Scaling of brain and body weight within modern and fossil hominids: implications for the Flores specimen

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Abstract

The recently discovered hominid from Flores has a cranial capacity and body size approximating fossil australopithecines. It has been argued that it is not pathological, but instead may represent some form of a *Homo erectus* endemic dwarf relic. While no modern analogs for endemic dwarfism exist in modern human populations, there does exist quite a large range of variation in brain/body sizes in populations that have presumably experienced a wide range of ecological environments selecting for varying brain and body sizes. Using Beals' cranial capacity and body weight estimates for 37 modern human populations, as well as Kappleman's (1996) estimates for a number of fossil hominids, the relationship between encephalization quotient (EQ) and body weight is found to be consistently negative within all hominid species (for which there were more than 2 data points). Within modern humans the correlation is $r=-.74$ ($p<.0001$, $N=37$); recent *Homo sapiens* fossil specimens $r=-.95$ ($p<.0001$, $N=12$), archaic *Homo sapiens* $r=-.55$ ($p=.10$, $N=10$); *Homo erectus* $r=-.54$ ($p=.27$, $N=6$); *Australopithecus boisei* $r=-.998$ ($p<.05$). These negative relationships indicate that brain size tends to decrease more slowly than body weight across specimens/populations. Flores brain/body values are not predicted by the relationships demonstrated for non-pathological modern human populations, nor any of the fossil populations except the australopithecines. This suggests either that Flores underwent a wholly different kind of selection regime than any of the populations studied here, or it is pathological. The difficulties with uncritically using EQ as a measure of behavioral complexity will also be addressed.

Introduction

The recently discovered specimen LB1 from Flores, dated to around 18,000 years ago, does not fit easily into any existing hominid taxon. Given its age, it is a clear outlier with respect to hominid brain evolution. Its discoverers argued that is not pathological, but instead represents a new species of hominid (Brown et al., 2004; Morwood et al., 2004). Originally, Brown et al. (2004) suggested that it was some form of endemic dwarf relic originally deriving from a *Homo erectus* population. "Dwarfing in LB1 may have been the end product of selection for small body size in a low calorific environment." (Brown et al., 2004, p. 1060). More recently, they have argued that – although its endocast is most similar to Homo erectus {Falk, 2005 #2661) – its body proportions are <u>not</u> consistent with an allometrically scaled-down version of a *Homo erectus* (Morwood et al., 2005). However, they continue to suggest that it "…could have evolved in situ as a response to island-specific conditions and associated behavioural changes." (Morwood et al., 2005, p. 1016).

A tendency towards reduced body size in island species has been documented for a range of larger mammals (larger than ~5 kg, Lomolino, 1985). Explanations for this general pattern have centered on resource limitations, sometimes combined with reduced predation pressure (Lomolino, 1985). The extent to which this is a valid explanation for body size in LB1 is not clear. While the original reports suggested that dwarf variants of *Stegodon* (an elephant relative) were found contemporaneous with LB1, thereby suggesting resource limitations generally, this needs to be clarified. Endemic dwarf *Stegodon* species had previously been thought to have become extinct by ~840 KYA, to be replaced by medium and large bodied *Stegodon* species (Rolland and Crockford, 2005). Regardless of the actual body size of the *Stegodon* remains found with LB1, however, it is clear that Flores had been able to support large mammals for much of its history, suggesting significant changes in resource availability (at least for *Stegodon*). Furthermore, it is unclear how resource limitations would affect a hominid species that is associated with Upper Paleolithic tools, may have utilized fire, and was found with a wide variety of animal remains, including fish, frog, snake, tortoise, birds, rodents, and bats. It is interesting to note, in this regard, that the mammals apparently least affected by endemic dwarfism are those such as mustelids and ursids that depend at least partly on aquatic resources (Lomolino, 1985).

In addition, it is not clear how resource limitations leading to general body size dwarfism would be expected to affect brain size. One report exists of an apparent decrease in relative brain size in an insular fossil bovid (Köhler and Moyá-Solá, 2004), however the extent to which this example is relevant to a hominid species is questionable (the niches occupied by bovids differ substantially from that of all later hominids). A more relevant comparative sample would involve body/brain size scaling relationships in hominids.

It is generally recognized that relative brain size increases with decreasing body size among closely related forms (Kappelman, 1996). Relative brain size is typically indexed by the encephalization quotient (EQ), which is simply the ratio of the actual brain size to the brain size expected for a mammal of its body size (Jerison, 1973). Brain size tends to decrease more slowly than body size among closely related species, which leads to EQ’s paradoxically being larger in these smaller species. LB1 has both the body weight and brain volume of an Australopithecine (its femoral cross-sectional area is about the same as AL288-1, and it cranial capacity is ~400 cc, Brown et al., 2004; Falk et al., 2005a), which suggests an encephalization quotient significantly less than what has been estimated for known *Homo erectus* specimens. This is a problem for any hypothesized phylogenetic relationship connecting *Homo erectus* (or any other non-australopithecine species) to LB1. To illustrate the strength of this scaling effect (and the extent of the problem for LB1), we plot EQ vs. body weight for several species, both fossil and extant. In addition, we estimate these relationships for a sample of 50 adult micrencephalics from (Hofman, 1984). Results indicate that LB1 scales as either a modern microcephalic or an australopithecine.

Methods

Data was compiled from a number of sources. LB1's brain size was assumed to be 400 cm^3 (Falk et al., 2005a), and its body weight was assumed to be the same as AL288-1: 27.3 kg (McHenry, 1992). Extant *Homo sapiens* data for non-pathological populations was obtained from the CRANDAT database, originally compiled by Beals and colleagues et al. (Beals et al., 1984). This data includes mean cranial capacity, body weight, and height data on 37 modern human populations. Data for individual fossil hominids was derived from Kappelman (1996), who estimated body weight using orbital dimensions, and compiled cranial capacity estimates from the literature. Kappelman's (1996) taxonomic groupings are used here: modern *Homo sapiens*: Tepexpan,Mexico, Gamble's Cave, Fish Hoek, Zhoukoudian 103, Zhoukoudian 101, Zhoukoudian 102, Grimaldi

(Grotte des Enfants), Wadjak I, Predmosti 3, Cro Magnon, Skhul 5, Qafzeh 9, Hotu Cave, Mladec, Star Mestro I, San Tendoro, Dolni Vestonice, Brno III; archaic *Homo sapiens*: Le Moustier, Amud I, La Chapelle, Gibralter 1, La Ferrassie, Jebel Irhoud I, Flosibad, Maba, Saccopastore, Kabwe, Zuttiyeh 1, Steinheim, Bodo; *Homo erectus*: Zhoukoudian XI, Zhoukoudian XII, Sangiran 17 (skull VIII), KNM-WT 15000, KNM-ER 3883, SK 847, KNM-ER 3733; *Homo habilis*: OH 24, KNM-ER 1813, KNM-ER 1470; *Australopithecus boisei*, KNM-ER 406, KNM-ER 732, OH 5; *Australopithecus aethiopicus*: KNM-WT 17000; *Australopithecus robustus*:
SK 48; *Australopithecus africanus*: STS 71, STS 5.

Data for Extant *Homo sapiens* micrencephalics (individuals with significantly smaller brains than normal, due to a variety of reasons) was obtained from by Professor Michel Hofman (Netherlands Institute for Neurosciences, Royal Netherlands Academy of Arts and Sciences), who had compiled the data from published sources for a previous study (Hofman, 1984), and kindly sent us a copy of the dataset. This data includes brain weights and body heights for 84 individuals aged 0 to 74. Hofman (1984) defined micrencephaly as individuals with brain sizes > 3 standard deviations lower than his comparison normal group. Thus, individuals were selected based solely on their small brain size, irrespective of aetiology. Of these, 50 individuals were older than 18 and had data for both brain weight and height, and these were used for the analyses below. Brain weights for this selected sample ranged from 200 g to 966 g. Because only body height was available for this sample, body weight was estimated from body height using the 2001-2002 National Health and Nutrition Examination Survey (NHANES) data. This dataset includes height and weight data for 5229 individuals over the age of 18, designed to broadly sample variation across the US. The regression of body weight on height for this sample was: [body weight kg] = -64.07+0.8503 x [body height cm] ($r=0.44$, $p<0.0001$).

Where only brain weights are reported, cranial capacities estimated using the conversion [cranial capacity cm^3] = 1.14 x [brain weight g] (Kappelman, 1996). EQ was calculated using the following formula: [brain weight g]/(11.22x[body weight kg]$^{0.76}$) (Martin, 1981).

Several types of comparisons were conducted. Both EQ and cranial capacity were plotted (separately) against body weight. Least-squares regression lines were calculated for each taxon/population, allowing the calculation of predicted EQ for an individual from that population if it were as small as LB1. From these predicted EQ's, the expected brain size necessary for it to follow the EQ/body size scaling trends for different taxon can be derived for direct comparison with LB1's estimated brain size: [expected brain size g] = [EQ predicted from regression] x (11.22 x [body weight]$^{0.76}$). Because only height was directly measured on the micrencephalics, brain weight was also plotted against body height for those samples where possible (i.e., extant normal and micrencephalic *Homo sapiens* samples).

Results

Figure **1** shows the relationships between EQ and body weight within each of the hominid taxon/populations included in this study. In every case, the relationship is negative (higher EQ's for smaller bodied individuals). The only taxons/populations that come close to predicting LB1 are Australopithecus boisei (the only australopithecine taxon with at least 3 data points in Kappelman, 1996) and the micrencephalics. We also note that the smallest bodied modern human normal populations in this sample are: Akha (minority peoples of Southern China and Southeast Asia), San (Bushmen from marginal environments in Africa), Andamanese (isolated islands in Bay of Bengal), Javanese (island population), Vedda (Sri Lanka). Their EQ's are among the highest of all modern populations in Beals sample, and are either live in marginal environments or on islands.

Predicted brain sizes for LB1-sized individuals/populations within each taxon were as follows: *H. sapiens* (extant populations) EQ = 6.1, leading to a predicted cranial capacity of 1024.0 cm^3; *H. sapiens* (recent – e.g., Cro Magnon, Skuhl, etc.) EQ = 7.3, predicted cranial capacity of 1223.0 cc cm^3; *H. sapiens* (archaic – e.g., Neanderthal, Bodo, etc.) EQ= 5.0, predicted cranial capacity = 829.0 cm^3; *H. erectus* EQ = 4.1, leading to a predicted cranial capacity of 488.7 cm^3. These compare to an estimated EQ for LB1 of 2.5. For each estimate except that derived from *H. erectus*, LB1's EQ falls outside the 95% confidence intervals for that taxon. The only reason it doesn't also for *H. erectus* is that this estimate is based on only 6 specimens, leading to very wide confidence intervals. However, all of the *H. erectus* specimens have EQ's and body weights larger than LB1. Given that EQ gets larger as body size decreases within each of the samples – as well among between closely related species in the same genus (such as Hylobatids, Kappelman, 1996), and even different dog breeds (Deacon, 1997; Lapicque, 1907) – the only way for LB1 to be predicted by the *H. erectus* scaling relationship is if we have a wildly biased sample of this taxon, or wildly incorrect body or brain sizes. Given that brain size in fossil hominids is likely more accurately estimated (through direct measurements of cranial capacity) than is body size, this would suggest that our estimates of body size in *H. erectus* would have to be gross underestimates to get EQ/body weight scaling relationships to predict LB1 values. Thus, LB1 scales like either an australopithecine or a modern micrencephalic, and is not reasonably predicted as some sort of dwarfed *H. erectus*.

The reason EQ scales negatively with body size can be seen from Figure **2**, which plots log endocranial volume cm^3 against log body weight g. As can be seen, the slopes of these relationships are all less than 1, which means that brain size changes less than body weight does as body weight changes. With respect to predicting LB1, brain size decreases less than body size as body size decreases. Once again, the only taxon/populations that have scaling relationships that best predict LB1 are the australopithecines and modern micrencephalic *H. sapiens*. Similar to the EQ/body weight relationships, LB1 is outside the 95% confidence intervals of all taxa/populations except *H. erectus*, *H. habilis*, the Australopithecines, and the modern micrencephalics. As noted above, *H. erectus* is based on only 6 specimens. *H. habilis* scaling is based on only 3 specimens, and include KNM-ER 1470 as part of this taxon. Thus, once again, LB1 falls with either Australopithecines or modern micrencephalics.

Finally, Figure **3** plots log endocranial volume cm^3 directly against log body height cm for the taxa/populations for which height is available. This plot does not require an estimation of body weight, but we can only compare LB1 with Beals' modern population estimates, Hofman's micrencephalics. The Nariokotome *H. erectus* specimen is also plotted on this graph, since the relatively complete nature of its skeleton allows a fairly accurate estimate of height (the estimated height at death is used here: 160 cm, Walker and Leakey, 1993). Once again, LB1 groups clearly with modern micrencephalics.

Discussion

There are 3 possible explanations for LB1: 1) LB1 is a dwarfed, non-pathological *H. erectus* with a very small brain. 2) LB1 is a derived australopithecine. 3) LB1 is a pathological modern human specimen – a microcephalic from an already diminutive population.

LB1 consistently groups with either modern microcephalics or Australopithecines with respect to brain/body scaling. This, combined with the robust finding of negative relationships between EQ and body weight, poses a problem for suggestions that LB1 represents a non-pathological, dwarfed population of *Homo*. The general argument for endemic dwarfing in other species centers on the idea of limited resource availability on islands. A range of modern human populations are diminutive in size, presumably also due to an evolutionary history of limited resource availability, yet they strongly point to a trend of greater EQ's (not smaller ones, as is needed to predict LB1) as body size decreases. To tie LB1 to any known *Homo* population, either fossil or extant, one has to propose a evolutionary selective regime that is not attested by any of them. In effect, if LB1 is truly not pathological, one has to assume that the selective processes leading to increased EQ's in *Homo* worked in reverse, if it is derived from some *Homo* taxon. This would be strikingly at odds with the behavioral traits associated with it (Upper Paleolithic tools, use of fire, and exploitation of a wide range of animals for meat). Among other things, it would raise the question of why other hominoids displaying LB1-sized brains (e.g., chimpanzee, gorilla and orangutan) do not also regularly (or even sometimes) display such elaborate behavioral adaptations. It also raises the question of why other *Homo* do not save the metabolic expense and maturational delays associated with larger brains, if LB1-sized brains would be sufficient. Arguing for some developmental constraints on brain/body size (Finlay et al., 2001; c.f. Schoenemann, 2001) is complicated by the fact that the larger-bodied hominoids demonstrate that one can have human-sized bodies with LB1-sized brains.

The fact that LB1 also scales with Australopithecines might suggest it is derived from them in some way. However, this would involve a series of completely-unattested intermediate populations spanning perhaps ~1 million years, traversing a continent. Although possible, it would seem unlikely given the range of hominids that are already known during this period of time.

The third possibility – that LB1 is pathological – is consistent with the present analysis. Modern micrencephalics clearly display brain/body scaling relationships that predict

LB1. Whether or not LB1 differs morphologically from all known types of micrencephaly is a different question – one that is currently under debate (Falk et al., 2005a; Falk et al., 2005b; Weber et al., 2005). It is clearly premature to argue that it could not *possibly* match any known type of microcephally, given that the assessment of this question is in the preliminary stages. Given the evolutionary difficulties associated with the first two possibilities, which assume that LB1 is not pathological, we suggest that serious consideration be given to the possibility that it is a microcephalic individual.

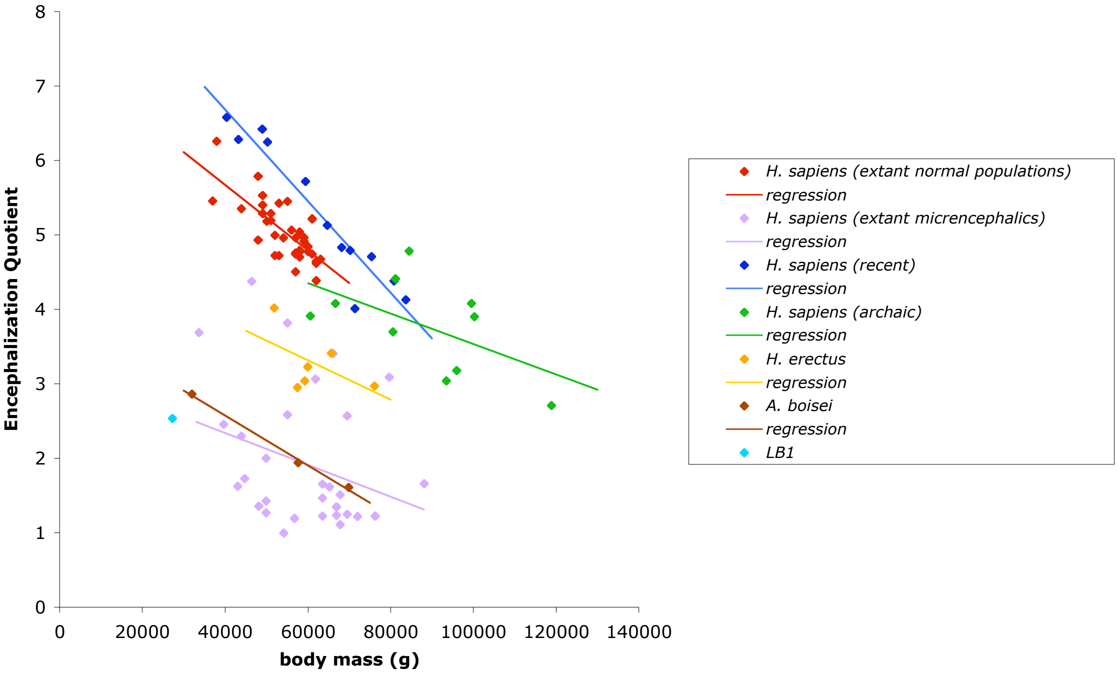

Figure 1: EQ vs. body mass in hominids

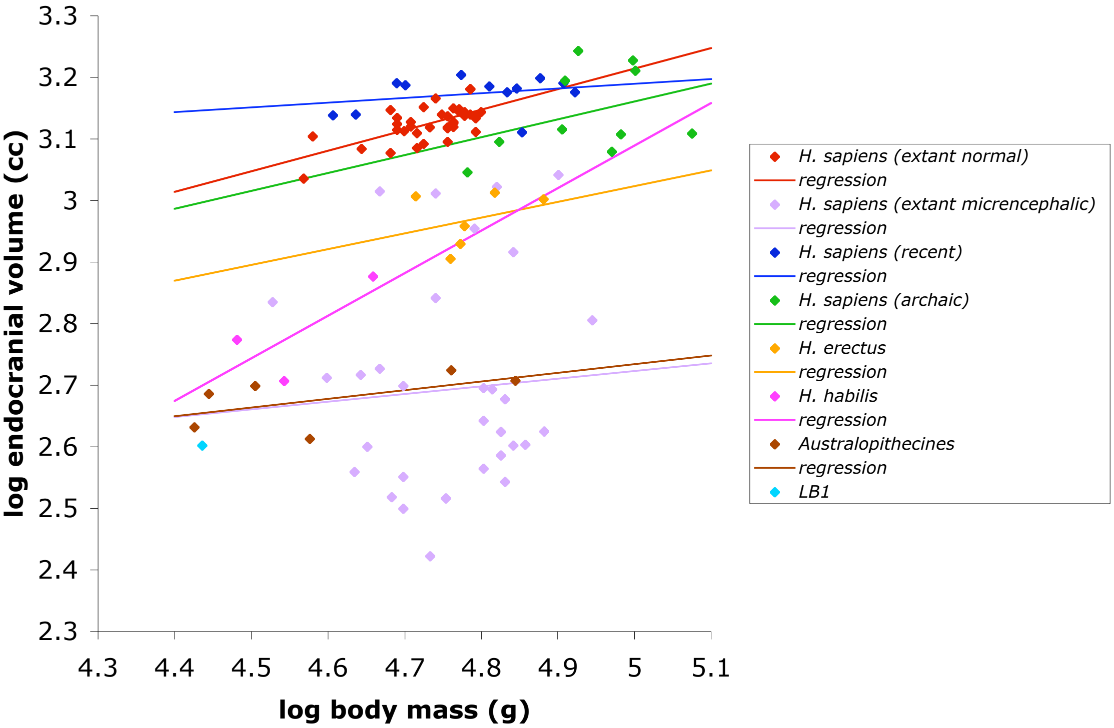

Figure 2: Endocranial volume vs. body mass in hominids

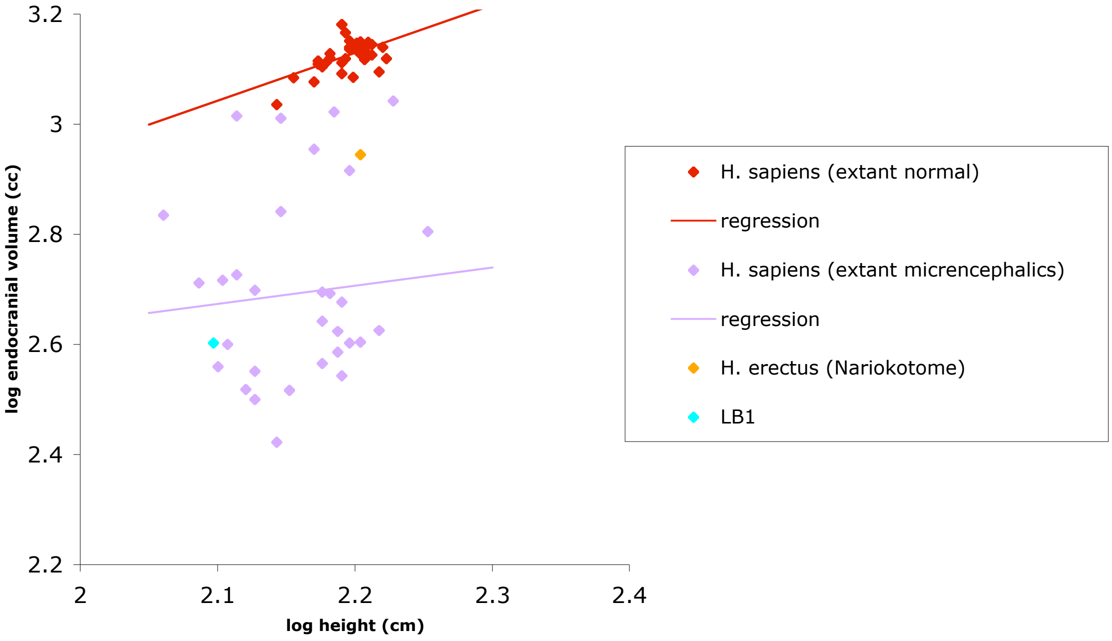

Figure 3: Cranial capacity vs. height in hominids

Figure notes:

Figure 1: EQ vs. body mass in hominids.

Figure 2: Endocranial volume vs. body mass in hominids

Figure 3: Cranial capacity vs. height in hominids

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