Energetics and the Evolution of Brain Size in Early *Homo*

William R. Leonard[1], Marcia L. Robertson[1], and J. Josh Snodgrass[2]

[1]Department of Anthropology, Northwestern University, Evanston, USA

[2]Department of Anthropology, University of Oregon, Eugene, USA

Introduction

Anthropologists have increasingly begun to rely on energetic models to understand the patterns and trends in hominin evolution (e.g. Aiello and Wheeler, 1995; Leonard and Robertson, 1994, 1997; Leonard, 2002). The acquisition of food energy, its consumption, and ultimately its allocation for biological processes are all critical aspects of an organism's ecology (McNab, 2002). In addition, from the perspective of evolution, the goal for all organisms is the same – to allocate sufficient energy to reproduction to ensure their genes are passed on to future generations. Consequently, by looking at the ways in which animals go about acquiring and then allocating energy, we can better understand how natural selection produces important patterns of evolutionary change. This approach is particularly useful in studying human evolution, because it appears that many important transitions in the hominin lineage – the evolution of bipedality, the expansion of brain size and the initial colonization of northern climes – had implications for energy allocation (Leonard, 2002).

In this chapter, we use an energetic approach to gain insights into the evolution of brain size with the emergence of the genus *Homo*. We begin by looking at the energy demands associated with large brain size in modern humans relative to other primates and other mammals. We then examine the hominin fossil record to gain insights into changes in brain size, foraging strategies and dietary patterns associated with the evolution of early *Homo*. Both the comparative and fossil evidence suggest that the increased metabolic costs of larger brain sizes in the genus *Homo* were dependent upon the changes in dietary quality and alterations in body composition. Although we do not know the specific components of the diet of early *Homo*, it does appear that these hominins consumed a diet of greater energy and nutritional density than their australopithecine ancestors. In addition, it also appears that expansion of the brain size in the hominin lineage was associated with

potential reductions in muscularity and/or gastrointestinal (GI) mass and increases in adiposity (body fatness).

Metabolic demands of large brain size

What is remarkable about the large human brain is its high metabolic cost. The energy requirements of brain tissue are about 29 kcal/100 grams/day, roughly 16 times that of skeletal muscle tissue (Kety, 1957; Holliday, 1986). This means that for a 70 kg adult human with a brain weight of about 1400 grams, over 400 kcal per day are allocated to brain metabolism. Yet despite the fact that humans have much larger brains than most other mammals, the total energy demands for our body – our resting energy requirements – are no greater than those of a comparably sized mammal (Kleiber, 1961; Leonard and Robertson, 1992).
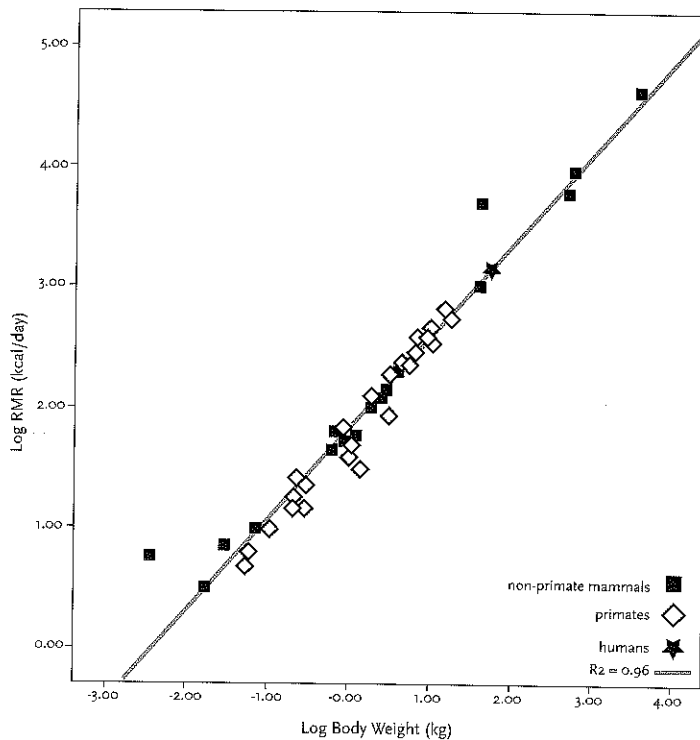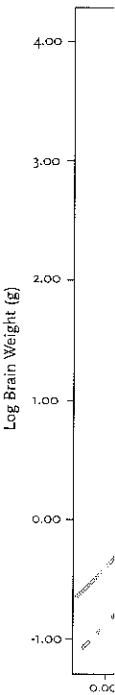

Fig. 1. Log-Log plot of resting metabolic rate (RMR; kcal/day) versus body weight (kg) for 51 species of terrestrial mammals (20 non-primate mammals, 30 primates, and humans). Humans conform to the general mammalian scaling relationship, as described by Kleiber (1961). The scaling relationship for the entire sample is: $RMR = 69(Wt^{0.755})$. Data are from Leonard et al. (2003) and Snodgrass et al. (1999).

WILLIAM R. LEONARD ET AL.

This point is evi

metabolic rate (R

primates, and hu

tionship between

ergy demands sc

RMR (kcal/da

The implication

energy budget to

which shows the

the same species

Fig. 2. Log-Log plot

trial mammals. Th

above the non-pri

mammals: BW = o.

mates have brain s

brain sizes that are t

ENERGETICS AND TH

This point is evident in Figure 1, which shows the relationship between resting metabolic rate (RMR; kcal/day) and body weight (kg) in non-primate mammals, primates, and humans. Humans conform to the general mammalian scaling relationship between RMR and body weight (the "Kleiber relationship"), in which energy demands scale to the $3/4^{th}$ power of body weight (Kleiber, 1961):

$$RMR \ (kcal/day) = 70wt^{0.75}$$

The implication of this is that humans allocate a much larger share of their daily energy budget to brain metabolism than other species. This is evident in Figure 2, which shows the scaling relationship between brain weight (grams) and RMR for the same species noted in Figure 1.
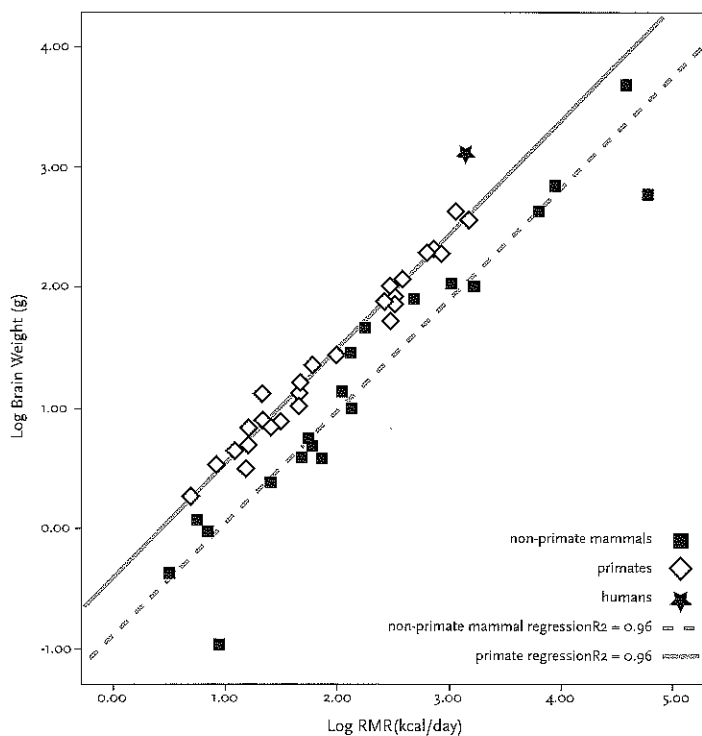
Fig. 2. Log-Log plot of brain weight (BW;g) versus RMR (kcal/day) for 51 species of terrestrial mammals. The primate regression line is systematically and significantly elevated above the non-primate mammal regression. The scaling relationships are: non-primate mammals: BW = 0.13(RMR$^{0.92}$); primates: BW = 0.38(RMR$^{0.95}$). Thus, for a given RMR, primates have brain sizes that are three times those of other mammals, and humans have brain sizes that are three times those of other primates.

We find that at a given metabolic rate, primates have systematically larger brain sizes than other mammals, and humans, in turn, have larger brain sizes than other primates. Adult humans allocate 20-25% of their RMR to brain metabolism, approximately three times that of other primates (~7-9% of RMR), and nine times that of non-primate mammals (about 3% of RMR).

Important dimensions of human nutritional biology appear to be associated with the high-energy demands of our large brains. Humans consume diets that are more dense in energy and nutrients than other primates of similar size. For example, Cordain et al. (2000) have shown that modern human foraging populations typically derive 45-65% of their dietary energy intake from animal foods. In comparison, modern great apes obtain much of their diet from low-quality plant foods. Gorillas derive over 80% of their diet from fibrous foods such as leaves and bark (Richard, 1985). Even among chimpanzees, only about 5% of their calories are derived from animal foods, including insects (Teleki, 1981; Stanford, 1996). Meat and other animal foods are more concentrated sources of calories and nutrients than most of the plant foods typically eaten by large-bodied primates. This
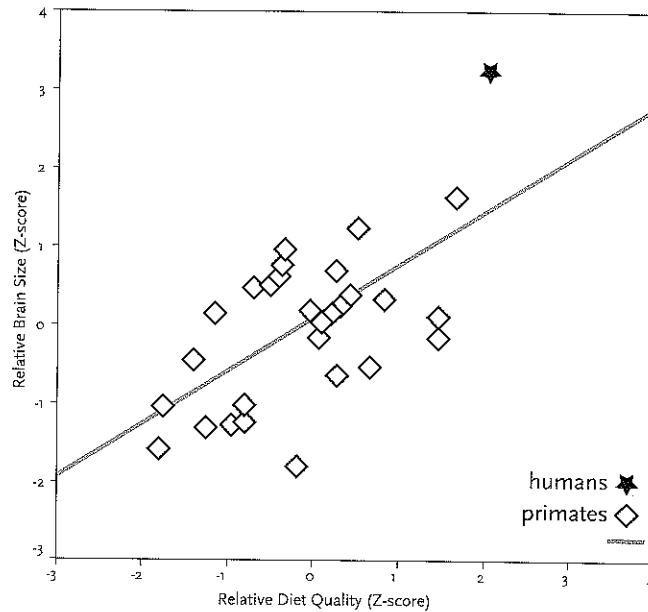
Fig. 3. Plot of relative brain size versus relative diet quality for 31 primate species (including humans). Primates with higher quality diets for their size have relatively larger brain size (r = 0.63; P < 0.001). Humans represent the positive extremes for both measures, having large brain:body size and a substantially higher quality diet than expected for their size. Adapted from Leonard et al. (2003).
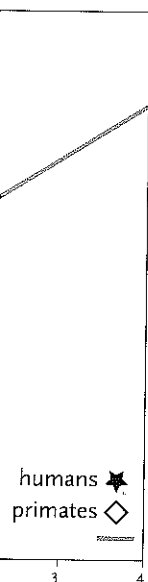
higher-quality diet n
the energy and nutri
Comparative analys
link between brain s
sus dietary quality (a
animal foods in the (
al., 2003). There is a
amount of energy al
diet. Across all prim
the positive extreme
and the highest qual
hominin brains wou
lity diet to support th
The relative size and
flect our high-qualit
tines (colons), an ada
ident in Figure 4, wh
in humans and the g
half of the GI volum
Humans, on the otl
duced colon.
The enlarged colons
quality plant fibers,
volatile fatty acids (N
morphology of hun
more similar to a car
ent-rich diet (Sussm
Together, these con
size over the course
tion of a diet that wa
the case for most lai
driving force behind
available evidence i
necessary condition
ing larger hominin l

Brain evolution ir

The human fossil re
change in hominin l

WILLIAM R. LEONARD *ET AL.*

ENERGETICS AND THE E

stematically larger brain
rger brain sizes than oth-
to brain metabolism, ap-
of RMR), and nine times

pear to be associated with
consume diets that are
of similar size. For exam-
an foraging populations
m animal foods. In com-
from low-quality plant
foods such as leaves and
bout 5% of their calories
1981; Stanford, 1996).
ces of calories and nutri-
e-bodied primates. This

humans ⚹
primates ◇

rimate species (including
relatively larger brain size
or both measures, having
an expected for their size.

higher-quality diet means that humans need to eat a smaller volume of food to get the energy and nutrients they require.

Comparative analyses of living primate species (including humans) support the link between brain size and dietary quality. Figure 3 shows relative brain size versus dietary quality (an index based on the relative proportions of leaves, fruit, and animal foods in the diet) for 31 different primate species (adapted from Leonard et al., 2003). There is a strong positive relationship ($r = 0.63$; $P < 0.001$) between the amount of energy allocated to the brain and the caloric and nutrient density of the diet. Across all primates, larger brains require higher-quality diets. Humans fall at the positive extremes for both parameters, having the largest relative brain size and the highest quality diet. This relationship implies that the evolution of larger hominin brains would have necessitated the adoption of a sufficiently high-quality diet to support the increased metabolic demands of greater encephalization.

The relative size and morphology of the human gastrointestinal (GI) tract also reflect our high-quality diet. Most large-bodied primates have expanded large intestines (colons), an adaptation to fibrous, low-quality diets (Milton, 1987). This is evident in Figure 4, which shows the relative sizes of the colon and small intestines in humans and the great apes. In all three ape species, the colon accounts for over half of the GI volume and is greatly expanded over the size of the small intestine. Humans, on the other hand, have relatively enlarged small intestines and a reduced colon.

The enlarged colons of most large-bodied primates permits fermentation of low-quality plant fibers, allowing for extraction of additional energy in the form of volatile fatty acids (Milton and Demment, 1988; Milton, 1993). In contrast, the GI morphology of humans (small colon and relatively enlarged small intestine) is more similar to a carnivore, and reflects an adaptation to an easily digested, nutrient-rich diet (Sussman, 1987; Martin, 1989).

Together, these comparative data suggest that the dramatic expansion of brain size over the course of human evolution likely would have required the consumption of a diet that was more concentrated in energy and nutrients than is typically the case for most large primates. This *does not* imply that dietary change was the driving force behind major brain expansion during human evolution. Rather, the available evidence indicates that a sufficiently high-quality diet was probably a necessary condition for supporting the metabolic demands associated with evolving larger hominin brains.

Brain evolution in early Homo

The human fossil record indicates that the first substantial burst of evolutionary change in hominin brain size occurred about 2.0 to 1.7 million years ago, associat-
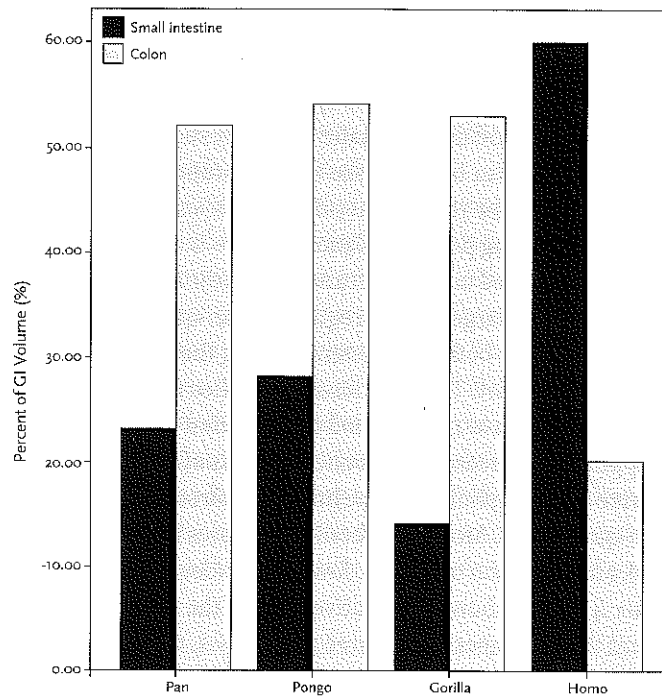
Fig. 4. Relative proportions of the small intestine and large intestine (colon) in modern humans (*Homo sapiens*) and the great apes (*Pan troglodytes, Pongo pygmaeus, Gorilla gorilla*). The colon volume of humans is markedly smaller than that of all three great apes (20% of GI volume vs. > 50% in the apes), and is indicative of adaptation to a higher-quality and more easily digested diet. Data derived from Milton (1987).

ed with the emergence and evolution of early members of the genus *Homo*. Table 1 presents data on evolutionary changes in hominin brain size (cm³), estimated adult male and female body weights (kg) and posterior tooth area (mm²). The australopithecines showed only modest brain size evolution from about 430 to 530 cm³ over more than 2 million years (from about 4 to 1.5 million years ago). However, with the evolution of the genus *Homo*, there were substantial increases in encephalization, with brain sizes of over 600 cm³ in *Homo habilis* (at 1.9 – 1.6 mya) and 800-900 cm³ in early members of *Homo erectus* (at 1.8 – 1.5 mya). Although the relative brain size of *Homo erectus* is smaller than the average for modern humans, it is outside of the range seen among other living primate species (Leonard and Robertson, 1994).

Changes in the craniofacial and dental anatomy of *Homo erectus* suggest that these forms were consuming different foods than their australopithecine ancestors. During the evolution of the australopithecines, the total surface area of the grinding teeth (molars and premolars) increased dramatically from 460 mm² in *A.*

WILLIAM R. LEONARD *ET AL.*

Homo

ntestine (colon) in modern hu-
ongo pygmaeus, Gorilla gorilla).
f all three great apes (20% of GI
on to a higher-quality and more

s of the genus *Homo.* Table 1
brain size (cm³), estimated
r tooth area (mm²). The aus-
tion from about 430 to 530
.5 million years ago). How-
substantial increases in en-
mo habilis (at 1.9 – 1.6 mya)
(at 1.8 – 1.5 mya). Although
the average for modern hu-
g primate species (Leonard

no erectus suggest that these
astralopithecine ancestors.
al surface area of the grind-
cally from 460 mm² in *A.*

Table 1. Geological ages (millions of years ago), brain size (cm³), estimated male and female body weights (kg), and postcanine tooth surface areas (mm²) for selected fossil hominid species.

| Species | Geological age (mya) | Brain size (cm³) | Body Weight | | Postcanine tooth surface (mm²) |
			Male (kg)	Female (kg)	
A. afarensis	3.9-3.0	438	45	29	460
A. africanus	3.0-2.4	452	41	30	516
A. boisei	2.3-1.4	521	49	34	756
A. robustus	1.9-1.4	530	40	32	588
Homo habilis (sensu stricto)	1.9-1.6	612	37	32	478
H. erectus (early)	1.8-1.5	863	66	54	377
H. erectus (late)	0.5-0.3	980	60	55	390
H. sapiens	0.4-0.0	1350	58	49	334

All data from McHenry and Coffing (2000), except for *Homo erectus.* Early *H. erectus* brain size is the average of African specimens as presented in McHenry (1994b), Indonesian specimens from Antón and Swisher (2001) and Georgian specimens from Gabunia et al. (2000, 2001). Data for late *H. erectus* are from McHenry (1994a).

afarensis to 756 mm² in *A. boisei.* In contrast, with the emergence of early *Homo* at approximately 2 million years ago, we see marked reductions in the posterior dentition. Postcanine tooth surface area is 478 mm² in *H. habilis* and 377 mm² in early *H. erectus.*

H. erectus also shows substantial reductions in craniofacial and mandibular robusticity relative to the australopithecines (Wolpoff, 1999). Yet, despite having smaller teeth and jaws, *H. erectus* was a much bigger animal than the australopithecines, being human-like in its stature, body mass and body proportions (McHenry, 1992, 1994a; Ruff and Walker, 1993; Ruff et al., 1997; McHenry and Coffing, 2000). Together these features indicate that early *Homo erectus* was consuming a richer, more calorically dense diet with less low-quality fibrous plant material. How the diet might have changed with the emergence of *H. erectus* is examined in the following section.

Dietary changes associated with brain evolution in early Homo

The marked increases in brain and body size coupled with the reductions of posterior tooth size and craniofacial robusticity all suggest that there was a shift in the composition and quality of the diet consumed by *H. erectus.* However, there re-

mains considerable debate over what kinds of dietary changes likely occurred during this period of human evolution. The most widely held view is that the diet of early *Homo* included more animal foods (Stanford and Bunn, 2001). The environment at the Plio-Peistocene boundary (2.0 – 1.8 mya) was becoming increasingly drier, creating more arid grasslands (Vrba, 1995; Reed, 1997; Owen-Smith, 1999). These changes in the African landscape made animal foods more abundant and, thus, an increasingly attractive food resource (Behrensmeyer et al., 1997). Specifically, when we examine modern ecosystems, we find that although savanna/grasslands have much lower net primary productivity than woodlands (4050 vs. 7200 kcal/m²/yr), the level of herbivore productivity in savannas is almost three times that of the woodlands (10.2 vs. 3.6 kcal/m²/yr) (Leonard and Robertson, 1997). Thus, fundamental changes in the ecosystem structure during the Plio-Pleistocene transition likely resulted in a net increase in the energetic abundance of game animals in the African landscape. Such an increase would have offered an opportunity for hominins with sufficient capability to exploit the animal resources.

The archaeological record provides evidence that this occurred with *Homo erectus* – the development of the first rudimentary hunting and gathering economy in which game animals became a significant part of the diet and resources were shared within foraging groups (Potts, 1988; Harris and Capaldo, 1993; Roche et al., 1999). These changes in diet and foraging behaviour would not have turned our hominin ancestors into carnivores; however, the addition of even modest amounts of meat to the diet (10-20% of dietary energy), combined with the sharing of resources that is typical of hunter-gatherer groups, would have significantly increased the quality and stability of hominin diets.

Greater consumption of animal foods also would have provided increased levels of key fatty acids that would have been necessary for supporting the rapid brain evolution seen with the emergence of *H. erectus*. Mammalian brain growth is dependent upon sufficient amounts of two long-chain polyunsaturated fatty acids (PUFAs): docosahexaenoic acid (DHA) and arachidonic acid (AA) (Crawford et al., 1999; Cordain et al., 2001). Because the composition of all mammalian brain tissue is similar with respect to these two fatty acids, species with higher levels of encephalization have greater requirements for DHA and AA (Crawford et al., 1999). It also appears that mammals have a limited capacity to synthesize these fatty acids from dietary precursors. Consequently, dietary sources of DHA and AA were likely limiting nutrients that constrained the evolution of larger brain size in many mammalian lineages (Crawford, 1992; Crawford et al., 1999).

Cordain and colleagues (2001) have shown that the wild plant foods available on the African savanna (e.g., tubers, nuts) contain, at most, trace amounts of AA and DHA, whereas muscle tissue and organ meat of wild African ruminants provide

WILLIAM R. LEONARD *ET AL.*

ENERGETICS AND

Table 2. Energy (k⟨
(DHA) contents o⟨
from Cordain et al.

Food item

African ruminant ⟨
African ruminant
African ruminant
African ruminant
African fish
Wild tuber/roots
Mixed wild plants

moderate to hig⟨
a rich source of
sources of AA ar⟨
are freshwater f⟨
Cordain et al.,
Broadhurst et a⟨
cephalization w⟨
trine resources.
use of aquatic re⟨
An alternative s⟨
posed by Wran⟨
controlled use ⟨
density of their
foods would ha⟨
tional content. ⟨
the small intes⟨
drate (Tagliabu⟨
the starch grar⟨
known as gelat⟨
by digestive en⟨
the nutritional
available for bi⟨
Although cook⟨
served to incre⟨
for the control.
1994; Brain ar⟨

changes likely occurred dur-
held view is that the diet of
Bunn, 2001). The environ-
was becoming increasingly
1997; Owen-Smith, 1999).
foods more abundant and,
smeyer et al., 1997). Speci-
nd that although savanna/
than woodlands (4050 vs.
savannas is almost three
(Leonard and Robertson,
structure during the Plio-
the energetic abundance
crease would have offered
to exploit the animal re-

ccurred with *Homo erectus*
nd gathering economy in
diet and resources were
Capaldo, 1993; Roche et
ur would not have turned
addition of even modest
combined with the shar-
would have significantly

provided increased levels
pporting the rapid brain
alian brain growth is de-
lyunsaturated fatty acids
acid (AA) (Crawford et
of all mammalian brain
cies with higher levels of
nd AA (Crawford et al.,
acity to synthesize these
sources of DHA and AA
ion of larger brain size in
al., 1999).

plant foods available on
race amounts of AA and
ican ruminants provide

Table 2. Energy (kcal), fat (g), protein (g), arachidonic acid (AA) and docosahexaenoic acid (DHA) contents of African ruminant, fish and wild plant foods per 100 grams. Data derived from Cordain et al. (2001).

Food item	Energy (kcal)	Fat (g)	Protein (g)	AA (mg)	DHA (mg)
African ruminant (brain)	126	9.3	9.8	533	861
African ruminant (liver)	159	7.1	22.6	192	41
African ruminant (muscle)	113	2.1	22.7	152	10
African ruminant (fat)	745	82.3	1.0	20-180	trace
African fish	119	4.5	18.8	270	549
Wild tuber/roots	96	0.5	2.0	0	0
Mixed wild plants	129	2.8	4.1	0	0

moderate to high levels of these key fatty acids. As shown in Table 2, brain tissue is a rich source of both AA and DHA, whereas liver and muscle tissues are good sources of AA and moderate sources of DHA. Other good sources of AA and DHA are freshwater fish and shellfish (Broadhurst et al., 1998; Crawford et al., 1999; Cordain et al., 2001). Cunnane and colleagues (Cunane and Crawford, 2003; Broadhurst et al., 1998) have suggested that the major increases in hominin encephalization were associated with systematic use of aquatic or marine or lacustrine resources. However, there is little archaeological evidence for the systematic use of aquatic resources until later in human evolution (Klein, 1999).

An alternative strategy for increasing dietary quality in early *Homo* has been proposed by Wrangham and colleagues (1999, 2003). These authors argue that the controlled use of fire for cooking allowed early *Homo* to improve the nutritional density of their diet. They note that the cooking of savanna tubers and other plant foods would have served to both soften them and increase their energy/nutritional content. In their raw form, the starch in roots and tubers is not absorbed in the small intestine and is passed through the body as non-digestible carbohydrate (Tagliabue et al., 1995; Englyst and Englyst, 2005). However, when heated, the starch granules swell and are disrupted from the cell walls. This process, known as gelatinization, makes the starch much more accessible to breakdown by digestive enzymes (García-Alonso and Goñi, 2000). Thus, cooking increases the nutritional quality of tubers by making more of the carbohydrate energy available for biological processes.

Although cooking is clearly an important innovation in hominin evolution, which served to increase dietary digestibility and quality, there is very limited evidence for the controlled use of fire by hominins before 1.5 million years ago (Bellomo, 1994; Brain and Sillen, 1988; Pennisi, 1999). The more widely held view is that

the use of fire and cooking did not occur until later in human evolution, at 200-250,000 years ago (Straus, 1989; Weiner et al., 1998). In addition, nutritional analyses of wild tubers used by modern foraging populations (e.g., Wehmeyer et al., 1969; Brand-Miller and Holt, 1998; Schoeninger et al., 2001) suggest that the energy content of these resources is markedly lower than that of animal foods, even after cooking (Cordain et al., 2001). Unlike animal foods, tubers are also devoid of both DHA and AA (Cordain et al., 2001; see Table 2). Consequently, there remain major questions about whether cooking and the heavy reliance on roots and tubers were important forces for promoting rapid brain evolution with the emergence of early *Homo*.

Overall, the available evidence seems to best support a mixed dietary strategy in early *Homo* that involved the consumption of larger amounts of animal foods than with the australopithecines. Ungar and colleagues (2006) have recently suggested that early *Homo* likely pursued a "flexible" and "versatile" subsistence strategy that would have allowed them to adapt to the patchy and seasonally variable distribution of food resources on the African savanna. They note that such a model is more plausible than ones proposing heavy reliance on one particular type of resource (e.g. meat or tubers). This is indeed true; however, what appears to be happening with early *Homo* – especially with *H. erectus* – is the development of a more stable and effective way of extracting resources from the environment. The increase in dietary quality and stability was likely achieved partly through changes in diet composition (Leonard and Robertson, 1994; Cordain et al., 2001) and partly through social and behavioural changes like food sharing and perhaps division of foraging tasks (Isaac, 1978; Kaplan et al., 2000). This greater nutritional stability provided a critical foundation for fueling the energy demands of larger brain sizes.

Implications of changes in body composition for brain evolution

In addition to improvements in dietary quality, the increased metabolic cost of larger brain size in human evolution also appears to have been supported by changes in body composition. Because humans allocate a substantially larger share of their daily energy budget to their brains than do other primates or other mammals, this implies that the size and metabolic demands of certain other organs/organ systems may be relatively reduced in humans compared with other species. Thus, the critical question is: which organs have been reduced or altered in their relative size over the course of human evolution to compensate for the expansion of brain size?

Analyses of human and primate body composition offer possible answers to this question. Aiello (1997; this volume) and Aiello and Wheeler (1995) have argued

that the increased
the reduction in siz
having very high er
size of the large int
vide the necessary
lism. Aiello and W
species (including
size. However, rec
strate the significa
mammals that are
tions remain about
dated the dramatic
Leonard and colle
ences in muscle ar
count for the varia
mates and other m
levels of body fatne
ness (adiposity) in
metabolism. First,
replacing muscle r
cated to the brain.
can be drawn upo
higher levels of bo
providing stored e
tional resources.

Table 3. Body weigh
(RMR; kcal/day), ar
mans from birth to a

Age

New born
3 months
18 months
5 years
10 years
Adult male
Adult female

)[a] All data are from
and younger, wh

WILLIAM R. LEONARD *ET AL.*

ENERGETICS AND TH

that the increased energy demands of the human brain were accommodated by the reduction in size of the GI tract. Since the intestines are similar to the brain in having very high energy demands (so-called "expensive tissues"), the reduction in size of the large intestines of humans, relative to other primates, is thought to provide the necessary energy "savings" required to support elevated brain metabolism. Aiello and Wheeler (1995) have shown that among a sample of 18 primate species (including humans), increased brain size was associated with reduced gut size. However, recent analyses by Snodgrass et al. (1999) have failed to demonstrate the significant differences in GI size between primates and non-primate mammals that are predicted from the "expensive tissue hypothesis". Thus, questions remain about the extent to which reductions in GI size may have accommodated the dramatic expansion of brain size during the course of human evolution. Leonard and colleagues (2003) and Kuzawa (1998) have suggested that differences in muscle and fat mass between humans and other primates may also account for the variation in budgeting of metabolic energy. Relative to other primates and other mammals, humans have lower levels of muscle mass and higher levels of body fatness (Leonard et al., 2003). The relatively high levels of body fatness (adiposity) in humans have two important metabolic implications for brain metabolism. First, because fat has lower energy requirements than muscle tissue, replacing muscle mass with fat mass results in energy "savings" that can be allocated to the brain. Additionally, fat provides a ready source of stored energy that can be drawn upon during periods of limited food availability. Consequently, the higher levels of body fat in humans may also help to support a larger brain size by providing stored energy to buffer against environmental fluctuations in nutritional resources.

Table 3. Body weight (kg), brain weight (g), percent body fat (%), resting metabolic rate (RMR; kcal/day), and percent of RMR allocated to brain metabolism (BrMet, %) for humans from birth to adulthood.)[a]

Age	Body weight (kg)	Brain weight (g)	Body fat (%)	RMR (kcal/day)	BrMet (%)
New born	3.5	475	16	161	87
3 months	5.5	650	22	300	64
18 months	11.0	1045	25	590	53
5 years	19.0	1235	15	830	44
10 years	31.0	1350	15	1160	34
Adult male	70.0	1400	11	1800	23
Adult female	50.0	1360	20	1480	27

)[a] All data are from Holliday (1986), except for percent body fat data for children 18 months and younger, which are from Dewey et al. (1993).

The importance of body fat is particularly notable in human infants, which have both high brain to body weight ratios and high levels of body fatness. Table 3 shows age-related changes in body weight (kg), brain weight (g), fatness (%), RMR (kcal/day) and percent of RMR allocated to the brain for humans from birth to adulthood. We see that in infants, brain metabolism accounts for upwards of 60% of RMR. Human infants are also considerably fatter than those of other mammalian species (Kuzawa, 1998). Body fatness in human infants is about 15-16% at birth, and continues to increase to 25-26% during the first 12 to 18 months of postnatal growth. Fatness then declines to about 15% by early childhood (Dewey et al., 1993). Thus, during early human growth and development, it appears that body fatness is highest during the periods of the greatest metabolic demand of the brain.

It is likely that fundamental changes in body composition (i.e., the relative sizes of different organ systems) during the course of hominin evolution allowed for the expansion of brain size without substantial increases in the total energy demands for the body. At present, we do not know which alterations were the most critical for accommodating brain expansion. Variation in body composition both within and between primate species is still not well understood. Among humans, our knowledge of variation in body composition is based largely on data from populations of the industrialized world. Consequently, more and better data on interspecific and ontogenetic variation in primate and human body composition are necessary to further resolve these issues.

New imaging techniques such as magnetic resonance imaging (MRI) and positron emission tomography (PET scans) offer the potential to directly explore variation in organ weight and organ-specific energy demands in living humans and primates. For example, Gallagher et al. (2006) recently used MRI technology to measure how differences in organ weights contribute to ethnic differences in RMRs among living humans. These authors demonstrated that the significant differences in RMR between their African-American and Euroamerican samples could be accounted for by differences in the summed weight of the most metabolically expensive organs (liver, heart, spleen, kidneys and brain). Similarly, Chugani (1998) has recently utilized PET scans to quantify changes in glucose utilization in the human brain from birth to adulthood. His findings suggest that the extremely high metabolic costs of brain metabolism characteristic of early human life (as outlined in Table 3) may extend further into childhood than previously realized. Together these studies highlight the potential use of new imaging techniques to improve our understanding of how interspecific variation in body composition contributes to differences in metabolic rate.

Conclusions

An energetic persp
brain size in the ho
bolic consequence:
ing energy budge
mammals. The hig
that are relatively i
relative proportion
ed with dietary qua
both a very high-q
Greater encephali:
body composition
muscled", having
species of similar
mans, particularly
els of muscle mas:
brains in two imp
the brain" and (2)
With the emerger
we find the first n
sponding change
with evidence fro
consuming a hig
the increases in b
Further research
that took place w
biomedical imag
and interspecific
metabolic rates.

n human infants, which have
of body fatness. Table 3 shows
eight (g), fatness (%), RMR
in for humans from birth to
accounts for upwards of 60%
er than those of other mam-
han infants is about 15-16% at
e first 12 to 18 months of post-
early childhood (Dewey et al.,
opment, it appears that body
st metabolic demand of the

ition (i.e., the relative sizes of
in evolution allowed for the
in the total energy demands
ations were the most critical
dy composition both within
stood. Among humans, our
largely on data from popula-
and better data on interspe-
body composition are nec-

ance imaging (MRI) and
potential to directly explore
demands in living humans
cently used MRI technology
ute to ethnic differences in
strated that the significant
nd Euroamerican samples
weight of the most meta-
eys and brain). Similarly,
uantify changes in glucose
. His findings suggest that
characteristic of early hu-
o childhood than previous-
al use of new imaging tech-
specific variation in body
e.

Conclusions

An energetic perspective is particularly useful for understanding the evolution of brain size in the hominin lineage. Large human brain sizes have important metabolic consequences as humans expend a relatively larger proportion of their resting energy budget on brain metabolism than other primates or non-primate mammals. The high costs of large human brains are supported, in part, by diets that are relatively rich in energy and other nutrients. Among living primates, the relative proportion of metabolic energy allocated to the brain is positively correlated with dietary quality. Humans fall at the positive end of this relationship, having both a very high-quality diet and a large brain size.

Greater encephalization also appears to have consequences for other aspects of body composition. Comparative primate data indicate that humans are "undermuscled", having relatively lower levels of skeletal muscle than other primate species of similar size. Conversely, levels of body fatness are relatively high in humans, particularly in infancy. These greater levels of body fatness and reduced levels of muscle mass allow human infants to accommodate the growth of their large brains in two important ways: (1) by having a ready supply of stored energy to "feed the brain" and (2) by reducing the total energy costs of the rest of the body.

With the emergence and evolution of the genus *Homo* between 2.0 and 1.7 mya, we find the first major pulse of brain evolution in the hominin lineage. The corresponding changes in craniofacial anatomy and postcanine tooth size, coupled with evidence from the archaeological record, suggest that these hominins were consuming a higher-quality and more stable diet that would have helped to fuel the increases in brain size.

Further research is needed to better understand the nature of the dietary changes that took place with the emergence of *Homo*. In addition, the application of new biomedical imaging techniques offers the potential to directly explore how intra- and interspecific variation in body composition may contribute to the variation in metabolic rates.

References

Aiello, L.C., 1997. Brains and guts in human evolution: The expensive tissue hypothesis. Brazilian Journal of Genetics 20, 141-148.

Aiello, L.C., Wheeler, P., 1995. The expensive-tissue hypothesis: The brain and the digestive system in human and primate evolution. Current Anthropology 36, 199-221.

Antón, S.C., Swisher, C.C. III, 2001. Evolution of cranial capacity in Asian *Homo erectus*. In: Indriati, E. (ed.), A Scientific Life: Papers in Honor of Dr. T. Jacob, 25-39. Bigraf Publishing, Yogyakarta, Indonesia.

Behrensmeyer, K., Todd, N.E., Potts, R., McBrinn, G.E., 1997. Late Pliocene faunal turnover in the Turkana basin, Kenya and Ethiopia. Science 278, 1589-1594.

Bellomo, R.V., 1994. Methods of determining early hominid behavioral activities associated with the controlled use of fire at FxJj 20 Main, Koobi Fora. Journal of Human Evolution 27, 173-195.

Brain, C.K., Sillen, A., 1988. Evidence from the Swartkrans cave for the earliest use of fire. Nature 336, 464-466.

Brand-Miller, J.C., Holt, S.H.A., 1998. Australian aboriginal plant foods: A consideration of their nutritional composition and health implications. Nutrition Research Reviews 11, 5-23.

Broadhurst, C.L., Cunnane, S.C., Crawford, M.A., 1998. Rift Valley lake fish and shellfish provided brain-specific nutrition for early *Homo*. British Journal of Nutrition 79, 3-21.

Chugani, H.T., 1998. A critical period of brain development: Studies of cerebral glucose utilization with PET. Prevent Med 27, 184-188.

Cordain, L., Brand Miller, J., Eaton, S.B., Mann, N., Holt, S.H.A., Speth, J.D., 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. American Journal of Clinical Nutrition 71, 682-692.

Cordain, L., Watkins, B.A., Mann, N.J., 2001. Fatty acid composition and energy density of foods available to African hominids. World Rev. Nutr. Diet. 90, 144-161.

Crawford, M.A., 1992. The role of dietary fatty acids in biology: Their place in the evolution of the human brain. Nutr. Rev. 50, 3-11.

Crawford, M.A., Bloom, M., Broadhurst, C.L., Schmidt, W.F., Cunnane, S.C., Galli, C., Gehbremeskel, K., Linseisen, F., Lloyd-Smith, J., Parkington, J., 1999.

Evidence for unique function of docosahexaenoic acid during the evolution of the modern human brain. Lipids 34, S39-S47.

Cunnane, S.C., Crawford, M.A., 2003. Survival of the fattest: Fat babies were the key to evolution of the large human brain. Comparative Biochemistry and Physiology, Part A 136, 17-26.

Dewey, K.G., Heinig, M.J., Nommsen, L.A., Peerson, J.M., Lonnerdal, B., 1993. Breast-fed infants are leaner than formula-fed infants at 1 y of age: The Darling Study. American Journal of Clinical Nutrition 52, 140-145.

Englyst, K.N., Englyst, H.N., 2005. Carbohydrate bioavailability. British Journal of Nutrition 94, 1-11.

Gabunia, L., Vekua, A., Lordkipanidze, D., Swisher, C.C., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Antón, S.C., Bosinski, G., Joris, O., Lumley, M.-A. de, Majsuradze, G., Mouskhelishivili, A., 2000. Earliest Pleistocene cranial remains from Dmanisi, Republic of Georgia: taxonomy, geological setting, and age. Science 288, 1019-1025.

Gabunia, L., Antón, S.C., Lordkipanidze, D., Vekua, A., Justus, A., Swisher, C.C. III, 2001. Dmanisi and dispersal. Evolutionary Anthropology 10, 158-170.

Gallagher, D., Albu, J., He, Q., Heshka, S., Boxt, L., Krasnow, N., Elia, M., 2006. Small organs with a high metabolic rate explain lower resting energy expenditure in African American than in white adults. American Journal of Clinical Nutrition 83, 1062-1067.

García-Alonso, A., Goñi, I., 2000. Effect of processing on potato starch: In vitro availability and glycemic index. Nahrung 44, 19-22.

Harris, J.W.K., Capaldo, S., 1993. The earliest stone tools: their implications for an understanding of the activities and behavior of late Pliocene hominids. In: Berthelet, A., Chavaillon, J. (eds), The Use of Tools by Human and Nonhuman Primates, 196-220. Oxford Science Publications, Oxford.

Holliday, M.A., 1986. Body composition and energy needs during growth. In: Falkner, F., Tanner, J.M. (eds), Human Growth: A Comprehensive Treatise, Volume 2. 101-117. (2nd ed.) Plenum Press, New York.

Isaac, G.L., 1978. Food sharing and human evolution: Archaeological evidence from the Plio-Pleistocene of East Africa. Journal of Anthropological Research 34, 311-325.

Kaplan, H., Hill, K., Lancaster, J., Hurtado, A.M., 2000. A theory of life history evolution: Diet, intelligence and longevity. Evolutionary Anthropology 9, 156-185.

Kety, S.S., 1957. The general metabolism of the brain *in vivo*. In: Richter, D. (ed.), Metabolism of the Central Nervous System, 221-237. Pergammon, New York.

Kleiber, M., 1961. The Fire of Life. Wiley, New York.

Klein, R.G., 1999. The Human Career: Human Biological and Cultural Origins (2nd Ed.). University of Chicago Press, Chicago.

Kuzawa, C.W., 1998. Adipose tissue in human infancy and childhood: An evolutionary perspective. Yearbook Physical Anthropology 41, 177-209.

Leonard, W.R., 2002. Food for thought: Dietary change was a driving force in human evolution. Scientific American 287(6), 106-115.

Leonard, W.R., Robertson, M.L., 1992. Nutritional requirements and human evolution: A bioenergetics model. American Journal of Human Biology 4, 179-195.

Leonard, W.R., Robertson, M.L., 1994. Evolutionary perspectives on human nutrition: The influence of brain and body size on diet and metabolism. American Journal of Human Biology 6, 77-88.

Leonard, W.R., Robertson, M.L., 1997. Comparative primate energetics and hominid evolution. American Journal of Physical Anthropology 102, 265-281.

Leonard, W.R., Robertson, M.L., Snodgrass, J.J., Kuzawa, C.W., 2003. Metabolic correlates of hominid brain evolution. Comparative Biochemistry and Physiology, Part A 135, 5-15.

Martin, R.D., 1989. Primate Origins and Evolution: A Phylogenetic Reconstruction. Princeton University Press, Princeton, NJ.

McHenry, H.M., 1992. Body size and proportions in early hominids. American Journal of Physical Anthropology 87, 407-431.

McHenry, H.M., 1994a. Tempo and mode in human evolution. Proceedings of the National Academy of Sciences (USA) 91, 6780-6786.

McHenry, H.M., 1994b. Behavioral ecological implications of early hominid body size. Journal of Human Evolution 27, 77-87.

McHenry, H.M., Coffing, K., 2000. *Australopithecus* to *Homo*: Transformations in body and mind. Annual Review of Anthropology 29, 125-146.

McNab, B.K., 2002. The physiological ecology of vertebrates: A view from energetics. Cornell University Press, Ithaca, NY.

Milton, K., 1987. Primate diets and gut morphology: Implications for hominid evolution. In: Harris, M., Ross, E.B. (eds), Food and Evolution: Toward a Theory of Human Food Habits, 93-115. Temple University Press, Philadelphia.

Milton, K., 1993. Diet and primate evolution. Scientific American 269(2), 86-93.

Milton, K., Demment, M.W., 1988. Digestion and passage kinetics of chimpanzees fed high and low fiber diets and comparison with human data. J. Nutr. 118, 1082-1088.

Owen-Smith, N., 1999. Ecological links between African savanna environments, climate change and early hominid evolution. In: Bromage, T.G., Schrenk, F. (eds), African Biogeography, Climate Change, and Human Evolution, 138-149. Oxford University Press, New York.

Pennisi, E., 1999. Did cooked tubers spur the evolution of big brains? Science 283, 2004-2005.

Potts, R., 1988. Early Hominid Activities at Olduvai. Aldine, New York.

Reed, K., 1997. Early hominid evolution and ecological change through the African Plio-Pleistocene. Journal of Human Evolution 32, 289-322.

Richard, A.F., 1985. Primates in Nature. WH Freeman, New York.

Roche, H., Delagnes, A., Brugal, J.P., Feibel, C., Kibunjia, M., Mourre, V., Texier, J.-P., 1999. Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. Nature 399, 57-60.

Ruff, C.B., Walker, A., 1993. The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge.

Ruff, C.B., Trinkaus, E., Holliday, T.W., 1997. Body mass and encephalization in Pleistocene *Homo*. Nature 387, 173-176.

Schoeninger, M.J., Bunn, H.T., Murray, S.S., Marlett, J.A., 2001. Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. Journal of Food Composition and Analysis 14, 3-13.

Snodgrass, J.J., Leonard, W.R., Robertson, M.L., 1999. Interspecific variation in body composition and its influence on metabolic variation in primates and other mammals. American Journal of Physical Anthropology (Suppl.) 28, 255 (abstract).

Stanford, C.B., 1996. The hunting ecology of wild chimpanzees: implications for the evolutionary ecology of Pliocene hominids. American Anthropologist 98, 96-113.

Stanford, C.B., Bunn, H.T., 2001. Meat-Eating and Human Evolution. Oxford University Press, Oxford.

Straus, L.G., 1989. On early hominid use of fire. Current Anthropology 30, 488-491.

Tagliabue, A., Raben, A., Heijnen, M.L., Duerenberg, P., Pasquali, E., Astrup, A., 1995. The effect of raw potato starch on energy expenditure and substrate oxidation. American Journal of Clinical Nutrition 61, 1070-1075.

Teleki, G., 1981. The omnivorous diet and eclectic feeding habits of the chimpanzees of Gombe National Park. In: Harding, R.S.O., Teleki, G. (eds), Omnivorous Primates, 303-343. Columbia University Press, New York.

Ungar, P.S., Grine, F.E., Teaford, M.F., 2006. Diet in early *Homo*: A review of the evidence and a new model of adaptive versatility. Annual Review of Anthropology 35, 209-228.

Vrba, E.S., 1995. The fossil record of African antelopes relative to human evolution. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burkle, L.H. (eds), Paleoclimate and Evolution, with Emphasis on Human Origins, 385-424. Yale University Press, New Haven.

Wehmeyer, A.S., Lee, R.B., Whiting, M., 1969. The nutrient composition and dietary importance of some vegetable foods eaten by the !Kung bushmen. S. Afr. Med. J. 95, 1529-1530.

Weiner, S., Qunqu, X., Goldberg, P., Liu, J., Bar-Yosef, O., 1998. Evidence for the use of fire at Zhoukoudian, China. Science 281, 251-253.

Wolpoff, M.H., 1999. Paleoanthropology, 2nd Ed. McGraw-Hill, Boston.

Wrangham, R.W., Conklin-Brittain, N.L., 2003. Cooking as a biological trait. Comparative Biochemistry and Physiology, Part A 136, 35-46.

Wrangham, R.W., Jones, J.H., Laden, G., Pilbeam, D., Conklin-Brittain, N.L., 1999. The raw and the stolen: Cooking and the ecology of human origins. Current Anthropology 40, 567-594.

The E
Histor

Hillard S. Kap

Introduction

This paper prese
both the primate
dress the simult
span, it extends s
search into the ev
(Cole, 1954; Gad
sion, *the embodie*
Robson, 2001b),
investments and
The chapter begi
applies it to unc
characteristics o:
ries in the prim
course is then co
tive developmen
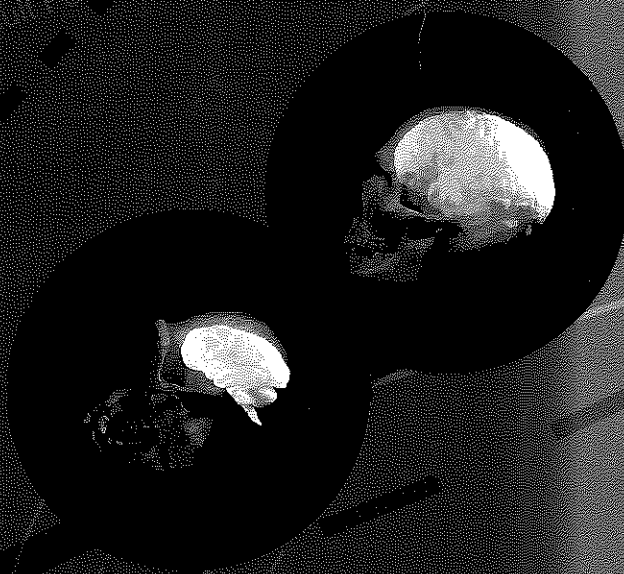evolution of the l
man developmer
issues raised at tl

The embodied

According to the
result of a proces
vironment and c

Guts
AND
Brains

*An Integrative Approach
to the Hominin Record*

Wil Roebroeks (ed.)