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Progressive Changes in Brain Size and Musculo-Skeletal Traits in Seven Hominoid Populations

Neurological complexity has increased over evolutionary time for invertebrates and vertebrates alike, with the hominid brain tripling in size over the last 3 million years. Since magnetic resonance imaging (MRI) studies among humans indicate a significant correlation (mean $r > 0.40$) between individual differences in brain size and general cognitive ability, it is reasonable to hypothesize that increasing brain size confers greater intelligence. However, larger brains have associated costs, taking longer to build and requiring more energy to run. Sufficient advantages must have accrued for them to override these trade-offs. The present paper documents that in hominoids, as brain size increased from 380 to 1364 cm^3 over seven hominoid groups (chimpanzees to australopithecines to *Homo habilis* to *Homo erectus* to differences among *Homo sapiens*), it was accompanied by changes in 74 musculo-skeletal traits ($rs = 0.90$). These occurred on both cranial traits (temporalis fossae, post-orbital constrictions, mandibles, dentition, nuchal muscle attachments) and on post-cranial traits (pelvic widths, femoral heads, tibial plateaus). It is concluded that in the evolutionary competition to find and fill new niches, there was "room at the top" for greater behavioral complexity and larger brain size, leading to cascading effects on other traits.

Keywords: Brain size; intelligence; evolution; life-history trade-offs.

1. Introduction

Increased neurological complexity over evolutionary time has occurred in several independently evolving lines of invertebrates and vertebrates alike, little of which can be explained by body size increases (Jerison, 1973, 1991, 2001; Russell, 1983; Falk & Gibson, 2001). The tripling in size of the hominoid brain over the last 5 million years may be a special case of this more general phenomenon. Yet, larger brains are energetically expensive, accounting for 5% of basal metabolic rate in rats, cats, and dogs, 10% in rhesus monkeys and other primates, and 20% in humans (Armstrong, 1990). Larger brains also require more prolonged life histories including longer gestations, slower maturation, higher offspring survival, lower reproductive output, and longer life

(Harvey & Pagel, 1991; Godfrey et al., 2001). This paper examines whether the evolution of increased brain size was accompanied by changes in the musculo-skeletal system.

Because australopithecines averaged 450 cm^3 (slightly larger than the average chimpanzee brain of 380 cm^3), *Homo erectus* about 1,000 cm^3, and *Homo sapiens*, about 1,350 cm^3, it is reasonable to hypothesize that bigger brains evolved via selection for increased intelligence (Jerison, 1973). Among humans, overall brain size, measured by total mass or volume, has been considered a neurological basis for increased cognitive ability since at least the time of Broca, Darwin, and Galton. As Darwin (1871) wrote:

> No one, I presume, doubts that the large size of the brain in man, relatively to his body, in comparison with that of the gorilla or orang, is closely connected with his higher mental powers. We meet the closely analogous facts with insects, in which the cerebral ganglia are of extraordinary dimensions in ants; these ganglia in all the Hymenoptera being many times larger than in the less intelligent orders, such as beetles. The belief that there exists in man some close relation between the size of the brain and the development of the intellectual faculties is supported by the comparison of ancient and modern people, and by the analogy of the whole vertebrate series (Darwin, 1871, Vol. 1, pp. 145-146).

Since Darwin, much additional data has suggested that his surmise was correct. For example, Bonner (1980, 1988) reviewed naturalistic data and found that the more recently an animal species had evolved, the larger was its brain and the more complex was its culture. Passingham (1982) reviewed experimental studies of "visual discrimination learning" that measured the speed with which children and other mammals abstracted such rules as "pick the same object each time to get food." More intelligent children, assessed by standardized intelligence (IQ) tests, learned faster than did those with lower IQ scores, and mammals with larger brains learned faster than did those with smaller brains (i.e., chimpanzees > rhesus monkeys > spider monkeys > squirrel monkeys > marmosets > cats > gerbils > rats = squirrels). Dunbar (1992) showed that brain size was the key factor in primates determining the upper limit on the size of the group maintained through time. Recently, Madden (2000) found that species of bowerbirds that build bowers have relatively larger brains than species that do not build bowers, and that species building more complex bowers have relatively larger brains.

Galton (1888) was one of the first to quantify the relation between brain size and cognitive ability among humans. He estimated brain (or cranial) volume by multiplying head length by breadth by height in 1,095 university students, plotted the results against class rank, and found that those who obtained high honors had a brain size 2 to 5%

greater than those who did not. Rushton and Ankney (1996) reviewed 32 studies with a total sample size of 51,493 that have since corroborated Galton's results using external head measures with people of all ages, both sexes, and various ethnic backgrounds and found correlations from 0.02 to 0.39, with a mean $r = 0.20$ ($p < 10^{-10}$) between estimated cranial volume and IQ score. Eight magnetic resonance imaging (MRI) studies of brain size were also reviewed, with a total sample size of 381 normal (non-clinical) subjects, and correlations between brain size and IQ ranged from 0.33 to 0.69, with a mean r of 0.44. Subsequent reviews (Vernon et al., 2000) and studies (Posthuma et al., 2002; Thompson et al., 2002) have corroborated the mean correlation of > 0.40 between MRI measured brain size and IQ, and also shown that brain size is about 90% heritable and the correlation between brain size and intelligence is also largely genetic in origin.

Increased brain size has had cascading effects on other life history traits, requiring a longer time to grow a bigger brain and, once built, more energy to run it. Smith (1989, see also Harvey & Pagel, 1991; Godfrey et al., 2001) found that across 21 primate species, brain size predicted (0.80 to 0.90) birth weight, body weight, gestation length, age at weaning, inter-birth interval, age at sexual maturity, age at first breeding, lifespan, age at eruption of first molar, and age at complete dentition. At the extreme of this set of life history characteristics are *Homo sapiens*. For example, gestational age approximates 33 weeks in chimpanzees and 38 weeks in modern humans; puberty is reached around 8 years in chimpanzees and 13 years in humans; life span averages 30 years in chimpanzees and around 70 years in humans.

The relation between increasing brain size and prolonged life history is also found within humans. A review of the world literature showed that East Asians averaged a 17-cm^3 larger mean brain volume than did Europeans who averaged 80 cm^3 larger than did Africans (Rushton, 1995, pp. 126-132, Table 6.6). These average differences in brain size were found using several independent procedures. For example, an endocranial study of 20,000 skulls from around the world showed that East Asians, Europeans, and Africans averaged volumes of 1,415, 1,362, and 1,268 cm^3, respectively (Beals et al., 1984). A study of cranial capacity based on external head measures from a random sample of 6,325 U.S. Army personnel showed that Asian Americans, European Americans, and African Americans averaged 1,416, 1,380, and 1,359 cm^3, respectively (Rushton, 1992). An autopsy study of 1,261 individuals showed that European Americans averaged a mean brain weight of 1,323 grams and African Americans, 1,223 grams (Ho et al., 1980). An MRI study of 108 people in Britain showed that Caucasians averaged a larger brain volume than did Africans and West Indians (Harvey et al., 1994).

Parallel population differences are found for other life history traits. East Asians and Europeans, whether tested in their home continents or in North America, give birth at later gestational ages than do Africans, and their children reach puberty later and are longer lived (Rushton, 1995). Reviews of the world literature show that East Asians and their descendants have mean IQs in the range of 101 to 111, Europeans and their descendants have means in the range of 85 to 115, and Africans and their descendants have means in the range of 70 to 90 (Rushton & Ankney, 1996; Vernon et al., 2000).

There is disagreement about how to correct for body size when examining brain-size/learning-ability relations. With humans, the effect of body size on brain size is often controlled using analysis of covariance. Controlling for body size changes the question from "is IQ correlated with absolute brain size?" to "is IQ correlated with relative brain size?" Although these are quite different questions, Rushton and Ankney's (1996) review of the evidence showed that the answer to both is "yes."

Jerison's (1973, 1991) encephalization quotient (EQ) enables comparisons to be made of brain to body size ratio across diverse animal species along a single linear dimension. The average EQ is defined as 1.0. If the brain is smaller than average for a given body size, the EQ has a value of less than 1.0, and if larger than average greater than 1.0. Three broad groups of mammals have been classified according to their EQs: insectivores and rodents have small brains for their body weight (EQs = 0.1 to 1.0); carnivores, ungulates, and prosimians have brains of a moderate size (EQs = 0.5 to 1.5); and monkeys and apes have large brains relative to their body size (EQs = 2.0 to 5.0). Human EQs are over 6, which is about three times larger than would be expected for a primate of similar body size.

Over evolutionary time, EQs have increased among both invertebrates and vertebrates (Figure 1). For mammals living 65 million years ago, the mean EQ was only about 0.30 compared to the average of 1.00 today. Despite the difficulty of always knowing what to include as "brain," Russell (1983) estimated that EQs for living molluscs varied between 0.043 and 0.31, and for living insects between 0.008 and 0.045, with the less encephalized living species resembling forms that appeared early in the geologic record and the more encephalized species resembling those that appeared later.

In this paper, we test the hypothesis that cascading effects on the musculo-skeletal traits have accompanied the evolution of brain size in hominoids. We do this by comparing data from seven hominoid groups that evolved during the last several million years. The seven groups (with their mean absolute brain sizes) are *Pan troglodytes* (380 cm^3), *Australopithecines* (450 cm^3), *H. habilis* (650 cm^3), *H. erectus* (1,000 cm^3) and then, as a stringent test of our hypothesis, the three geographic populations of *Homo sapiens*, Africans (1,267 cm^3), Europeans (1,364 cm^3), and East Asians (1,346 cm^3).

It may be important to note that chimpanzees are the sister clade of all true hominids, but they have also been used as a proxy for the species that would have come prior to all hominids and, thus, are used in this way here. Perhaps when more is pub-

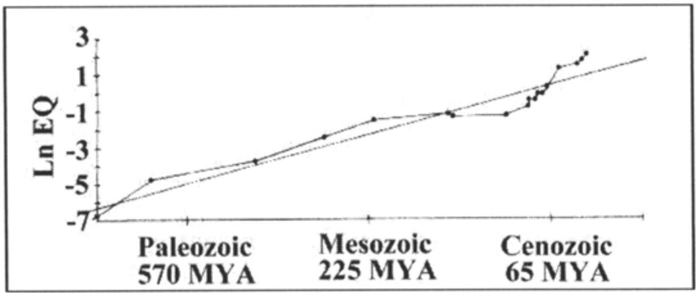

Figure 1. Encephalization quotient (natural log) plotted against elapsed geologic time in millions of years (After Russell, 1983)

lished about the earliest hominid fossils (e.g., *Ardipithecus ramidus*) these correlations can be reexamined using the fossil evidence. Furthermore, it may be argued that we have over-simplified the fossil record by grouping *H. erectus* and *H. ergaster* together and *H. habilis* and *H. rudolfensis* together, but the naming of species has always been a contentious issue and we have decided to use the classification system from Aiello and Dean (1990), Conroy (1993) and Fleagle (1999).

Materials and Methods

The appendix gives a brief description of 76 musculo-skeletal traits and the rank order for each of the seven population groups based on an "average" individual (e.g., collapsed across sex). It begins with absolute brain size (trait 1) and relative brain size (trait 2), after which it is divided into eight sections. Section A reports data on 17 cranial traits (3-19), section B on 11 teeth and mandibular traits (20-30), section C on 6 nuchal traits (31-36), section D on 3 spinal traits (37-39), section E on 8 pelvic traits (40-47), section F on 3 upper limb traits (48-50), section G on 18 lower limb traits (51-68), and section H on 8 body proportions (69-76). Tied ranks are given the average of the ranks that they would have received without ties. Missing data are given as dashes.

Traits were chosen to sample as much of the skeleton as possible and were included only when data were available for at least 3 of the 7 groups. Standard texts of evolutionary anatomy provided data on the one ape and the three fossil species (Aiello & Dean, 1990; Conroy, 1993; Fleagle, 1999). Standard forensic anthropology textbooks provided data on the three *H. sapiens* groups (Binkley, 1989; Reichs, 1998; Byers, 2002). As many variables as possible were taken from this limited number of sources so as to minimize selectivity bias. When a different reference was used, to fill-in a missing data point, a footnote is provided to the table.

To test the hypothesis that both absolute and relative brain size (traits 1 and 2) are associated with the size and shape of the other 74 musculo-skeletal traits, Pearson product-moment correlations (*r*) were calculated. The Pearson *r* is a parametric test that assumes the variables being correlated are normally distributed and are based on ratio level measurements. Neither of these assumptions is true in this study, so the main results are also reported from two non-parametric procedures: Spearman's rank order correlation rho, and Kendall's tau (which is especially useful for handling tied data). However, the Pearson *r* is typically robust enough to overcome most violations of its assumptions and its use here makes the results comparable to those already published (e.g., Smith, 1998; Godfrey et al., 2001).

Results

There were missing data in 131/532 (25%) of the categories and ties in 90 of the 399 remaining ones (23%). The Pearson correlation between absolute brain size (trait 1) and relative brain size (trait 2) was 0.93 ($n = 7$; $p < 0.001$, one-tailed; Spearman's rho = 0.93; Kendall's tau = 0.81). Both absolute and relative brain size were correlated with each of the 74 musculo-skeletal traits (3 to 76), first using a pair-wise deletion method to handle missing data (in this case variables rather than subjects), thereby retaining as many traits as possible for analysis (all 74 traits), and then using a list-wise deletion method, which calculated the correlation only where complete data were available (27 traits).

Using pair-wise deletion, absolute brain size (trait 1) was correlated with 74 musculo-skeletal traits with mean and median Pearson *r*s of 0.93 and 0.99 (range from 0.80 to 1.00; Spearman's mean and median rho = 0.96, 0.98; Kendall's mean and median tau = 0.94, 0.98). The high correlations also occurred for the separate trait categories, viz., the 17 cranial traits (3-19), $r = 0.97$; the 11 teeth and mandibular traits (20-30), $r = 0.95$; the 6 nuchal traits (31-36), $r = 0.98$; the 3 vertebral traits (37-39), $r = 1.00$; the 8 pelvic traits (40-47), $r = 0.97$; the 3 upper limb traits (48-50), $r = 0.96$; the 18 lower limb traits, (51-68), $r = 0.97$; and the 8 body proportions (69-76), $r = 0.93$. Using list-wise deletion, absolute brain size also was correlated with the 27 traits that remained, with mean and median Pearson *r*s of 0.97 and 1.00 (range from 0.80 to 1.00; Spearman's mean and median rho = 0.97, 1.00; Kendall's mean and median tau = 0.95, 1.00).

Again using pair-wise deletion, relative brain size (trait 2) was correlated with the 74 musculo-skeletal traits with mean and median Pearson *r*s of 0.76 and 0.91(range from 0.26 to 0.99; Spearman's mean and median rho = 0.76, 0.86; Kendall's mean and median tau = 0.63, 0.73). The high correlations occurred for all the separate categories, viz., the 17 cranial traits (3-19), $r = 0.79$; the 11 teeth and mandibular traits (20-30), $r = 0.77$; the 6 nuchal traits (31-36), $r = 0.79$; the 3 vertebral traits (37-39), $r = 0.56$; the 8 pelvic traits (40-47), $r = 0.59$; the 3 upper limb traits (48-50), $r = 0.77$; the 18 lower limb traits (51-68), $r = 0.79$; and the 8 body proportions (69-76), $r = 0.75$. Using list-wise deletion, relative brain size was correlated with the 27 traits that remained, with mean and median Pearson *r*s of 0.91 (range from 0.80 to 0.96; Spearman's mean and median rho = 0.91, 0.93; Kendall's mean and median tau = 0.80, 0.81).

Across Africans, Europeans, and East Asians, absolute and relative brain size intercorrelated 1.00 and both were correlated with the 42 traits on which data were available, with mean and median Pearson *r*s of 0.81. Where data were available, the high correlation occurred for the separate trait categories, viz., on 11 of 17 cranial traits (3-19), $r = 0.91$; on 8 of 11 teeth and mandibular traits (20-30), $r = 0.83$; on 3 of 6 nuchal traits (31-36), $r = 1.00$; on 1 of 8 pelvic traits (40-47), $r = 0.50$; on 1 of 3 upper limb traits (48-50), $r = 1.00$; and on 2 of 18 lower limb traits (51-68), $r = 0.98$. Only on 6 of 8 body proportions (69-76) did the effect not show (*r*s = 0.10). Virtually identical results occurred using list-wise deletion, with brain size being correlated with the 36 traits that remained, with mean and median Pearson *r*s of 0.83. Six traits lacked data on East Asians, and eight traits had ties or reversals that involved Asians and Europeans (traits 26, 30, 42, 62, 68, 69, 71 and 72); two had ties or reversals that involved Africans (traits 6 and 70). Out of the 36 traits on which full data were available, 26 gave a perfect three-way ranking. The probability of getting this predicted East Asian-European-African ranking once in a row is 3! or 1 in 6; to get it 26/36 times has an associated binomial probability of less than 10^{-10}.

Discussion

As brain size increased from 380 to 1364 cm^3 across seven hominoid groups, it was accompanied by systematic changes in 74 musculo-skeletal traits measured from the crania to the knee (*r*s = 0.90). These changes occurred on both cranial traits (temporalis fossae, post-orbital constrictions, mandibles, dentition, nuchal muscle attachments), and post-cranial traits (pelvic widths, femoral heads, tibial plateaus). The correlations were stronger for absolute brain size (mean and median Pearson *r*s of 0.93 and 0.99) than for relative brain size (mean and median Pearson *r*s of 0.76 and 0.91), although both absolute and relative brain size were significant predictors. The body proportions showed the least reliable relationships, perhaps because of the problem of ratio measurements in biology (Packard & Boardman, 1988). The most parsimonious explanation for *all* of these observed changes is that they were accommodations for increased brain size. In engineering design (both evolutionary and non-evolutionary), form follows function. Evolution selects for behavior. Thus, in the competition to find and fill new niches, there likely has always been "room at the top" for greater behavioral complexity, more intelligence, and larger brain size.

To convey the multifarious character of the musculo-skeletal changes, six illustrations are provided. For example, Figure 2 illustrates that as brain size expanded over evolutionary time, it was accompanied by broader, shorter, increasingly spherically-shaped heads, with less keeling or sagittal outline (cranial traits 3 to 5). The brain case also expanded over the top of the face rather than behind it (cranial trait 12). *Homo sapiens* have a broader, shorter, and more spherically-shaped head with less keeling or sagittal outline than did *Homo habilis* or australopithecines.

Figure 3 illustrates that as brain tissue expanded to make the more spherically-shaped head illustrated above, it did so at the expense of the large jaw-closing muscles (the temporal and masseter muscles) that run through the temporalis fossa and the post-orbital constriction (cranial traits 18 and 19) and attach to the forward process on the branch of the jaw and to the lower corner of the jaw, respectively. *Homo habilis* had greater indentations than did *Homo erectus*, which had greater indentations than did *Homo sapiens*.

Figure 4 illustrates that as brains expanded, a flatter and wider face emerged (maxilla and mandibular traits 7, 23, 24, 25, and 30). This is because the smaller muscles that resulted from filling in the cranial indentations illustrated above could no longer close such large and heavy jaws. With selection for smaller jaws there was, in turn, selection for fewer and smaller teeth with shorter roots, and finally, for incisor shoveling (traits

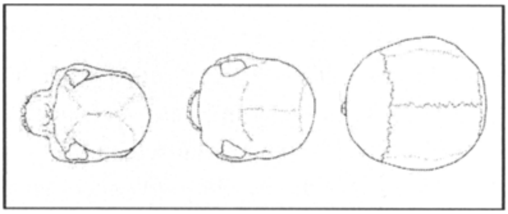

Figure 2. With increasing brain size heads became spherical in shape. From left to right, Australopithecus, Homo habilis, *and* Homo sapiens *(after Aiello & Dean, 1990).*

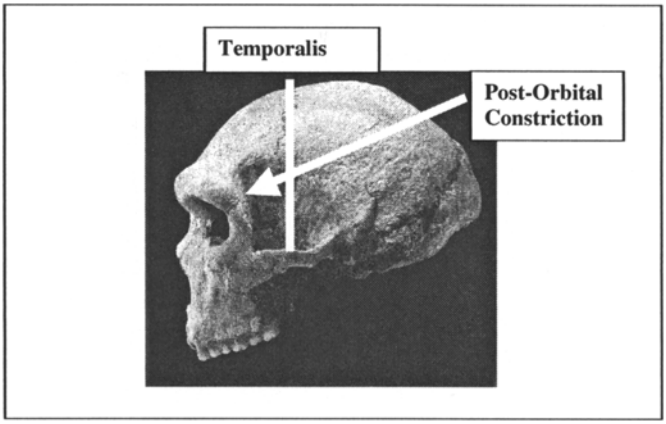

Figure 3. With increasing brain size there are decreases in the post-orbital constriction and temporalis fossa.

20-23). Along with decreasing jaw size came a concomitant decrease in size of neck muscles and the bony crests to which they attach, now no longer required for supporting heavy, forward-jutting faces (neck traits 33-34, 36). Australopithecines had a more forward-jutting face with larger jaws and larger teeth and decreased neck muscles than did *Homo habilis* or *Homo erectus* or modern *Homo sapiens*.

Figure 5 illustrates that *Homo sapiens* have a larger birth canal than did Australopithecus. As brains expanded, a larger pelvic opening was required to allow for the birth of larger-brained infants (pelvic trait 40). A larger pelvic opening in turn led to an increased sacral site, which joins the two halves of the pelvis together in the back (pelvic trait 47).

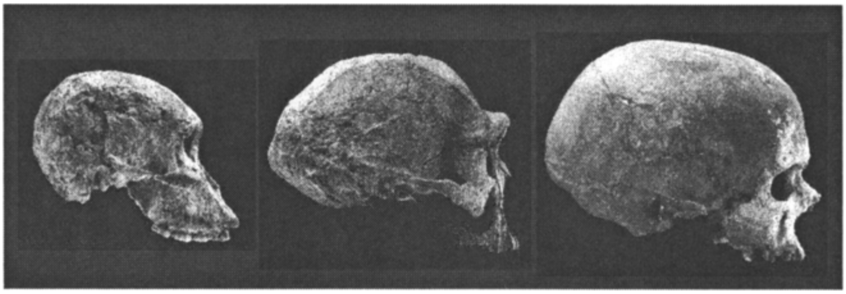

Figure 4. With increasing brain size there is decreased prognathism. Muscles are no longer available to hold up a forward jutting jaw. From left to right, Australopithecus, Homo erectus, *and* Homo sapiens *(after Aiello & Dean, 1990).*

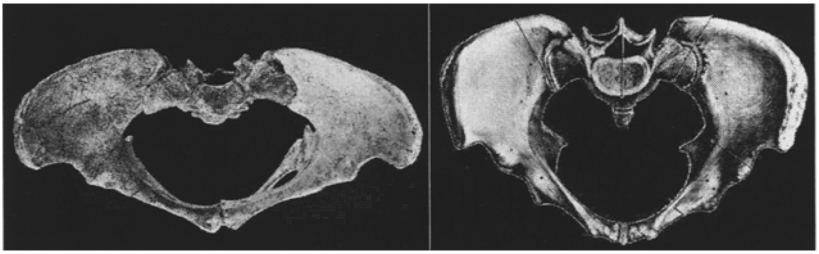

Figure 5. With increasing brain size there is increased pelvic transverse diameter to allow for the birth of larger brained infants.

Figure 6 illustrates the curvature of the femur (leg traits 56 and 60). When the pelvic bone expanded, as illustrated above, the femur needed a greater curvature to remain in contact with the weight-bearing knee, near the center of gravity. In turn the curving of the femur led to the formation of the linea aspera, which is a pilaster that prevents the bone from breaking due to bending stresses (leg trait 59). Although the linea aspera has been said to be due to muscle attachments, similar muscles attach in similar areas for nearly all mammals and yet the linea aspera occurs late in mammalian evolution, which is why we believe brain size has a role to play in the formation of the linea aspera.

Figure 7 illustrates that the upper part of the knee joint, the femoral condyles (leg traits 53, 55) increased in size and flatness to produce a more stable structure for a femur that curves back inwards to make contact with the knee. Consequently, too, the tibial plateau increased in size and concavity to form a more stable joint (leg traits 61-64).

These results show that increasing brain size has cascading effects on the skeleton and so join those already showing that increasing brain size results in delayed maturation and greater metabolic activity. For example, Smith (1989) found similar orders of magnitude ($r = 0.90$) between brain size and various life-history traits across primate species. It requires longer time to grow a bigger brain and, once built, more energy to run it. Thus, selection for increased brain size had cascading effects on other traits. The selective advantage of larger brains must have overridden these costs and contributed substantially to evolutionary fitness.

These results raise questions of broader theoretical interest. Over 570 million years, EQs have increased among both invertebrates and vertebrates (Figure 1). Jerison (1973, 1991, 2001), Russell (1983), and others, have found evolutionary convergence for increasing EQs in several independent branches of the phylogenetic tree. For example, Russell (1989) calculated that for 140 million years, dinosaurs too showed increas-

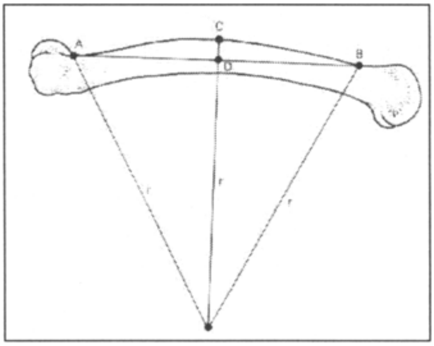

Figure 6. The calculation of femoral curvature (after Aiello & Dean, 1990).

ing encephalization before going extinct 65 millions years ago. He provided evidence that dinosaurs were evolving into large-brained bipeds, showing the same cascading effects now found in the hominid line (delayed maturation, greater metabolic expenditure, a more gracile skeletal form).

Several problems can be identified in our manuscript. It is problematic, for example, to define our various groups – chimpanzees, Australopithecenes, *H. habilis*, *H. erectus*, etc. in the way that we have. Each of these groups contain many populations of individuals with complex histories. To reduce variability to simple nominal categories is to risk oversimplification. Moreover, some researchers will want to argue about our rationale for combining different species with different geographic units within a

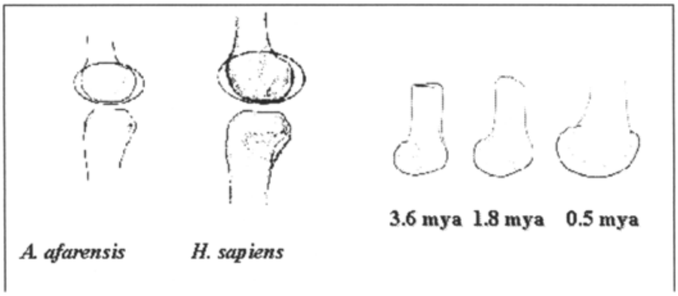

Figure 7. With increasing brain size there is increased size of knee joints in order to provide greater stability for curved femurs.

species or about whether a common evolutionary pattern exists across these groups. Nonetheless, it is difficult to see how objections of these kinds could undermine our strong results. Variation and oversimplification tend to work in the opposite direction and to reduce the chance of finding strong effects.

It is also clear that biological characters do not evolve in a simple linear order but emerge in response to a mosaic of local and unique pressures (e.g., changing climates, diets, styles of locomotion, reproductive strategies, arms races between predators and prey, and overall body size). Nonetheless, convergent trends may occur due to selection for increasing behavioral complexity. We agree that fossil hominids cannot be arranged in linear order, each one evolving into the next until the penultimate one evolves into living humans, a position recently clarified by Tattersall and Schwartz (2000) who presented evidence that as many as fifteen hominid species may have co-existed during the last three million years. We also agree that studying the linear evolution of whole brain size using a general intelligence model can obscure phylogenetic differences among species with similar learning abilities, and that it is useful to look for connections between specific morphological components of the brain and specific intellectual abilities (Hodos, 1988). However, we also think that general patterns can be as informative as particular ones. Restricting attention to the origins and functioning of the parts without concern for the whole is as unproductive as a concern for the whole without considering the parts.

Across-species comparisons show that increasing brain size confers the kind of behavioral advantages normally referred to as intelligence, as when Bonner (1980, 1988) showed that the later an animal species had emerged in earth history, the larger was its brain, and the more complex was its culture. Most researchers have focused on particular adaptations in specific organisms rather than on the longer trends of evolution. The systematic nature of the changes in the musculo-skeletal system found with increasing brain size suggests there may be much to be gained from a broader perspective.

Appendix. Rank Order of Size and Shape Across Seven Populations in 76 Musculo-Skeletal Traits.

Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	*H. sapiens* Africans	 Europeans	 East Asians
1. Cranial capacity (cm^3)	380 (1)	450 (2)	650 (3)	1000 (4)	1267^1 (5)	1346^1 (6)	1364^1 (7)
2. Encephalization Quotient	3.01 (2)	2.79 (1)	3.38 (4)	3.34 (3)	6.38^2 (5)	6.50^2 (6)	6.95^2 (7)
			A. Cranial Traits (17)				
3. Cranial shape	Narrowest (1)	Narrow (2)	Broader than Australopithecines (3)	Broader than *H. habilis* (4)	Broader than *H. erectus*, narrowest of moderns^3 (5)	Broader than Africans^3 (6)	Broadest^3 (7)
4. Cranial length	Longest (1)	Long (2)	Shorter than Australopithcines (3)	Shorter than *H. habilis* (4)	Shorter than *H. erectus*, longest of moderns (5)	Shorter than Africans and longer than Asians (6)	Shortest (7)
5. Sagittal outline	Lowest vault (1)	Low vault but slightly higher than *P. troglodytes* (2)	Higher vault than Australopithecines (3)	Higher vault than *H. habilis* (4)	Higher vault than *H. erectus*, lowest of moderns, depressed post-bregma (5)	Higher than Africans, lower than Asians (6)	Highest (7)
6. Nasal bone prominence	Flat (2)	Flat (2)	Flat (2)	Slight prominence (5)	Slight prominence (5)	Most prominent (7)	Slight prominence (5)
7. Facial prognathicism	Most prognathic (1)	Very prognathic (2)	Less prognathic than Australopithecines (3)	Less prognathic than *H. habilis* (4)	Less prognathic than *H. erectus*, most prognathic of moderns^4 (5)	Less prognathic than Africans, more so than Asians^4 (6)	Orthognathic^4 (7)

					H. sapiens		
Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	Africans	Europeans	East Asians
8. Bizygomatic breadth (reverse keyed)	Widest[5] (1)	Wide[5] (2)	Slightly narrowed[5] (3)	Narrower than *H. habilis*[5] (4)	Narrower than *H. erectus*, widest of moderns (5)	Narrower than Africans, Wider than Asians (6)	Narrowest (7)
9. Palatal form	U-shaped (1)	Slightly less U-shaped (2)	Nearly V-shaped (3)	More V-shaped and nearing parabolic (4)	Least parabolic of moderns (5)	Parabolic /elliptic (6)	Widest parabolic (7)
10. Supraorbital ridge shape (reverse keyed)	Un-arched and largest (1)	Un-arched and large (2)	Arched and slightly smaller (3)	Smaller, arched and rounded with glabellar depression (4)	Table-like with glabellar depression, largest of modern (5)	Small, smooth and arched (6)	Arched and smallest (7)
11. Mastoid process (reverse keyed)	Largest (1)	Large (2)	Smaller than Australopithecines (3)	Smaller than *H. habilis* (4)	Largest of moderns, two heads (5)	Small and pointy (6)	Smallest and stubby (7)
12. Neurocranium position	Behind face (1.5)	Behind face (1.5)	Higher but still behind face (3)	Higher than *H. habilis* but still (4)	Higher than *H. erectus*, but lowest of moderns[4] (5)	Over top of face[4] (6)	Most over the top of face[4] (7)
13. Circularity of temporal foramen	Long and narrow, oval (1)	Short and wide, but not quite circular (2)	--	Short and narrow, circular (3)	--	--	--
14. Face rotation	Absent (1)	Absent to slight (2)	Slight (3)	Present and more prominent (4)	--	--	--

Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	*H. sapiens* Africans	Europeans	East Asians
15. Anterior position of foramen magnum and occipital condyle	Posteriorly oriented (behind bitympanic line) (1)	More anterior than *P. troglodytes*, less than in *H. habilis* (2)	More anterior than Australopithecines (3)	Close to *H. sapiens* position (4)	--	--	--
16. Curvature of squamosal suture	Straight and low (1.5)	Straight and low (1.5)	Curved and low (3)	More curved and higher than *H. habilis* (4)	--	--	--
17. Orientation of occipital condyle	Vertical (1)	Horizontal (3)	Horizontal (3)	Horizontal (3)	--	--	--
18. Size of masseter muscle	Large (1.5)	Large (1.5)	Smaller than Australopithecines (3)	Smaller than *H. habilis* (4)	--	--	--
19. Post-orbital constriction size	Largest (1)	Slightly smaller than *P. troglodytes* (2)	Slightly smaller than Australopithecines (3)	Smaller than *H. habilis* (4)	Smaller than *H. erectus*, largest of moderns (5)	Larger than Africans, smaller than Asians (6)	Smallest (7)
B. Teeth and Mandible Traits (11)							
20. Incisor shape	Flat (2.5)	Flat (2.5)	Flat (2.5)	Flat (2.5)	Rarely shoveled (5)	Sometimes shoveled (6)	Frequently shoveled (7)
21. Number of teeth	32 (3)	32 (3)	32 (3)	32 (3)	32 (3)	30-32 (6)	28-32 (7)
22. Size of molars	Smaller than Australopithecines (2)	Largest (1)	Smaller than *P. troglodytes* (3)	Smaller than *H. habilis* (4)	Smaller than *H. erectus*, largest of moderns[5] (5)	Smaller than Africans[5] (6)	Smallest[5] (7)

					H. sapiens		
Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	Africans	Europeans	East Asians
23. Orthognathism of mandible	Long, low, prognathic (1)	Slightly shorter and higher, but still prognathic (2)	Shorter, higher than Australopithcines (3)	Short and high (4)	Longest and lowest of moderns (5)	Medium length and height (6)	Short and high (orthognathic) (7)
24. Shape of mandibular	U-shaped (1)	Nearing to V-shape (2)	Nearly V-shaped (3.5)	Nearly V-shaped (3.5)	Least V-shaped of moderns (5)	Less V-shaped than Asians (6)	Most V-shaped (7)
25. Width of Mandibular condyles	Close together (1)	Wider apart than *P. troglodytes* closer than *H. habilis* (2)	Wider apart than Australopithecines (3)	Wider apart than *H. habilis* (4)	Wider than *H. erectus* and closest of moderns[6] (5)	Wider apart than Africans closer than Asians[6] (6)	Widest apart[6] (7)
26. Chin prominence	Absent (2)	Absent (2)	Absent (2)	Absent (mental trigone present) (3)	Reduced (4)	Prominent (7)	Moderate (6)
27. Height of condyle relative to coronoid	Shorter condyle (1)	Slightly taller condyle than *P. troglodytes* (2)	Equal (3.5)	Equal (3.5)	--	--	--
28. Mandibular notch	Shallow (1.5)	Shallow (1.5)	Deep (3)	Deep (4)	--	--	--
29. Narrowness of Ascending ramus	Widest anteroposteriorly (1)	Wide anteroposteriorly (2.5)	Wide anteroposteriorly (2.5)	Narrow anteroposteriorly (4)	--	--	--
30. Length of tooth roots (reverse keyed)	Longest (1)	Long (2)	Shorter than Australopithecines (3)	Shorter than *H. habilis* (4)	Shorter than *H. erectus*[5] (5)	Shortest[5] (6.5)	Shortest[5] (6.5)

C. Neck Traits (6)

						H. sapiens	
Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	Africans	Europeans	East Asians
31. Height of nuchal region (reverse keyed)	Highest (1)	High (2)	Low (3)	Lowest (4)	--	--	--
32. Neck shape	Broad and squat (1.5)	Broad and squat (1.5)	--	--	Broad and strait (5)	Narrow, curved and long (6)	--
33. Mass of nuchal muscles (reverse keyed)	Largest (1)	Reduced compared to *P. troglodytes* (2)	Reduced compared to Australopithecines (3)	Reduced near moderns (4)	Reduced and largest of moderns (5)	Small (6)	Smallest (7)
34. Muscle complexity (reverse keyed)	Complex (many bellies and bodies) (1)	Less complex than *P. troglodytes* (2)	Similar to Australopithecines (3)	Simple (few bellies and bodies) (4)	--	--	--
35. Close of rectus capitis muscles	Side by side (1)	Spread apart (2)	Spread apart further (3.5)	Similar to *H. habilis* (3.5)	--	--	--
36. Size of nuchal crest and bony markings	Present and large (1)	Present in large specimens, reduced in small specimens (2)	Few pronounced markings (3)	Fewer pronounced markings (4)	Very few pronounced markings (5)	Smoother to Absent (6)	Absent (7)
			D. Vertebral Traits (3)				
37. Longest spinous process	5th or 6th (1)	Most likely 6th (2)	--	7th, like moderns (3)	--	--	--
38. Size of spinous process	Longest (1)	Long (2)	--	Short, but slightly longer than moderns (3)	--	--	--

Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	*H. sapiens* Africans	*H. sapiens* Europeans	*H. sapiens* East Asians
39. Convexity of atlas superior facet	Concave (1)	Less concave (2)	--	Flat (3)	--	--	--
E. Pelvic Traits (8)							
40. Size of transverse diameter (mm)	98 (1)	99.1 (2)	--	*H. sapiens* range (3.5)	122 (3.5)	132 (5)	--
41. Size of anteroposterior diameter (mm)	85 (1.5)	85 (1.5)	--	*H. sapiens* range (3.5)	103 (3.5)	118 (5)	--
42. Bi-Iliac width (mm)	132 (1)	200 (2)	--	--	250 (3)	270 (5)	252 (4)
43. Shape of iliac blade	Tall and narrow (1)	Short and wide (2)	--	Short and wide (3)	--	--	--
44. Sciatic notch	Absent, poorly developed (1)	Present, well developed (2)	--	Sexually dimorphic, well developed like moderns (3)	--	--	--
45. Convexity of inferior pubic ramus	Convex (1)	Straight (2.5)	Straight (2.5)	--	--	--	--
46. Size of acetabulum (mm)	.82 (1)	.78-.83 (2)	--	Near modern size ~.90 (3)	--	--	--
47. Size of sacrum	Smallest (1)	Larger (2)	--	Large, like moderns (3)	--	--	--
F. Upper Limb Traits (3)							

					H. sapiens		
Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	Africans	Europeans	East Asians
48. Orientation of glenoid cavity	Cranially oriented (1)	Less cranially oriented than *P. troglodytes* (2)	--	Laterally oriented, like moderns (3)	--	--	--
49. Arm size (reverse keyed)	Large (1)	Large (2)	--	Modern human range (3)	Largest of moderns (4)	Larger than Asians, smaller than Africans (5)	Smallest (6)
50. Capacity of elbow extension	Hyperextension possible (1.5)	Hyperextension possibly (1.5)	Slight hyperextension capabilities (3)	--	--	--	--
			G. Lower Limb Traits (18)				
51.Intertrochanteric line	Absent (1)	Present in large specimens only (2)	--	Present (3)	--	--	--
52. Femoral head size	Smallest (1)	Intermediate between apes and humans (2)	Intermediate between Australopiethecines (3)	Large (4)	Smallest of moderns (5)	Intermediate between Africans and Asians (6)	Largest (7)
53. Femoral condylar lateral profile	Circular (1)	Circular in small specimens, but circcular to oval in large specimens (2)	Same as Australopithecines, but less circular (3)	Nearly like moderns (4)	Most circular of moderns[7] (5)	Elliptical[7] (6)	Oval[7] (7)
54. Symmetry of femoral condyles	Asymmetrical (1)	Asymmetrical in some small specimens, more symmetrical in other specimens (2.5)	Like Australopithecines (2.5)	Symmetrical (4)	--	--	--

Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	*H. sapiens*		
					Africans	Europeans	East Asians
55. Femoral bicondylar width (mm)	Smallest (1.5)	Smallest (1.5)	Slightly larger (3)	Larger, nearing modern values (4)	79.50[7] (5)	83.05[7] (6)	--
56. Shaft to condyle angle (reverse keyed)	Largest (1.5)	Ape-like (1.5)	Slightly reduced (3)	Smaller than *H. habilis* (4)	--	--	--
57. Thinness of femoral neck cross-section	Cortical bone thick throughout, round (1)	Cortical bone compressed (2.5)	Cortical bone compressed (2.5)	Like moderns, but slightly thicker cortical bone (4)	--	--	--
58. Shallowness of femoral trochanteric fossa	Deep (1.5)	Deep (1.5)	--	Less deep (3)	--	--	--
59. Femoral pilaster	No pilaster (2)	No pilaster (2)	No pilaster (2)	None to small pilaster (4)	Small pilaster[8] (5)	Large pilaster[8] (6)	Largest pilaster[8] (7)
60. Femoral shaft curvature index	77.5 (straight) (2)	80 (3)	--	--	76.6[8, 9] (1)	97.0[8, 9] (4)	102. 2[8, 9] (5)
61. Size of tibial plateau	Smallest (1)	Slightly larger than *P. troglodytes* (2)	--	--	Smallest of moderns[7] (3)	Intermediate between Africans and Asians[7] (4)	Largest[7] (5)
62. Tibial plateau flatness	Most curved (1.5)	Most curved (1.5)	--	--	Curved[12] (3)	Flat[12] (4.5)	Flat[12] (4.5)
63. Lateral tibial condyle concaveness	Most convex (1.5)	Convex (1.5)	Slightly less convex than Australopitheines (3)	--	Flat[12] (4)	Varies[12] (5)	Concave[12] (6)

					H. sapiens		
Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	Africans	Europeans	East Asians
64. Knee congruency	Lowest (1)	Low (2)	Moderate (3)	High (4)	--	--	--
65. Tibial plateau angle (reverse keyed)	Highest (1)	High (2)	Lowest (3)	--	Highest of moderns[12] (4)	Low[12] (5)	--
66. Tibial condyle size	Smallest and narrowest (1)	Small and narrow (2.5)	Small and narrow (2.5)	Larger, nearly modern (4)	Larger than *H. erectus*, smallest of moderns (5)	Larger than Africans (6)	Largest (7)
67. Size of distal tibial head	Small (2)	Small (2)	Small (2)	Slightly enlarged (4)	Larger than *H. erectus*, 47.07[7] (5)	Largest, 53.23[7] (6)	--
68. Tibial anterior border sharpness	Round (2)	Round (2)	Round (2)	--	Rounded (4)	Sharp (5.5)	Sharp (5.5)
			H. Body Proportion Traits (8)				
69. Height (meters)	Less than 1 (1.5)	Less than 1 (1.5)	1-1.5 (3)	1.3-1.5 (4)	1.42-1.69 (5.5)	1.64-1.74 (7)	1.59-1.68 (5.5)
70. Intermembral index (upper limb compared to lower limb lengths) (reverse keyed)	108.7 (1)	85 (2)	86.5 (3)	*H. sapiens* range (4)	70.3 (7)	70.5 (5)	71.1 (6)
71. Brachial index	80.1 (1)	--	--	--	78.5 (2)	75.5 (4)	76.5 (3)
72. Crural index	101.9 (1)	--	--	--	86.2 (2)	83.3 (4)	86.5 (3)

					H. sapiens		
Trait number and name	*P. troglodytes*	Australopithecines	*H. habilis*	*H. erectus*	Africans	Europeans	East Asians
73. Arm length as % of body height	Highest (1)	High (2.5)	High (2.5)	Like modern humans (4.5)	45.76 (4.5)	44.54 (6)	--
74. % body weight upper limbs	Highest, 15.8 (1)	High, 12 (2)	High (3)	Low, like moderns (4)	--	--	--
75. Leg length as % of body height	Lowest (1)	Low (2.5)	Low (2.5)	Like modern humans (4)	56.42 (6)	54.98 (5)	--
76. % body weight lower limbs	24.2 (1)	28 (2)	--	30 (3)	--	--	--

Notes. Dashes indicate missing data. Superscripts indicate reference source. [1]Rushton (1995, p. 131); [2]calculated from data in Rushton (1992, p. 405); [3]Iscan & Helmer (1993, p. 77-78); [4]Stibbe (1938); [5]Coon (1962, Table 39); [6]Stringer et al (1999, p. 260); [7]Farralley & Moore (1975, p. 66-67); [8]Steele & Bramblett (1988, p. 59); [9]Gilbert (1976, p. 601); [7]Farralley & Moore (1975, p. 63); [10]Craig (1995, p. 777-780).

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