensmeier, 1975, 1976). Clearly, the availability of a rich food source stored in belowground plant parts is of critical significance in evaluating the potential for hominid subsistence at such sites. Coursey (1973) and Geist (1978) have explored other aspects of this potential food source for hominids.

Workers in the Omo Basin have recovered sufficient pollen samples to allow a sketch of the floristics of hominid sites of 2.5-2 million years ago. The

findings of Bonnefille (1976) and Carr (1976) suggest the broad similarity of the vegetational patterns of the period 2 million years BP with those of today, and also provide direct palynological evidence of the occurrence of hydrophilic vegetation throughout the period. For instance, the pollen of rhizomatous sedges and herbs (e.g., *Typha*) is well represented in the early (2.5 million year BP) community at Omo (Bonnefille, 1976). In the Omo Basin today *Typha* occurs on riverine silt berms and deltas, as well as lake margins (Carr, 1976; Mitchell, 1978). While the generalized pollen profile for the period between 2.5 and 2 million years BP shows an overall desiccation, *Typha* pollen continues to dominate certain localized areas (Bonnefille, 1976). Thus, hydric vegetation, much like that which occurs in present-day wetlands, persisted during this time at Omo, and remained a critical and exploitable resource.

As in many other reconstructions of hominid habitat, Hay (1976) pictures a "savannah grassland, probably with areas of brush and shrub" surrounding the lake site at Olduvai. Though the marked distribution of biomass belowground has been referred to, an additional point must be made: in semiarid as well as marsh landscapes, a significant part of the richest food resource is out of reach of terrestrial herbivores.

As was suggested earlier, the intermeshing of biotic (grazing) and physical (fire and drought) conditions regulates the amount of belowground nutrient reserves. At the same time, the extent to which these forces control the short-term quality and amount of food for aboveground herbivores is suggested by the features of present-day systems. For example, Vesey-Fitzgerald (1965) notes that the natural pastures which occur on the low, seasonally exposed flood plains of shallow lakes in semiarid regions of East Africa today are often fringed by a boundary of alkaline grassland, and criss-crossed by the drainages of freshwater streams. During the dry season the upper stretches of such drainages become seams of high-quality forage. Yet the richest areas of productivity are the natural pastures occurring on the uncovered flood plain during the dry season. Vesey-Fitzgerald (1965) emphasizes the shifting nature of the aboveground lakeshore resource, which is affected mainly by drought and the trampling of stems by large ungulates. Since the crushing of stems has a "rejuvenating" effect similar to that of fire on the pastures, the seasonal visitation of large herbivores to lakesides serves not only to maintain but also to heighten the quality of these areas for ungulate species. The effect of grazing by ungulates is amplified by the tendency toward hierarchical social organization in species feeding either on highly localized, rich pockets of resources – as in this example – or on highly diffused resources such as could be expected in arid or semiarid situations. The feeding behavior of groups of ungulates fitting this model tends to be at once cooperative and intensively focused on specific sites (Geist, 1974), and would presumably have a drastic impact (as a result of both trampling and cropping) on the availability of key food sources.

The natural pastures bordering the uncovered flood plain in the example above, much like perennial-dominated arid lands and shallow littorals, offered important but constantly fluctuating food resources. The task of seeking food for an early hominid dependent on aboveground vegetation would have involved dealing with behavioral patterns and population movements of the dominant ungulates, as well as pulses of herb and seed production.

The observed effect of these perturbations on grasslands and shrublands provides an important clue to understanding how the course of evolution in these systems had affected consumer members of earlier communities. Since grazers seem to have evolved with savannah grass and shrubland vegetation types (Van Couvering, 1976), it is not surprising that large herbivores are coming to be seen as a vital regulatory factor in the disposition of plant production. Recent work suggests a complex of mutualistic interactions between animals and plants: the facilitation of energy flow between grazers (McNaughton, 1976), the maintenance of herb diversity by normal grazing and trampling (Chew, 1974; Trlica, 1977; Stoddart *et al.*, 1975; Ellison, 1960), species turnover stemming from overgrazing (Peterides, 1974), and the stimulation of herbaceous productivity (Owen and Wiegert, 1976; Detling *et al.*, 1979; Dyer, 1979). All of these interrelations suggest that over evolutionary time there has been a progressive tightening of the energy pathways between the producer and consumer compartments, a fact of significance for other animals seeking a living as something other than a herbivore in the same system.

Hamilton *et al.* (1978), in their account of omnivory in two populations of flood plain-dwelling Chacma baboons (*Papio ursinus*), provide a suggestive example of the difficulties involved for a consumer species existing outside the grassland-large terrestrial herbivore linkage. The baboons feed on many of the same plant species as the dominant ungulates of the area, but avoid competition by utilizing stem bases and shallow rhizomes that are too close to the ground to be cropped by grazers and require manipulative skill to collect. The kneeling warthog that grazes tiller bases at ground level is another example. Because these omnivores are exploiting a niche that is strongly shaped in terms of periodicity and productivity by herbivores, their strategy seems to be to move away from overlap with the main pathway of production and to feed as predators, rather than participate in a coevolutionary mechanism (Hamilton *et al.*, 1978; cf. Geist, 1978).

The omnivore diet reflects the seasonal availability of various food items (Bennett *et al.*, 1943; Dunbar, 1976; Field, 1970), an observation of great importance to our understanding of Pliocene and early Pleistocene hominids. The dry season is the time of greatest stress in semiarid environments (Whitaker, 1970). Belowground plant storage parts are one food item not seriously affected at this time of year (Trlica, 1977). In addition, many roots and tubers

offer valuable supplies of rather scarce water (Tanaka, 1976; Noy-Meir, 1973). Fieldwork with semiarid grassland omnivores has shown that the widest exploitation of plant rhizomes and tiller bases occurs during the dry season (Field, 1970; Tanaka, 1976; Dunbar, 1976). It is unlikely that evolving hominids could afford to ignore the relatively stable and nutritionally rich zone of belowground production during this time of the year.

Earlier speculation on hominid diets based on baboon analogies (Jolly, 1970) has failed to grasp the full range of resources in the environments of Pliocene and early Pleistocene hominids. Preoccupation with aboveground foods has, in paleoecological analyses, placed hominids in a zone of resources constantly fluctuating under the influence of biotic and physical factors. While it is important to realize that the early hominid diet probably included a wide variety of both plant and animal (scavenged or hunted) matter (see Geist, 1978), the role of belowground plant storage parts during the dry season, and perhaps during the entire year, cannot be underestimated.

The analogies that have been drawn here between past and present plant communities suggest the existence of a rich alternative food source. Belowground storage parts of water-edge plants and perennials of semiarid areas comprised a nutrient cache that was an integral part of the habitats of early hominids. The strategy of keying into a resource that was largely free from the effects of grazing, fire, and seasonal drought would assure a more reliable food source than that offered by aboveground vegetation.

It is interesting to note that all three of the families of large omnivores either originated or underwent adaptive radiations in Miocene and Pliocene times. Origins and adaptive radiations are related to the movement or adaptive shift of a group into a new adaptive zone (Simpson, 1953). An adaptive shift can result from a number of different factors (Von Wahlert, 1965), with one of these being the appearance of a new set of resources.

Although the evolution of belowground plant storage parts is not well documented, it seems possible that the increasing aridity of Miocene and Pliocene times (Andrews and Van Couvering, 1975; Peters, 1979), along with the need of some plants to escape the pressures of grazing and fire, are factors responsible for an accelerated trend begun in the Oligocene toward the development of belowground storage parts (Bruce Tiffney, personal communication). This in itself represents an adaptive shift on the part of the plants. The sinking of nutrients belowground produced a new and exploitable resource. It appears then that the three different families of mammals each evolved functionally analogous solutions to the problems of utilizing the resources of this new adaptive zone. We suggest that such an adaptive shift was in part responsible for the origins and/or adaptive radiations of ursids, suids, and hominids that are seen during the Miocene and Pliocene times.

CONCLUSION

Partial convergence by ursids, suids, and hominids upon belowground plant resources resulted in functionally analogous food-gathering structures (claws = snout = digging stick) and similar postcanine dentitions.

Belowground plant storage parts offer a nutritionally rich food resource. These plants parts are relatively unaffected by grazing, fire, and drought. The belowground food source therefore would have allowed an important measure of security, stability, and independence for hominids seeking a living in Pliocene and early Pleistocene times. The entry of hominids into a food base that was independent of the uncertainties of fire, drought, and ungulate movements possibly played a profound role in the later evolution of this group.

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