Brain size at birth throughout human evolution: A new method for estimating neonatal brain size in hominins

Jeremy M. DeSilva*, Julie J. Lesnik

Department of Anthropology University of Michigan, Ann Arbor, MI 48109-1107, USA

ABSTRACT

An increase in brain size is a hallmark of human evolution. Questions regarding the evolution of brain development and obstetric constraints in the human lineage can be addressed with accurate estimates of the size of the brain at birth in hominins. Previous estimates of brain size at birth in fossil hominins have been calculated from regressions of neonatal body or brain mass to adult body mass, but this approach is problematic for two reasons: modern humans are outliers for these regressions, and hominin adult body masses are difficult to estimate. To accurately estimate the brain size at birth in extinct human ancestors, an equation is needed for which modern humans fit the anthropoid regression and one in which the hominin variable entered into the regression equation has limited error. Using phylogenetically sensitive statistics, a resampling approach, and brain-mass data from the literature and from National Primate Research Centers on 362 neonates and 2802 adults from eight different anthropoid species, we found that the size of the adult brain can strongly predict the size of the neonatal brain ($r^2 = 0.97$). This regression predicts human brain size, indicating that humans have precisely the brain size expected as an adult given the size of the brain at birth. We estimated the size of the neonatal brain in fossil hominins from a reduced major axis regression equation using published cranial capacities of 89 adult fossil crania. We suggest that australopiths gave birth to infants with cranial capacities that were on average 180 cc (95% CI: 158–205 cc), slightly larger than the average neonatal brain size of chimpanzees. Neonatal brain size increased in early *Homo* to 225 cc (95% CI: 198–257 cc) and in *Homo erectus* to approximately 270 cc (95% CI: 237–310 cc). These results have implications for interpreting the evolution of the birth process and brain development in all hominins from the australopiths and early *Homo*, through *H. erectus*, to *Homo sapiens*.

© 2008 Elsevier Ltd. All rights reserved.

Introduction

Encephalization in the hominin lineage is one of the most frequently studied aspects of human evolution. The large human brain presents two evolutionary dilemmas. First, growing a large brain is energetically expensive (Passmore and Durnin, 1955; Aiello and Wheeler, 1995; Leonard et al., 2003), and second, delivering a large-brained infant through a relatively small pelvic opening makes human birth a difficult and sometimes dangerous endeavor (Rosenberg and Trevathan, 2002). Both of these challenges are intimately related to the size of the brain at birth in human neonates.

However, because of the fragile nature of the newborn skeleton, discoveries of the fossilized crania of infant and juvenile hominins are unusual (Dart, 1925; Howell and Coppens, 1974; Kimbel et al.,

1982; Alemseged et al., 2006). Furthermore, because of the difficulty in precisely aging infant cranial remains, and because rapid brain growth occurs in both chimpanzees and humans in the first few months after birth (Vrba, 1998; Leigh, 2004), directly measuring the size of the brain at birth in fossil hominins may not be possible. Therefore, indirect methods have been used to approximate the size of the neonatal cranium in Plio-Pleistocene hominins.

It has been estimated, for example, that *Australopithecus africanus* gave birth to infants with a cranial capacity between 110 and 163 cc (Leutenegger, 1972). This calculation was based on a regression of neonatal body mass on female body mass and an estimate of 22.5 kg for *A. africanus* female body mass. From this equation, Leutenegger (1972) estimated that *A. africanus* gave birth to infants that were between 760 and 1660 g in body mass. However, modern humans have unusually large babies relative to female body mass when compared to other primates (Leutenegger, 1973; Martin, 2003). Leutenegger (1972) assumed that *A. africanus* had already begun to evolve towards the modern human condition and consequently revised the body mass estimate of *A. africanus* at birth to between 1120 and 1660 g. Finally, because humans and

* Corresponding author.
E-mail addresses: jdesilva@worcester.edu (J.M. DeSilva), lesnikju@umich.edu (J.J. Lesnik).

chimpanzees have a comparable percentage of neonatal body mass composed of brain tissue (9.7 and 9.9% respectively), Leutenegger (1972) argued that *A. africanus* presumably did as well. Application of this percentage to neonatal body-mass estimates resulted in a 110–163 cc estimate for brain size at birth in *A. africanus* (Leutenegger, 1972). These results were applied by both Berge et al. (1984) and Tague and Lovejoy (1986) in their interpretations of the A.L. 288-1 (Lucy) *Australopithecus afarensis* pelvis.

Fifteen years later, Leutenegger (1987) revised his estimate of brain size at birth in the australopiths based on direct regression of neonatal brain mass to female body mass in 21 anthropoid species, including five hominoids, though modern humans were not included in the regression. An anthropoid regression resulted in predicted neonatal brain masses of 134.6 g (109.3–165.8 g) for *A. afarensis* and 126.3 g (103.2–154.7 g) for *A. africanus*. However, Leutenegger (1987) argued that using a hominoid-only regression was more appropriate and application of this equation resulted in lower neonatal brain-mass estimates of 120.7 g (106.6–136.7 g) for *A. afarensis* and 115.3 g (102.1–130.2 g) for *A. africanus*.

Häusler and Schmid (1995) utilized two regression equations in building their argument that the A.L. 288-1 pelvis was actually from a male individual. These authors suggested that Leutenegger's (1987) regression of anthropoid neonatal brain mass on female body mass is probably more appropriate for estimating the size of the brain at birth in australopiths than the hominoid-only regression because it used a larger sample of brain masses to generate the regression. Second, these authors calculated neonatal brain size from an all-primate ($n = 27$) regression of neonatal brain mass on adult brain mass (Martin, 1983). These methods resulted in a prediction that australopith neonates had brains that were between 135 and 160 g, with a maximum estimate of 210 g. Based on pelvic morphology, the authors noted that *A. afarensis*, as represented by Lucy, had infants with a 131 g brain mass and *A. africanus*, as represented by the South African partial skeleton Sts 14, had infants with brains that were about 176 g in mass. Because the pelvic dimensions of their reconstruction of the A.L. 288-1 pelvis did not accommodate their estimated size of the neonatal australopith head, Häusler and Schmid (1995), argued that Lucy may actually be a male. These neonatal brain masses, however, were regarded as overestimates in studies that reaffirmed Lucy's status as a female *A. afarensis* (Wood and Quinney, 1996; Tague and Lovejoy, 1998). First, although error is inherent when using a regression equation to calculate neonatal brain size, Häusler and Schmid (1995) did not report their australopith neonatal brain-size estimates with error ranges and confidence intervals (Wood and Quinney, 1996). Second, Häusler and Schmid (1995) circuitously used a regression of adult brain mass to adult body mass (Martin, 1983) to approximate the adult brain size in *A. afarensis* (492 g), and then used a regression of neonatal brain mass to adult brain mass in primates (Martin, 1983) to suggest that the *A. afarensis* neonatal brain was as large as 210 g. If Häusler and Schmid (1995) are correct that female body mass and neonatal brain mass are correlated, it is unclear why *Pongo* would have a larger body mass than *A. afarensis*, but have smaller-brained infants (Tague and Lovejoy, 1998).

There are three potential problems with how neonatal brain size in australopiths has been calculated to date. First, many of the previous estimates of australopith neonatal brain mass have been calculated from regressions of neonatal body mass or neonatal brain mass to adult female body mass. For these regressions, modern humans are an outlier, having significantly larger neonates with larger brains than expected given our adult body mass (Fig. 1). Because modern humans are an outlier for these regressions, one must decide whether australopiths were more apelike, more humanlike, or somewhere in between. This frequently subjective exercise can be avoided by using a regression in which human values are not outliers.

A **Relationship between neonatal brain and female body mass in primates**

◇ Non-human primates ■ Human
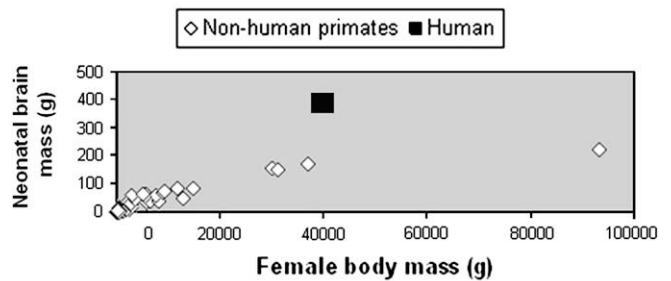
B **Relationship between neonatal body and female body mass in primates**
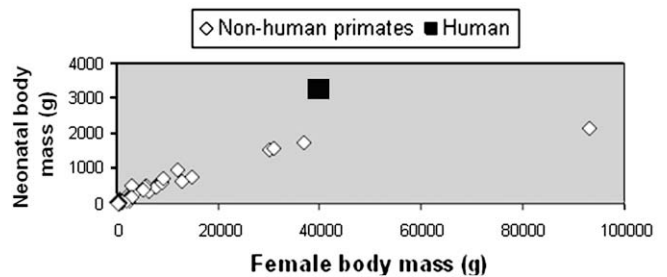
◇ Non-human primates ■ Human

Fig. 1. Previous methods to estimate neonatal brain mass in fossil hominins. Previous attempts to calculate the size of the brain at birth in extinct human ancestors have used regression equations derived from the relationship between the mass of the adult female body and the neonatal brain (a) or neonatal body (b). Notice that modern humans are an outlier for both.

The second issue with these regressions is that Leutenegger's (1972, 1987) approach necessitates accurate estimates of hominin body sizes based on fragmentary fossil remains, which has obvious problems (Smith, 1996). The 95% confidence interval of female body mass in *A. afarensis* is between 15 and 45 kg (McHenry, 1994). Applying these values to the equations used by Häusler and Schmid (1995) results in a range of potential neonatal brain masses for *A. afarensis* between 78 and 210 grams (Wood and Quinney, 1996). Estimates of neonatal brain size in australopiths should ideally be calculated from regressions in which the australopith input variable has considerably less error than female body mass.

Third, although the size of the adult brain mass in primates ($n = 27$) is highly correlated with the size of the brain at birth ($r = 0.99$) (Martin, 1983, 1990) and has been used to estimate neonatal brain size in australopiths (Häusler and Schmid, 1995), the published brain-size-at-birth values for many primate species are based on data from only a single individual (e.g., Sacher and Staffeldt, 1974). A paucity of neonatal brain-mass data raises the possibility that australopith brain-volume estimates based on these regressions may not be reliable. Additionally, this regression (Martin, 1983) includes the distantly related prosimian primates, which may result in a regression line that may not be as applicable to australopiths as one that is restricted to anthropoids, Old World primates, or apes.

We investigated whether a more accurate estimate of brain size at birth in human ancestors can be calculated using a larger data set of neonatal and adult brain masses, and a new regression using a resampling technique. With the calculated size of the brain at birth and the known adult brain volume from fossil crania, we estimated the percentage of brain growth that occurred in utero in the australopiths, early representatives of the genus *Homo*, *Homo erectus*, and middle Pleistocene *Homo* to determine whether extinct hominin brain growth better fits a chimpanzee pattern or a human pattern.

It is important to note that calculating characteristics of extinct hominins from modern regressions can be influenced by the choice of the right line-fitting technique (Smith, 1994; Hens et al., 2000) and by the populations from which the regression equation is calculated (Konigsberg et al., 1998). In this study, we applied both reduced major axis (RMA) and least-squares regression techniques, and attempted to control for phylogeny using independent contrasts. However, our population from which the regression equations were drawn is constrained by the availability of data and should be reevaluated when more neonatal brain data are available.

Materials

Nonhuman primate neonatal and adult brain masses were compiled from the literature (Keith, 1885; Kennard and Willner, 1941; Schultz, 1944, 1965; Kretschmann et al., 1970; Sacher and Staffeldt, 1974; Harvey and Clutton-Brock, 1985). Brain masses from the sources listed above are not fully reliable, however, because the protocols for weighing the brain varied, and the brain mass reported is often based on a single individual. We therefore obtained larger samples of neonatal and adult brain-mass data from the Southwest National Primate Research Center (*Papio anubis*), Oregon National Primate Research Center (*Macaca fuscata, Macaca mulatta*), and Yerkes National Primate Research Center (*Saimiri sciureus, Macaca nemestrina, Cercocebus atys*, and *Pan troglodytes*). Together, the data from the literature and from the NPRCs represent 28 different anthropoid species, including 17 catarrhines. Our analysis prioritized those adult and neonatal data sets collected at the same facility or by the same author to reduce the error introduced by measurement differences (Tobias, 1970; Peters et al., 1998). The descriptive statistics of these neonatal and adult brain masses obtained from the National Primate Research Centers are listed in Table 1. The neonatal brains were from full-term primates that died at birth or within one week after birth. Brain mass data for neonatal and adult humans were compiled from Bischoff (1880) and Marchand (1902).

Cranial capacities of *Sahelanthropus*, 25 australopiths, eight members of early *Homo*, 38 *Homo erectus*, and 17 middle Pleistocene *Homo* were compiled from Holloway et al. (2004) and from additional sources listed in Table 2. Fossil crania identified by Holloway et al. (2004) as coming from infants or juveniles were excluded from the analysis, as these individuals had not finished their cranial growth. These include DIK-1-1, A.L. 333–105, Taung, the Type 3 endocast from Sterkfontein, SK 54, SK 859, KNM-ER 1590, and Modjokerto. Estimates of the cranial capacity of KNM-WT 17400 range from 390 cc (Falk et al., 2000) to 500 cc (Brown et al., 1993), and because of this wide range and KNM-WT 17400's subadult status, this fossil was not included in the analysis. Subadult fossil crania estimated to be at least 8 years old at death

and for which adult estimates were within 5% of the measured cranial capacity were included in the analyses. These specimens included Omo L338y-6, OH 7, OH 13, OH 16, and KNM-WT 15000 (Holloway, 1981; Tobias, 1991; Begun and Walker, 1993; Holloway et al., 2004). Holloway et al. (2004) rated the accuracy of the cranial capacity estimates from 1 (most accurate) to 3 (least accurate). Removal of the three specimens that Holloway et al. (2004) put in categories 2–3 or 3 (MLD 1, OH 24, KNM-ER 3732) did not change the results of this study. Falk et al. (2000) reported slightly smaller cranial capacity estimates for *Paranthropus boisei, P. robustus*, and *A. africanus* than did Holloway et al. (2004). The predicted neonatal brain size for those three species is only 2% lower if Falk et al.'s (2000) numbers are used instead of Holloway et al.'s (2004), and does not change the general results of this study.

Because there is an increase in cranial capacity in fossil hominins through the Pleistocene (Ruff et al., 1997; Lee and Wolpoff, 2003; Rightmire, 2004), we separated these crania into three groups. Twenty crania identified by Antón (2003) as early members of *H. erectus* older than 0.75 Myr were analyzed separately from the temporally later and larger-brained *H. erectus* fossils ($n = 18$) from the Asian sites of Zhoukoudian, Nanjing, Hexian, Yunxian, Ngandong, and Sambungmacan (Antón, 2003; Holloway et al., 2004; Liu et al., 2005). Seventeen crania from the middle Pleistocene that have been assigned by some to *Homo heidelbergensis* (e.g., Tattersall, 1986; Rightmire, 1998, 2004, 2008) were also analyzed as a separate group. There are no differences in the results when the middle Pleistocene crania from Africa are analyzed separately from those considered to be pre-Neandertal European specimens (Stringer, 1996; Dean et al., 1998).

We are aware of the problems associated with the term "brain size" (Smith et al., 1995), as this can refer to the mass, volume, or cranial capacity. Because the most useful measure of brain size in paleoanthropology is cranial capacity, masses in this study were converted to cranial capacities by dividing the mass by the specific gravity of brain tissue (1.036) (Blinkov and Glezer, 1968).

Methods

The correlation between adult brain mass and neonatal brain mass and 95% confidence intervals for the slope and y-axis were determined using both least-squares and RMA regression (Bohonak, 2002). Two separate regressions were calculated: one using data from all of the anthropoids ($n = 28$) and another using data from the catarrhines only ($n = 17$). However, the mean neonatal brain mass of the majority of the species in the above regressions is based on single newborns. We therefore generated another regression based on eight species for which larger data sets are available.

A regression of neonatal brain mass on adult brain mass was generated for individuals of the following eight species: *Saimiri*

Table 1
Descriptive statistics for brain size at birth and as adult in eight anthropoid species*

Species	Neonates (*n*)	Neonatal brain mass (g) Mean ± SD (range)	Adults (*n*)	Adult brain mass (g) Mean ± SD (range)	Source
Saimiri sciureus	24	15.3 ± 2.0 (11.0–19.7)	62	26.2 ± 2.5 (19.7–30.3)	Yerkes NPRC
Cercocebus atys	41	57.5 ± 11.4 (24.2–80.1)	96	107.9 ± 11.2 (88.5–137.6)	Yerkes NPRC
Macaca fuscata	5	69.4 ± 5.5 (63.0–76.0)	18	109.7 ± 13.4 (89.1–132.2)	Oregon NPRC
Macaca mulatta	77	58.3 ± 5.5 (32.6–69.9)	572	91.1 ± 9.6 (62.4–129.0)	Oregon NPRC
Macaca nemestrina	93	61.8 ± 8.8 (37.7–78.8)	200	104.6 ± 12.3 (71.9–114.0)	Yerkes NPRC
Papio anubis	35	82.9 ± 6.2 (70.9–98.3)	20	161.4 ± 16.7 (134.7–195.7)	Southwest NPRC
Pan troglodytes	22	150.9 ± 17.0 (109.0–180.9)	70	381.7 ± 37.2 (308.0–530.0)	Yerkes NPRC; Herndon et al., 1999
Homo sapiens	41	381.8 ± 42.9 (255.0–540.0)	902	1336.1 ± 127.7 (982.0–1705.0)	Bischoff, 1880
Homo sapiens	24	367.7 ± 66.4 (295.0–443.0)	862	1306.9 ± 130.0 (820.0–1925.0)	Marchand, 1902

* A Microsoft Excel spreadsheet of the individual data summarized in this table is available upon request. Those interested should contact the first author.

Table 2
Predicted size of the brain at birth in different hominin species

Species[a] (n)	Specimens	Adult brain mean ± SD (cc)	Sources	Predicted neonatal brain mean ± SD (cc)	95% CI for mean neonatal brain (cc)
Sahelanthropus tchadensis (1)	TM 266-01-060-1	365	Zollikofer et al., 2005	148.3	130.8–168.2
Australopithecus afarensis (4)	A.L. 162-28,[b] 288-1, 333-45, 444-2[c]	455.6 ± 79.4	Holloway, 1983; Holloway et al., 2004; Kimbel et al., 2004	173.8 ± 21.9	152.9–197.5
Australopithecus africanus (8)	MLD 1, 37/38; Sts 5, 19/58, 60, 71; Stw 505; Type 2	466.8 ± 46.4	Conroy et al., 1990, 1998, 2000; Holloway et al., 2004	177.1 ± 12.6	155.8–201.3
Australopithecus garhi (1)	BOU-VP-12/130	450	Holloway et al., 2004	172.6	151.9–196.2
Australopithecus aethiopicus (1)	KNM-WT 17000	410	Walker et al., 1986; Falk et al., 2000; Holloway et al., 2004	161.4	142.1–183.2
Australopithecus robustus (2)	SK 1585; Drimolen 7	530	Holloway et al., 2004; Schwartz and Tattersall, 2005	194.4	170.7–221.3
Australopithecus boisei (9)	KNM-ER 406, 407, 732, 23000, 13750; OH 5; Omo L338-y; Omo-323-1976-896; KGA 10-525	499.6 ± 30.3	Holloway, 1981; Brown et al., 1993; Falk et al., 2000; Holloway et al., 2004	186.2 ± 7.1	163.6–211.8
Early *Homo*[d] (8)	KNM-ER 1805, 1813, 1470, 3732; OH 7, 13, 16, 24	651.6 ± 88.9	Tobias, 1991; Holloway et al., 2004	225.4 ± 22.4	197.5–257.2
Homo erectus[e] (20)	KNM-ER 3733, 3883, 42700; KNM-WT 15000; D2280, 2282, 2700, 3444; OH 9, 12; BOU-VP-2/66; UA 31; Sangiran 2, 3, 4, 10, 12, 17; Trinil 2; Gongwangling	839.6 ± 138.6	Begun and Walker, 1993; Abbate et al., 1998; Gabunia et al., 2000; Asfaw et al., 2002; Vekua et al., 2002; Holloway et al., 2004; Lordkipanidze et al., 2006; Spoor et al., 2007	270.5 ± 32.6	236.5–309.6
Later Asian *H. erectus* (18)	Zhoukoudian II, III, X, XI, XII; Nanjing 1; Hexian; Ngandong 1, 6, 7, X, 13, 14; Sambungmacan 1, 3, 4; Yunxian; Ngawi	1056.7 ± 123.7	Holloway et al., 2004; Liu et al., 2005	320.0 ± 27.2	279.1–367.1
Middle Pleistocene *Homo* (17)	Bodo; Kabwe; Ndutu; Salé; Saldanha; Narmada; Arago; Ceprano; Petralona; Reilingen; Steinheim; Swanscombe; Atapuerca 4, 5, 6; Dali; Jinniushan	1218.9 ± 223.1	Holloway et al., 2004	355.0 ± 28.7	309.1–407.8

[a] Hominid taxonomy is contentious and our grouping of these particular specimens into the species indicated above may be problematic. The raw data on adult brain size provided in Holloway et al. (2004) and other sources listed above can be entered into the regression equations provided in Table 4 for any combination of specimens thought to represent a taxonomic unit.

[b] Schwartz and Tattersall (2005) considered this specimen to be nonhominid. If A.L. 162-28 is removed from the analysis, the australopith average changes little (180.3 ± 13.6 cc) and the mean neonatal brain-size estimate for *A. afarensis* increases slightly to 179.5 ± 22.8 cc.

[c] Specimen A.L. 444-2 is a large individual that is found late in the Hadar sequence (Lockwood et al., 2000; Kimbel et al., 2004) and therefore may skew the results presented for *A. afarensis*. When this specimen is removed from *A. afarensis*, the mean neonatal brain-size estimate for *A. afarensis* decreases slightly to 165.2 ± 16.6 cc.

[d] Early *Homo* consists of specimens typically grouped as either *H. habilis* or *H. rudolfensis*.

[e] *Homo erectus* consists of specimens older than 0.75 Myr.

sciureus, *Cercocebus atys*, *Macaca fuscata*, *Macaca mulatta*, *Macaca nemestrina*, *Papio anubis*, *Pan troglodytes*, and *Homo sapiens*. We also generated a regression using only the seven catarrhines (i.e., the New World primate *Saimiri* was removed for this analysis). The National Primate Research Centers and literature sources listed in Table 1 provided individual brain masses for 362 neonates and 2802 adults from the above-mentioned eight species. Because longitudinal data on brain growth have not been compiled for these species, it is unknown how large the brain of any one neonatal primate would have been, or how large the brain of any one adult was at birth. However, all of the possible longitudinal relationships can be generated by resampling from the cross-sectional data. If the 362 neonatal primates had not died at birth, their brains presumably would have grown to a size that can be estimated using the large pool of 2802 adult primate brain masses. Likewise, the size of the brain at birth in any of these adult primates can be approximated using the data known from the 362 neonates. Individual neonate-adult pairings were made using a resampling technique described below.

We assumed that the neonatal brain mass for any infant of a given species could develop into any of the reported brain masses of the same species and the same sex. The brain mass of a single neonate of a given species and sex was randomly sampled with replacement and paired with a randomly sampled brain mass of a single adult primate of the same species and sex (Fig. 2). This procedure was repeated for 50 females and 50 males of a given species to generate a total of 100 possible neonatal-adult brain-mass values for each primate species. This approach was repeated for each of the eight primate species for a total of 800 individual neonate-adult brain-mass data points. To ensure that each species contributed equally to the regression equation, this method was used over an exact-permutation approach. It is important to note that the method employed in this study is more conservative and produces larger confidence intervals for the regression coefficients than exact permutations, which would have resulted in over 50,000 neonatal-adult brain mass pairings. We prefer this more conservative approach until a longitudinal study of brain growth in primates assesses the validity of our resampling cross-sectional data to approximate longitudinal data.

Least-squares and RMA regression coefficients were calculated using the 800 individual resampled neonatal-adult brain-mass pairings. Each of the 89 individual hominin cranial capacities was then entered as dependent variables into the regression equation to calculate the brain size at birth and the 95% confidence interval around that estimate.

The percentage of brain growth that occurred prenatally in the australopiths, early *Homo*, *H. erectus*, and mid-Pleistocene *Homo*
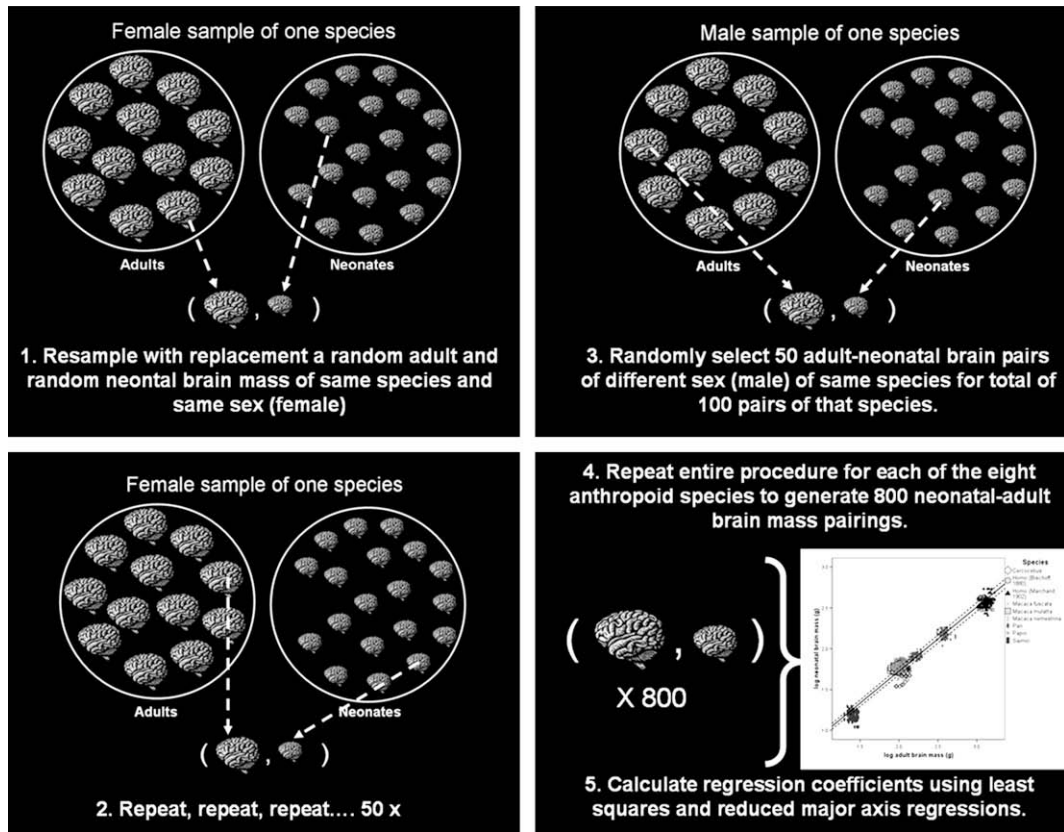
Fig. 2. This figure illustrates the five steps used to generate a regression equation of neonatal brain mass to adult brain mass in individual anthropoid primates. This equation is then used to estimate the size of the neonatal brain in extinct hominins from cranial capacity estimates of fossil crania.

was then calculated. Each calculated neonatal cranial capacity was divided by all possible adult cranial capacities for the hominin group being studied using exact permutation.

Phylogenetically sensitive statistics were also employed to test whether the relationship between neonatal and adult brain mass differed once phylogeny was controlled. Different primate species used in this study are related to one another through common ancestry, and may therefore violate the assumption of independence in a linear regression (Felsenstein, 1985; Harvey and Purvis, 1991). We generated a least-squares regression of neonatal on adult brain mass using phylogenetically independent contrasts calculated using the software COMPARE v.4.6 (Martins, 2004). Branch lengths were all assumed to be equal and the primate phylogeny followed Smith and Cheverud (2002).

Results

Table 3 lists the slope, *y*-intercept, and 95% confidence intervals for both least-squares and RMA regression coefficients of primate neonatal brain mass to adult brain mass. Results of these analyses using data from all anthropoids, catarrhines-only, and our resampling approach are detailed below.

Anthropoids (28 species)

Adult brain mass is highly predictive of the size of the brain at birth in primates (Fig. 3). Using the mean adult and neonatal brain masses for 28 anthropoid species, adult brain mass explains 97% of the variance in neonatal brain mass; the RMA regression equation is:

$$\log (\text{neonatal brain mass}) = 0.9483 \times \log (\text{adult brain mass})$$
$$- 0.2092.$$

The 95% confidence interval for the slope is 0.869–1.026, and the 95% confidence interval for the *y*-intercept is −0.35718 to −0.03172. Application of this regression to the australopith adult cranial capacity data set ($n = 25$) suggests a neonatal brain size of

Table 3
Coefficients for regressions of primate neonatal brain mass to adult brain mass

| Regression subjects	Species (*n*)	Regression model	r^2	Slope (*m*)	Slope 95% CI	*y*-intercept	*y*-intercept 95% CI
Anthropoids	28	Least squares	0.97	0.94	0.86 to 1.01	−0.19	−0.34 to −0.04
Anthropoids	28	RMA	0.97	0.95	0.87 to 1.03	−0.21	−0.36 to −0.03
Catarrhines	17	Least squares	0.95	0.72	0.63 to 0.82	0.32	0.11 to 0.54
Catarrhines	17	RMA	0.96	0.76	0.70 to 0.84	0.23	0.02 to 0.39
Catarrhines	17	Least squares with independent contrasts	0.99	0.71	0.65 to 0.77	0.36	0.24 to 0.48
Catarrhines resampled	7	Least squares	0.97	0.77	0.76 to 0.78	0.19	0.17 to 0.21
Catarrhines resampled	7	RMA	0.97	0.73	0.71 to 0.74	0.32	0.29 to 0.34
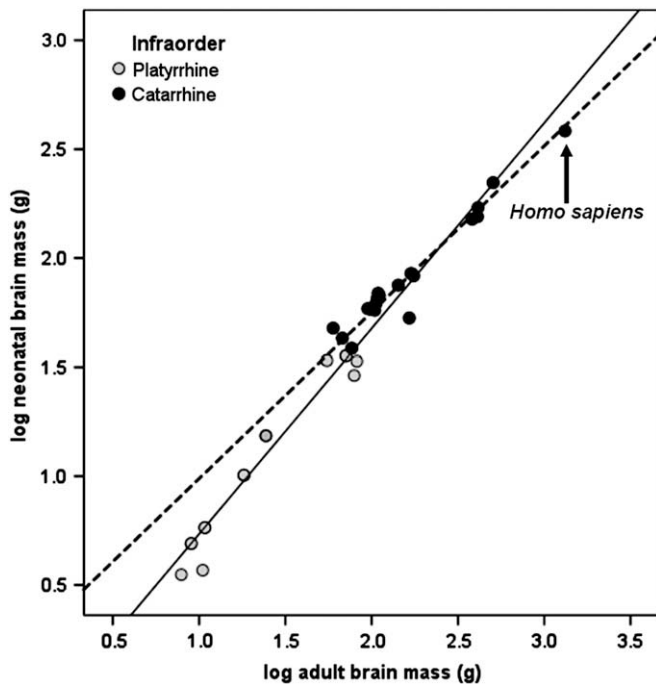
Fig. 3. Relationship between adult brain mass and neonatal brain mass in anthropoid primates. Two RMA regressions have been drawn: one through all of the anthropoids (solid line) and one through only the Old World primates (dotted line). Notice that the slopes are not equal and that anthropoids scale close to isometry ($m = 0.95$) whereas the Old World primates scale with negative allometry ($m = 0.76$). Also notice that humans are not an outlier for this regression.

214.1 ± 20.7 cc. However, the confidence intervals are large, yielding estimates of 93.3–520.3 cc.

Catarrhine primates (17 species)

Using the mean adult and neonatal brain masses for just the 17 catarrhine primate species, adult brain mass explains 96% of the variance in neonatal brain mass and the RMA regression equation is:

$$\log (\text{neonatal brain mass}) = 0.7631 \times \log (\text{adult brain mass})$$
$$+ 0.2255.$$

The 95% confidence interval for the slope is 0.6951–0.8427, and the 95% confidence interval for the *y*-intercept is 0.0240–0.3897. Application of this regression to the australopiths suggests a neonatal brain size of 185.7 ± 14.5 cc. However, the confidence intervals are again quite large and produce estimates of 76.8–443.0 cc for the size of the brain at birth in the australopiths. Using least-squares regression yields a similar estimate for neonatal brain size in australopiths of 177.0 ± 13.0 cc.

Catarrhine primates (phylogenetic controls)

It was important to test whether phylogeny was influencing the relationship between neonatal and adult brain mass. A least-squares regression was generated from the phylogenetically independent contrasts of neonatal to adult brain mass using the software COMPARE v. 4.6b. When phylogeny was controlled in this manner, adult brain mass explained 99.3% of the variance in neonatal brain mass, and the regression equation generated was:

$$\log (\text{neonatal brain mass}) = 0.71 \times \log (\text{adult brain mass}) + 0.36.$$

Applying this equation to australopiths yields an estimated brain volume of 182.5 ± 13.3 cc. This cranial capacity is not

different from the estimates generated without controlling for phylogeny.

Catarrhine primates (resampled data from seven species)

Using resampling statistics and the larger data set of neonatal and brain masses for seven catarrhine species and 700 pairs of resampled individuals, we also found that the adult brain mass is highly predictive of the neonatal brain mass in anthropoids ($r^2 = 0.97$) (Fig. 4). The RMA regression equation is:

$$\log (\text{neonatal brain mass}) = 0.7246 \times \log (\text{adult brain mass})$$

$$+ 0.3146.$$

The 95% confidence interval for the slope of the line is 0.7141–0.7356, and the 95% confidence interval for the *y*-intercept is 0.2869–0.3409. Because we treated the data points as individuals, and not as means, the 95% confidence interval is more constrained, and we can calculate a more informative estimate for the range of brain size in hominin neonates. Application of this regression to the australopith adult cranial capacity data set suggests a neonatal brain size of 179.8 ± 13.3 cc with a 95% CI of 158.1–204.5 cc. If *Saimiri* is included in the analysis, then the predicted australopith neonatal brain is nearly identical in size (179.9 ± 14.4 cc with a 95% CI of 161.1–204.0 cc). When the fossil specimens are clustered into one of many hypothesized taxonomic groupings (Table 2), the estimated size of the brain at birth does not vary considerably from one australopith species to another. However, in early *Homo*, the increase in estimated neonatal brain size to 225.4 ± 22.4 cc (95% CI: 197.5–257.2 cc) reflects the proportional increase in adult cranial capacity to 651.6 ± 88.9 cc (Table 2). Likewise, the increase in *H. erectus* adult cranial capacity results in a larger predicted neonatal brain size of 270.5 ± 32.6 cc (95% CI: 263.8–346.5 cc). Later Asian *H.*
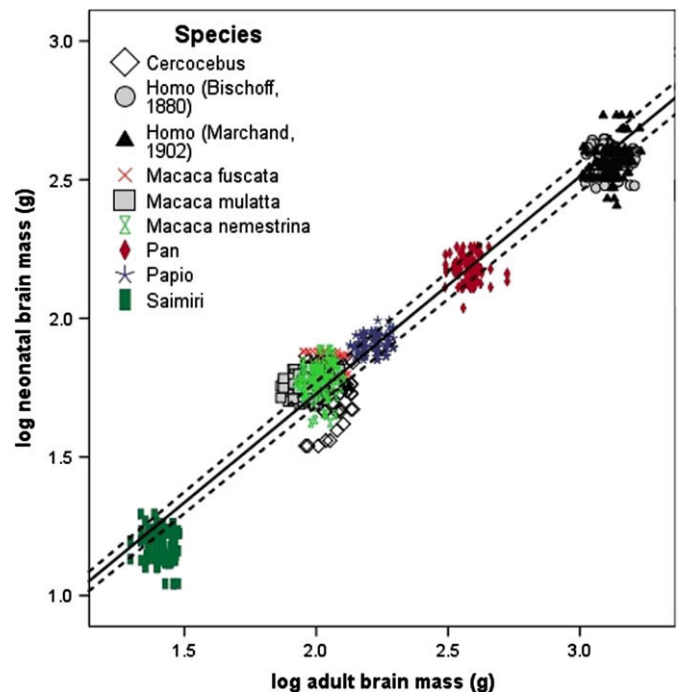

Fig. 4. Relationship between adult brain mass and nonatal brain mass using resampled data. A regression is generated from 100 resampled data points for eight species of anthropoid primate. For these species, including chimpanzees and humans, adult brain mass is a strong predictor of neonatal brain mass ($r^2 = 0.97$). The solid line is the RMA regression and the dotted lines are the 95% confidence interval of the mean.

Table 4
Gradual evolution in proportion of prenatal brain growth in hominids

Species	Number of resamples	% brain growth in utero	Source
Chimpanzee	789	40.1 ± 5.7	DeSilva and Lesnik, 2006
Australopiths	625	38.1 ± 4.9	This study
Early *Homo*	64	35.2 ± 5.5	This study
Homo erectus	400	33.1 ± 6.8	This study
Later Asian *H. erectus*	324	30.5 ± 4.4	This study
Middle Pleistocene *Homo*	289	29.5 ± 4.2	This study
Homo sapiens	10,000	29.9 ± 4.7	DeSilva and Lesnik, 2006 (from Bischoff, 1880)
Homo sapiens	10,000	28.0 ± 5.0	DeSilva and Lesnik, 2006 (from Marchand, 1902)

erectus neonates possessed brains that were 320.0 ± 27.2 cc (95% CI: 279.1–367.l cc) and middle Pleistocene members of the genus *Homo* gave birth to infants with brains that were 355.0 ± 28.7 cc (95% CI: 309.1–407.8 cc).

The percentage of brain growth that occurred in utero for the australopiths was 38.1 ± 4.9% (Table 4). The percentage of brain growth that occurred in utero for early *Homo* was 35.2 ± 5.5%. *Homo erectus* experienced approximately 33.1 ± 6.8% of its brain growth prenatally. Later Asian *H. erectus* specimens had on average 30.5 ± 4.4% of their brain growth prenatally, whereas middle Pleistocene *Homo* experienced 29.5 ± 4.2% of their brain growth in utero.

To test the predictive strength of the regression equation generated above, we used it to predict the size of the neonatal brain in four extant hominoid species (*Pan paniscus, Gorilla gorilla, Pongo pygmaeus,* and *Hylobates lar*). Because there are few data on brain size at birth in these species, they were not used to generate the regression. Because of their omission in generating the regression, however, what data are available can be used to test the predictive strength of the regression equation. For all four extant hominoids tested, the known brain size at birth is within the 95% confidence interval for the average size of the neonatal brain predicted by the regression equation generated in this study (Table 5).

Discussion

Modern humans are unique among primates in having unusually large-bodied neonates with large brains relative to the size of the mother (Fig. 1). However, given the size of the adult brain, humans have precisely the brain size at birth expected for a catarrhine primate (Fig. 3). These results contrast with those of Martin (1983), who suggested that humans have smaller brains at birth than expected given their adult brain size. Although we found that humans have slightly smaller brains at birth than expected based on the anthropoid regression (Fig. 3), the human average is well within the 95% confidence interval of this regression, and falls directly on the catarrhine-only regression line. We suggest that the larger sample size of individual primate neonatal brain masses

presented here account for the difference between the two studies. Because of the scaling relationship between neonatal brain size and adult brain size, we were able to estimate the size of the brain at birth in extinct hominin species using relatively reliable data on the adult cranial capacity of 89 fossilized crania. Importantly, the results did not change when phylogeny was considered as a variable in the analysis.

On average, australopiths gave birth to infants with brains slightly larger than those of infant chimpanzees. Modern chimpanzees give birth to neonates with brains that are 145.7 ± 16.4 cc (DeSilva and Lesnik, 2006), whereas we estimate that infant australopiths had a cranial capacity of 179.8 ± 13.3 cc. In contrast, modern human neonates have brains that are about 367 cc at birth ($n = 252$) (Ho et al., 1981).

Brain size at birth in Lucy's children

Our estimates of cranial capacity at birth in the australopiths are larger than those previously proposed (Leutenegger, 1972, 1987). Given the strong allometric relationship between adult brain size and neonatal brain size across anthropoid primates (Martin, 1983, 1990; this study), we find it unlikely that australopiths would have had adult brains that were on average larger than those of chimpanzees while giving birth to infants with brains on average smaller than those of chimpanzee neonates. Instead, we suggest that Häusler and Schmid's (1995) higher neonatal brain size estimates are more accurate than Leutenegger's (1972, 1987) estimates, although *A. afarensis* having infants with 203 cc (210 g) brains is probably an overestimate, as noted by Tague and Lovejoy (1998). Nevertheless, even with the larger neonatal brain-size estimates for australopiths calculated in this study, we concur with Tague and Lovejoy (1998) that *A. afarensis*, as represented by A.L. 288-1 (Lucy), could have successfully given birth. Neonatal brain size is strongly correlated with the size of the mother's brain in studies of macaques (Cheverud et al., 1990), baboons (Mahaney et al., 1993; Rogers et al., 2007), and humans (Lunde et al., 2007). Data also suggest that neonatal head circumference is more highly correlated with maternal than paternal head circumference (Lunde et al., 2007). Therefore, the offspring of the small-brained Lucy (estimated 340–400 cc by Häusler and Schmid, 1997) were more than likely on the low end of the *A. afarensis* range. Entering the larger estimate of 400 cc into the regression equation yields neonatal brain-size estimates in Lucy's children of 158.5 cc (139.7–179.9 cc). Tague and Lovejoy (1998) demonstrated that a neonate with a brain of this size (160 g) could be birthed through Lucy's pelvic outlet using either Häusler and Schmid's (1997) or Tague and Lovejoy (1986) reconstruction.

Brain size at birth in African *Homo erectus*

The methodology used here allows us to assess the brain size at birth estimated from the pelvis of the KNM-WT 15000 *H. erectus* skeleton (Walker and Ruff, 1993). Using the diameter of the pelvic inlet, and making adjustments for the age and sex of the Nariokotome boy, Walker and Ruff (1993) suggested that a female *H. erectus* would have been able to give birth to an infant with

Table 5
Predictive strength of the regression equation

Species	Adult brain mass (g)	Source	Predicted neonatal brain mass (g) (95% CI)	Actual neonatal brain mass (g)	Source
Pan paniscus	381.7	*Pan troglodytes* in DeSilva and Lesnik, 2006 ($n = 70$)	153.2 (135.1–173.8)	154.9	Yerkes NPRC ($n = 1$)
Gorilla gorilla	522.7	Tobias, 1971 ($n = 668$)	192.4 (169.1–219.0)	217.0	Yerkes NPRC ($n = 1$)
Pongo pygmaeus	419.4	Tobias, 1971 ($n = 199$)	164.0 (144.5–186.3)	165.1	Schultz, 1941 ($n = 3$)
Hylobates lar	102.5	Schultz, 1944 ($n = 180$)	59.1 (52.8–66.1)	65.0	Schultz, 1944 ($n = 3$)

a brain between 200 and 240 g (193–232 cc). The cranial capacity of the Nariokotome boy was 880 cc, and was unlikely to grow much larger given that the human brain reaches adult size by the age of 5–6 years (Jolicoeur et al., 1988; Leigh, 2004) and the Nariokotome boy was at least eight (Dean et al., 2001) or 10–12 years (Smith, 1993) of age. Using our regression equation, we suggest that *H. erectus*, as represented by KNM-WT 15000, would have given birth to a neonate with a brain of approximately 280 cc (245–321 cc).

If our estimate is correct, there are two possible reasons for the slight discrepancy between our results and Walker and Ruff's (1993). First, *H. erectus* may have been more sexually dimorphic than modern humans and the 4% increase in pelvic inlet diameter used by Walker and Ruff (1993) to convert the Nariokotome boy into a female may have been an underestimate. Recent analysis of *H. erectus* craniodental material from Koobi Fora, Kenya (Spoor et al., 2007), supports the hypothesis that *H. erectus* exhibited a greater degree of sexual dimorphism than modern humans. Second, only a small change in the fronto-occipital diameter would change the head circumference, and thus the estimated cranial volume of a *H. erectus* infant. Using both the Dobbing and Sands (1978) equation employed by Walker and Ruff (1993) to convert fronto-occipital diameter to cranial volume and Lindley et al. (1999) equation based on CT scans of neonates, a change of only 1 mm in fronto-occipital diameter would equal a change of 10 g of brain tissue. Therefore, only 4–8 mm in the fronto-occipital diameter is needed to account for the difference between Walker and Ruff's (1993) estimates of brain size at birth in *H. erectus* and ours.

Strategies of brain development

In this study, we made the assumption that human ancestors never strayed from the catarrhine regression of adult-neonatal brain size. This assumption needs further explanation. Although the size of the neonatal brain is strongly correlated with the size of the adult brain across primates, including both modern chimpanzees and humans (Martin, 1983, 1990; this study), there is variation around the regression line, with some species having slightly larger brains at birth than expected and some having slightly smaller than expected given their adult brain size. Studies of brain development in primates have revealed two basic strategies of brain development related to maternal investment. Leigh (2004) suggested that Old World monkeys tend to have more brain growth prenatally, thus incurring a heavy energy cost on the pregnant mother, whereas hominoids and platyrrhines tend to have more brain growth postnatally, shifting the energy requirements for brain development to lactation and the infant's own ability to acquire food resources (Martin, 1996; Leigh, 2004). Our results are consistent with this hypothesis. Figure 3 demonstrates that, relative to catarrhines, platyrrhines have smaller brains at birth, and thus would require energy in part from increased lactation to achieve adult brain size. Furthermore, *Cercocebus atys* (white diamonds in Fig. 4), a cercopithecoid primate with a slightly smaller brain at birth than expected, weans unusually late in the wild (Leigh, 2004). Given these two strategies for brain development, we must consider the possibility that, relative to modern humans, australopiths and other human ancestors may have invested more heavily in either prenatal or postnatal brain development. Adoption of either strategy by these extinct hominins would shift the value of neonatal brain mass either above or below the catarrhine regression and would result in an overestimation or underestimation of brain size at birth using the regression equation employed in this study.

Three scenarios for australopith brain development are illustrated in Fig. 5. The cluster of resampled neonatal-adult brain size pairs for chimpanzees (white diamonds) and humans [gray and black diamonds, separately representing data from Bischoff (1880) and Marchand (1902)], with the catarrhine regression line and 95%
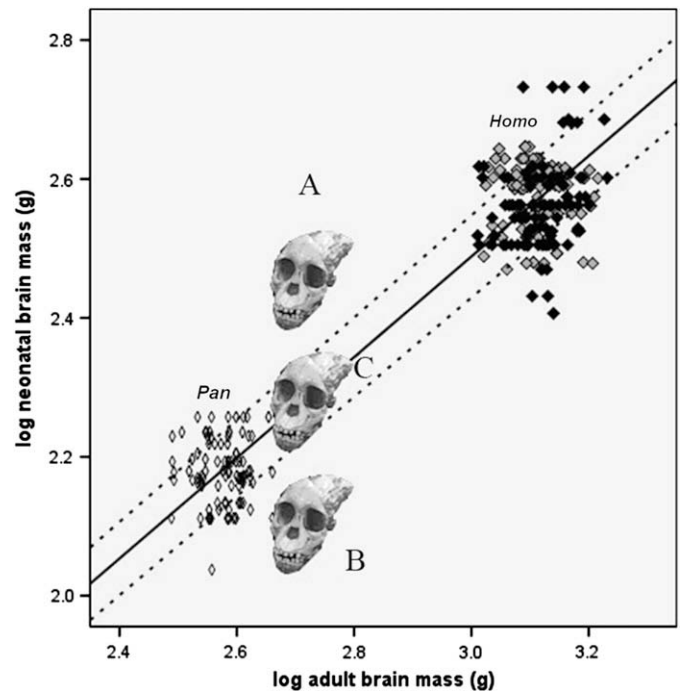

Fig. 5. Three models of brain development in the australopiths. The data points in the lower left are modern chimpanzees and those in the upper right are modern humans (enlarged from Fig. 4). Scenario A predicts that australopiths had larger brains at birth than expected given the size of their brains as adults. Scenario B predicts that australopiths had smaller brains at birth than expected given the size of their brains as adults. Scenario C is the null hypothesis that australopiths never deviated from the catarrhine regression of adult brain size and neonatal brain size. These three hypotheses are described further in the text.

confidence intervals, are enlarged from that portion of Fig. 4. In scenario A, adult and neonatal brains are decoupled and australopiths invested more energy in prenatal brain development and have larger brains than expected at birth. Scenario B also represents a decoupling of adult and neonatal brain size and hypothesizes that australopiths invested more in postnatal brain development and had infants with smaller brains than expected at birth. Scenario C represents the null hypothesis depicting australopiths as devoting prenatal and postnatal resources to brain growth in a manner similar to modern chimpanzees and humans.

Scenario A would result only if natural selection favored larger-brained and larger-bodied australopith infants. This scenario seems unlikely given the fact that the evolution of bipedalism resulted in (or from) the restructuring of the pelvis in a manner that changed the shape and reduced the size of the birth canal (Lovejoy et al., 1999; Lovejoy, 2005).

Scenario B suggests a reduction in the amount of brain growth that occurs prenatally. This scenario implies that selection favored smaller brains at birth in the australopiths compared to their ancestors and therefore an accelerated amount of brain growth postnatally. Although this scenario may initially be favored because of the pelvic constraints prohibiting scenario A, it is important to recognize that, eventually during the course of human evolution, hominins would have had to evolve back onto the regression line because that is where modern humans are today. This shift back to the anthropoid regression would necessitate selection for larger-brained neonates relative to the size of the adult female at some point during the Plio-Pleistocene. Again, because of pelvic constraints, and the potential advantages of having brain development occurring in a postnatal environment (Rosenzweig and Bennett, 1996; Bogin, 1999), it is unlikely that selection would have favored an increase in prenatal brain development in hominins at

any stage. This scenario also implies earlier birth in australopiths relative to either chimpanzees or humans, thus necessitating elevated and immediate postnatal care.

Given the difficulties with scenarios A and B, we instead suggest that australopiths, and other human ancestors, have never strayed from the catarrhine regression of neonatal brain mass to adult brain mass and that scenario C best characterizes the evolutionary trajectory of brain development in Plio-Pleistocene hominins. The regression equation may therefore be valid in predicting neonatal brain size from fossil adult cranial volumes.

Evolution of percentage of brain growth achieved by birth

The allometric relationship between adult and neonatal brain mass also reveals important information regarding the frequently used measure of percentage of total brain size achieved in utero. The slope of the regression of neonatal brain mass on adult brain mass in catarrhines is less than one (0.73) and therefore represents negative allometry. Consequently, as the adult brain mass increases in size, the proportion of brain growth that occurs in utero (neonatal brain divided by adult brain) necessarily decreases simply because of the scaling relationship between the adult and neonatal brain (Fig. 6). This relationship occurs particularly in Old World primates, which exhibit a decrease in prenatal brain growth as the adult brain size increases. For example, macaques complete 60% of their brain growth before birth (Passingham, 1982; Table 1), chimpanzees complete about 40% of brain growth neonatally (Coqueugniot et al., 2004; DeSilva and Lesnik, 2006), and humans achieve roughly 30% by birth (Leigh, 2006; DeSilva and Lesnik, 2006).
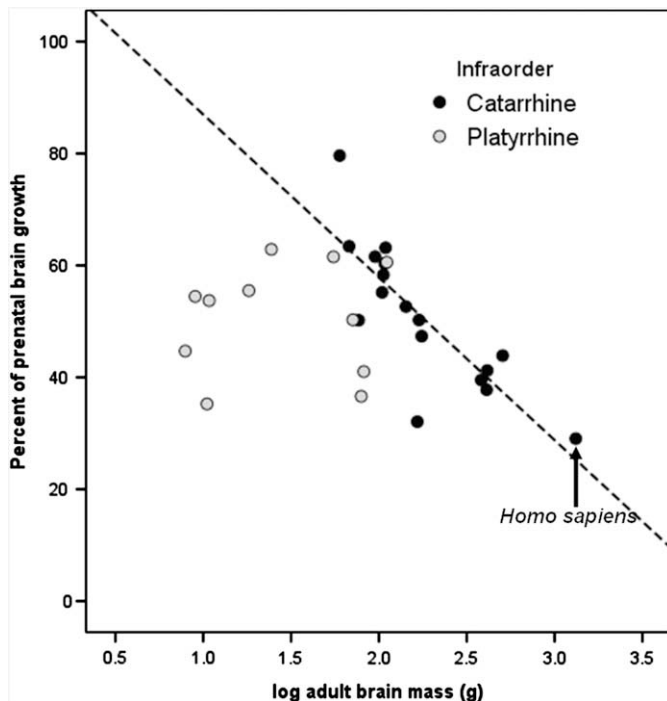

Fig. 6. Allometry of primate brain development. For New World primates (gray circles), the size of the adult brain and the percentage of brain development that occurs before birth appear to be independent of one another. This is being driven primarily by the small, twinning callitrichids and by three members of the large-brained genus *Cebus*. However, for Old World primates (black circles), the percentage of total brain size that is achieved prenatally decreases as the absolute size of the adult brain increases ($r^2 = 0.66$). Humans, with their unusually large adult brains, experience the smallest percentage of brain growth in utero. The single Old World primate data point far below the main regression is the baboon *Papio papio*, represented by a single neonate (Sacher and Staffeldt, 1974).

A comparison of the percentage of brain growth that occurs in utero for chimpanzees and humans has been used quite often to address questions of primate life history (Martin, 1983; Dienske, 1986; Smith and Tompkins, 1995; Fragaszy and Bard, 1997; Kennedy, 2005), hominid brain growth, development, and cognitive ability (Schultz, 1940; Passingham, 1982; Foley et al., 1991; Coqueugniot et al., 2004; Vinicius, 2005; Leigh, 2006; Hublin and Coqueugniot, 2006), and early hominid obstetrics (Häusler and Schmid, 1995). The above studies cite a wide range of values for in utero brain growth for both humans and chimpanzees.

Recently, we used a larger data set of neonatal and adult brain masses to suggest that chimpanzees experience 40.1% (± 5.7%) and humans between 27–29% of their brain growth prenatally (DeSilva and Lesnik, 2006). Based on these results, we argued that *H. erectus* did not have a chimpanzeelike proportion of brain growth in utero, supporting the hypothesis of Walker and Ruff (1993) that the Nariokotome *H. erectus* skeleton was evidence for secondary altriciality in the human lineage by 1.6 million years ago. It was still unclear to us whether this hominin species had already adopted a completely modern-human-like distribution of prenatal and postnatal brain growth.

Based on the results of this study, however, we now suggest that the dichotomy of a chimpanzeelike versus humanlike pattern of in utero brain growth is most likely a false one and instead argue that the Plio-Pleistocene hominins attained a proportion of prenatal and postnatal brain growth between the chimpanzeelike ancestral condition and that experienced by modern humans. Using the data from this study, we calculated prenatal brain-growth percentages for australopiths at 38.1% (± 4.9%), early *Homo* at 35.2% (± 5.5%), and *H. erectus* at 33.1% (± 6.8%). Later *H. erectus* fossils and middle Pleistocene *Homo* specimens are within the modern human range of prenatal brain growth. These data are consistent with the hypothesis that neonatal brain development in human evolution has proceeded in a gradual fashion. Given the large standard deviations in the percentages of brain growth reported above, however, the hypothesis of a sudden shift from a chimpanzeelike pattern of brain growth to a humanlike pattern cannot be completely ruled out.

Conclusion

Human mothers give birth to unusually large infants. However, given the size of the adult human brain, human neonates have precisely the brain size that is expected for an anthropoid primate. The correlation between adult and neonatal brain size across anthropoid primates established that australopiths gave birth to infants with brain volumes of about 180 cc. Because neonatal brain mass scales negatively with the adult brain mass, Old World primates with larger brains experience less brain growth in utero, and therefore larger-brained species, like African apes and humans, necessarily have more postnatal brain development. We argue that early hominin ancestors never strayed from the regression of neonatal brain size to adult brain size. Thus, as the adult brain became larger, the proportion of brain growth that occurred postnatally increased as well. Because selection may favor both absolute brain size and the amount of brain growth that occurs postnatally in certain environments, the interrelatedness of these two variables may have accelerated encephalization in the genus *Homo* during the Plio-Pleistocene until pelvic constraints blocked any further increase in neonatal brain size.

References

Abbate, E., Albianelli, A., Azzaroli, A., Benvenuti, M., Tesfamariam, B., Bruni, P., Cipriani, N., Clarke, R.J., Ficcarelli, G., Macchiarelli, R., Napoleone, G., Papini, M., Rook, L., Sagri, M., Madhin Tecle, T., Torre, D., Villa, I., 1998. A one-million-year-old *Homo* cranium from the Danakil (Afar) Depression of Eritrea. Nature 393, 458–460.

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

Alemseged, Z., Spoor, F., Kimbel, W.H., Bobe, R., Geraads, D., Reed, D., Wynn, J.G., 2006. A juvenile early hominin skeleton from Dikika, Ethiopia. Nature 443, 296–301.

Antón, S.C., 2003. Natural history of *Homo erectus*. Yearb. Phys. Anthropol. 46, 126–170.

Asfaw, B., Gilbert, W.H., Beyene, Y., Hart, W.K., Renne, P.R., WoldeGabriel, G., Vrba, E., White, T.D., 2002. Remains of *Homo erectus* from Bouri, Middle Awash, Ethiopia. Nature 416, 317–320.

Begun, D., Walker, A., 1993. The endocast. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 326–358.

Berge, C., Orban-Segebarth, R., Schmid, P., 1984. Obstetrical interpretation of the australopithecine pelvic cavity. J. Hum. Evol. 13, 573–587.

Bischoff, T.L.W.v., 1880. Das Hirngewicht des Menschen. Druck und Verlag von P. Neusser, Bonn.

Blinkov, S.M., Glezer, I.I., 1968. The Human Brain in Figures and Tables: A Quantitative Handbook. Plenum Press and Basic Books, New York.

Bogin, B., 1999. Patterns of Human Growth. Cambridge University Press, Cambridge.

Bohonak, A.J., 2002. RMA: software for reduced major axis regression. Available online at: http://www.bio.sdsu.edu/pub/andy/BohonakCV.html.

Brown, B., Walker, A.C., Ward, C.V., Leakey, R.E., 1993. New *Australopithecus boisei* calvaria from east Lake Turkana. Am. J. Phys. Anthropol. 91, 137–159.

Cheverud, J.M., Falk, D., Vannier, M., Konigsberg, L., Helmkamp, R.C., Hildebolt, C., 1990. Heritability of brain size and surface features in rhesus macaques (*Macaca mulatta*). J. Hered. 81, 51–57.

Conroy, G.C., Vannier, M.W., Tobias, P.V., 1990. Endocranial features of *Australopithecus africanus* revealed by 2- and 3-D computed tomography. Science 247, 838–841.

Conroy, G.C., Weber, G.W., Seidler, H., Tobias, P.V., Kane, A., Brunsden, B., 1998. Endocranial capacity in an early hominid cranium from Sterkfontein, South Africa. Science 280, 1730–1731.

Conroy, G.C., Falk, D., Guyer, J., Weber, G.W., Seidler, H., Recheis, W., 2000. Endocranial capacity in Sts 71 (*Australopithecus africanus*) by three-dimensional computed tomography. Anat. Rec. 258, 391–396.

Coqueugniot, H., Hublin, J.J., Veillon, F., Houët, F., Jacob, T., 2004. Early brain growth in *Homo erectus* and implications for cognitive capacity. Nature 431, 299–302.

Dart, R.A., 1925. *Australopithecus africanus*: the man-ape of South Africa. Nature 115, 195–199.

Dean, C., Leakey, M.G., Reid, D., Friedmann, S., Schwartz, G.T., Stringer, C., Walker, A., 2001. Growth processes in teeth distinguish modern humans from *Homo erectus* and earlier hominins. Nature 414, 628–631.

Dean, D., Hublin, J.-J., Holloway, R., Ziegler, R., 1998. On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. J. Hum. Evol. 34, 485–508.

DeSilva, J.M., Lesnik, J.J., 2006. Chimpanzee neonatal brain size: implications for brain growth in *Homo erectus*. J. Hum. Evol. 51, 207–212.

Dienske, H., 1986. A comparative approach to the question of why human infants develop so slowly. In: Else, J.G., Lee, P.C. (Eds.), Primate Ontogeny, Cognition and Social Behavior. Cambridge University Press, Cambridge, pp. 145–154.

Dobbing, J., Sands, J.E., 1978. Head circumference, biparietal diameter and brain growth in fetal and postnatal life. Early Hum. Dev. 2, 81–87.

Falk, D., Redmond Jr., J.C., Guyer, J., Conroy, G.C., Recheis, W., Weber, G.W., Seidler, H., 2000. Early hominid brain evolution: a new look at old endocasts. J. Hum. Evol. 38, 695–717.

Felsenstein, J., 1985. Phylogenies and the comparative method. Am. Nat. 126, 1–25.

Foley, R.A., Lee, P.C., Widdowson, E.M., Knight, C.D., Jonxis, H.P., 1991. Ecology and energetics of encephalization in hominid evolution [and discussion]. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 334, 223–232.

Fragaszy, D.M., Bard, K., 1997. Comparison of development and life history in *Pan* and *Cebus*. Int. J. Primatol. 18, 683–701.

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

Harvey, P.H., Clutton-Brock, T.H., 1985. Life history variation in primates. Evolution 39, 559–581.

Harvey, P.H., Purvis, A., 1991. Comparative methods for explaining adaptations. Nature 351, 619–624.

Häusler, M., Schmid, P., 1995. Comparison of the pelves of Sts 14 and AL 288-1: implications for birth and sexual dimorphism in australopithecines. J. Hum. Evol. 29, 363–383.

Häusler, M., Schmid, P., 1997. Assessing the pelvis of AL 288-1: a reply to Wood and Quinney. J. Hum. Evol. 32, 99–102.

Hens, S.M., Konigsberg, L.W., Jungers, W.L., 2000. Estimating stature in fossil hominids: which regression model and reference sample to use? J. Hum. Evol. 38, 767–784.

Herndon, J.G., Tigges, J., Anderson, D.C., Klumpp, S.A., McClure, H.M., 1999. Brain weights throughout the lifespan of the chimpanzee. J. Comp. Neurol. 409, 567–579.

Ho, K.C., Roessmann, U., Hause, L., Monroe, G., 1981. Newborn brain weight in relation to maturity, sex, and race. Ann. Neurol. 10, 243–246.

Holloway, R.L., 1981. The endocast of the Omo L338y-6 juvenile hominid: gracile or robust *Australopithecus*? Am. J. Phys. Anthropol. 54, 109–118.

Holloway, R.L., 1983. Cerebral brain endocast pattern of *Australopithecus afarensis* hominid. Nature 303, 420–422.

Holloway, R.L., Broadfield, D.C., Yuan, M.S., 2004. The Human Fossil Record, Vol. 3: Brain Endocasts—The Paleoneurological Evidence. Wiley-Liss, Hoboken.

Howell, F.C., Coppens, Y., 1974. Inventory of remains of Hominidae from Pliocene/Pleistocene formations of the Lower Omo Basin, Ethiopia (1967–1972). Am. J. Phys. Anthropol. 40, 1–16.

Hublin, J.-J., Coqueugniot, H., 2006. Absolute or proportional brain size: that is the question. A reply to Leigh's (2005) comments. J. Hum. Evol. 50, 109–113.

Jolicoeur, P., Baron, G., Cabana, T., 1988. Cross-sectional growth and decline of human stature and brain weight in 19th century Germany. Growth Dev. Aging 52, 201–206.

Keith, A., 1885. The growth of the brain in man and monkeys, with a short criticism of the usual method of stating brain-ratios. J. Anat. Physiol. 24, 282–303.

Kennard, M.A., Willner, M.D., 1941. Weights of brains and organs of 132 New and Old World monkeys. Endocrinology 28, 977–984.

Kennedy, G.E., 2005. From the ape's dilemma to the weanling's dilemma: early weaning and its evolutionary context. J. Hum. Evol. 48, 123–145.

Kimbel, W.H., Johanson, D.C., Coppens, Y., 1982. Pliocene hominid cranial remains from the Hadar Formation, Ethiopia. Am. J. Phys. Anthropol. 57, 453–499.

Kimbel, W.H., Rak, Y., Johanson, D.C., 2004. The Skull of *Australopithecus afarensis*. Oxford University Press, Oxford.

Konigsberg, L.W., Hens, S.M., Jantz, L.M., Jungers, W.L., 1998. Stature estimation and calibration: Bayesian and maximum likelihood perspectives in physical anthropology. Yearb. Phys. Anthropol. 41, 65–92.

Kretschmann, H.-J., Schleifenbaum, L., Wingert, F., 1970. Quantitative studies on the postnatal development of the central nervous system of *Cercopithecus aethiops*. In: Biegert, J., Leutenneger, W. (Eds.), Proceedings of the Third International Conference on Primatology, Zurich, Vol 1. Karger, Basel, pp. 108–114.

Lee, S.-H., Wolpoff, M.H., 2003. The pattern of evolution in Pleistocene human brain size. Paleobiology 29, 186–196.

Leigh, S.R., 2004. Brain growth, life history, and cognition in primate and human evolution. Am. J. Primatol. 62, 139–164.

Leigh, S.R., 2006. Brain ontogeny and life history in *Homo erectus*. J. Hum. Evol. 50, 104–108.

Leonard, W.R., Robertson, M.L., Snodgrass, J., Kuzawa, C.W., 2003. Metabolic correlates of hominid brain evolution. Comp. Biochem. Physiol., Part A Mol. Integr. Physiol. 136, 5–15.

Leutenegger, W., 1972. Newborn size and pelvic dimensions of *Australopithecus*. Nature 243, 568–569.

Leutenegger, W., 1973. Maternal-fetal weight relationships in primates. Folia Primatol. 20, 280–293.

Leutenegger, W., 1987. Neonatal brain size and neurocranial dimensions in Pliocene hominids: implications for obstetrics. J. Hum. Evol. 16, 291–296.

Lindley, A.A., Benson, J.E., Grimes, C., Cole III, T.M., Herman, A.A., 1999. The relationship in neonates between clinically measured head circumference and brain volume estimates from head CT-scans. Early Hum. Dev. 56, 17–29.

Liu, W., Zhang, Y., Wu, X., 2005. Middle Pleistocene human cranium from Tangshan (Nanjing), southeast China: a new reconstruction and comparisons with *Homo erectus* from Eurasia and Africa. Am. J. Phys. Anthropol. 127, 253–262.

Lockwood, C.A., Kimbel, W.H., Johanson, D.C., 2000. Temporal trends and metric variation in the mandibles and dentition of *Australopithecus afarensis*. J. Hum. Evol. 39, 23–55.

Lordkipanidze, D., Vekua, A., Ferring, R., Rightmire, G.P., Zollikofer, C.P., Ponce de León, M.S., Agusti, J., Kiladze, G., Mouskhelishvili, A., Nioradze, M., Tappen, M., 2006. A fourth hominin skull from Dmanisi, Georgia. Anat. Rec. 288, 1146–1157.

Lovejoy, C.O., Cohn, M.J., White, T.D., 1999. Morphological analysis of the mammalian postcranium: a developmental perspective. Proc. Natl. Acad. Sci. U.S.A. 96, 13247–13252.

Lovejoy, C.O., 2005. The natural history of human gait and posture. Part 1. Spine and pelvis. Gait Posture 21, 95–112.

Lunde, A., Klungsøyr, M., Gjessing, H.K., Skjærven, R., Irgens, L., 2007. Genetic and environmental influences on birth weight, birth length, head circumference, and gestational age by use of population-based parent-offspring data. Am. J. Epidemiol. 165, 734–741.

Mahaney, M.C., Williams-Blangero, S., Blangero, J., Leland, M.M., 1993. Quantitative genetics of relative organ weight variation in captive baboons. Hum. Biol. 65, 991–1003.

Marchand, F., 1902. Ueber das Hirngewicht des Menschen. B.G. Teubner, Leipzig.

Martin, R.D., 1983. Human Brain Evolution in an Ecological Context. Fifty-Second James Arthur Lecture on the Evolution of the Human Brain. American Museum of Natural History, New York.

Martin, R.D., 1990. Primate Origins and Evolution. Princeton University Press, Princeton.

Martin, R.D., 1996. Scaling of the mammalian brain: the maternal energy hypothesis. News Physiol. Sci. 11, 149–156.

Martin, R.D., 2003. Human reproduction: a comparative background for medical hypotheses. J. Reprod. Immunol. 59, 111–135.

Martins, E.P., 2004. COMPARE, version 4.6b. Computer programs for the Statistical Analysis of Comparative Data. Department of Biology, Indiana University, Bloomington. Available online at: http://compare.bio.indiana.edu/.

McHenry, H.M., 1994. Behavioral ecological implications of early hominid body size. J. Hum. Evol. 27, 77–87.

Passingham, R., 1982. The Human Primate. Freeman, San Francisco.

Passmore, R., Durnin, J.B.G., 1955. Human energy expenditure. Physiol. Rev. 35, 801–835.

Peters, M., Jänke, L., Staiger, J.F., Schlaug, G., Huang, Y., Steinmetz, H., 1998. Unsolved problems in comparing brain sizes in *Homo sapiens*. Brain Cogn. 37, 254–285.

Rightmire, G.P., 1998. Human evolution in the middle Pleistocene: the role of *Homo heidelbergensis*. Evol. Anthropol. 6, 218–227.

Rightmire, G.P., 2004. Brain size and encephalization in early to mid-Pleistocene *Homo*. Am. J. Phys. Anthropol. 124, 109–123.

Rightmire, G.P., 2008. *Homo* in the middle Pleistocene: hypodigms, variation, and species recognition. Evol. Anthropol. 17, 8–21.

Rogers, J., Kochunov, P., Lancaster, J., Shelledy, W., Glahn, D., Blangero, J., Fox, P., 2007. Heritability of brain volume, surface area and shape: an MRI study in an extended pedigree of baboons. Hum. Brain Mapp. 28, 576–583.

Rosenberg, K., Trevathan, W., 2002. Birth, obstetrics and human evolution. Br. J. Obstet. Gynaecol. 109, 1199–1206.

Rosenzweig, M.R., Bennett, E.L., 1996. Psychobiology of plasticity: effects of training and experience on brain and behavior. Behav. Brain Res. 78, 57–65.

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

Sacher, G.A., Staffeldt, E.F., 1974. Relation of gestation time to brain weight for placental mammals. Am. Nat. 108, 593–616.

Schultz, A.H., 1940. Growth and development of the chimpanzee. Contrib. Embryol. 28, 1–63.

Schultz, A.H., 1941. Growth and development of the orang-utan. Contrib. Embryol. 29, 57–111.

Schultz, A.H., 1944. Age changes and variability in gibbons. Am. J. Phys. Anthropol. 2, 1–129.

Schultz, A.H., 1965. The cranial capacity and orbital volume of hominoids according to age and sex. In: Caso, A. (Ed.), Homenaje a Juan Comas en su 65 Anniversario, Vol. 2. Libros de Mexico, Mexico City, pp. 337–357.

Schwartz, J.H., Tattersall, I., 2005. The Human Fossil Record, Vol. 4: Craniodental Morphology of Early Hominids and Overview. Wiley-Liss, Hoboken.

Smith, B.H., 1993. The physiological age of KNM-WT 15000. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 195–220.

Smith, B.H., Tompkins, R.L., 1995. Toward a life history of the Hominidae. Annu. Rev. Anthropol. 24, 257–279.

Smith, R.J., 1994. Regression models for prediction equations. J. Hum. Evol. 26, 239–244.

Smith, R.J., 1996. Biology and body size in human evolution: statistical inference misapplied. Curr. Anthropol. 37, 451–481.

Smith, R.J., Gannon, P.J., Smith, B.H., 1995. Ontogeny of australopithecines and early *Homo*: evidence from cranial capacity and dental eruption. J. Hum. Evol. 29, 155–168.

Smith, R.J., Cheverud, J.M., 2002. Scaling of sexual dimorphism in body mass: a phylogenetic analysis of Rensch's rule in primates. Int. J. Primatol. 23, 1095–1135.

Spoor, F., Leakey, M.G., Gathogo, P.N., Brown, F.H., Antón, S.C., McDougall, I., Kiarie, C., Manthi, F.K., Leakey, L.N., 2007. Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya. Nature 448, 688–691.

Stringer, C., 1996. Modern human origins: progress and prospects. Philos. Trans. R. Soc. Lond., B, Biol. Sci. 357B, 563–579.

Tague, R.G., Lovejoy, C.O., 1986. The obstetric pelvis of A.L. 288-1 (Lucy). J. Hum. Evol. 15, 237–255.

Tague, R.G., Lovejoy, C.O., 1998. AL 288-1— Lucy or Lucifer: gender confusion in the Pliocene. J. Hum. Evol. 35, 75–94.

Tattersall, I., 1986. Species recognition in human paleontology. J. Hum. Evol. 15, 165–175.

Tobias, P.V., 1970. Brain-size, grey matter and race—fact or fiction? Am. J. Phys. Anthropol. 32, 3–26.

Tobias, P.V., 1971. The Brain in Hominid Evolution. Columbia University Press, New York.

Tobias, P.V., 1991. Olduvai Gorge, Vol. 4: The Skulls, Endocasts, and Teeth of *Homo habilis*. Cambridge University Press, Cambridge.

Vekua, A., Lordkipanidze, D., Rightmire, G.P., Agusti, J., Ferring, R., Maisuradze, G., Mouskhelishvili, A., Nioradze, M., Ponce de León, M., Tappen, M., Tvalchrelidze, M., Zollikofer, C., 2002. A new skull of early *Homo* from Dmanisi, Georgia. Science 297, 85–89.

Vinicius, L., 2005. Human encephalization and developmental timing. J. Hum. Evol. 49, 762–776.

Vrba, E., 1998. Multiphasic growth models and the evolution of prolonged growth exemplified by human brain evolution. J. Theor. Biol. 190, 227–239.

Walker, A.C., Leakey, R.E., Harris, J.M., Brown, F.H., 1986. 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. Nature 322, 517–522.

Walker, A., Ruff, C.B., 1993. The reconstruction of the pelvis. In: Walker, A., Leakey, R. (Eds.), The Nariokotome *Homo erectus* Skeleton. Harvard University Press, Cambridge, pp. 221–233.

Wood, B.A., Quinney, P.S., 1996. Assessing the pelvis of AL 288-1. J. Hum. Evol. 31, 563–568.

Zollikofer, C.P., Ponce de León, M.S., Lieberman, D.E., Guy, F., Pilbeam, D., Likius, A., Mackaye, H.T., Vignaud, P., Brunet, M., 2005. Virtual cranial reconstruction of *Sahelanthropus tchadensis*. Nature 434, 755–759.