The human adaptations to meat eating: a reappraisal

Claude Marcel Hladik, Patrick Pasquet

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C.M. Hladik

éco-Anthropologie, CNRS (FRE 2323) and Museum National d'Histoire Naturelle, Laboratoire d'Ecologie, 4 avenue du Petit Château. 91800 Brunoy (France)

P. Pasquet

Dynamique de l'évolution humaine CNRS (UPR 2147) 44 rue de l'Amiral Mouchez. 75014 Paris (France)

In this paper we discuss the hypothesis, proposed by some authors, that man is a habitual meat-eater. Gut measurements of primate species do not support the contention that human digestive tract is specialized for meat-eating, especially when taking into account allometric factors and their variations between folivores, frugivores and meat-eaters. The dietary status of the human species is that of an unspecialized frugivore, having a flexible diet that includes seeds and meat (omnivorous diet). Throughout the various time periods, our human ancestors could have mostly consumed either vegetable, or large amounts of animal matter (with fat and/or carbohydrate as a supplement), depending on the availability and nutrient content of food resources. Some formerly adaptive traits (e. g. the "thrifty genotype") could have resulted from selective pressure during transitory variations of feeding behavior linked to environmental constraints existing in the past.

Key Words: meat eating, hominids, gut allometry, thrifty genotype

Introduction

In a paper presented in this journal, Henneberg, Safaris and Mathers (1998), argued that Homo sapiens is a habitual rather than a facultative meat eater. As an extension of the "expensive-tissue hypothesis" proposed by Aiello and Wheeler (1995) the idea that a major trend toward carnivory occurred in hominid evolution was also supported by data on coevolved parasites and metabolic adaptations.

Recent data and discussions concerning primate gut morphology in relation to diet (Hladik et al. 1999), as well as the fact that the evolutionary history of the hominids is much longer than previously recognized (Senut et al., 2001) may highlight in a different way the fundamental dietary trend of our species.

Current hypotheses on dietary trends

Based on the remarks made by Dart (1953) about stone artifacts and faunal remains being associated with Australopithecinae, Ardrey (1976) suggested the "hunting hypothesis" namely that meat eating was a milestone in hominid evolution. The complex social bonds and technical skills necessary for the collective organization of hunting parties would have complemented morphological and behavioral adaptations. Using as analogies the baboon model (Devore and Washburn, 1963), and present-day human groups of hunter-gatherers (Lee and Devore, 1968), discussions and speculations focused on the relationships between game acquisition, feeding ecology and social organization. The adaptive biological significance of meat eating was summarized by Milton (1999), who stated that "the incorporation of animal matter into the diet played an absolutely essential role in human evolution", otherwise the arid and seasonal environment likely to be the cradle of hominids would not have provided enough protein.

In their often cited paper, Aiello and Wheeler (1995) proposed the "expensive-tissue hypothesis" which focus on the evolutionary forces responsible for the increase in the hominid brain size. They stressed the importance of the shift to a high-quality diet with its corresponding gut adaptation. By lowering considerably the energetic cost for basal metabolism, a reduced intestinal mass may permit disposal of sufficient energy to cover the extra-expenditure required by a larger brain. Aiello and Wheeler based their argument on the relationship between body mass and Basal Metabolic Rate (BMR): the Kleiber line characterizing relationship between BMR and body size is identical for all mammals, including humans. Since maintenance of gut and brain tissues are equally expensive, Aiello and Wheeler proposed that gut reduction allowed the emergence of the large brain in hominids.

Henneberg et al. (1998) developed further arguments concerning the role of meat eating in human evolution. For these authors, the quantitative similarity of human gut morphology to that of carnivorous mammals is a strong argument for the proposition that the human status is that of a "well evolved meat eater". These authors also provided additional arguments concerning the evolution of taenioids, the parasites linked to meat eating. Initially transmitted by domesticated dogs, these parasites coevolved with humans and acquired a strict host status as a result of regular meat eating during long time periods. Another argument for habitual meat-eating in humans is their capacity to digest heam and other porphyrin-iron compounds derived from meat (although this might be a common trait of most primates), whereas herbivorous mammals cannot absorb such compounds.

Diet and gut size revisited

To support their hypothesis, Aiello and Wheeler (1995) refer to a set of measurements of the intestinal tract of primates published by one of us (Hladik, 1977; Chivers and Hladik, 1980) –with some adjustments– compared to human intestinal tract measurements (data from Aschoff et al., 1971). However, the sample they used to determine non-human primate gut weight includes species of primates with partly folivorous diets rich in fiber. For this reason, the expected gut size for a "standard human"–derived from this sample and larger than observed– reflected mostly the actual differences in diet between the reference primate sample and human beings (Hladik and Pasquet, 1999).

Furthermore, because data on gut areas are more accurate than weights, they should be used instead to compare the dietary adaptations of different species. Most weighing was done after excess moisture from gut parts dissected in water was removed; hence published weights must be used with caution. Area measurement of relaxed gut parts were conducted to assess functional capacity (i.e., absorption and the size of fermenting chambers) in relation to functional body size (Hladik, 1977).

Figure 1 shows the scaling of the gut area to body size for three groups of species of non human primates, and some other mammals, according to whether they were folivores, frugivores, or faunivores in their major dietary preferences. The slopes of the best fit lines corresponding to these three groups differ significantly. Accordingly, the comparison of gut absorptive areas of animals with unlike body sizes should take into account different allometric relationships. The absorptive areas vary according to body length (L), scaled to $L2.64$, $L2.37$ and $L1.98$, respectively for folivores, frugivores and faunivores (that is a large range of morphological variation, between $L2$ and $L3$). We (Chivers and Hladik, 1980) proposed a geometrical model to explain the functional effect of allometry so that animals with high-quality diet (faunivores, and to a lesser extent, frugivores) show a reduced absorptive area when compared to folivores; assuming, of course, a constant flux per unit mucosal area for all species. Thus, in humans, a clear-cut adaptation to meat eating would imply that the gut allometric relationship coincides with that of the "faunivores", having the lowest absorptive area. This is not supported by measurements of human gut size as plotted in fig 1; all these measurements were grouped on the best fit line of the frugivores (Hladik et al., 1999). Such measurements of human guts, carried on with a method similar to that used for non human primate, were not taken into account in the analysis of Aiello and Wheeler.

The type of "frugivore" adaptation characterizing Homo sapiens and several other primate species does not exclude small proportions of insects and/or leafy materials in the diet, especially to balance the amino acid intake. The unspecialized morphology of this frugivorous type also corresponds to the most flexible and opportunistic feeding behavior of primates (Hladik, 1981).

Energy, nutrient needs, and diets

Together with their aguments on parasitology and digestive physiology, Henneberg et al. (1998) presented some data on energy intake. These suggest that human absorption efficiency is intermediate between that of herbivores and carnivores, but closer to that of carnivores. Taking into account the fact that a part of the data has been recorded in zoos, and the possibility that net energy rather than gross energy intake was used for some species, these considerations highlight, once again, the necessity for humans to find energy in an easily digestible form. Similarly, the "coefficient of gut differentiation" (after correcting the mismatch in the figures' legends of the published paper) do not support the claim that of human beings are closer to cats and dogs than to monkeys and apes; clearly, this type of measurement does not take into account the allometric factor, necessary when comparing species with different body sizes (Chivers and Hladik, 1980).
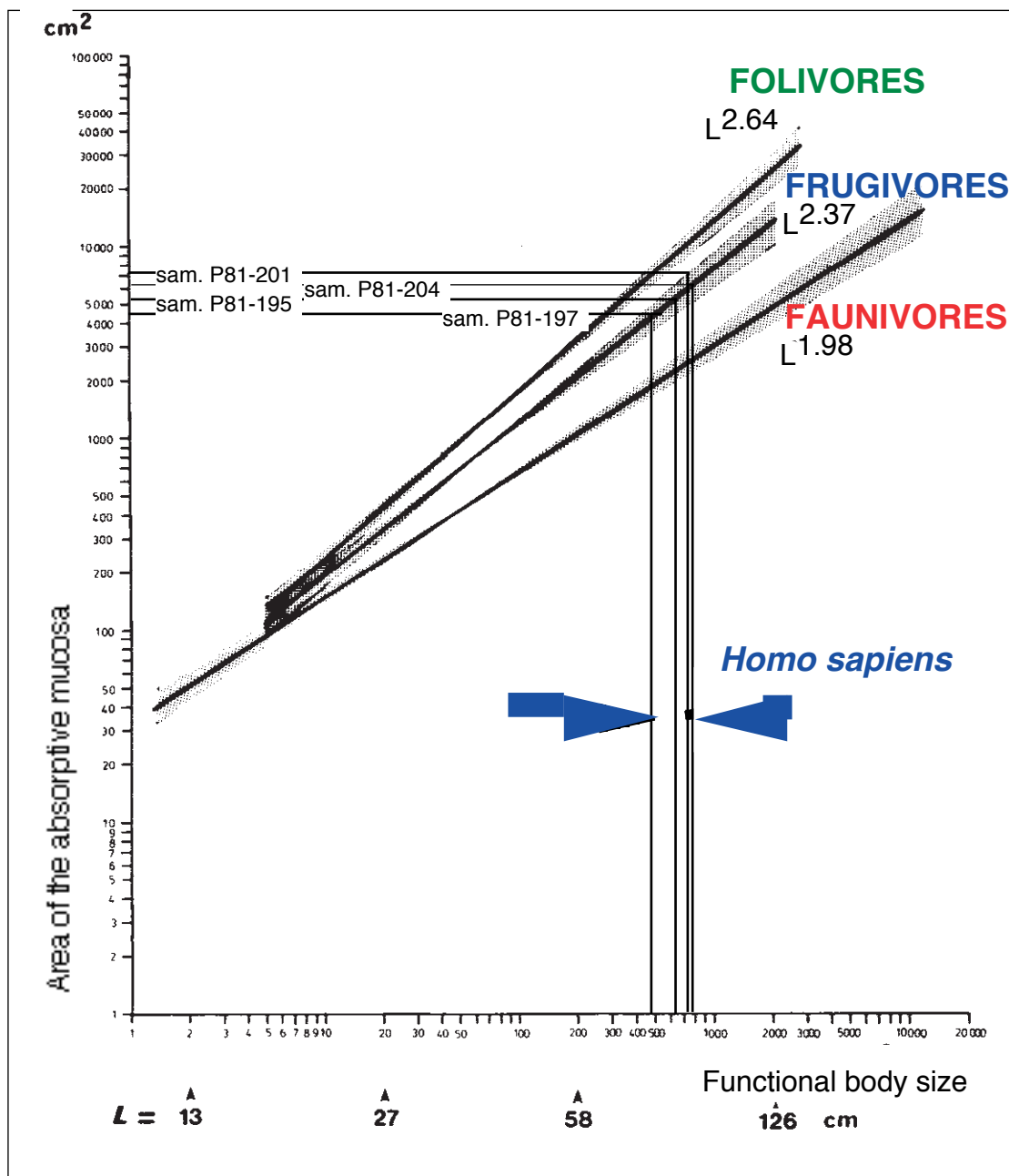
Figure 1. Allometric relationship between the area of the absorptive mucosa of the digestive tract and functional body size in three distinct group of species, according to major dietary patterns (in a total of 117 primates of 50 species, among 180 mammals). Similar measurements of 4 post-mortem human specimens (samples P81 of Hladik and Chivers) are reported on this figure. Functional body size ($10-3L3$) is plotted along a logarithmic scale (L= nose to anus for animals; sitting height for humans). (taken from Chivers and Hladik, 1980; Hladik et al., 1999)

The link between a high quality diet (eventually including animal matter), and the enlargement of the brain characterizing hominid evolution, previously highlighted by several authors (Martin, 1983; Foley and Lee, 1991; Leonard and Robertson, 1997) can be the result of a behavioral change, followed or not by morphological adaptation (i.e. a redistribution in the size of the different organs). In his allometric analysis of the evolution of the mammal brain Martin (1983) identified four separate "grades" of relative brain size (fig. 2) characterized by the slope and position of the major axis of the relationship between cranial capacity and body weight. Since each of these "grades" includes species with various diets (folivores, fugivores, carnivores), there is no clear-cut relationship between brain size and dietary adaptation. Thus, it is likely that a compensatory energetic reduction allowing the functioning of the large brain of Homo (with respect to Kleiber's law) may affect all body parts rather than being exclusively focused on gut tissue (Hladik et al., 1999).

With relation to the energy needs, primate feeding strategies vary from a type involving low-energy cost / low energy yield (i.e. for most folivore±frugivore), to a type involving the opposite, namely high energy expenditure / high energy intake, such as in baboons and chimpanzees (Hladik, 1981). The latter corresponds to a diet focused on the most "packed" (in terms of energy density), dispersed but rewarding plant foodstuffs (the sweetest fruits and fatty arils). Such a diet may also include fatty insects and, occasionally, meat.

To cover their other nutritional needs, primate species with a frugivorous diet supplement their food intake with proteins from young shoots and leaves, or from animal matter (mostly invertebrates). This is the most flexible dietary adaptation possible, for it allows switching among the various categories of food items available in different habitats throughout the seasonal cycle (Hladik, 1988). The ambiguous term omnivore is used to either describe such a flexibility, or to emphasize that a meat supplement is eventually included into a frugivorous diet. However, one should notice that the largest primate species, especially anthropoids, use mainly vegetable matter to meet their protein requirements. Chimpanzees, may occasionally eat the meat of small mammals, but they do not cover their protein requirements from this source; anyhow, this source is rarely available to females and never used by the youngest animals (Hladik, 1981).
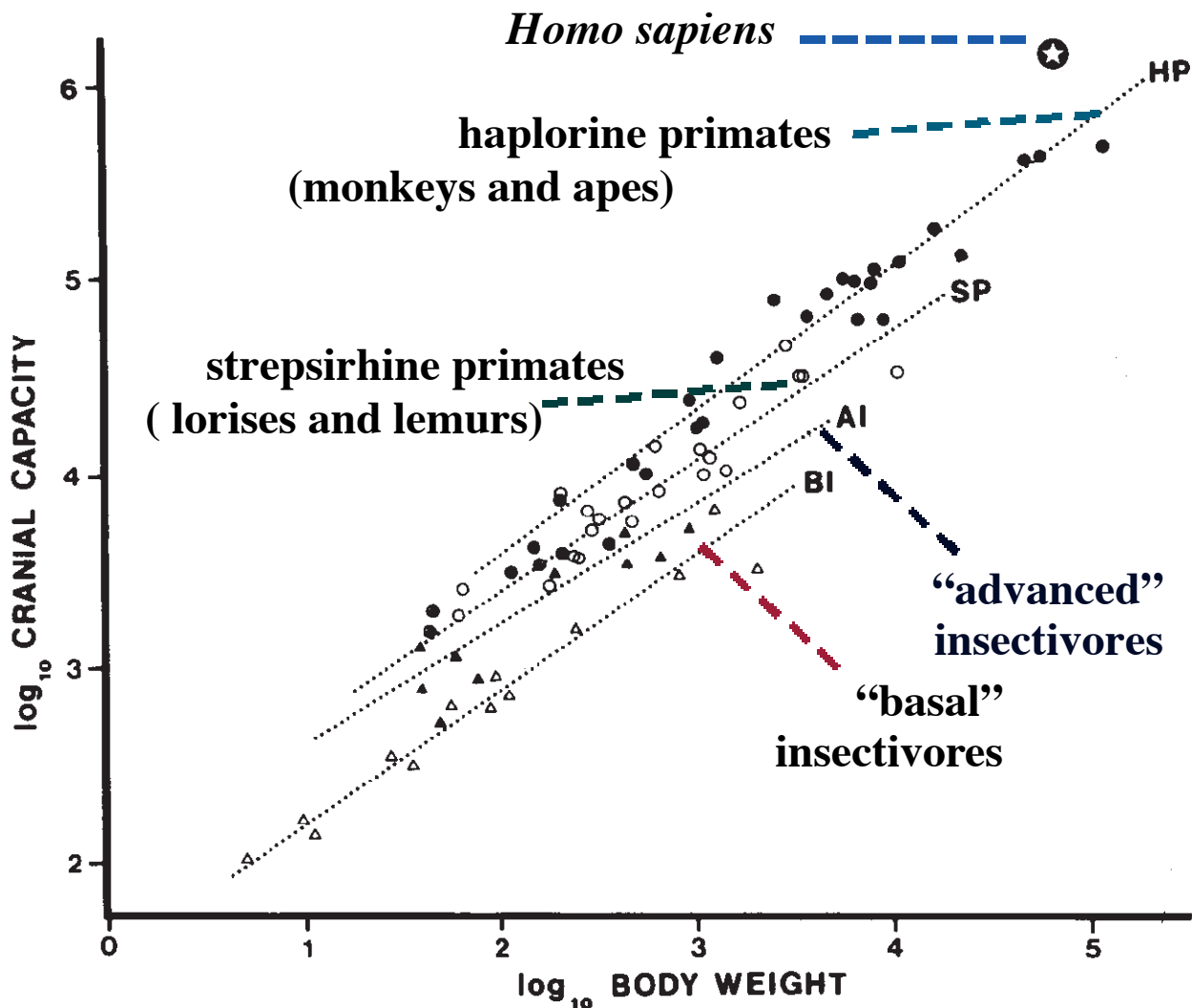
Human evolution and dietary changes

Figure 2. Allometric relationships between cranial capacity and body weight in different categories of primates and insectivorous mammals (after R.D. Martin, 1983).

There is no reason to think that, during the last 6 million years during which hominids evolved (among others) forms closer and closer to Homo sapiens (Senut et al., 2001), there was a significant departure from this unspecialized and flexible dietary adaptation. However, the dietary history of hominids is likely to show several changes. Throughout the various periods, human ancestors could have consumed mostly vegetable, or mostly animal matter depending on the availability and nutrient content of food resources,(Gordon, 1987, Couplan, 1997). The present consensus scenario of our past feeding behavior posits three major phases: (1) After the late Miocene climate shift, hominid feeding behavior, progressively shifted from a mainly vegetarian diet to a diet including more and more animal matter, either from hunting and/or from scavenging, under changing environmental circumstances. (2) The hunter-gatherer way of life, and the resulting diet, characterized conditions up to the mid-Pleistocene. In the late Pleistocene, during the ice-ages, hominids had to specialized on large game. (3) These successive phases, as described by Gordon (1987), have been followed by the progressive control over animal and vegetable resources through domestication and cultivation, thus allowing some human groups to eat more vegetable matter than during most previous periods.

Meat has been obviously consumed, but it is unlikely that animal flesh (especially lean meat) was a staple food for long periods. As highlighted by Speth (1989, 1991), fat and fatty meat provide energy to meat eaters, but lean meat can become rapidly unhealthy if used as a unique food. During "lean periods", meat must be complemented with vegetable matter as an energy source, especially when it is necessary to cover the extra energy needed for reproduction. During such periods, the energy derived from protein should not exceed 25% of the total intake.

Nevertheless, the consumption of large amounts of protein (mostly from large mammals, especially during the ice-ages) could have triggered selective pressure for an increase in the post-absorptive insulin response - with insulin-resistance as a major consequence - a trait adapted to an environment where carbohydrate availability is reduced (Brand-Miller and Colagiuri, 1994). Such a "thrifty genotype" would have persisted among some modern populations not or lately faced to the transition to agriculture (determining a shift to larger amounts of available carbohydrates), such as the West American Indians (Neel, 1982; Young, 1993), for whom the high prevalence of diabetes mellitus and associated obesity results from the westernization of their diet. In other populations (i.e. in Europe) the disappearance of selective pressure for the insulin response with the advent of plant and animal domestication between 8,000 and 5,000 BP explains the relatively low prevalence of diabetes mellitus and obesity at the present time (Brand-Miller and Colagiuri, 1994).

In the same vein, the persistence for more than 100,000 years, of taenioid parasites that had coevolved with humans as they hunted with dogs during periods of large game consumption - a hypothesis proposed by Henneberg et al. (1998) as evidence for habitual meat consumption - can be viewed as an inheritance from these ancient times. It is generally recognized that specialized forms (such as parasites) cannot return to their initial, unspecialized forms. For this reason, teaniods could have persisted, even during periods of low meat consumption.

A carnivorous diet may be supported by several lines of evidence recorded in the archaeological literature (Isaac and Crader, 1981). Nevertheless, a lack of evidence for the presence of vegetable materials is no proof that some edible plant were not abundant, even during the ice-ages (Reichholf, 1990).

Dietary variation and cultural changes

With respect to the origin of hominids, it must be stated that the high quality foods necessary to provide enough energy could have been found in sources other than the fat meat of large game. Wrangham et al. (1999) provided a new and very exciting hypothesis linking the process of hominization to the early use of fire for cooking. As long ago as 1.9 million years (Plio-Pleistocene), the initial Homo erectus forms of both sexes tended to have large body (and brain) sizes, with a reduction of the teeth. This was possible (and likely to be selected for) when a shift to a high calorie diet that did not necessitate long lasting mastication occurred. Either cooked fatty meat, or cooked wild tubers may provide this type of food. Cooking in embers considerably improves the taste and texture of both foods; it may explain why it would have been rapidly adopted by hominids able to master the technique of fire (with brain increase obviously related to technical skills). However, the most efficient way of obtaining calories would be to cook starchy tubers (50% more energy from starch after cooking). Furthermore, most wild yam species are non toxic and available in large quantities throughout Africa's forests and savannas (A. Hladik and Dounias, 1993). Archaeologists have not yet found clearly identified long-lasting hearths (with the trace left by high temparatures on the surrounding

ground), dating from before the mid-Pleistocene. But the presence of tiny charcoal remains mentioned by Wrangham et al. could be quite convincing evidence for the early utilization of fire, as anybody who has recently visited an abandoned Pygmy forest settlement could attest. A few months after the Pygmies left the encampment, no obvious trace of a hearth was visible, even though the occupants has cooked meat and tubers, wrapped in large leaves, in the embers of small fires. This cooking technique, as well as the various technical processes that allow plant parts to be detoxified (Johns, 1990) may have lasted for several millenium without leaving visible tracxes for archaeologists to identify.

The behavioral and social consequences for Homo spp., of the utilization of foods easily digestible and high in energy (including meat as well as vegetable matter) imply complex social bonds and technical skills such as those that underpin the organization of hunting parties. Meat eating obviously played a part in hominid history. But the unspecialized gut anatomy that allowed adaptation to various diets in various environments was plobably a facilitating factor - among others - of the exponential increase in technical skills and cultural traits, that accompanied the enlargment of the brain.

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