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## Comparative context of Plio-Pleistocene hominin brain evolution

One of the distinguishing features of *Homo sapiens* is its absolutely and relatively large brain. This feature is also seen in less extreme form in some fossil *Homo* species. However, are increases in brain size during the Plio-Pleistocene only seen in *Homo*, and is brain enlargement among Plio-Pleistocene primates confined to hominins? This study examines evidence for changes in brain size for species and lineage samples of three synchronic East African fossil primate groups, the two hominin genera *Homo* and *Paranthropus*, and the cercopithecoid genus *Theropithecus*. Hominin endocranial capacity data were taken from the literature, but it was necessary to develop an indirect method for estimating the endocranial volume of *Theropithecus*. Bivariate and multivariate regression equations relating measured endocranial volume to three external cranial dimensions were developed from a large (ca. 340) sample of modern African cercopithecoids. These equations were used to estimate the endocranial volumes of 20 *Theropithecus* specimens from the African Plio-Pleistocene. Spearman's rho and the Hubert nonparametric test were used to search for evidence of temporal trends in both the hominin and *Theropithecus* data. Endocranial volume apparently increased over time in both *Homo* and *Paranthropus boisei*, but there was no evidence for temporal trends in the endocranial volume of *Theropithecus*. Thus, hypotheses which suggest a mix of environmental, social, dietary, or other factors as catalysts for increasing brain in Plio-Pleistocene primates must accommodate evidence of brain enlargement in both *Homo* and *Paranthropus*, and explain why this phenomenon appears to be restricted to hominins.

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### Introduction

The large brain and encephalization of *Homo sapiens*, along with the retracted face, flexed cranial base, manual dexterity, habitually upright posture and obligate bipedalism, are the cardinal distinguishing features of modern humans. The absolutely and relatively large brain is widely regarded as the crucial factor facilitating the evolution and maintenance of the complex language and culture that sets modern human behaviour apart from that of the apes. There is also a widespread assumption that significant trends in the evolution of absolute and

relative size of the hominin neurocranium are restricted to our own genus, *Homo*. Falk (1991) and Tobias (1991) have both argued that, whereas there was no substantial brain size increase in australopith species, brain size increased dramatically in *Homo*, from 2 Ma onwards, and their arguments have been reinforced by further work on trends in hominin brain size (Aiello & Wheeler, 1995; Kappelman, 1996; Ruff *et al.*, 1997). Furthermore, it has been suggested that brain size should be one of the main criteria for including taxa in *Homo* (Tobias, 1991). The traditional link between the stone tool industries of the Plio-Pleistocene and *Homo*

also assumes that the enlarged, and enlarging, brain of *Homo* was the key to the development of stone tool manufacture. The dominant paradigm is that the ability to conceive of the form of a finished stone tool, and then plan and carry out the sequence of actions necessary to manufacture it, were conceptual and motor skills that were confined to large-brained members of the genus *Homo* [see Wood & Collard (1999a) for a recent review].

The view that significant brain size increase is restricted to hominin species in the genus *Homo* is problematic, not only on taxonomic grounds, but also because of recent research into early hominin brain evolution and reassessments of the links between early hominin species and stone tools. It has been suggested that species classified as “early *Homo*” (*H. habilis* and *H. rudolfensis*) are more similar morphologically (and probably behaviourally) to the australopiths than to later *Homo*, and should therefore be removed from *Homo* (Wood & Collard, 1999a). Thus, if substantial brain size increase is evident before *H. ergaster*, in *H. habilis sensu lato*, and if the revised taxonomy is accepted, brain size increase is not restricted to members of our own genus. In addition, there is an increasing body of morphological evidence indicating that brain size increases may have occurred much earlier in hominin evolution than is conventionally supposed. By 3 Ma, at least one australopith species had brains that were absolutely larger, and perhaps also relatively larger, than those of *Pan* (Kimbel *et al.*, 1994), and Falk *et al.* (2000), in a recent reappraisal of early hominin brain evolution, argue that trends for increased brain size and cortical reorganization may have begun in the australopith ancestors of “early *Homo*”. It has also been shown in recent work that non-*Homo* hominins are synchronous with stone tool industries at Plio-Pleistocene sites in both East and southern Africa (Heinzelin *et al.*, 1999; Kuman &

Clarke, 2000). Last, the suggestion that features of the hand of *Paranthropus robustus* are compatible with stone tool manufacture (Susman, 1994) also invites re-examination of the assumption that brain enlargement and stone tool manufacture were restricted to the *Homo* lineage.

The period between ca. 2.5 and ca. 1.5 Ma (hereinafter referred to for brevity as the Plio-Pleistocene) was particularly crucial for the evolution of the hominin brain. During this time we see unambiguous evidence of hominin taxa with brain sizes exceeding those of living nonhuman primates, but, until recently (Conroy *et al.*, 1998; Falk, 1998; Falk *et al.*, 2000), most research on hominin brain evolution in this time period has focused on *Homo* taxa. The results of these recent studies indicate that investigations of hominin brain evolution must be extended to include non-*Homo* taxa, especially as the assumed association between particular hominin species and stone tool manufacture is under reinvestigation. Thus, in this study, we test three hypotheses concerning primate brain evolution in the Plio-Pleistocene. The first is that, during this period, the origin and early stages of the evolution of *Homo sensu lato* are associated with significant increases in brain size. Second, that during the Plio-Pleistocene, brain enlargement among hominins was confined to the taxa assigned to *H. sensu lato*. Third, in order to justify focusing on the hominin evidence, we also test the hypothesis that hominins were the only large-bodied primates to show significant increases in brain size during the Plio-Pleistocene. The background to the three components of this investigation are described in more detail below.

Despite the traditional view that significant increases in hominin brain size only occurred in post-2 Ma *Homo*, there is no consensus about the pattern and rate of hominin brain enlargement. Rapid brain size increase in late Pleistocene hominins is well

documented (Leigh, 1992; Kappelman, 1996; Ruff *et al.*, 1997), but the pace and pattern of enlargement prior to this time seems, at least to some researchers, to be neither gradual, nor obviously punctuated (McHenry, 1982, and summarized in Tobias, 1987). Ruff *et al.* (1997) argued that *Homo* was the focus of hominin brain evolution, but suggested that there are several grades of relative brain size within *Homo*, and that the earliest putative members of the genus, “early *Homo*” or *H. habilis* and *H. rudolfensis*, “may represent another grade” (Ruff *et al.*, 1997:175). Thus, this study begins by re-examining the evidence for the link between the appearance and early evolution of the *Homo* lineage (taken for the purposes of this study to include *H. habilis* and *H. rudolfensis*) with an increase in absolute brain size, with or without any increase in relative brain size.

Researchers familiar with the evidence have proposed that, during the Plio-Pleistocene, brain size may also have increased over time within another hominin genus, namely within the lineage represented by *P. boisei sensu lato* (Carney *et al.*, 1971; Holloway, 1988; Walker & Leakey, 1988; Brown *et al.*, 1993). Wolpoff (1988:493) went further, suggesting that these increases were “at least to some extent independent of body size and thus are a real evolutionary trend within the lineage”. It is important to formally test the hypothesis that brain enlargement among the Plio-Pleistocene hominins is confined to *Homo sensu lato*. This is not only necessary for assessing the logic of the evolutionary scenario that confines brain expansion and a facility for culture to *Homo sensu lato*, but it is also important to investigate brain evolution in non-*Homo* hominins for its own sake (Falk, 1998; Falk *et al.*, 2000). Interpretations of human evolution that imply a non-linear, more “bushy” phylogeny (e.g., Wood, 1996), together with the results of recent cladistic analyses (Skelton &

McHenry, 1992; Strait *et al.*, 1997; Wood & Collard, 1999b) make it clear that there has probably been a substantial amount of morphological and functional convergence, or homoplasy, within hominin evolution. Thus, we must take particular care to investigate whether the “unique” pattern of brain evolution proposed for *Homo sensu lato* really is confined to that taxon. To test the hypothesis that changes in brain size are confined to the *Homo* clade, we investigated brain evolution in the only other comparable East African hominin lineage, *Paranthropus*. We focus on the East African evidence for *Paranthropus* because it is relatively well-dated, and also because the *P. boisei sensu lato* hypodigm includes several specimens for which it is possible to measure, or estimate, endocranial volume (Brown *et al.*, 1993).

To provide an even broader comparative context for brain size evolution in early *Homo*, the possibility of similar trends in the brain sizes of other synchronic and sympatric nonhominin primate lineages should also be considered. It may appear obvious that trends in hominin brain evolution which culminated in modern humans are unique among primates, but this hypothesis has never been formally tested. In the absence of non-hominin hominid fossils from the African Plio-Pleistocene fossil record, coeval primates with the closest evolutionary relationship to hominins are the cercopithecoids. Of this group, one primate, *Theropithecus*, is particularly well-represented at hominin sites through the Plio-Pleistocene. Theropithecids have been compared to hominins in a number of studies, most notably in Jolly’s (1970) “seed-eating hypothesis” (but see also Wrangham, 1980; Dunbar, 1983; Foley, 1984, 1993; Elton, 2000), and can be used to provide a comparative perspective when examining patterns in human evolution. It is likely that *Theropithecus* inhabited similar environments as some early hominin

species, and may even have competed with hominins at some localities. It has been argued that environmental change may force evolutionary change (e.g., Coppens, 1975; Vrba, 1980, 1985, 1995), and if one examines two relatively closely related groups of animals living in the same places and at the same time, it may be possible to assess which evolutionary trends are the result of a shared environment and which are novel for that particular group. Thus, in a hominin–theropithecoid comparison, the monkeys are, in effect, used as a “control group”.

Despite the relatively large number of *Theropithecus* cranial specimens, surprisingly little attention has been paid to evolutionary trends in its endocranial volume. Falk (1981) compared and contrasted sulcal patterns in fossil and modern *Theropithecus* species, but did not provide endocranial volume estimates. Martin (1993) measured the cranial capacities of three *T. oswaldi* crania from East Africa (Peninj DAT 600/82, a *T. oswaldi* female, Kanjera BM 32102, a *T. oswaldi* male, and Kanjera BM 14936, a *T. oswaldi* female), and concluded that *T. oswaldi* was probably smaller-brained than modern *Papio*, and may even have had a smaller brain relative to body mass than *T. gelada*. To date, however, there has been no investigation of temporal trends in endocranial volume within *Theropithecus*.

The paucity of endocranial volume estimates for Plio-Pleistocene cercopithecoids is in part due to the large number of crania filled with matrix, making it difficult to measure cranial capacity directly. The need to estimate quantities, such as brain size, that cannot always be measured directly is a common problem in palaeontology (Vaisnys *et al.*, 1984). The estimation of endocranial volume from external dimensions has been attempted in several ways. Foramen magnum area was used to estimate cranial capacity in *Oreopithecus bambolii* skull Bac. 63 (Harrison, 1989; see also Martin, 1990).

Bregma-asterion (a chord on the parietal) was used to predict cranial capacity in the *H. habilis* skull OH 7 (Vaisnys *et al.*, 1984), and Walker *et al.* (1983) used a midline endocranial arc measurement (from opisthion to the most anterior point of the frontal lobe impression) to estimate the cranial capacity of the Rusinga Island *Proconsul heseloni* skull KNM-RU 7290. The relationships between skull height (basion–bregma) and endocranial volume in catarrhines has also been investigated, and the resulting regressions have been used to predict cranial capacities in a number of fossil hominins (Trevor-Jones *et al.*, 1995). Martin (1990) devised several regression equations to estimate primate cranial capacity from external cranial dimensions, but when applied to cercopithecoids they produce inaccurate estimates (see below). This may be because the sample of primates used to devise the regressions included both strepsirrhines and haplorhines (Martin, 1990), so may not provide a good prediction model for primates like cercopithecoids that are of intermediate body and brain size. In this study, the relationship between endocranial volume and three external linear dimensions (cranial length, width and height) in cercopithecoids was investigated using least-squares bivariate and multiple regression analyses. The resulting regressions were used to estimate endocranial volume for a sample of an East and southern African Plio-Pleistocene *Theropithecus* lineage, *T. darti*–*T. oswaldi*. These data were then used to test the hypothesis that brain expansion in Plio-Pleistocene large-bodied primates was restricted to hominins.

## Materials and methods

*Indirect estimates of endocranial volume for the Theropithecus sample*

*Comparative sample of extant cercopithecoids.* The composition of the sample is shown in

**Table 1** Extant cercopithecoïd comparative sample

Species	Male ( <i>h</i> )	Female ( <i>h</i> )	Total ( <i>h</i> )	Male mean endocranial volume (cc)	Female mean endocranial volume (cc)
<i>Mandrillus sphinx</i>	8	6	14	163	129
<i>M. leucophaeus</i>	8	5	13	160	136
<i>Cercocebus torquatus</i>	12	9	21	103	86
<i>C. galeritus</i>	3	5	8	114	91
<i>Cercopithecus neglectus</i>	17	8	25	63	53
<i>Lophocebus albigena</i>	17	14	31	100	82
<i>Colobus guereza</i>	21	19	40	68	63
<i>C. aethiops</i>	21	13	34	61	55
<i>Papio cynocephalus</i>	14	12	26	153	140
<i>P. anubis</i>	27	19	46	180	141
<i>P. ursinus</i>	20	14	34	191	165
<i>P. hamadryas</i>	13	3	16	157	125
<i>P. papio</i>	5	1	6	167	118
<i>Theropithecus gelada</i>	10	15	25	129	116
Total	196	143	339		

Cranial capacity data from this study.

**Table 1.** All crania used in the analysis were from wild-shot adult individuals without obvious skeletal pathology. Maturity was assessed on the basis of M3 eruption in all species except *T. gelada*, which has been shown to have relatively delayed eruption of this tooth (Jolly, 1972). For *T. gelada*, maturity was assessed by epiphyseal fusion if the postcranial skeleton was available, and by cranial suture closure and M2 wear if not. In all specimens with associated postcranial material, adult status determined by dentition was confirmed by the assessment of long bone epiphyseal fusion. The 339 crania included in the analysis were unequally distributed by sex, with 143 females and 196 males.

*Measurements and methods.* Measurements taken on the cranium of each specimen were basion–bregma (cranial height), maximum bi-temporal width (cranial width), glabella–inion (cranial length), and orbital height and width. Measurements were taken with Sylvac digital callipers, and entered directly into a laptop computer using a calliper interface. Spreading callipers were used for

basion–bregma and maximum temporal width in the larger crania; these measurements were entered manually into the database package. Cranial capacity was measured using the “mustard seed” technique of Gingerich & Martin (1981), with small plastic beads in place of seed. The orbits were plugged with cotton wool, beads were introduced and settled according to a simple, standard protocol. The cranial capacity was then taken to be the volume of beads decanted from the graduated measuring cylinder into the cranial cavity.

Bivariate and multiple least-squares regression analyses were used to examine the relationship between cranial capacity and external cranial dimensions. These analyses were undertaken using two datasets, one comprising the whole cercopithecoïd sample, and another comprising *T. gelada* only, as it has been argued that the modern gelada has a smaller relative brain size than other similarly-sized cercopithecoïds (Martin, 1990, 1993). Thus, we needed to investigate the possibility that there might be a different relationship between endocranial volume and external

**Table 2** Regression values for cercopithecoid and *Theropithecus* datasets

Independent variable	Sample	a Intercept	b Slope	Adjusted $r^2$
Cranial length	Cercopithecoid	-137.8	2.7	0.90
	<i>Theropithecus</i>	-69.1	1.9	0.48
Cranial height	Cercopithecoid	-184.8	5.1	0.91
	<i>Theropithecus</i>	-46.2	2.6	0.41
Cranial width	Cercopithecoid	-165.9	4.1	0.91
	<i>Theropithecus</i>	-116.0	3.3	0.66
Multiple (cranial length, height, width)	Cercopithecoid	-177.2	2.0 height 0.5 length 1.8 width	0.94
	<i>Theropithecus</i>	-121.5	-0.3 height 0.3 length 3.2 width	0.63

cranial dimensions in *Theropithecus* specimens. The intercept, slope and adjusted  $r^2$  values for both samples are given in Table 2 (see also Figures 1–6). The intercept and slope values are different in the two datasets, as are the adjusted  $r^2$  values, which are 0.9, or above, in the whole cercopithecoid regression, but range from 0.41 to 0.66 in the *Theropithecus*-specific sample.

The method for estimating endocranial volume was tested by applying the whole sample cercopithecoid equations to extant and fossil Old World monkey crania of known endocranial volume not included in the original regression analysis (Table 3). The *Theropithecus*-specific equations were tested on two extant *T. gelada* crania, and four fossil *Theropithecus* crania of known endocranial volume (although the measured endocranial volumes for these specimens, especially that for the KNM-ER 969 unsexed calvaria, may be an underestimate of the actual value due to the presence of some matrix inside the neurocranium) (Table 4). In all cases, estimates taken from the regression equations developed in this study were closer to the measured cranial capacity than estimates taken from the published equations (Martin, 1990:386). In general, the *Theropithecus*-specific equations more accurately estimated the endocranial

volumes of the *Theropithecus* specimens. However, as the statistical relationships between external cranial dimensions and endocranial volume are weaker (but still significant) in the *Theropithecus* dataset than they are in the cercopithecoid sample, due in part to a smaller *Theropithecus* sample size, the final analyses were undertaken twice, using estimates from both the cercopithecoid and the *Theropithecus* regressions.

The regression equations derived from the extant sample were applied to measurements taken on Plio-Pleistocene fossil cercopithecoid crania (Table 5). In many cases, only one of the three measurements was available. When there was a choice of two dimensions, the equation with the largest  $r^2$  was used to estimate endocranial volume, and when all three dimensions were available, multiple regression equations were used. The four fossil *Theropithecus* measured endocranial volumes were added to the sample of estimated cranial capacities. In total, 20 fossil *Theropithecus* specimens were included in the trend analyses.

#### *Body mass estimation and scaling for fossil Theropithecus specimens*

Body mass in extant and extinct cercopithecoids varies according to species and sex (Harvey *et al.*, 1987; Smith & Jungers,

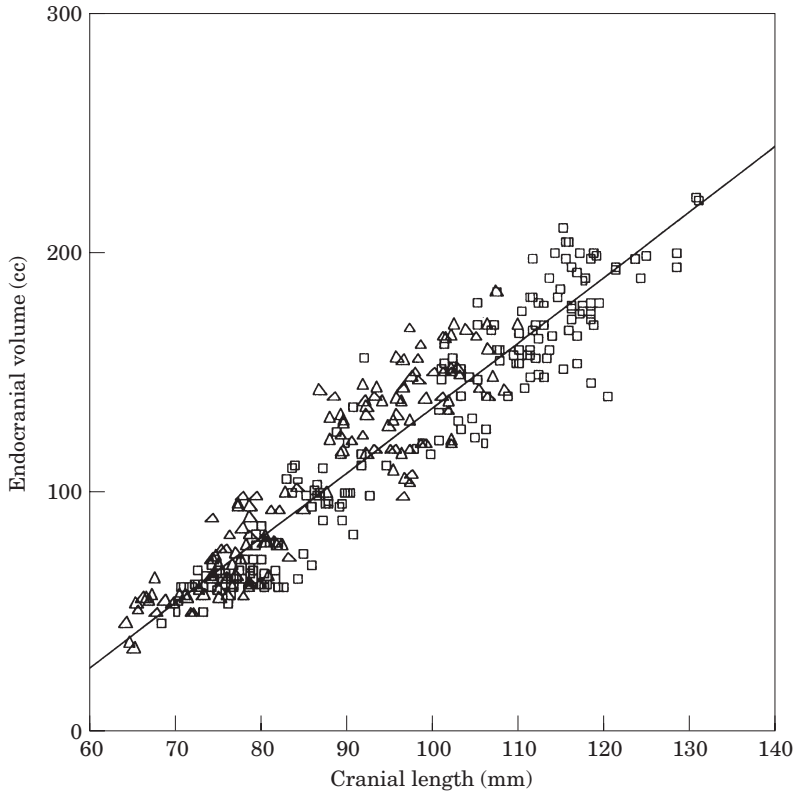


Figure 1. Cercopithecoid regression (endocranial volume/cranial length).  $\square$  male,  $\triangle$  female. Total population  $R_{sq}=0.90$ .

1997). Thus, in order to make cross-species comparisons of brain size it is important to scale brain size to body size. One method of doing this for animals of known brain and body mass is through the use of the encephalization quotient, or EQ (Jerison, 1973; Eisenberg, 1981; Martin, 1990). This method is of limited use for extinct taxa, owing to difficulties obtaining accurate body mass values for many fossil specimens. It has been demonstrated that there is a significant difference between EQ calculated with observed body mass and EQ calculated with predicted body mass, and that the cumulative effect of using a series of predicted values results in data with little or no practical value (Smith, 1996). For example, in this study an estimated endocranial volume

used in conjunction with an estimated actual body mass would introduce two levels of error into the data. The use of a body mass proxy allows endocranial volume to be scaled without making crude estimates of body mass, thus removing one of these levels of error. It has been shown that there is a strong correlation ( $r=0.99$ ) between orbit area and body mass across Old World primates (Kappelman, 1996), so in this work, orbit area (calculated as the product of orbit height and breadth) has been used as a proxy for body mass. A recent investigation of the relationship between cranial variables and body mass in cercopithecoids has shown that orbit area is not a consistent predictor of body mass in the superfamily (Delson *et al.*, 2001). However, in this study

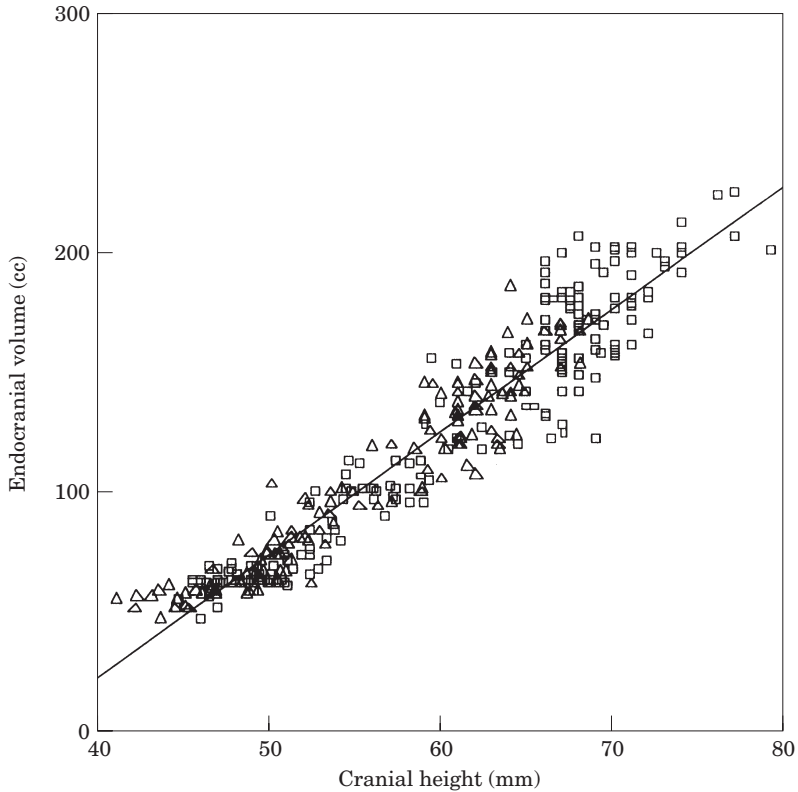


Figure 2. Cercopithecoid regression (endocranial volume/cranial height).  $\square$  male,  $\triangle$  female. Total population  $R_{sq}=0.91$ .

we do not use orbit area to predict body mass directly, but instead use it as a proxy. In the absence of more suitable body mass proxies (i.e., measurements of fossil *Theropithecus* crania not used to predict endocranial volume), orbit area at least provides a skeletally-based means of scaling endocranial volume for use in what is a “narrow” allometry study (*sensu* Smith, 1980).

#### *Fossil Theropithecus datasets*

Two southern African *T. darti* and 18 East and southern African *T. oswaldi* crania were suitable for inclusion in the final analyses of absolute brain size. Of these, only 11 specimens were included in the final analyses of relative brain size (Table 5). The criteria for

inclusion were that they had to be capable of having their absolute cranial capacity estimated and have at least the margin of one orbit preserved. Analysis of absolute endocranial volume was undertaken on four separate datasets (East and southern African *T. darti* and *T. oswaldi*; East and southern African *T. oswaldi*; East African *T. oswaldi*, and East African *T. oswaldi* females), and an analysis of relative endocranial volume was undertaken on three separate datasets (East and southern African *T. darti* and *T. oswaldi*; East and southern African *T. oswaldi*, and East African *T. oswaldi*) (Table 6). Temporal trends in the *T. darti*–*T. oswaldi* lineage were also examined, as the two taxa have been described as a “chronospecies” (Jablonski, 1993).

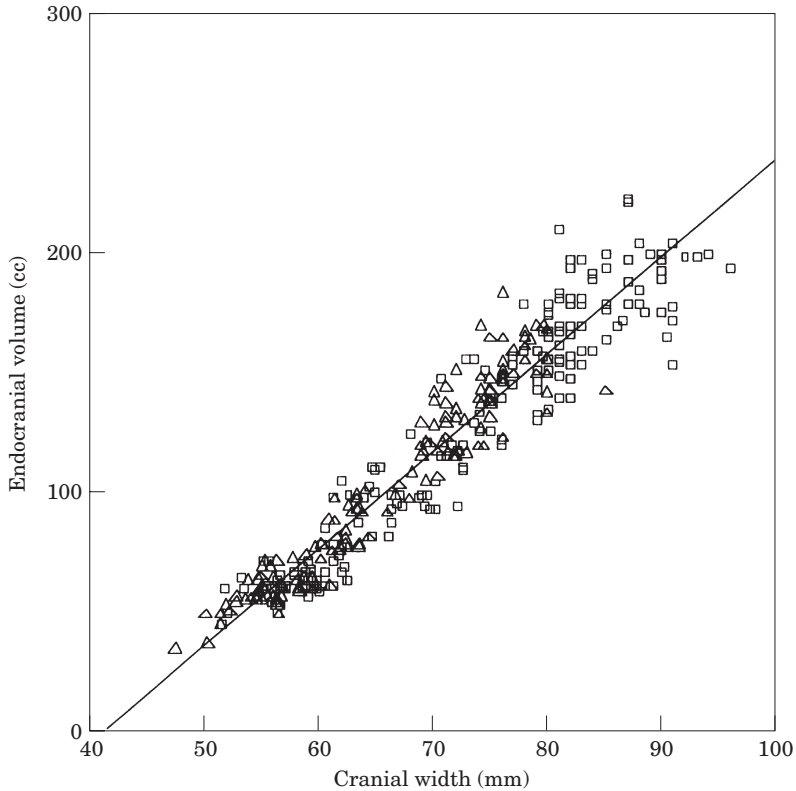


Figure 3. Cercopithecoid regression (endocranial volume/cranial width).  $\square$  male,  $\triangle$  female. Total population  $R_{sq}=0.91$ .

#### *Fossil hominin datasets*

The endocranial volumes of 23 early hominin specimens, representing six species (*P. aethiopicus*, *P. boisei*, *H. habilis sensu stricto*, *H. rudolfensis*, *H. ergaster*, *H. erectus*) were used in this study (Table 7). Endocranial volumes were taken from the literature (Holloway, 1973, 1978, 1983, 1988; Stringer, 1986; Brown *et al.*, 1993; Suwa *et al.*, 1997; Falk *et al.*, 2000), with the exception of the estimate used for the juvenile *P. boisei* specimen, Omo L338y-6. This specimen is estimated to have been seven to eight years of age at death (White & Falk, 1999), with an estimated endocranial volume of 427 cc (Falk *et al.*, 2000). It is possible that this figure represents the actual adult brain volume, as maximum (or near-maximum)

brain size is attained in *Pan* by four years of age (Passingham, 1982) and in humans by seven (Cabana *et al.*, 1993) to ten years (Tanner, 1988) of age. That this figure represents adult brain volume is especially probable given that early hominin development rate was likely to have been more similar to that of modern apes than it was to modern humans (Bromage, 1987). However, growth and development is not complete in *Pan* until approximately 12 years of age, and in humans until 15–18 years, so Omo L338y-6 may not have reached maturity. To account for this, and also to account for any differences between the *P. boisei* developmental rate and that of the appropriate extant comparators, the published endocranial volume for Omo L338y-6

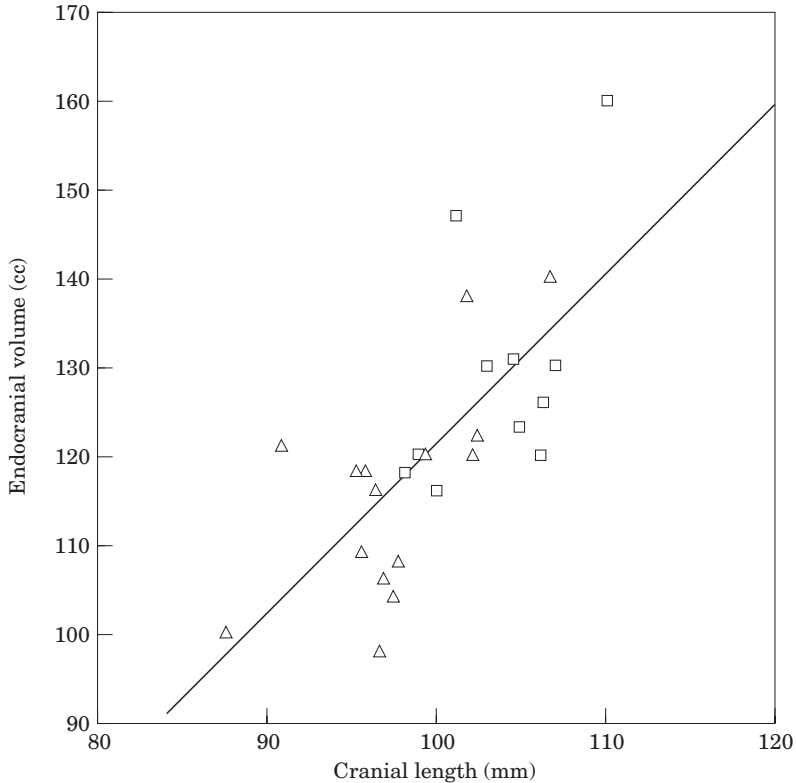


Figure 4. *Theropithecus* regression (endocranial volume/cranial length).  $\square$  male,  $\triangle$  female. Total population  $R_{sq}=0.48$ .

was increased by 4% (based on the likely chronological age and developmental stage of the specimen), giving a predicted adult endocranial volume of 444 cc.

The hominin specimens were divided into six datasets (Table 8): *P. boisei sensu stricto* and *sensu lato*, *H. habilis sensu stricto*, “early Homo” (i.e. *H. habilis sensu lato*, including both *H. habilis sensu stricto* and *H. rudolfensis*), a hypothetical “early Homo”–*H. ergaster* (early African *H. erectus*) lineage, and a hypothetical “early Homo”–*H. ergaster*–African *H. erectus sensu stricto* lineage.

#### *Statistical analysis of cranial capacity trends*

The fossil data were ranked, from earliest to most recent, so that the datasets were comparative within themselves, and analysed

using Spearman’s rho, a correlation procedure for nonnormally distributed samples, to assess whether there was any significant association between the estimated geological age of the fossils (their rank) and their endocranial volume. Another simple, non-parametric test for trend, the “Hubert test” (Hubert *et al.*, 1985; Konigsberg, 1990; Leigh, 1992), was also used to analyse the data, as statistical tests traditionally used to examine trends in a set of data ordered by time can have major limitations when applied to fossil data (Leigh, 1992). This is due in part to the unequal time intervals between data points and the presence of more than one observation for a given date (Vandaele, 1983); it is argued that the “Hubert test” minimizes these limitations (Leigh, 1992). Observations were ranked,

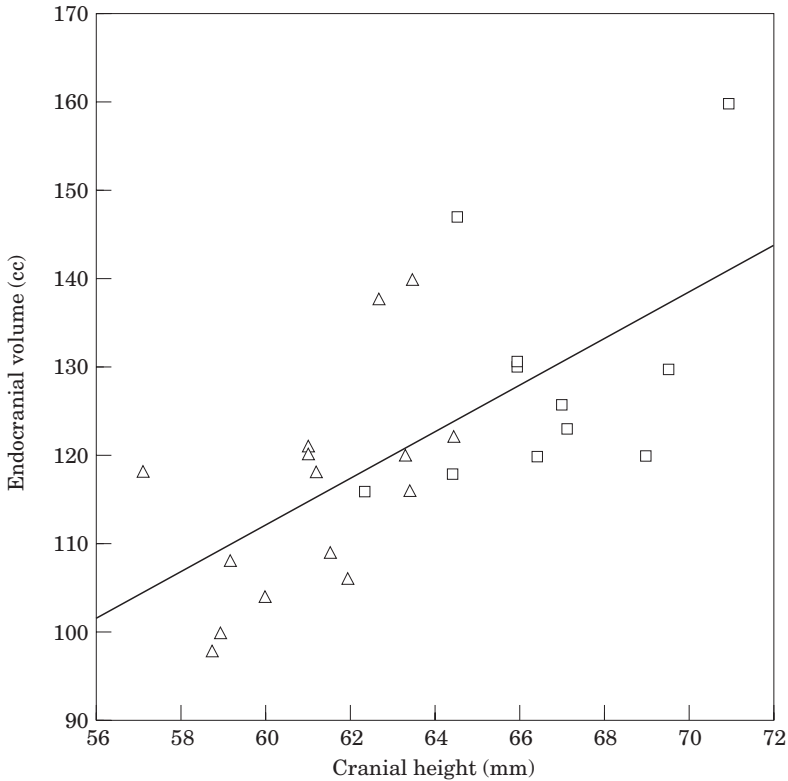


Figure 5. *Theropithecus* regression (endocranial volume/cranial height). □ male, △ female. Total population  $R_{sq}=0.41$ .

with the endocranial volume and the rank number in corresponding vectors. These vectors are then multiplied and the dot products summed to give an overall numerical value for the dataset. One of the two vectors is then randomly re-ordered and the multiplication repeated, so that each set of vectors has its own numerical value. This process is repeated 50,000 times, and the significance of the association between vectors estimated using the equation  $(M+1)/(N+1)$ , where  $M$  is the number of values as large, or larger, than the initial summed dot product and  $N$  is the number of permutations (Hubert *et al.*, 1985). A significant positive trend is implied when only a very small number of randomly-obtained summed dot products exceeds the initial summed dot product, and a significant

negative trend is shown when most randomly-obtained summed dot products exceed the initial summed dot product. No trend is assumed when the initial value lies near the centre of the distribution of the dot products obtained from random permutations (Leigh, 1992). This simulation model is therefore based on the observation that a data series with no statistical significance for trend is most likely to come from the middle of a bell-curve distribution of all possible orders of that dataset.

Randomization tests have been used successfully in several palaeoanthropological studies (see, for example, Lockwood *et al.*, 1996). Specifically, the Hubert test has been used to test trends in the morphology of prehistoric human skeletons (Konigsberg, 1990), brain size trends in *H. erectus* (Leigh,

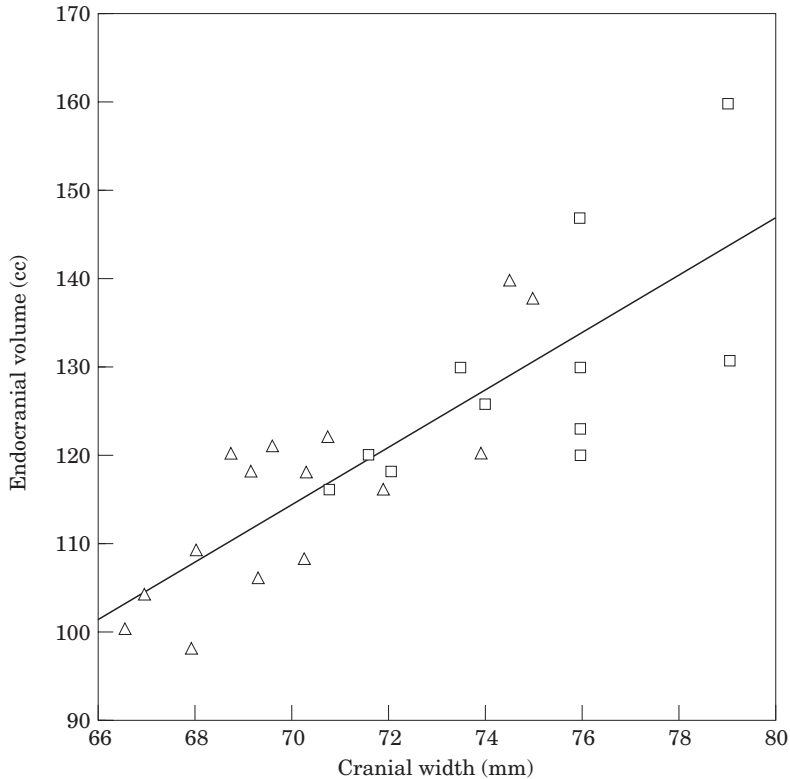


Figure 6. *Theropithecus* regression (endocranial volume/cranial width). □ male, △ female. Total population  $R_{sq}=0.66$ .

1992), and temporal trends in mandibular and dental morphology in *P. boisei* (Wood *et al.*, 1994).

## Results

### Theropithecus

There was no increase or decrease in either absolute or relative brain size over time in any of the *Theropithecus* datasets (Table 6). The Spearman's rho correlation coefficients were all non-significant ( $P>0.05$ ), and the  $P$  values generated by the Hubert test were all either  $>0.05$ , or  $<0.95$ , demonstrating that there was no significant relationship, either positive or negative, between the relative, or absolute, endocranial volume of fossil *Theropithecus* and time.

### Hominins

Due to the difficulties in obtaining adequate body mass proxies in many of the fossil hominin specimens, only absolute endocranial volumes were used in the hominin analyses. For the most part, the results obtained from analyses using Spearman's rho conformed to those obtained using the Hubert test (Table 8).

In the *P. boisei sensu stricto* sample (which excluded KNM-WT 17000, *P. aethiopicus*), there was an increase in absolute brain size over time (Table 8 and Figure 7), significant to the 0.05 level in both the Hubert test ( $P=0.016$ ) and Spearman's rho ( $r=0.63$ ). This trend was also seen in *P. boisei sensu lato*, the addition of the relatively small-brained *P. aethiopicus* specimen KNM-WT

**Table 3 Comparison of actual and estimated endocranial volumes for cercopithecoid specimens not included in the original (cercopithecoid-based) regression**

Taxon	Sex	Measured endocranial volume (cc)	Endocranial volume (cc) estimated from linear cranial dimensions using cercopithecoid equations from this study				Endocranial volume (cc) estimated from linear cranial dimensions using equations from Martin (1990:386)			
			Multi	Length	Height	Width	Multi 2‡	Length	Height	Width
<i>C. guereza</i>	Female	60	62	60	65	63	73	54	100	84
<i>C. guereza</i>	Male	70	78	91	73	79	94	86	109	105
<i>C. aethiops</i>	Female	50	54	69	59	46	69	62	93	66
<i>C. aethiops</i>	Male	60	63	71	62	64	76	64	96	86
<i>C. neglectus</i>	Female	56	50	65	42	56	66	58	75	76
<i>C. neglectus</i>	Male	60	61	60	69	59	73	53	104	79
<i>L. albigena</i>	Female	80	84	75	93	81	95	68	136	108
<i>L. albigena</i>	Male	80	79	80	88	72	92	74	129	95
<i>P. anubis</i>	Female	148	145	149	129	154	190	181	193	250
<i>P. anubis</i>	Male	172	158	147	178	142	210	177	294	221
<i>P. cynocephalus</i>	Female	158	134	150	134	126	174	183	202	185
<i>P. cynocephalus</i>	Male	166	168	186	160	162	243	271	253	271
<i>P. ursinus</i>	Female	166	169	172	175	158	236	233	288	261
<i>P. ursinus</i>	Male	195	187	198	180	183	284	304	300	329
<i>T. gelada</i>	Female	118	124	123	130	119	153	132	195	171
<i>T. gelada</i>	Male	130	144	144	154	132	188	171	243	198
<i>T. oswaldi</i>	—	145	191	202	160	207	289	315	253	410
KNM-ER 969*										
<i>T. oswaldi</i>	Female	140	172	186	185	150	251	269	313	240
M 14836										
<i>T. oswaldi</i>	Female	150	—	205	—	162	—	327	—	271
M 32102										
<i>T. oswaldi</i>	Female	150	168	158	154	179	224	201	243	317
SK 561										

\*Matrix.

†Using the modulus of the linear dimensions.

‡Using the product of the linear dimensions.

**Table 4** Comparison of actual and estimated endocranial volumes (*Theropithecus*-specific equation)

Taxon /specimen	Sex	Measured endocranial volume (cc)	<i>Theropithecus</i> -specific equations			
			Multi	Length	Height	Width
<i>T. gelada</i> extant	Male	130	126	127	128	126
<i>T. gelada</i> extant	Female	118	115	112	116	115
<i>T. oswaldi</i> KNM-ER 969*	Unknown	145	192	167	131	187
<i>T. oswaldi</i> M 14836	Female	140	143	156	144	141
<i>T. oswaldi</i> M 32102	Female	150	—	170	—	151
<i>T. oswaldi</i> SK 561	Female	150	165	137	128	164

\*Matrix.

17000 giving rise to a higher significance level,  $P < 0.01$  in both tests ( $P = 0.007$  in Hubert test, with a Spearman's correlation co-efficient of 0.73) (Table 8 and Figure 8).

The *H. habilis sensu stricto* sample that excluded *H. rudolfensis* showed no increase in absolute brain size over time according to the analysis using Spearman's rho ( $r = 0.56$ ,  $P > 0.05$ ), although the Hubert  $P$  value, equal to 0.055, was on the boundary of significance at the 0.05 level (Table 8 and Figure 9). However, when *H. rudolfensis* was included (to form an "early *Homo*" or *H. habilis sensu lato* sample), the Spearman's rho correlation co-efficient decreased dramatically ( $r = 0.15$ ,  $P > 0.05$ ), with a corresponding increase in the Hubert  $P$  value ( $P = 0.32$ ) (Table 8 and Figure 10). This shows that when *H. rudolfensis* and *H. habilis sensu stricto* are combined there is no increase in endocranial volume in the resulting taxon during the Plio-Pleistocene. This is due mainly to the large brain size of the relatively early *H. rudolfensis* specimen KNM-ER 1470.

There was an increase in endocranial volume over time in the hypothetical "early *Homo*"–*H. ergaster* lineage sample, the results being significant to the 0.05 level in

both the Hubert test ( $P = 0.02$ ) and the Spearman's rho ( $r = 0.58$ ,  $P < 0.05$ ) (Table 8 and Figure 11). A comparable result was obtained in the analysis of the hypothetical "early *Homo*"–*H. ergaster*–African *H. erectus sensu stricto* lineage sample, with a Hubert test  $P$  value of 0.02, and a Spearman's correlation co-efficient of 0.58 ( $P < 0.05$ ) (Table 8 and Figure 12).

To summarize (Figure 13), there were significant increases in absolute endocranial volume in two hypothetical hominin lineages over the course of the Plio-Pleistocene. There was an increase in endocranial volume in the hypothetical lineage that includes *H. habilis sensu stricto*/*H. rudolfensis* and *H. ergaster*/*H. erectus*. There was no change in endocranial volume over time in either the *H. habilis sensu stricto*, or *H. habilis sensu lato* samples. It is worth noting, however, that for the former sample, the Hubert test  $P$  value was on the boundaries of significance, and that the correlation coefficient from the Spearman's rho analysis was relatively high, which indicates a weak trend towards increasing absolute brain size over time in this taxon. Finally, there was a definite trend towards increasing endocranial volume over the course of the Plio-Pleistocene in the two

Table 5 Fossil *Theropithecus* endocranial volume data

Taxon	Sex	Specimen	Date (Ma)	Site	Estimated endocranial volume (cc)		Estimation dimension	Orbit area (cm <sup>2</sup> )	Relative brain size	
					<i>Theropithecus</i> equation	Cercopithecoid equation			Gelada equation	Cercopithecoid equation
<i>T. oswaldi</i>	—	KNM-ER 1532 a	2·5	Koobi Fora	180	199	Width	—	—	—
<i>T. oswaldi</i>	—	KNM-ER 1567	2·5	Koobi Fora	151	162	Width	—	—	—
<i>T. oswaldi</i>	—	KNM-ER 151	2·5	Koobi Fora	132	140	Width	—	—	—
<i>T. oswaldi</i>	—	KNM-ER 969	1·6	Koobi Fora	145*	145*	Direct	—	—	—
<i>T. oswaldi</i>	—	KNM-ER 581	1·6	Koobi Fora	150	161	Width	—	—	—
<i>T. oswaldi</i>	Female	KNM-ER 418	2·5	Koobi Fora	160	168	Multi	—	—	—
<i>T. oswaldi</i>	Female	O68/6511	1·7	Olduvai	174	193	Multi	—	—	—
<i>T. oswaldi</i>	Male	OLD66 589	1·7	Olduvai	187	207	Width	—	—	—
<i>T. oswaldi</i>	Female	8400 b	0·7	Hopefield	141	151	Width	—	—	—
<i>T. oswaldi</i>	Female	KNM-WT 17435	2·0	Nachukui	144	169	Length	9·07	1·50	1·55
<i>T. oswaldi</i>	Male	KNM-ER 1531	2·5	Koobi Fora	173	190	Multi	8·30	1·62	1·65
<i>T. oswaldi</i>	Male	KNM-ER 18925	2·5	Koobi Fora	212	246	Multi	8·99	1·63	1·67
<i>T. oswaldi</i>	Female	M 14836	1·85	Kanjera	140*	140*	Direct	6·40	1·78	1·78
<i>T. oswaldi</i>	Female	M 32104	1·85	Kanjera	128	126	Multi	6·97	1·67	1·66
<i>T. oswaldi</i>	Female	M 32102	1·85	Kanjera	150*	150*	Direct	8·04	1·60	1·60
<i>T. oswaldi</i>	Female	KNM-ER 6001	2·5	Koobi Fora	155	128	Multi	6·40	1·81	1·74
<i>T. oswaldi</i>	Female	KNM-ER 971	2·5	Koobi Fora	162	160	Multi	8·34	1·60	1·59
<i>T. oswaldi</i>	Female	SK 561	1·9	Swartkrans	150*	150*	Direct	8·15	1·59	1·59
<i>T. dari</i>	Female	MP 222	3·0	Makapansgat	122	134	Multi	6·83	1·67	1·70
<i>T. dari</i>	Female	M 3073	3·0	Makapansgat	143	153	Multi	6·77	1·73	1·75
<i>T. baringsensis</i> †	Male	KNM-BC 2	3·2	Chemeron	129	135	Width	6·24	1·77	1·79
<i>T. brumpti</i> †	Male	KNM-WT 16828	3·1	Nachukui	187	207	Width	10·08	1·51	1·54

\*Measured endocranial volume; for estimated volumes, please see Tables 3 and 4.

†Included for information only; not used in final analysis.

**Table 6** Fossil *Theropithecus* datasets and results

Dataset	Spearman's rho correlation coefficient		Hubert test value	
	<i>Theropithecus</i> equation	Cercopithecoid equation	<i>Theropithecus</i> equation	Cercopithecoid equation
East and southern African <i>T. darti</i> and <i>T. oswaldi</i> , absolute endocranial volume $n=20$	-0.39 ( $P>0.05$ , ns)	-0.02 ( $P>0.05$ , ns)	$P=0.64$	$P=0.61$
East and southern African <i>T. oswaldi</i> , absolute endocranial volume $n=18$	-0.35 ( $P>0.05$ , ns)	-0.16 ( $P>0.05$ , ns)	$P=0.87$	$P=0.77$
East African <i>T. oswaldi</i> , absolute endocranial volume $n=16$	-0.26 ( $P>0.05$ , ns)	-0.11 ( $P>0.05$ , ns)	$P=0.77$	$P=0.70$
East African <i>T. oswaldi</i> females, absolute endocranial volume $n=8$	-0.20 ( $P>0.05$ , ns)	0.10 ( $P>0.05$ , ns)	$P=0.62$	$P=0.32$
East and southern African <i>T. darti</i> and <i>T. oswaldi</i> , relative endocranial volume $n=11$	-0.20 ( $P>0.05$ , ns)	-0.25 ( $P>0.05$ , ns)	$P=0.62$	$P=0.73$
East and southern African <i>T. oswaldi</i> , relative endocranial volume $n=9$	0.03 ( $P>0.05$ , ns)	0.03 ( $P>0.05$ , ns)	$P=0.42$	$P=0.43$
East African <i>T. oswaldi</i> , relative endocranial volume $n=8$	0.07 ( $P>0.05$ , ns)	0.07 ( $P>0.05$ , ns)	$P=0.46$	$P=0.42$

**Table 7** Fossil hominin endocranial volumes. *P. boisei* and *H. habilis* refer to *P. boisei sensu stricto*, and *H. habilis sensu stricto*, respectively

Taxon	Specimen	Endocranial volume (cc)	Date (Ma)	Site	Reference
<i>P. aethiopicus</i>	KNM-WT 17000	410	2.6	Nachukui	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	Omo L338y-6*	444	2.4	Shungura	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	O. 323-1976-896	490	2.2	Shungura	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	KNM-ER 13750	475	1.9	Koobi Fora	Holloway, 1988
<i>P. boisei</i>	KNM-ER 23000	491	1.9	Koobi Fora	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	KNM-ER 407	438	1.88	Koobi Fora	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	OH 5	500	1.85	Olduvai	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	KNM-WT 17400	500	1.82	Nachukui	Brown <i>et al.</i> , 1993
<i>P. boisei</i>	KNM-ER 732	466	1.72	Koobi Fora	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	KNM-ER 406	525	1.7	Koobi Fora	Falk <i>et al.</i> , 2000
<i>P. boisei</i>	KGA 10-525	545	1.4	Konso	Suwa <i>et al.</i> , 1997
<i>H. habilis</i>	OH 24	590	1.9	Olduvai	Holloway, 1973
<i>H. habilis</i>	KNM-ER 1813	510	1.9	Koobi Fora	Holloway, 1983
<i>H. habilis</i>	OH 7	687	1.85	Olduvai	Holloway, 1978
<i>H. habilis</i>	KNM-ER 1805	582	1.85	Koobi Fora	Holloway, 1978
<i>H. habilis</i>	OH16	667	1.7	Olduvai	Stringer, 1986
<i>H. habilis</i>	OH 13	650	1.6	Olduvai	Holloway, 1973
<i>H. rudolfensis</i>	KNM-ER 1470	752	1.9	Koobi Fora	Holloway, 1978
<i>H. ergaster</i>	KNM-ER 3733	848	1.78	Koobi Fora	Holloway, 1983
<i>H. ergaster</i>	KNM-WT 15000	900	1.6	Nachukui	Holloway, 1988
<i>H. ergaster</i>	KNM-ER 3883	804	1.58	Koobi Fora	Holloway, 1983
<i>H. erectus</i>	OH 9	1067	1.2	Olduvai	Holloway, 1983
<i>H. erectus</i>	OH 12	727	0.75	Olduvai	Holloway, 1983

\*Omo L338y-6 corrected for maturity (value here represents a 4% increase of the actual volume).

**Table 8 Fossil hominin datasets and results**

Dataset	Spearman's rho correlation co-efficient	Hubert test value
<i>P. boisei sensu lato</i> (n=11)	0.73 (P<0.01)	P=0.007
<i>P. boisei sensu stricto</i> (n=10)	0.63 (P<0.05)	P=0.016
<i>H. habilis sensu stricto</i> (n=6)	0.56 (P>0.05, ns)	P=0.055
<i>H. habilis sensu lato</i> (n=7)	0.15 (P>0.05, n.s.)	P=0.32
"Early Homo" ( <i>H. habilis</i> + <i>H. rudolfensis</i> )– <i>H. ergaster</i> (n=10)	0.58 (P<0.05)	P=0.02
"Early Homo"– <i>H. ergaster</i> + <i>H. erectus</i> (n=12)	0.58 (P<0.05)	P=0.02

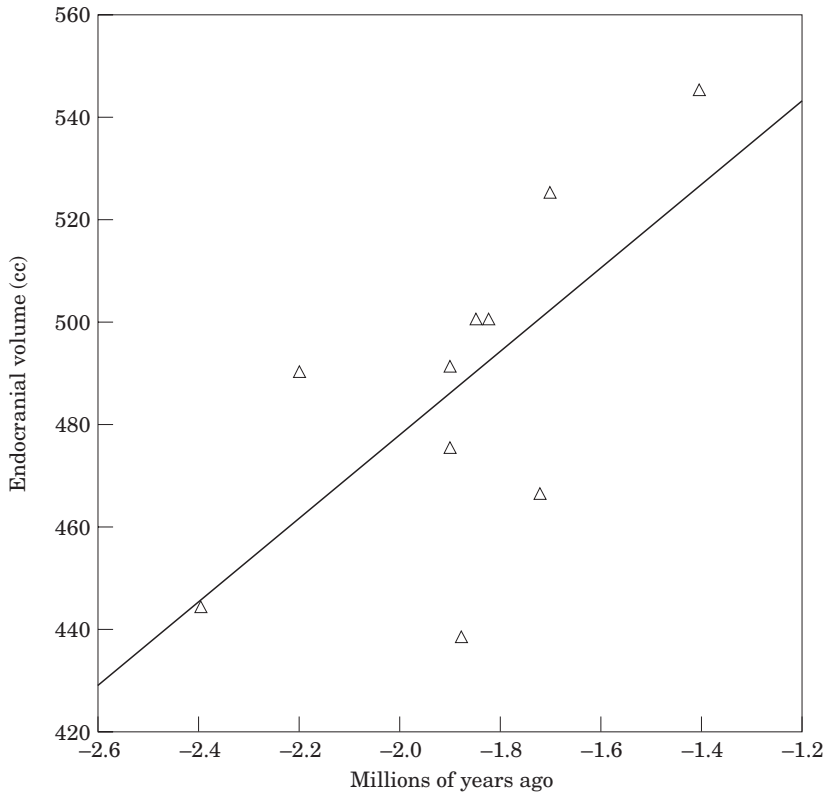


Figure 7. *P. boisei sensu stricto* regression (endocranial volume/time). *P. boisei s. s.* Rsq=0.4380.

*Paranthropus* samples: *P. boisei sensu stricto* and *P. boisei sensu lato* (i.e., *P. boisei* and *P. aethiopicus*).

**Discussion**

The absolutely and relatively large size of the modern human brain is one of the crucial

aspects of biology that distinguishes modern humans from other primates. Moreover, the large size of the human brain is assumed to be critical for the evolution of the uniquely elaborate culture that characterizes modern humans and our immediate ancestors. Brain enlargement is also widely assumed to be a feature confined to our own genus, *Homo*

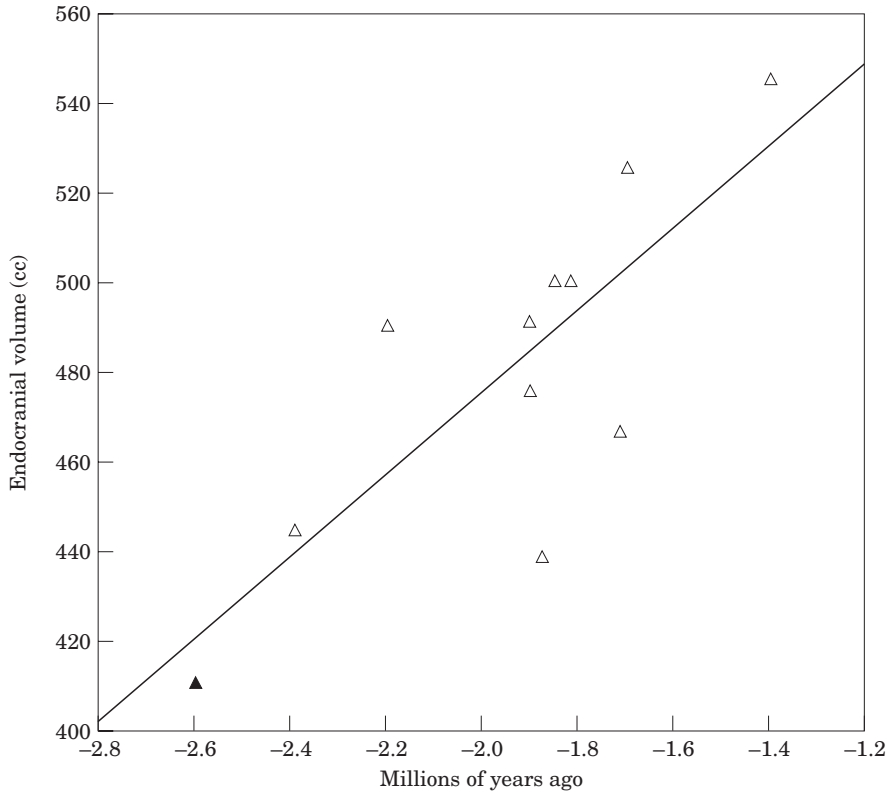


Figure 8. *P. boisei sensu lato* regression (endocranial volume/time).  $\triangle$  *P. boisei s. s.*,  $\blacktriangle$  *P. aethiopicus*. Total population  $R_{sq}=0.6240$ .

(Falk, 1991; Tobias, 1991; Aiello & Wheeler, 1995; Kappelman, 1996; Ruff *et al.*, 1997). The results from this study do indeed support brain enlargement within the taxonomic series *H. habilis sensu stricto*–*H. rudolfensis*–*H. ergaster*. However, our examination of the evidence for trends within these taxa does not imply that the sequence necessarily comprises either a clade or lineage, and we note that there is also a positive trend in estimates of body mass for the taxa in this series (Aiello & Wood, 1994). Our results also provide support for the suggestion that there was an increase in absolute brain size through time in *P. boisei* (Wolpoff, 1988). However, in contradistinction to the evidence for the *Homo sensu lato* lineage referred to above, researchers have argued

that there is no evidence for a temporal increase in body mass within *P. boisei* (Aiello & Wood, 1994; Wood *et al.*, 1994). If an increase in absolute brain size within *P. boisei* was not associated with a concurrent increase in body mass, then during the Plio-Pleistocene there is stronger evidence for an increase in relative brain size within *P. boisei sensu stricto*, or *sensu lato* than there is within *Homo sensu lato*.

Elsewhere, it has been argued that, by 3 Ma, *A. afarensis* had brains that were absolutely larger, and perhaps also relatively larger, than those of *Pan* (Kimbel *et al.*, 1994). The implication of this, combined with brain size increase in at least one non-*Homo* lineage, is that changes in the hominin brain that distinguished hominins from

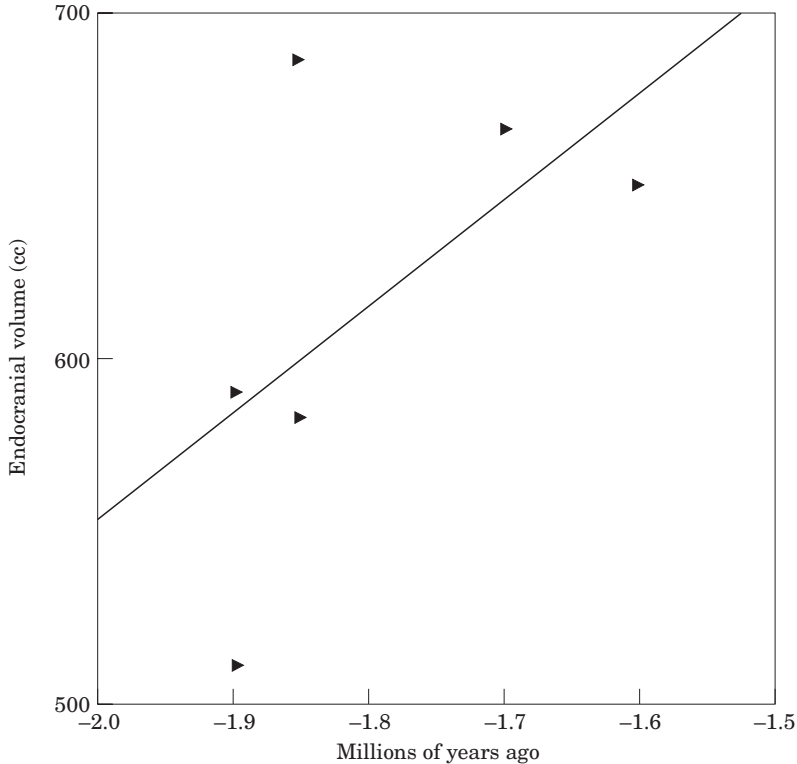


Figure 9. *H. habilis sensu stricto* regression (endocranial volume/time). *H. habilis s. s.*  $R_{sq}=0.3299$ .

other African apes occurred before the emergence of *Homo sensu stricto*. Arguments about the uniqueness of the *Homo* brain are often framed within the context of the prior assumption that the manufacture and use of stone tools is a feature that separates *Homo* and non-*Homo* hominins. Thus, “early *Homo*” (*H. habilis sensu lato*) is sometimes assumed to have a different pattern of brain evolution to that of other hominins, such as *Paranthropus*. This reasoning is circular, and fundamentally unsound on this basis alone. In addition, it is likely, based on both morphology and association in the archaeological record, that non-*Homo* hominins made and used stone tools (Susman, 1994; Heinzelin *et al.*, 1999; Kuman & Clarke, 2000). Thus, one of the most important arguments for linking *Homo*’s unique pattern of brain evolution with the manufacture

and use of stone tools no longer withstands close scrutiny.

There is a paucity of information about the brain size and body mass of many fossil hominin taxa, especially the earliest members of the Hominini, for which the published fossil record of well-preserved crania is still comparatively poor. It would be desirable to track temporal trends in relative brain size through time for early (i.e., pre-2 Ma) hominin taxa, but the data are presently not good enough to do this. However, the Plio-Pleistocene data presented here can be put into context by examining patterns of brain size evolution in *Theropithecus*, another large-bodied primate, across the same time period. This primate has been used as a “control group” in several studies of human evolution (Jolly, 1970; Dunbar, 1983; Elton, 2000). Plio-Pleistocene species of

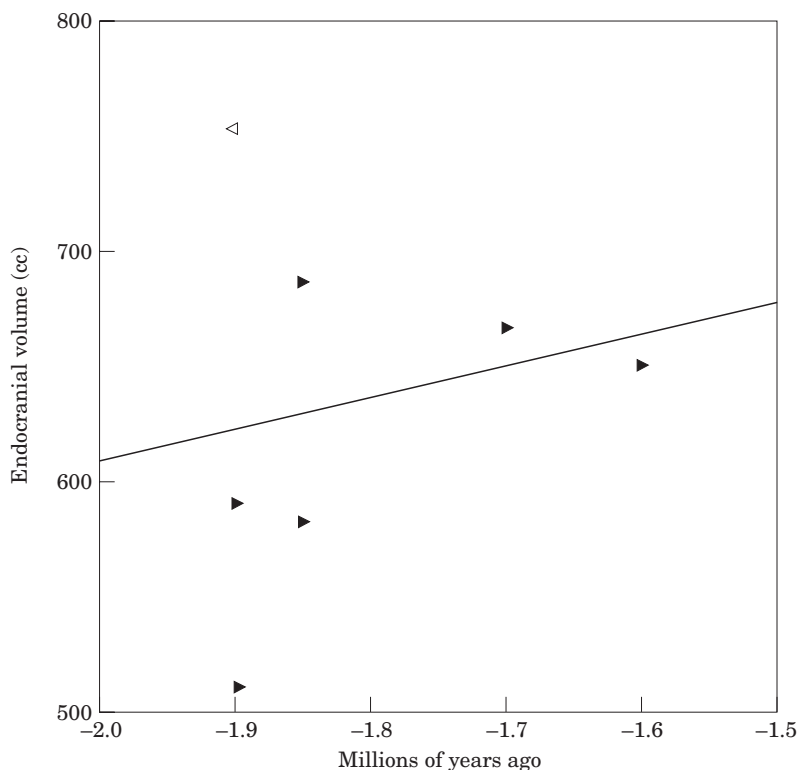


Figure 10. *H. habilis sensu lato* regression (endocranial volume/time). ◁ *H. rudolfensis*, ▶ *H. habilis s. s.* Total population  $R_{sq}=0.0412$ .

*Theropithecus* are found at the same localities as early hominins and their artefacts, and the two taxa probably inhabited similar environments. Thus, it is possible that many similar selective pressures acted on both hominins and theropiths, so that any differences in their evolutionary trajectories are likely to be due to behavioural factors rather than environmental influences. The results of both the Spearman's rho and the Hubert test for *Theropithecus* are unambiguous: there is no significant increase or decrease in fossil *Theropithecus* endocranial volume over time. This indicates that increase in brain size over time was not a feature common to all large-bodied African primates in the Plio-Pleistocene. It appears that a distinction can be made between hominin and non-hominin primates, for while absolute brain size

increases in at least two hominin lineages, *P. boisei* and "early *Homo-H. ergaster*", it does not increase in the comparable large-bodied non-hominin primate lineage.

Various theories have been put forward to explain increases in hominin brain size. These include hypotheses that focus on social behaviour as a selective pressure (Humphrey, 1976; Aiello & Dunbar, 1993), ones that concentrate on the influence of dietary change, particularly increased meat eating, on brain size (Foley & Lee, 1991; Aiello & Wheeler, 1995; Kappelman, 1996), and others that link hominin brain size increase with stone tool manufacture and use (Tobias, 1991), or climate change (Vrba, 1994).

In an elegant hypothesis linking heterochrony and climate change, Vrba (1994)

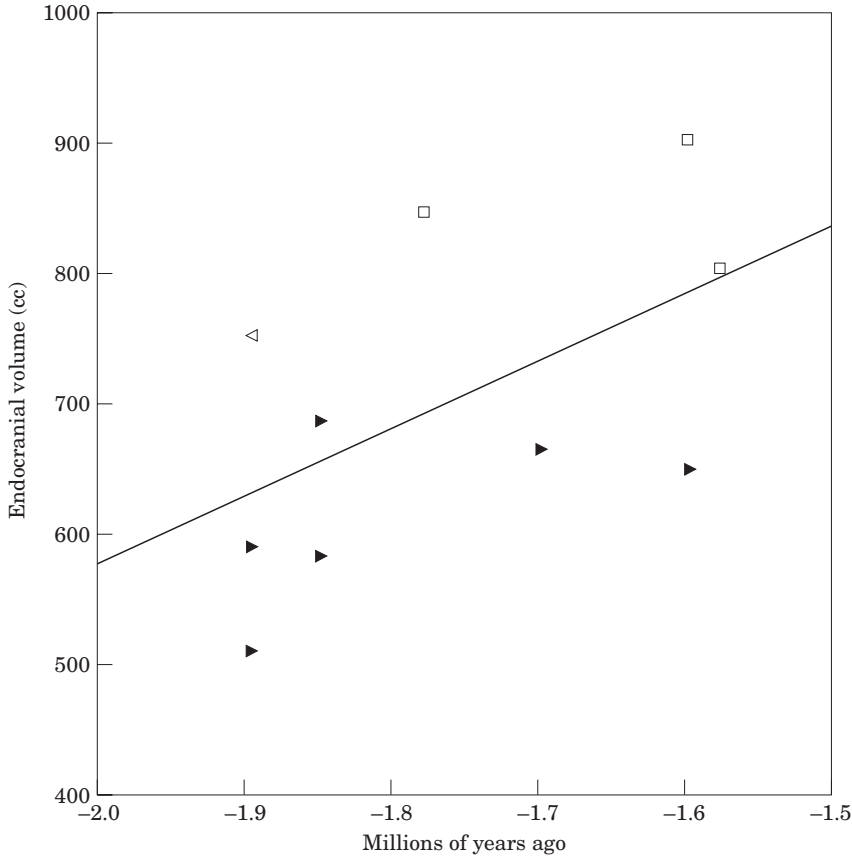


Figure 11. “Early *Homo*”–*H. ergaster* regression (endocranial volume/time). □ *H. ergaster*, ◁ *H. rudolfensis*, ▶ *H. habilis* s. s. Total population  $R_{sq}=0.3095$ .

argues that *time* hypermorphosis induced by a cooling trend may explain the increase in the size of the brain in *Homo sensu lato*. She contrasts this with evidence for *rate* hypermorphosis in *Paranthropus*, suggesting that this latter heterochrony lacked any mechanism that would have caused brain size to increase around 2.5 Ma. The results of the present study do not support such a neat dichotomy. Attention should now be focused on developing testable hypotheses to explain why the same climate failed to induce brain enlargement in *Theropithecus*.

Dietary strategy is one of the most obvious differences between hominins and theropithecids. Whereas there is evidence for the

inclusion of meat in the diets of *A. africanus* and *P. robustus* (Lee-Thorp *et al.*, 1994; Sponheimer & Lee-Thorp, 1999), making it likely that early East African hominins also supplemented their diets with meat, it is unlikely that the predominantly graminivorous *Theropithecus* species incorporated meat, or even high-energy plant food, into the diet. Energetic constraints have been invoked as an explanation for the relatively small brain of the modern *T. gelada* (Martin, 1993), and it is possible that increased meat-eating in hominins removed energetic constraints on brain growth (Foley & Lee, 1991; Aiello & Wheeler, 1995). Dunbar (1992) has argued that brain growth will not occur

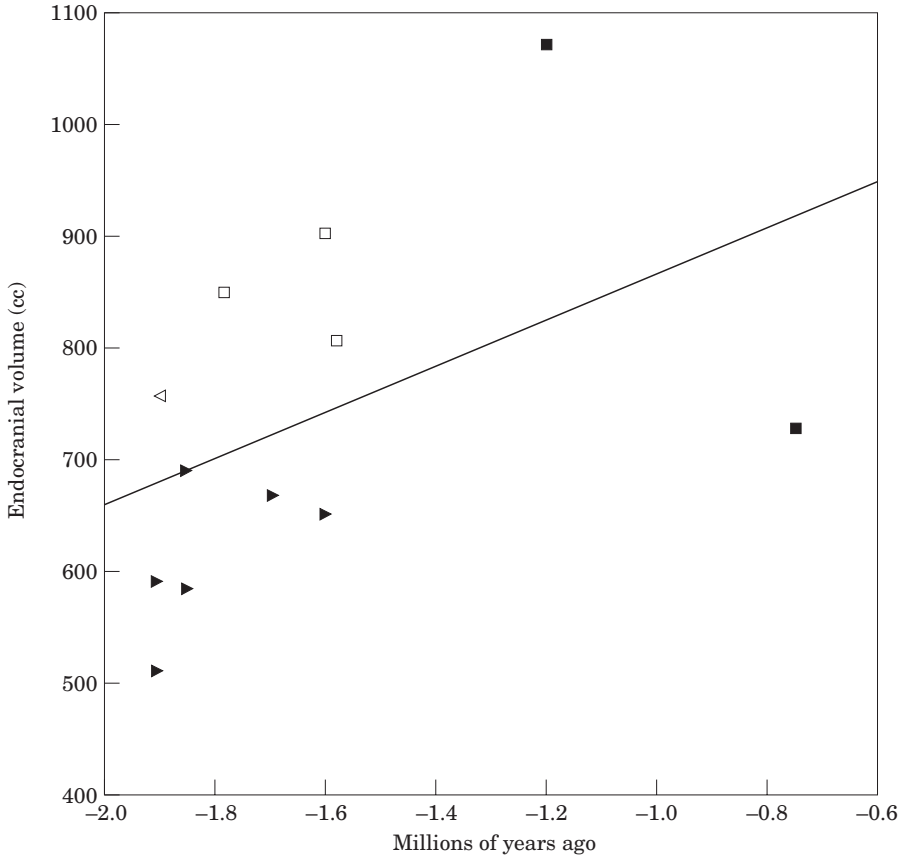


Figure 12. “Early *Homo*”–*H. ergaster*–African *H. erectus* regression (endocranial volume/time).  
 □ *H. ergaster*, ■ *H. erectus*, △ *H. rudolfensis*, ► *H. habilis s. s.* Total population  $R_{sq}=0.2091$ .

simply because of lack of energetic constraints, preferring to believe that there must have been positive selection for increased brain size. It is therefore difficult to translate energetic arguments of this sort into a selective pressure sufficient to cause the hominin brain to increase in size without combining it with complementary hypotheses in a feedback relationship, such as interaction with carnivores who may have been competing for the same resources (Wynn & McGrew, 1989) and selection for increased brain size through complex foraging. Thus, it is more likely that if nutrition influenced hominin brain size, it did so because a higher energy diet facilitated rather than

initiated increased brain growth while simultaneously requiring increased brain power.

It is possible that the act of food procurement was an important selective pressure in hominin brain size increase. There have been several ecological theories for the large brain size of primates in general. Some foods that primates eat must be prepared before consumption, through removing the embedded edible part from a surrounding inedible matrix, and this “extractive foraging” has been put forward as an explanation for the need for increased cognitive abilities in primates (Gibson, 1986). It has been shown that frugivores have significantly larger brains relative to body mass than folivores,

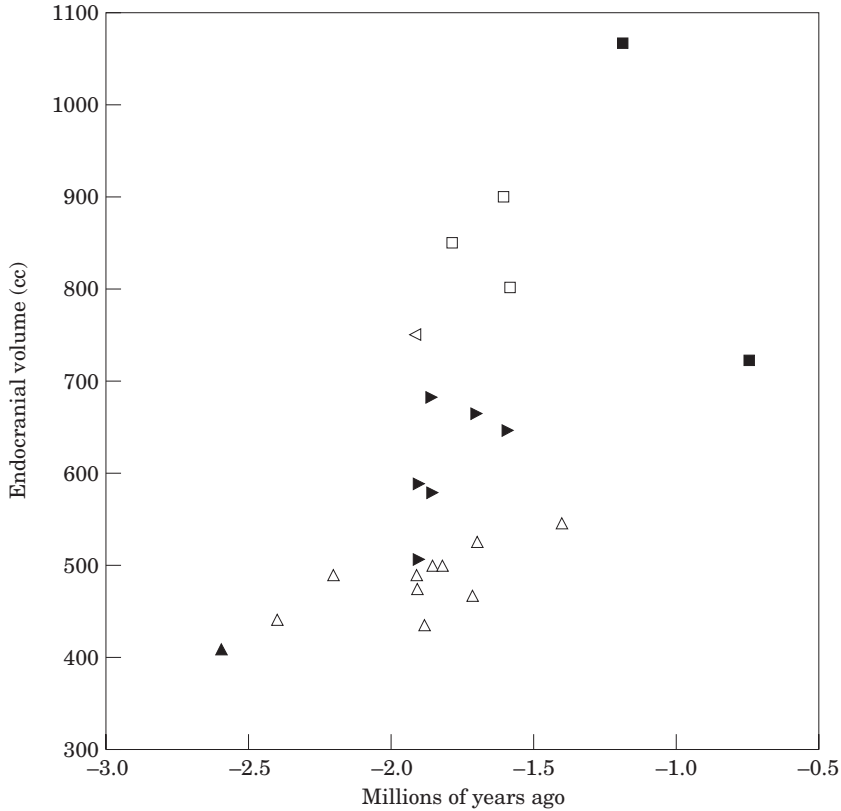


Figure 13. Summary illustration of all the specimens used in the analyses (endocranial volume/time).  
 $\triangle$  *P. boisei s. s.*,  $\blacktriangle$  *P. aethiopicus*,  $\square$  *H. ergaster*,  $\blacksquare$  *H. erectus*,  $\triangleleft$  *H. rudolfensis*,  $\blacktriangleright$  *H. habilis s. s.*

suggesting the need for greater cognitive ability in the former in order to monitor dispersed, patchy and more unpredictable food sources (Clutton-Brock & Harvey, 1980). It has also been suggested that as relative brain size correlates with mean home range size, frugivores may need larger brains to accommodate mental maps for larger areas (Milton, 1988). The above arguments can be applied to the acquisition of meat by hominins. Animals are unpredictable and potentially mobile food sources, and home ranges in hominins are argued to have increased at the same time that the environment changed (Foley, 1992; Leonard & Robertson, 1997). Carcasses, whether hunted or scavenged, must be prepared in some way before being eaten, and

cut marks on bones, along with bones apparently smashed to extract marrow, show that this was occurring early in hominin evolution (Blumenschine, 1986, 1987; Heinzelin *et al.*, 1999). The manufacture and use of stone tools as a means to access meat eating might have been a crucial factor in hominin encephalization. However, it is also possible that increased meat eating and exploitation of patchy resources occurred because the existing cognitive ability and skills of hominins enabled them to make tools, and therefore facilitated meat eating (Bilsborough, 1992). Increased cognitive abilities may have enabled early hominin scavengers to compete with each other, and with taxa such as *Crocota* that were highly morphologically and behaviourally-specialized

scavengers. It has been suggested that the type of deception and Machiavellian intelligence observed in nonhuman primate mating behaviour (Byrne & Whiten, 1988), may have been employed by hominins to give them a foraging advantage (Wynn & McGrew, 1989).

The arguments presented in this paper suggest that the patterns of hominin brain size change, and the context in which they occurred, were considerably more complex than is commonly supposed. Four recent lines of evidence can be cited in support. First, there is evidence that stone tools were being manufactured and used by non-*Homo* hominins as early as ca. 2.5 Ma (Heinzl et al., 1999; Kuman & Clarke, 2000). Second, absolute, and probably also relative, brain sizes were increasing in at least one non-*Homo* lineage during the period that also saw an increase in the complexity of stone artefacts (Asfaw et al., 1992). Third, the only evidence for an increase in brain size within *Homo sensu lato* in the same time period is for an increase in absolute brain size between *H. habilis sensu lato* and *H. ergaster*. Fourth, increases in body mass in the hypothetical phylogenetic series *H. habilis sensu lato*–*H. ergaster* make it unlikely that there was an increase in relative brain size in *Homo sensu lato* prior to the emergence of *H. ergaster*. These factors indicate that debates about the ecological and behavioural contexts of hominin brain evolution must now be more sophisticated, and take into account the possibility that there were multiple patterns of brain evolution in the Hominini.

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