

Theories of Human Evolutionary Trends in Meat Eating and Studies of Primate Intestinal Tracts

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ABSTRACT

Theories of hominid evolution have postulated that switching to meat eating permitted an increase in brain size and hence the emergence of modern man. However, comparative studies of primate intestinal tracts do not support this hypothesis and it is likely that, while meat assumed a more important role in hominid diet, it was not responsible for any major evolutionary shift.

INTRODUCTION

Despite the enormous variation in current human diet in different cultural and environmental settings (Farb and Armelagos, 1980; Garine, 1990), whether or not there is such a thing as a “basic” human diet is a long-

standing and controversial issue both for nutritionists and anthropologists. The evolutionary trends of our ancestors that may shed light on past diets have been investigated via a number of different approaches including studies that compare them with other primates and mammals (e.g. Kay and Hylander, 1978; Whiten and Widdowson, 1992); analysis of isotopic composition of fossil hominid bones and teeth (Ambrose and De Niro, 1986); palaeo-environments (Bunn and Kroll 1986), and studies on contemporary hunter-gatherers (Hill, 1982, O'Connell *et al.* 1988; Kaplan *et al.*, 2000). However, the various research approaches available at present cannot yield a definite representation of our past dietary history, especially when the focus is on a long-term study of meat eating.

In spite of a consensus among modern researchers that large amounts of meat were consumed by hominids during prolonged periods of history (Gordon, 1987), the reality of biological adaptation to meat eating is questionable. To address this issue, we will examine data concerning gut morphology that might be used as evidence of adaptive dietary trends.

MEAT EATING AND HOMINIZATION

Based on the remarks of Dart (1953) about stone artefacts and faunal remains associated with Australopithecinae, Ardrey (1976) suggested the "hunting hypothesis", which implies that meat eating was a milestone in hominid evolution. The morphological, behavioural and social consequences of meat eating would have been linked to the complex social bonds and technical skills that imply group organization of hunting parties. A number of speculative debates on this matter, using the baboon model (Devore and Washburn, 1963) and analogies with current human groups of hunter-gatherers (Lee and Devore, 1968), have 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 came to the conclusion 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 have been the cradle of hominids would not have provided enough protein. The link between a high quality diet (including animal matter) and the enlargement of the brain (characterizing

hominization) has been highlighted by several authors (Martin, 1983; Foley and Lee, 1991; Leonard and Robertson, 1997).

In their most quoted paper, the argument of Aiello and Wheeler (1995) supports this view, proposing the “expensive-tissue hypothesis”, related to the evolutionary forces implied in the increase of hominid brain size. They focus on the shift to a high-quality diet and corresponding gut adaptation. A reduced intestinal mass would considerably lower the relative energy cost and permit disposal of sufficient energy to cover the extra-expenditure of a larger brain. The main point of Aiello and Wheeler is based on the relationship between body mass and Basal Metabolic Rate (BMR): the Kleiber line characterizing the relationship between BMR and body size is identical for all mammals, including humans. Since maintenance of gut tissue is as expensive as that of brain tissue, Aiello and Wheeler proposed that gut reduction compensated for brain increase.

Henneberg *et al.* (1998), following this point of view, developed further arguments on the role of meat eating in human evolution. For these authors, the “quantitative similarity of human gut morphology to guts of carnivorous mammals” is a strong argument for a human status of “well evolved meat eater”. In fact, one should ask if there is actual evidence of human gut adaptation to meat eating in the past that would have permitted a characteristic swing towards carnivorousness.

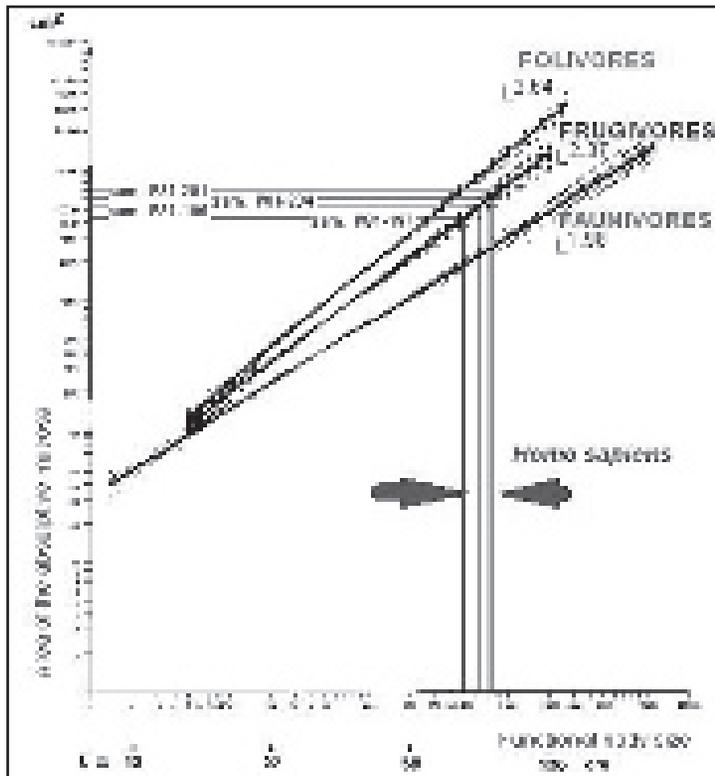
PRIMATE DIETS, DIGESTIVE TRACT AND BRAIN

To support their hypothesis, Aiello and Wheeler (1995) refer to a set of measurements of the intestinal tract of primates published by Hladik (Hladik, 1977; Chivers and Hladik, 1980), with certain adjustments, as compared to the human intestinal tract (data from Aschoff *et al.*, 1971). However, since the sample they used to determine non-human primate gut size (or gut weight) includes several species of primates with folivorous diets rich in fibre (such as gorillas), the expected gut size for a “standard human” – derived from this sample and larger than normally observed – could reflect, to some extent, differences in diet between the reference primate sample and humans (Hladik and Pasquet, 1999).

Gut areas rather than weight were used in Hladik's studies. Data on areas is more accurate than weight because most weighing is performed after the removal of excess moisture of gut parts dissected in water; hence published weights must be used with caution. Furthermore, area measurement of relaxed gut parts was aimed at comparing functional capacity (i.e. absorption and the size of fermenting chambers) in relation to functional body size (Hladik, 1977).

FIGURE 1

Allometric relationship between the area of the absorptive mucosa of the digestive tract and functional body size in three distinct groups 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 in this graph. Functional body size (10-3L3) is plotted along a logarithmic scale (L= nose to anus for animals; sitting height for humans)

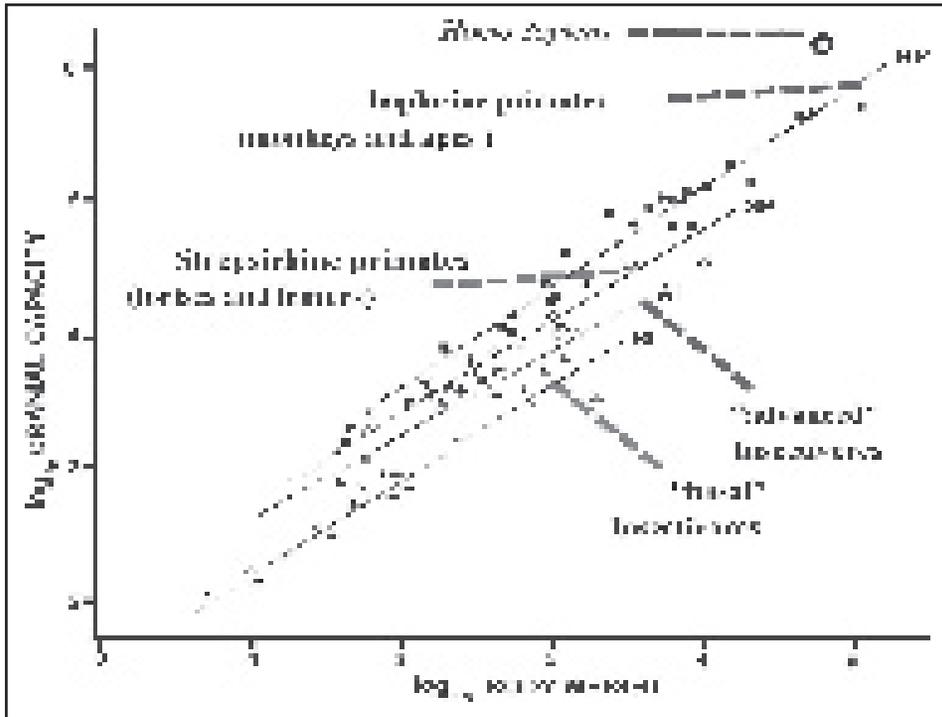
SOURCE: Hladik *et al.*

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 their major dietary tendencies: folivorous, frugivorous and faunivorous. The slopes of the best fit lines corresponding to these three groups differ significantly. Accordingly, the comparison of gut absorptive areas of animals differing in body size would seem to account for different allometric relationships. The absorptive areas vary according to body size, scaled to $L^{2.64}$, $L^{2.37}$ and $L^{1.98}$, respectively for folivores, frugivores and faunivores. A geometrical model was proposed 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, as compared to folivores, assessing for all species a constant flux per unit of mucosal area (Chivers and Hladik, 1980).

Thus, in humans, a clear-cut adaptation to meat eating would imply that the gut allometric relationship coincides with that of the “faunivores”, with the lowest absorptive area. This is not supported by the measurements of human gut size that are plotted in Fig 1, all these measurements being grouped on the best fit line of the frugivores (Hladik *et al.*, 1999). These measurements of human guts, carried out by a method similar to that used for non-human primates some time after the study of non-human primates, were not taken into account in the analysis of Aiello and Wheeler.

Returning to the issue of relating increase in brain size to dietary adaptation, there is obviously no direct relationship. Similarly, Martin (1983) in his allometric analysis of the evolution of the mammal brain identified four separate “grades” of relative brain size (Fig. 2) characterized by the slope of the major axis of the relationship between cranial capacity and body weight.

FIGURE 2
Allometric relationships between cranial capacity and body weight in different categories of primates and insectivorous mammals



SOURCE: R. D. Martin, 1983.

Since each of these “grades” includes species with different diets (folivorous, frugivorous, carnivorous), there is no clear-cut relationship between brain size and dietary adaptation. It is thus likely that a compensatory energetic reduction that allows 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.

DISCUSSION: DIET AND HOMINIZATION

Most forest primates have a frugivorous diet, with a supplement of protein provided either by young vegetable shoots and leaves, or by animal matter (mostly invertebrates). This is a most flexible dietary adaptation that allows

them to switch between the various categories of food items available in different habitats throughout the seasons of the year (Hladik, 1988). The ambiguous term omnivore is used either to describe such flexibility or to emphasize a supplement of meat included from time to time in a mainly frugivorous diet. However, it is noticeable that the largest primate species, especially anthropoids, consume mainly vegetable matter to provide their protein requirements. Chimpanzees, that occasionally eat the meat of small mammals, do not receive all their protein requirements from this source, which is anyway rarely available to females and never exploited by the youngest animals (Hladik, 1981).

Considering the unspecialised frugivorous-type human gut anatomy, the dietary history of the genus *Homo* is likely to display a wide range of variation. During various historical periods, depending on availability and the nutrient content of food resources, our human ancestors would mostly have consumed either vegetable or animal matter (Isaac *et al.*, 1981; Gordon, 1987; Couplan, 1997). The present consensual picture of our past feeding behaviour includes three major phases: (1) After the late Miocene climate shift, hominid feeding behaviour in changing environments progressively shifted from a mainly vegetarian diet to a diet including more and more animal matter, either from hunting and/or from scavenging; (2) the hunter-gatherer way of life and the resulting diet characterized the mid-Pleistocene period, but in the late Pleistocene, during the ice-ages, hominids had to specialize in large game; (3) these successive phases, as described by Gordon (1987), were followed by progressive control of animal and vegetable resources through domestication and cultivation, allowing some human groups to eat more vegetable matter than during previous periods.

Meat was consumed, but it is unlikely that animal flesh (especially lean meat) was a staple for long periods. As highlighted by Speth (1989, 1991), fat and fatty meat provide energy for meat eaters, and lean meat can rapidly become unhealthy if used as an only food. During “lean periods”, meat must be complemented with vegetable matter as an energy source, especially to provide the necessary energy for reproduction.

The high quality foods needed to provide enough energy for the incipient hominids could have been drawn from alternative sources rather than the fat meat of large game. Wrangham *et al.* (1999) have provided a new and very

exciting hypothesis on the possible process of hominization, made possible by the early use of fire for cooking. As far back as 1.9 My (Plio-Pleistocene), the first *Homo Erectus* tended towards a large body (and brain size), for both sexes, with a reduction of teeth. This was possible by (and likely to be selected for) a shift to a high caloric diet that did not require much mastication. Either a cooked fatty meat or a cooked wild tuber may have provided this type of diet. Cooking in embers considerably improves the taste and texture of both kinds of food and may explain why it could have been rapidly adopted by hominids able to master the technique of fire (with brain increase obviously related to technical skills). However, the best efficiency for obtaining calories would be with cooked starchy tubers (50% more energy from starch after cooking). Furthermore, most wild yam species are non-toxic and available in large quantities throughout African forests and savannas (A. Hladik and Dounias, 1993). Although clearly identified long-lasting hearth locations have never been found by archaeologists before the mid-Pleistocene, the evidence of early utilisation of fire based on charcoal residue fragments mentioned by Wrangham *et al.* would be quite a convincing argument for anyone who has recently visited an abandoned Pygmy forest settlement, and searched for tiny pieces of charcoal. After a few months, no obvious trace of a hearth is visible, although meat and tubers, wrapped in large leaves, have been cooked in the embers by the Pygmies.

Consequently, meat eating certainly played an essential part in hominid history, but the hominid flexible gut anatomy permitted adaptation to various diets. Taking into account the allometric factors in the comparative study of primate gut anatomy, there is no evidence to support theories such as a change in gut anatomy that allowed carnivorousness and a simultaneous increase in brain size. Alternatively, the early cooking of gathered foods – and the nutritional, behavioural and social consequences of this pattern – could have been a major milestone in the hominization process.

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