

# Hominid Brain Evolution

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## INTRODUCTION

Understanding brain evolution involves identifying both the physical changes that occurred, as well as understanding the reasons for these changes. There are two ways in which inferences about evolutionary changes are made. By comparing a species of interest against other modern species, one can determine what exactly is different, and in what way it is different. By studying the fossil record, one assesses the time-course of evolutionary changes. Both of these approaches have strengths and weaknesses. Significantly more data are available from modern forms, both in terms of the number of species one can assess and the specific details and subtleties of the adaptations studied, parts of the brain, connectivity between regions, neurotransmitter systems, cyto-architecture, integrated functioning, and so forth. However, one cannot unequivocally reconstruct the common ancestral states with this method because modern forms are themselves the end-products of separate evolutionary lineages. In some cases it appears that many lineages have evolved in parallel from a common ancestor different from any living species. In addition, one cannot determine the time-course of evolutionary change from a comparative analysis of the anatomy alone. For this, one needs the fossil record. The time-course may hold clues about the functional significance of brain evolution, depending on the timing and sequence of other features or factors that might be related to brain evolution (e.g., climate, technological, and biological changes). However, fossil data on brain evolution are limited, since brains themselves do not fossilize, leaving us with only their surrounding braincases (if we are even that lucky). Thus, both approaches, comparing modern species and assessing fossil evidence, are essential. Since there was one actual evolutionary history, our inferences about what happened – however derived – should all point towards the same conclusions if we are truly on the right track (Vincent Sarich, personal communication).

## BRAIN SCALING

The earliest comparative studies of brain and body size revealed that bigger-bodied species tended to have bigger brains. The relationship approximates a power function of the form:  $[\text{brain}] = k[\text{body}]^a$ . Log transforming both variables results in a (reasonably) straight line:  $[\log \text{ brain}] = [\log k] + a[\log \text{ body}]$ . Thus, the slope of the line describing the relationship between log brain and log body represents the exponent of the power function. Empirical studies of mammals show that the relationship is statistically very strong (e.g.,  $r=0.95$ ; Martin 1981). Nevertheless, the 95 percent confidence intervals for mammals encompass at least a 10-fold range in possible brain sizes at a given body size (Schoenemann 2006). This indicates that whatever influence body size might have on brain size, it is actually relatively weak. This is consistent with experiments showing that selection on body weight causes very little change in brain weight, which should not be the case if there really were a strong intrinsic developmental constraint tying brain size with body size (Atchley 1984; Riska et al. 1984).

Empirically, the power function exponent describing brain/body scaling appears to be close to 0.76 (Martin 1981), significantly less than 1 (isometry). There are two major explanations that have been offered for this pattern. Jerison (1973) suggests that brains serve to create a model of the external world, based on the array of sensory inputs they obtain. He believes the most important inputs for this are somatosensory (touch, pain, heat, body position), which correspond to information from the body surface. Since surface area scales to the two-thirds power of volume, brains should scale at the two-thirds power of body size. He later refined this model to argue that only the cortex (which is devoted to modeling the external world) should scale with body surface area, not the whole brain (Jerison 1988). Further, since cortical thickness also increases with brain size (at about the 0.17 power), brain size would actually be expected to increase at greater than the two-thirds power of body size (Jerison 1988). By combining known empirical scaling estimates for both brain-to-body size (0.76; Martin 1981), and brain-to-cortical surface area (0.91; Jerison 1982), one can directly predict how cortical surface area should scale with body size:

If:

$$[\text{cortical surface area}] = k_1 [\text{brain size}]^{0.91}$$

$$[\text{brain size}] = k_2 [\text{body size}]^{0.76}$$

Then:

$$[\text{cortical surface area}] = k_1 [k_2 [\text{body size}]^{0.76}]^{0.91} = k_3 [\text{body size}]^{0.69}$$

This exponent (0.69) is very close to the two-thirds exponent predicted by Jerison.

One problem with this model is that cross-sectional area of the spinal cord, which is as good a proxy as any for the number of afferent and efferent fibers connecting the brain with the body surface, actually scales much lower than the two-thirds power of body size (Fox and Wilczynski 1986). The model also requires that there be a simple, isometric relationship between cortical volume and the complexity of processing done on these sensory inputs. Exactly how this type of processing is accomplished at the neural level is unknown at present, however.

The other explanation for the 0.76 power scaling of brain-to-body size is related to the fact that total metabolic resources also scale with body size at the 0.76 power in mammals. Since brain tissue is particularly metabolically expensive (Hofman 1983; Aiello and Wheeler 1995), total metabolic resources would be an important upper constraint on brain size (Martin 1981; Armstrong 1983). Because of various types of evolutionary cognitive “arms races”, species may be expected to tend towards larger brain sizes generally, but the most adaptive brain size for a given species would be highly niche-dependent. This model is consistent with the finding of a substantial degree of variation in brain size at a given body size.<sup>1</sup>

Because both of these hypotheses predict approximately the same scaling relationship between brain and body size, it is not possible, based on the scaling relationship itself, to judge which is more likely (Deacon 1990). From a theoretical perspective, however, it is unclear why the degree of complexity of an organism’s model of the world should necessarily scale with its body surface area, whereas the metabolic costs of large brains are obvious. It may be that the association between cortex size and body surface area is accidental.

Regardless of why it occurs, the empirical relationship between brain and body size has led to an emphasis on controlling for body size when comparing brain size between species. The most widely used is probably Jerison’s (1973) Encephalization Quotient (EQ), which is simply the actual brain size of a species divided by the (empirically-derived) estimate of the average brain size for a mammal of that body size. Human EQs are in the 5–7 range (depending on the exact slope of the empirical line derived for mammals). The *behavioral* relevance of EQ over absolute brain size is highly questionable, however (see below).

## COMPARATIVE PERSPECTIVES ON BRAIN EVOLUTION

Most comparative studies have primarily focused on how humans differ from expectations based on primate trends, though ape disproportions have also been highlighted when found. These studies have clearly shown that the human brain is not simply an enlarged version of a chimpanzee brain (Deacon 1992; Rilling 2006). Some of the differences appear to be allometric (i.e., the result of predictable scaling patterns between parts), while others do not. Both types of differences probably have non-trivial behavioral implications (contrary to what is often assumed).

An example of an important difference explained by allometry is the size of the neocortex. In humans, it accounts for over 80 percent of the entire size of the brain, compared with less than half in some primates (Schoenemann 2009). This appears to be mostly a predictable result of brain size increase: humans have about as much neocortex as one would predict given a primate brain of our brain size. Another such pattern involves the proportion of the cortex that is made up of white matter (primarily connective axons) vs. gray matter (primarily dendrites and neuron cell bodies). More than 40 percent of the human cerebral cortex is white matter compared with only 21 percent of macaque (*Macaca mulatta*) brains. This turns out to be a function of cerebral cortex size (Hofman 1985). Interestingly, the empirical relationship suggests that white matter does not actually increase fast enough to keep areas as directly interconnected with one another in larger brains. This means that there is an inherent

structural bias towards increasing cortical specialization as brains increase in size. Based on published diagrams of currently-mapped, cytoarchitecturally-defined cortical areas for 19 mammal species, Changizi and Shimojo (2005) showed that the number of distinct cortical areas appears to be a function of increasing brain size. Using the equation derived from all mammals, humans should have approximately 150 cortical areas, compared with only approximately 100 in chimpanzees and approximately 75 in the largest-brained monkeys (e.g., *Papio papio*). Although data for only three primates were available (*Callithrix*, *Aotus*, *Macaca*), they all had greater estimated total numbers of cortical areas than the general mammal prediction, suggesting that among mammals primates might be particularly biased towards cortical specialization. In any case, even though the trend towards increasing cortical specialization is 'explained' by allometry, it nevertheless has fundamentally important behavioral implications (Schoenemann 2009).

Within the neocortex itself, the size of functional areas appear to be relatively unconstrained by allometry. The relative size of particular neocortical areas in mammals is predicted by the behavioral specializations of a given species. About half of the neocortex of the echo-locating Ghost Bat (*Macroderma gigas*) is involved in processing auditory information, for example (Krubitzer 1995). In humans, at least three neocortical areas appear to be significantly smaller than expected, given a primate brain our size (calculated from Blinkov and Glezer 1968; Stephan et al. 1981): primary motor cortex (approximately 33 percent as large as predicted), premotor (approximately 60 percent as large), and primary visual (VI; approximately 60 percent as large). Since our neocortex as a whole is not smaller than expected, some other parts must therefore be larger. The human frontal cortex is not larger overall (Semendeferi et al. 2002), but because two of its subdivisions are significantly smaller than expected (premotor and primary motor), the remainder must be significantly larger. Most empirical studies, dating back to Brodmann's initial cytoarchitectural studies (Brodmann 1909), seem to support this view (see review in Schoenemann 2006). The temporal lobe also appears to be somewhat larger than predicted, though apparently not by as much as the prefrontal (Rilling and Seligman 2002). Although comparative studies of the parietal lobe area are lacking, morphometric studies of endocranial surfaces suggest significant changes in this area as well (Bruner 2004).

Some non-neocortical areas also show interesting patterns. The olfactory bulb (sense of smell) is only approximately 31 percent as large as predicted (data from Stephan et al. 1981). The cerebellum, though slightly smaller than expected for a primate brain size as large as ours, is still almost three times larger than expected based on body size (Rilling and Insel 1998; MacLeod et al. 2003). Apes as a group appear to have undergone a grade shift in cerebellar proportions. Compared with monkeys, their cerebellar hemispheres are 2.7 times larger than expected for their cerebellar vermis sizes (MacLeod et al. 2003). With respect to body size, apes have cerebellar hemispheres approximately 2.4 times larger than monkeys, and humans 5.8 times larger (MacLeod et al. 2003). This is intriguing because the cerebellum has long been known to play a major role in moderating motor control, and as such would be expected to scale only with body size.

As with the cerebellum, the basal ganglia in humans are only approximately 65 percent as large as predicted for a primate brain our size (Stephan et al. 1981; Schoenemann 1997), but about twice as large with respect to body size. The basal

ganglia are known to be involved in a variety of motor functions, but they have also been implicated in language processing (Hochstadt et al. 2006), suggesting that the increase over body size predictions might have important behavioral consequences.

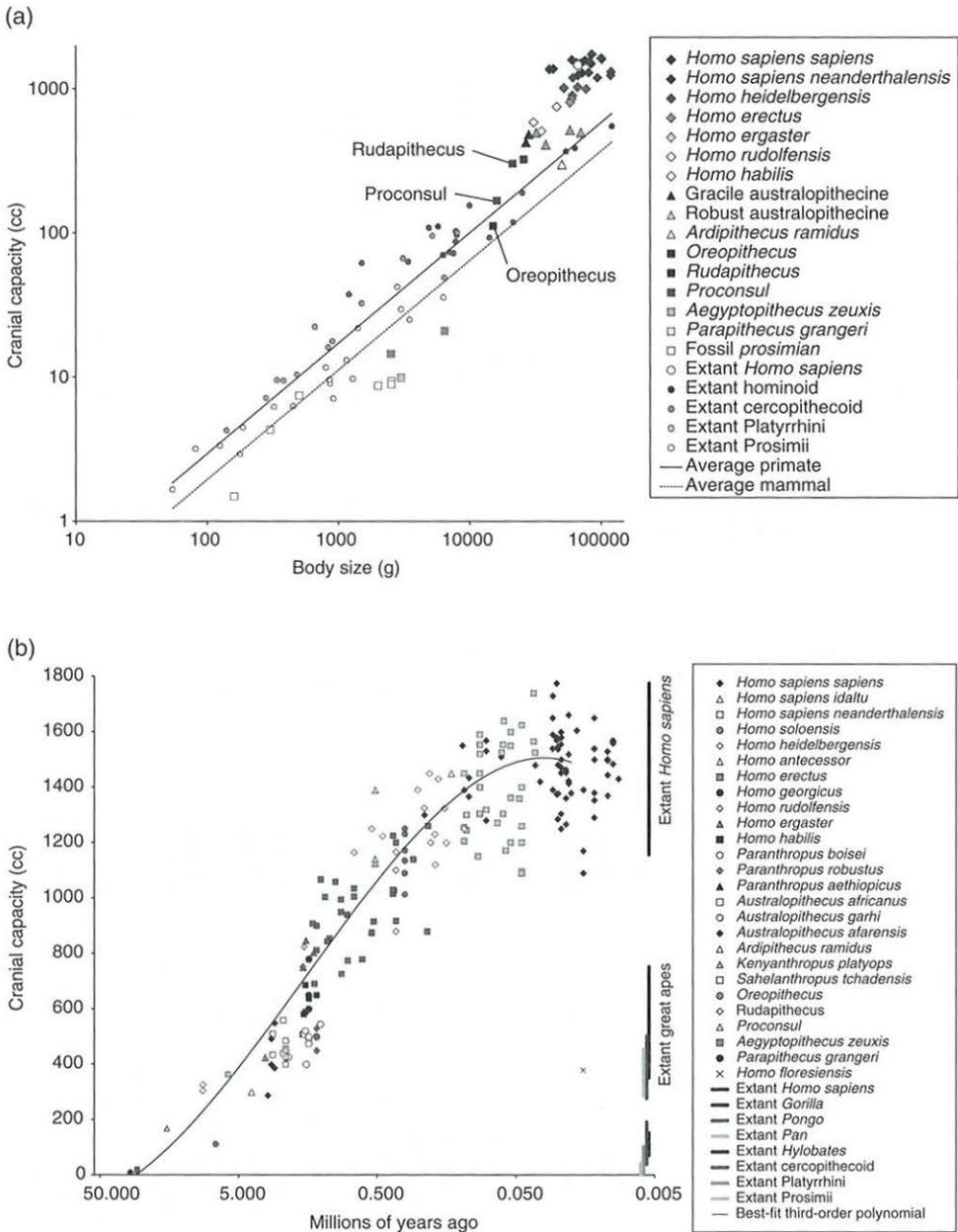
Potentially independent of gross anatomical changes, there are important suggestions of differences in the existence, elaboration, and/or organization of neuronal cell types, which is currently the focus of much study (Preuss 2006; Sherwood and Hof 2007). In apes and humans, unique patterns are found in anterior cingulate cortex (attentional and emotional processing), primary motor cortex (motor control), and fronto-insular cortex (involved in social cognition) (Sherwood and Hof 2007). One particular type of neuron (CR-ir pyramidal) is found in the primary motor and anterior cingulate cortices of both apes and humans, but only humans appear to have them in the anterior paracingulate cortex (Sherwood and Hof 2007). There also appears to have been a change in the visual pathway in humans, particularly the fibers that carry information about motion and luminance contrast (Preuss and Coleman 2002). The behavioral significance of these uniquely human attributes – if any – are difficult to establish at present.

## FOSSIL RECORD OF BRAIN EVOLUTION

Larger brains appear to have evolved independently several times in many different animal lineages. Birds, for example, are more encephalized than their reptile ancestors. The earliest mammals were significantly less encephalized than modern mammals (Jerison 1973). Delphinids (dolphins and killer whales) have some of the largest relative brain sizes among all living mammals, yet their closest relatives among terrestrial mammals are relatively small-brained artiodactyls (Jerison 1973; Murphy et al. 2004). Relative brain size in both carnivores and ungulates have increased since the Paleogene, with carnivore relative brain size outpacing that of ungulates in each major geologic time period (Jerison 1973), presumably representing some sort of cognitive evolutionary arms race.

The earliest primates resemble modern prosimians, and date back to the early Eocene (approximately 55–50 Ma; Fleagle 1999; see Silcox, this volume, Chapter 18). There are three species from this time period for which brain size and body size has been estimated, *Tetonius homunculus*, *Smilodectes gracilis* and *Adapis parisiensis* (Radinsky 1977). At 1.5 cc, *Tetonius homunculus* had a brain slightly smaller than that of the smallest-brained living primate, the mouse lemur (*Microcebus murinus*), even though it probably weighed about three times as much (Radinsky 1977; Stephan et al. 1981). Both *Smilodectes gracilis* and *Adapis parisiensis* had brains within the range of modern primates, but appeared to have had significantly larger body sizes than any living primate with similar sized brains (Figure 8.1a, Table 8.1). These Early Eocene primate specimens thus had lower EQs than any modern primate (about half the size of modern mammals). Thus, it appears that brain size increased significantly in the primate lineage as a whole over the past 50–55 Ma. With respect to brain morphology, these early primates appear similar to early mammals in having only the lateral sulcus (or Sylvian fissure; Radinsky 1977; Szalay 1969).

Relative brain size appears to have further increased in both platyrrhines (New World monkeys) and catarrhines (Old World monkeys, apes and humans) independently.



**Figure 8.1** Evolution of cranial capacity. (a) Cranial capacity vs. body size in modern and fossil primates. Data from Table 8.1. Average mammal: cranial capacity (cc) =  $0.059(\text{body mass g})^{0.76}$  (based on Martin 1981); average primate: cranial capacity (cc) =  $0.087(\text{body mass g})^{0.77}$  (data from Stephan et al. 1981). (b) Evolution of primate cranial capacity. Data from Table 8.2. Best-fit third-order polynomial of anthropoids through *Homo sapiens sapiens*, excluding robust australopithecines (*Paranthropus aethiopicus*, *P. boisei*, and *P. robustus*) and immature specimens: cranial capacity (cc) =  $76814(\log \text{Ma})^3 - 53694(\log \text{Ma})^2 - 68144(\log \text{Ma}) + 86331$  ( $r^2 = 0.90$ ,  $N = 183$ ).

Table 8.1 Estimated cranial capacities and body weights for primate fossils.

Specimen	Putative taxon	Location	Age (Ma)	Cranial capacity (cc)	Body mass (g) <sup>a</sup>	Developmental age <sup>b</sup>	Sources <sup>c</sup>
AMNH 4194	<i>Tetonius homunculus</i>	United States	55	1.5	160		1
YPM 12152 & USNM 17997	<i>Smilodectes gracilis</i>	United States	52.5	9.5	2540		1; date: 2
BM 20192 & AMNH 11045	<i>Adapis parisiensis</i>	France	52.5	9.0	2540		1
Cambridge M.538	<i>Adapis parisiensis</i>	France	52.5	8.8	2000		3
YPM 18302	<i>Necrolemur antiquus</i>	France	37.5	4.4	300		1
UT 40688-7	<i>Rooneyia viejaensis</i>	United States	33	7.5	500		1
CGM 40237	<i>Aegyptopithecus zeuxis</i>	Egypt	29.5	21.2	6403		body: 4; brain: 5
CGM 85785	<i>Aegyptopithecus zeuxis</i>	Egypt	29.5	14.6	2512		body: 4; brain: 5
DPC 18651	<i>Parapithecus grangeri</i>	Egypt	33	10	2995		6
KNM-RU 7290	<i>Proconsul</i>	Kenya	18	168	16,000		7
RUD 77	<i>Dryopithecus</i>	Hungary	9.85	326	25,450		4; date: 8
RUD 200	<i>Dryopithecus</i>	Hungary	9.85	305	21,100		4; date: 8
BAC-208	<i>Oreopithecus</i>	Italy	8	112	15,000		4
TM 266- 01-060-1	<i>Sahelanthropus tchadensis</i>	Chad	6.5	365			9
ARA-VP-6/500	<i>Ardipithecus ramidus</i>	Ethiopia	4.4	300	50,000		10; 11
KNM-WT 40000	<i>Kenyanthropus platyops</i>	Kenya	3.5	400–450			12
AL 162-28	<i>Australopithecus afarensis</i>	Ethiopia	3.18	400			
AL 288-1	<i>Australopithecus afarensis</i>	Ethiopia	3.0	387			
AL 333-105	<i>Australopithecus afarensis</i>	Ethiopia	3.18	400		juvenile	
AL 333-45	<i>Australopithecus afarensis</i>	Ethiopia	3.18	492			
AL 444-2	<i>Australopithecus afarensis</i>	Ethiopia	3	550			
Dikika 1-1	<i>Australopithecus afarensis</i>	Ethiopia	3.3–3.4	275–300			12
KNM-WT 17000	<i>Paranthropus aethiopicus</i>	Kenya	2.5	410	37,666		
KNM-ER 406	<i>Paranthropus boisei</i>	Kenya	1.5	500	69,843		
KNM-ER 407	<i>Paranthropus boisei</i>	Kenya	1.85	510			

KNM-ER 732	<i>Paranthropus boisei</i>	Kenya	1.7	500	31,979	
KNM-WT 13750	<i>Paranthropus boisei</i>	Kenya	1.7	475		
Konso (KGA-10-525)	<i>Paranthropus boisei</i>	Ethiopia	1.4	545		
OH 5	<i>Paranthropus boisei</i>	Tanzania	1.8	520	57,603	
SK 54	<i>Paranthropus robustus</i>	South Africa	1.5	500		juvenile
SK 859	<i>Paranthropus robustus</i>	South Africa	1.5	450		juvenile
SK 1585	<i>Paranthropus robustus</i>	South Africa	1.5	530		
MLD 1	<i>Australopithecus africanus</i>	South Africa	3.1	510		
MLD 37/38	<i>Australopithecus africanus</i>	South Africa	3.1	435		
Sts 5	<i>Australopithecus africanus</i>	South Africa	2.5	485	27,850	
Sts 19/58	<i>Australopithecus africanus</i>	South Africa	2.5	436		
Sts 60	<i>Australopithecus africanus</i>	South Africa	2.5	400		
Sts 71	<i>Australopithecus africanus</i>	South Africa	2.5	428	26,638	
Stw 505	<i>Australopithecus africanus</i>	South Africa	2.6	560		
Taung	<i>Australopithecus africanus</i>	South Africa	2.6	440		juvenile
Type 2	<i>Australopithecus africanus</i>		2.5	457		
Bouri (Bou-VP-12/130)	<i>Australopithecus garhi</i>	Ethiopia	2.5	450		
KNM-ER 1805	<i>Homo habilis</i>	Kenya	1.85	582		
KNM-ER 1813	<i>Homo habilis</i>	Kenya	1.88	509	34,883	
OH 7	<i>Homo habilis</i>	Tanzania	1.8	687		
OH 13	<i>Homo habilis</i>	Tanzania	1.5	650		
OH 16	<i>Homo habilis</i>	Tanzania	1.7	638		
OH 24	<i>Homo habilis</i>	Tanzania	1.8	590	30,286	
KNM-ER 3732	<i>Homo ergaster</i>	Kenya	1.88	750		
KNM-ER 3733	<i>Homo ergaster</i>	Kenya	1.78	848	59,200	
KNM-ER 3883	<i>Homo ergaster</i>	Kenya	1.57	804	57,458	
KNM-ER 1470	<i>Homo rudolfensis</i>	Kenya	1.88	752	45,597	
KNM-ER 1590	<i>Homo rudolfensis</i>	Kenya	1.85	825		

(continued)

Table 8.1 (cont'd)

<i>Specimen</i>	<i>Putative taxon</i>	<i>Location</i>	<i>Age (Ma)</i>	<i>Cranial capacity (cc)</i>	<i>Body mass (g)<sup>a</sup></i>	<i>Developmental age<sup>b</sup></i>	<i>Sources<sup>c</sup></i>
Dmanisi D2280	<i>Homo georgicus</i>	Republic of Georgia	1.7	650			
Dmanisi D2282	<i>Homo georgicus</i>	Republic of Georgia	1.7	780			
Dmanisi D2700	<i>Homo georgicus</i>	Republic of Georgia	1.7	600			13
Buia (UA 31)	<i>Homo erectus</i>	Eritrea	0.78–1.0	750–800			13
Daka (Bou-VP-2/66)	<i>Homo erectus</i>	Ethiopia	1.0	995			
Hexian	<i>Homo erectus</i>	China	0.412	1025			
KNM-ER 42700 (Illeret)	<i>Homo erectus</i>	Kenya	1.55	691			14
KNM-WT 15000 (Nariokotome Boy)	<i>Homo erectus</i>	Kenya	1.5	900	59,939		
Lantian (Gongwang 1)	<i>Homo erectus</i>	China	0.7	780			
Nanjing (Hulu Cave) 1	<i>Homo erectus</i>	China	0.580–0.620	876			15
Narmada	<i>Homo erectus</i>	India	0.236	1260			
Ngawi	<i>Homo erectus</i>	Java		870		immature	
OH 12	<i>Homo erectus</i>	Tanzania	0.78–1.2	727			date: 13
OH 9	<i>Homo erectus</i>	Tanzania	1.4	1067			date: 13
Salé	<i>Homo erectus</i>	Moroco	0.24	880			
Sambungmacan 1	<i>Homo erectus</i>	Java	0.8	1035			
Sambungmacan 3	<i>Homo erectus</i>	Java	0.4	917			
Sambungmacan 4	<i>Homo erectus</i>	Java	0.8	1006			
Sangiran 2	<i>Homo erectus</i>	Java	1.5	813			date: 13
Sangiran 3	<i>Homo erectus</i>	Java	1.0	950			
Sangiran 4	<i>Homo erectus</i>	Java	1.6	908			date: 13
Sangiran 10	<i>Homo erectus</i>	Java	1.2	855			date: 13
Sangiran 12	<i>Homo erectus</i>	Java	1.1	1059			date: 13
Sangiran 17	<i>Homo erectus</i>	Java	1.3	1004	76,062		date: 13
Sangiran IX	<i>Homo erectus</i>	Java	1.1–1.4	845			13
Trinil 2	<i>Homo erectus</i>	Java	0.9	940			

Yunxian (1 and 2)	<i>Homo erectus</i>	China	0.4	1200		
Zhoukoudian (Z 11)	<i>Homo erectus</i>	China	0.42	1015	51,796	date: 13
Zhoukoudian I, L (Z 10)	<i>Homo erectus</i>	China	0.42	1225		date: 13
Zhoukoudian III, E (Z 2)	<i>Homo erectus</i>	China	0.58	915		date: 13
Zhoukoudian III, L (Z 12)	<i>Homo erectus</i>	China	0.42	1030	65,649	date: 13
Zhoukoudian V	<i>Homo erectus</i>	China	0.3	1140		13
Atapuerca (Sima de los Huesos) 4	<i>Homo antecessor</i>	Spain	0.530–0.600	1390		date: 16
Atapuerca (Sima de los Huesos) 5	<i>Homo antecessor</i>	Spain	0.530–0.600	1125		date: 16
Atapuerca (Sima de los Huesos) 6	<i>Homo antecessor</i>	Spain	0.530–0.600	1140		date: 16
Ngandong (Solo IX)	<i>Homo soloensis</i>	Java	0.143–0.546	1135		date: 20
Ngandong 1 (Solo I)	<i>Homo soloensis</i>	Java	0.143–0.546	1172		date: 20
Ngandong 6 (Solo V)	<i>Homo soloensis</i>	Java	0.143–0.546	1251		date: 20
Ngandong 7 (Solo VI)	<i>Homo soloensis</i>	Java	0.143–0.546	1013		date: 20
Ngandong 13 (Solo X)	<i>Homo soloensis</i>	Java	0.143–0.546	1231		date: 20
Ngandong 14 (Solo XI)	<i>Homo soloensis</i>	Java	0.143–0.546	1090		date: 20
Arago 21	<i>Homo heidelbergensis</i>	France	0.4	1166		
Biache	<i>Homo heidelbergensis</i>	France	0.160–0.190	1200		date: 12
Bodo	<i>Homo heidelbergensis</i>	Ethiopia	0.6	1250	117,236	
Ceprano	<i>Homo heidelbergensis</i>	Italy	0.8	1165		
Dali 1	<i>Homo heidelbergensis</i>	China	0.209	1120		taxon: 13
Ehringsdorf	<i>Homo heidelbergensis</i>	Germany	0.23	1450		
Jinniushan	<i>Homo heidelbergensis</i>	China	0.28	1390		taxon: 13
Kabwe (Broken Hill)	<i>Homo heidelbergensis</i>	Zambia	0.18	1325	118,890	
Le Lazaret	<i>Homo heidelbergensis</i>	France	0.13	1250		child
Ndutu	<i>Homo heidelbergensis</i>	Tanzania	0.4	1100		12
Petalona	<i>Homo heidelbergensis</i>	Greece	0.21	1230		

(continued)

Table 8.1 (cont'd)

<i>Specimen</i>	<i>Putative taxon</i>	<i>Location</i>	<i>Age (Ma)</i>	<i>Cranial capacity (cc)</i>	<i>Body mass (g)<sup>a</sup></i>	<i>Developmental age<sup>b</sup></i>	<i>Sources<sup>c</sup></i>
Reilingen	<i>Homo heidelbergensis</i>	Germany	0.2	1430			
Saldanha (Elandsfontein)	<i>Homo heidelbergensis</i>	South Africa	0.5	1225			
Salé	<i>Homo heidelbergensis</i>	Morocco	0.4	880			12
Steinheim	<i>Homo heidelbergensis</i>	Germany	0.225	1200	60,513		
Swanscombe	<i>Homo heidelbergensis</i>	England	0.25	1325			
Amud 1	<i>Homo sapiens neanderthalensis</i>	Israel	0.041	1740	84,481		12
Dederiyeh 1	<i>Homo sapiens neanderthalensis</i>	Syria	0.05	1096		infant	12
Dederiyeh 2	<i>Homo sapiens neanderthalensis</i>	Syria	0.05	1089		infant	12
Engis 2	<i>Homo sapiens neanderthalensis</i>	Belgium	0.06	1362		child	
Feldhofer	<i>Homo sapiens neanderthalensis</i>	Germany	0.040?	1525			date: 12
Gánovce	<i>Homo sapiens neanderthalensis</i>	Slovakia	0.09	1320			
Gibraltar (Devil's Tower)	<i>Homo sapiens neanderthalensis</i>	Gibraltar	0.05	1400		child	
Gibraltar (Forbe's Quarry)	<i>Homo sapiens neanderthalensis</i>	Gibraltar	0.05	1200	93,432		
Jebel Irhoud 1	<i>Homo sapiens neanderthalensis</i>	Morocco	0.1	1305	80,481		
Jebel Irhoud 2	<i>Homo sapiens neanderthalensis</i>	Morocco	0.1	1400			
Krapina 3 (Cranium C)	<i>Homo sapiens neanderthalensis</i>	Croatia	0.13	1255			
Krapina 6 (Cranium E)	<i>Homo sapiens neanderthalensis</i>	Croatia	0.13	1205			
Krapina B	<i>Homo sapiens neanderthalensis</i>	Croatia	0.13	1450			
La Chapelle aux Saints	<i>Homo sapiens neanderthalensis</i>	France	0.05	1625	100,237		
La Ferrassie	<i>Homo sapiens neanderthalensis</i>	France	0.060–0.075	1640	99,507		
La Quina 18	<i>Homo sapiens neanderthalensis</i>	France	0.06	1200		child	
La Quina 5	<i>Homo sapiens neanderthalensis</i>	France	0.065	1172			
Le Moustier	<i>Homo sapiens neanderthalensis</i>	France	0.041	1565	81,190		
Monte Circeo (Guattari 1)	<i>Homo sapiens neanderthalensis</i>	Italy	0.052	1360			
Neanderthal	<i>Homo sapiens neanderthalensis</i>	Germany	0.04	1525			

Pech de L'Azé	<i>Homo sapiens neanderthalensis</i>	France	>0.103	1150		juvenile	12
Roc de Marsal	<i>Homo sapiens neanderthalensis</i>	France	>0.050	1260		infant	12
Saccopastore 1	<i>Homo sapiens neanderthalensis</i>	Italy	0.125	1245	66,573		
Saccopastore 2	<i>Homo sapiens neanderthalensis</i>	Italy	0.125	1300			
Shanidar 1	<i>Homo sapiens neanderthalensis</i>	Iraq	0.06	1600			
Shanidar 5	<i>Homo sapiens neanderthalensis</i>	Iraq	0.06	1550			
Skhul 1	<i>Homo sapiens neanderthalensis</i>	Israel	0.1	1450			
Skhul 4	<i>Homo sapiens neanderthalensis</i>	Israel	0.1	1554			
Skhul 5	<i>Homo sapiens neanderthalensis</i>	Israel	0.1	1520	70,166		
Skhul 9	<i>Homo sapiens neanderthalensis</i>	Israel	0.1	1590			
Spy I	<i>Homo sapiens neanderthalensis</i>	Belgium	0.068	1305			
Spy II	<i>Homo sapiens neanderthalensis</i>	Belgium	0.068	1553			
Tabun 1	<i>Homo sapiens neanderthalensis</i>	Israel	0.070–0.080	1271			date: 12
Teshik-Tash	<i>Homo sapiens neanderthalensis</i>	Uzbekistan	0.07	1525		child	
Herto 1/16	<i>Homo sapiens idaltu</i>	Ethiopia	0.16	1450			
Abri Pataud 1	<i>Homo sapiens sapiens</i>	France	0.022	1380			date: 12
Arene Candide 1	<i>Homo sapiens sapiens</i>	France	0.023	1414			date: 12; cranial capacity: 17
Arene Candide 2	<i>Homo sapiens sapiens</i>	France	0.023	1424			date: 12; cranial capacity: 17
Arene Candide 4	<i>Homo sapiens sapiens</i>	France	0.023	1520			date: 12; cranial capacity: 17
Arene Candide 5	<i>Homo sapiens sapiens</i>	France	0.023	1661			date: 12; cranial capacity: 17
Border Cave	<i>Homo sapiens sapiens</i>	South Africa	0.07	1510			
Brno I	<i>Homo sapiens sapiens</i>	Czech Republic	0.026	1600			
Brno II	<i>Homo sapiens sapiens</i>	Czech Republic	0.026	1500			
Brno III	<i>Homo sapiens sapiens</i>	Czech Republic	0.026	1304	79,551		
Bruniquel 2	<i>Homo sapiens sapiens</i>	France		1555			

(continued)

Table 8.1 (cont'd)

<i>Specimen</i>	<i>Putative taxon</i>	<i>Location</i>	<i>Age (Ma)</i>	<i>Cranial capacity (cc)</i>	<i>Body mass (g)<sup>a</sup></i>	<i>Developmental age<sup>b</sup></i>	<i>Sources<sup>c</sup></i>
Cap Blanc 1	<i>Homo sapiens sapiens</i>	France		1434			
Chancelade	<i>Homo sapiens sapiens</i>	France	0.012	1530			date: 12
Combe Capelle	<i>Homo sapiens sapiens</i>	France	0.028	1570			
Coobol Creek	<i>Homo sapiens sapiens</i>	Australia	0.012	1444			12
Cro-Magnon 1	<i>Homo sapiens sapiens</i>	France	0.03	1730			
Cro-Magnon 3	<i>Homo sapiens sapiens</i>	France	0.03	1590	59,407		
Dolni Vestonice 3	<i>Homo sapiens sapiens</i>	Czech Republic	0.0275	1285			
Dolni Vestonice 14	<i>Homo sapiens sapiens</i>	Czech Republic	0.0275	1538			
Dolni Vestonice 18	<i>Homo sapiens sapiens</i>	Czech Republic	0.0275	1481			
Dolni Vestonice 20	<i>Homo sapiens sapiens</i>	Czech Republic	0.0275	1547			
Dolni Vestonice 21	<i>Homo sapiens sapiens</i>	Czech Republic	0.0275	1378			
Grotte des Enfants (Grimaldi) 4	<i>Homo sapiens sapiens</i>	Italy/France	0.028	1775			date: 17
Grotte des Enfants (Grimaldi) 5	<i>Homo sapiens sapiens</i>	Italy/France	0.028	1375	40,405		date: 17
Grotte des Enfants (Grimaldi) 6	<i>Homo sapiens sapiens</i>	Italy/France	0.028	1580			date: 17
Keilor	<i>Homo sapiens sapiens</i>	Australia	0.012	1497			12
KNM-ES 11693 (Eliye Springs)	<i>Homo sapiens sapiens</i>	Kenya	0.20-0.30	>1300			18
Kostenki 14	<i>Homo sapiens sapiens</i>	Russia		1222			
Kostenki 2	<i>Homo sapiens sapiens</i>	Russia	0.02	1605			
Laetoli 18	<i>Homo sapiens sapiens</i>	Tanzania	0.12	1367			taxon: 12
Liujiang	<i>Homo sapiens sapiens</i>	China	0.04	1480			
Minatogawa 1	<i>Homo sapiens sapiens</i>	Japan	0.018	1390			
Minatogawa 2	<i>Homo sapiens sapiens</i>	Japan	0.018	1170			
Minatogawa 4	<i>Homo sapiens sapiens</i>	Japan	0.018	1090			

Mladeč 1	<i>Homo sapiens sapiens</i>	Czech Republic	0-03	1540			
Mladeč 2	<i>Homo sapiens sapiens</i>	Czech Republic	0-03	1390			
Mladeč 5	<i>Homo sapiens sapiens</i>	Czech Republic	0-03	1650			
Nazlet Khater 2	<i>Homo sapiens sapiens</i>	Egypt	0-037	1420			
Obercassel 1	<i>Homo sapiens sapiens</i>	Germany	0-012	1500			date: 12
Obercassel 2	<i>Homo sapiens sapiens</i>	Germany	0-012	1370			date: 12
Omo 2 (Kibbish)	<i>Homo sapiens sapiens</i>	Ethiopia	0-12	1435			
Pavlov 1	<i>Homo sapiens sapiens</i>	Czech Republic	0-026	1472			
Predmosti 3	<i>Homo sapiens sapiens</i>	Czech Republic	0-026	1580	75,313		
Predmosti 4	<i>Homo sapiens sapiens</i>	Czech Republic	0-026	1250			
Predmosti 9	<i>Homo sapiens sapiens</i>	Czech Republic	0-026	1555			
Predmosti 10	<i>Homo sapiens sapiens</i>	Czech Republic	0-026	1452			
Qafzeh 6	<i>Homo sapiens sapiens</i>	Israel	0-09	1568			
Qafzeh 9	<i>Homo sapiens sapiens</i>	Israel	0-09	1531	64,625		
Qafzeh 11	<i>Homo sapiens sapiens</i>	Israel	0-09	1280		adolescent	12
San Teodoro 1	<i>Homo sapiens sapiens</i>	Italy	0-011	1565			date: 17
San Teodoro 2	<i>Homo sapiens sapiens</i>	Italy	0-011	1569			date: 17
San Teodoro 3	<i>Homo sapiens sapiens</i>	Italy	0-011	1560			date: 17
San Teodoro 5	<i>Homo sapiens sapiens</i>	Italy	0-011	1484			date: 17
San Teodoro 7	<i>Homo sapiens sapiens</i>	Italy	0-012	1500			17
Singa 1	<i>Homo sapiens sapiens</i>	Sudan	0-133	1550			
St. Germain-la-Rivie	<i>Homo sapiens sapiens</i>	France	0-015	1354			date: 17
Sungir 1	<i>Homo sapiens sapiens</i>	Russia	0-024	1464			
Sungir 2	<i>Homo sapiens sapiens</i>	Russia	0-024	1267			
Sungir 3	<i>Homo sapiens sapiens</i>	Russia	0-024	1361			
Sungir 5	<i>Homo sapiens sapiens</i>	Russia	0-024	1453			
Veyrier 1	<i>Homo sapiens sapiens</i>	France	0-01	1430			date: 17
Wadjak 1	<i>Homo sapiens sapiens</i>	Java	0-015	1539			17
Wadjak 2	<i>Homo sapiens sapiens</i>	Java	0-015	1650			17

(continued)

Table 8.1 (cont'd)

<i>Specimen</i>	<i>Putative taxon</i>	<i>Location</i>	<i>Age (Ma)</i>	<i>Cranial capacity (cc)</i>	<i>Body mass (g)<sup>a</sup></i>	<i>Developmental age<sup>b</sup></i>	<i>Sources<sup>c</sup></i>
Willandra Lakes	<i>Homo sapiens sapiens</i>	Australia	0.018–0.012	1540			12
Yinkou (Jinniushan)	<i>Homo sapiens sapiens</i>	China	0.13	1390			
Zhoukoudian (Upper Cave) 1	<i>Homo sapiens sapiens</i>	China	0.015	1500	83,635		
Zhoukoudian (Upper Cave) 2	<i>Homo sapiens sapiens</i>	China	0.015	1380	43,241		
Zhoukoudian (Upper Cave) 3	<i>Homo sapiens sapiens</i>	China	0.015	1290	71,312		
LB1	<i>Homo floresiensis</i>	Flores, Indonesia	0.018	417			19

<sup>a</sup>From Kappelman (1996); estimates derived from orbit size.

<sup>b</sup>Specimens are known or believed to be adult unless otherwise noted.

<sup>c</sup>Data from Holloway et al. (2004) except as noted.

Codes for additional sources:

1. Radinsky (1977); 2. Gingerich (1979); 3. Gingerich and Martin (1981); 4. Begun and Kordos (2004); 5. Simons et al. (2007); 6. Bush et al. (2004); 7. Walker et al. (1983); 8. Bernor et al. (2002); 9. Guy et al. (2005); 10. Suwa et al. (2009); 11. White et al. (2009); 12. Lieberman (2011); 13. Antón (2003); 14. Spoor et al. (2007); 15. Wu et al. (2011); 16. Bischoff et al. (2007); 17. De Miguel and Henneberg (2001); 18. Bräuer (1989); 19. Falk et al. (2005); 20. Indriati et al. (2011).

The EQ of one of the earliest fossil catarrhines, *Aegyptopithecus*, dating to approximately 30 Ma, is smaller than any modern primate (and in fact is relatively small compared with modern mammals as well; Figure 8.1a, Tables 8.1 and 8.2). Estimates of brain size range from 21.2 cc (CGM 40237) and 14.6 cc (CGM 85785), with body sizes of 6.4 kg and 2.5 kg respectively (Begun and Kordos 2004; Simons et al. 2007).

All living anthropoids have relative brain sizes larger than the fossil primates dating to the apparent platyrrhine/catarrhine split, approximately 35 Ma (Figure 8.1a, Table 8.1). Endocranial reconstructions suggest that brain organization in *Aegyptopithecus* had begun to approximate modern anthropoids, with reduced olfactory bulbs (suggesting a reduced sense of smell), an elaborated visual cortex, and the development of a central sulcus separating primary somatic sensory and motor cortex (Radinsky 1974), thus differing from most fossil and modern prosimians. Although it was anthropoid-like in these ways, *Aegyptopithecus* appears not to have had as large a frontal lobe as is seen in modern anthropoids (Radinsky 1974).

Fossil evidence of hominoid brain evolution is relatively sparse, but we can sketch a rough outline. A *Proconsul* specimen (KNM-RU 7290) dating to 18 Ma has a brain size of approximately 168 cc (Walker et al. 1983). This is much larger in absolute terms than any prior fossil primate. With an estimated body size of approximately 16 kg, it sits comfortably within the range of modern primate brain sizes for its body size (Figure 8.1a, Tables 8.1 and 8.2). Using *Aegyptopithecus* as a gauge of the brain size of early catarrhines, *Proconsul* represents about a nine-fold increase in absolute brain size over approximately 14 million years.

*Proconsul* does not appear to have had an anatomy suggesting suspensory locomotion, unlike all modern hominoids. Given that molecular evidence suggests that the last common ancestor of modern hominoids lived approximately 12 Ma (Sarich 1987; see Disotell, this volume Chapter 15), *Proconsul* may not have been directly ancestral to modern hominoids. The earliest fossil primate brains from relatively large-bodied suspensory apes are two specimens of *Rudapithecus* (RUD 77 and RUD 200) (Begun, this volume Chapter 21), both of which date to close to 10 Ma. Their estimated brain sizes are just over 300 cc, placing them at the low end of modern great apes with respect to absolute size (Begun and Kordos 2004). However, because their estimated body sizes are relatively small (21 kg for RUD 200; 25 kg for RUD 77) they have relatively high EQs (higher than any living non-human ape; Figure 8.1a, Tables 8.1 and 8.2).

Another Late Miocene suspensory ape, *Oreopithecus*, had a brain size of approximately 112 cc and a body size of approximately 15 kg (Begun and Kordos 2004), giving it an absolute brain size similar to modern hylobatids (gibbons and siamangs) even though it weighed about twice as much. This translates to a low EQ for modern primates (close to that of gorillas), though still within the modern range (Figure 8.1a, Tables 8.1 and 8.2). *Oreopithecus* is generally thought to be an early great ape (Begun and Kordos 2004).

Fossil evidence of primate evolution thus suggests numerous independent increases in both relative and absolute brain size. Hominoid brain evolution appears most pronounced with respect to absolute size, rather than relative brain size. Because both body size and brain size increased in hominoid lineages, modern great apes do not have larger relative brain sizes than is typical for monkeys. Sulcal patterns of *Rudapithecus* suggest that relatively little neural organizational change occurred, with the exception of the frontal regions.

**Table 8.2** Estimated cranial capacities and body weights for extant primate species.

<i>Superfamily</i>	<i>Genus species</i>	<i>Common name</i>	<i>Cranial capacity (cc)<sup>a</sup></i>	<i>Body mass (g)</i>	<i>Source<sup>b</sup></i>
Hominoidea	<i>Homo sapiens</i>	human	1156–1775	66,242	1
Hominoidea	<i>Pan troglodytes</i>	chimpanzee	282–454	53,700	2
Hominoidea	<i>Pan paniscus</i>	bonobo	275–381		2
Hominoidea	<i>Gorilla</i>	gorilla	350–752	120,500	2
Hominoidea	<i>Pongo</i>	orangutan	276–502	62,750	2
Hominoidea	<i>Hylobates</i>	gibbon	70–152	5732	2
Cercopithecoidea	<i>Papio papio</i>	baboon	155.44	9885	3
Cercopithecoidea	<i>Macaca nemestrema</i>	pigtail macaque	108.87	4888	4
Cercopithecoidea	<i>Macaca cynomolgus</i>	crab-eating macaque	61.85	1504	4
Cercopithecoidea	<i>Presbytis entellus</i>	langur	119.40	21,319	5
Cercopithecoidea	<i>Macaca mulatta</i>	rhesus monkey	87.90	7800	6
Cercopithecoidea	<i>Cercocebus albigena</i>	mangabey	97.60	7900	6
Cercopithecoidea	<i>Papio anubis</i>	olive baboon	190.96	25,000	6
Cercopithecoidea	<i>Cercopithecus mitis</i>	blue monkey	70.56	6300	6
Cercopithecoidea	<i>Cercopithecus ascanius</i>	red-tailed monkey	63.51	3400	6
Cercopithecoidea	<i>Cercopithecus talapoin</i>	guenon	37.78	1200	6
Cercopithecoidea	<i>Erythrocebus patas</i>	patas monkey	103.17	7800	6
Cercopithecoidea	<i>Pygathrix nemacus</i>	red-shanked douc langur	72.53	7500	6
Cercopithecoidea	<i>Nasalis larvatus</i>	proboscis monkey	92.80	14,000	6
Cercopithecoidea	<i>Colobus badius</i>	red colobus	73.82	7000	6
Ceboidea	<i>Callithrix jacchus</i>	common marmoset	7.24	280	6
Ceboidea	<i>Cebuella pygmaea</i>	pygmy marmoset	4.30	140	6
Ceboidea	<i>Saguinus oedipus</i>	cotton-top tamarin	9.54	380	6
Ceboidea	<i>Saguinus</i>	tamarin	9.57	340	6
Ceboidea	<i>Callimico goeldii</i>	Goeldi's monkey	10.51	480	6
Ceboidea	<i>Aotus trivirgatus</i>	Northern/three-striped night monkey	16.20	830	6
Ceboidea	<i>Callicebus moloch</i>	red-bellied/dusky titi	17.94	900	6
Ceboidea	<i>Pithecia monacha</i>	monk saki	32.87	1500	6
Ceboidea	<i>Alouatta</i> sp.	howler monkey	49.01	6400	6

Ceboidea	<i>Ateles geoffroyi</i>	spider monkey	101-03	8000	6
Ceboidea	<i>Lagothrix lagotricha</i>	woolly monkey	95-50	5200	6
Ceboidea	<i>Cebus</i> sp.	capuchin monkey	66-94	3100	6
Ceboidea	<i>Saimiri sciureus</i>	squirrel monkey	22-57	660	6
Prosimii	<i>Cheirogaleus major</i>	greater dwarf lemur	6-37	450	6
Prosimii	<i>Cheirogaleus medius</i>	fat-tailed dwarf lemur	2-96	177	6
Prosimii	<i>Microcebus murinus</i>	gray mouse lemur	1-68	54	6
Prosimii	<i>Lepilemur</i> <i>ruficaudatus</i>	red-tailed sportive lemur	7-18	915	6
Prosimii	<i>Lemur fulvus</i>	brown lemur	22-11	1400	6
Prosimii	<i>Varecia variegata</i>	ruffed lemur	29-71	3000	6
Prosimii	<i>Avahi l. laniger</i>	Eastern woolly lemur	9-80	1285	6
Prosimii	<i>Avahi l. occidentalis</i>	Western woolly lemur	9-12	860	6
Prosimii	<i>Propithecus verreauxi</i>	white sifaka	25-19	3480	6
Prosimii	<i>Indri Indri</i>	idri	36-29	6250	6
Prosimii	<i>Daubentonia</i> <i>madagasc ariensis</i>	aye aye	42-61	2800	6
Prosimii	<i>Loris tardigradus</i>	red slender loris	6-27	322	6
Prosimii	<i>Nycticebus coucang</i>	slow loris	11-76	800	6
Prosimii	<i>Perodicticus potto</i>	potto	13-21	1150	6
Prosimii	<i>Galago crassicaudatus</i>	greater galago	9-67	850	6
Prosimii	<i>Galago demidoff</i>	Demidoff's dwarf galago	3-20	81	6
Prosimii	<i>Galago senegalensis</i>	lesser bush baby	4-51	186	6
Prosimii	<i>Tarsius</i> sp.	tarsier	3-39	125	6

<sup>a</sup>Range if given.

<sup>b</sup>Sources: 1. Parenti (1973); 2. Tuttle (1986); 3. Riese and Riese (1952); 4. Count (1947); 5. Jerison (1973); 6. Stephan et al. (1981).

## HOMININ BRAIN EVOLUTION

The most obvious evolutionary change in hominin brains has been in overall size. Figure 8.1b illustrates the cranial capacities plotted against time for most of the specimens discussed in this chapter (see Table 8.2 for sources). It is evident that the trend has been a roughly linear function of log time from the earliest anthropoids to the present. It also illustrates that the earliest hominins appear to have had brains approximately the size of modern apes. The cranial capacities of modern chimpanzees (*Pan troglodytes*) range from approximately 280 to approximately 450 cc, bonobos (*Pan paniscus*) from approximately 275 to approximately 380 cc, and gorillas (*Gorilla gorilla*) from approximately 350 to approximately 750 cc (Tuttle 1986). *Rudapithecus*, as discussed above, already had brain sizes in the lower end of this range as far back as approximately 10 Ma. *Sabelanthropus tchadensis*, which has been dated to approximately 6.5 Ma, had a cranial capacity of approximately 365 cc. Though it has been suggested to be an early hominin on morphological grounds (Guy et al. 2005), molecular phylogenetic studies suggest the last common ancestor of modern chimpanzees, gorillas and humans may have lived as late as 5 Ma (Sarich 1987; see Disotell, this volume, Chapter 15). If this is correct, *Sabelanthropus* may simply be a large-bodied Late Miocene ape. In either case, the earliest hominins likely had brain sizes ranging in the low end of modern large-bodied African apes.

*Ardipithecus ramidus*, with a cranial capacity of approximately 300 cc and dating to approximately 4.4 Ma, appears to be an early hominin (Suwa et al. 2009; Simpson, this volume, Chapter 22). *Australopithecus afarensis*, an early gracile bipedal form dating to between approximately 3.7 and 3.2 Ma, had cranial capacities ranging from 387 cc (AL 288-1, Lucy's) to approximately 550 cc (AL 444-2), thus overlapping and extending beyond the upper range of modern chimpanzee values (Holloway et al. 2004) (Hammond and Ward, this volume). Furthermore, body size estimates for these species suggest they were somewhat smaller than modern chimpanzees (McHenry 1992), suggesting EQs somewhat larger than modern chimpanzees (>3, compared with less than 2 for chimpanzees; see Figure 8.1a). As mentioned above, however, the behavioral significance of EQ vs. absolute brain size is unclear (see below). There is no obvious archeological evidence indicating any behavioral elaboration beyond modern great apes. Undisputed evidence of stone tool manufacturing, for example, does not occur until approximately 2.6 Ma (Semaw et al. 2003).

Specimens of *Australopithecus africanus*, dating between 3.1 and 2.5 Ma, have estimated cranial capacities of 400 cc (Sts 60) to 560 cc (Stw 505). One *Australopithecus garhi* specimen, dating to 2.5 Ma, has an estimated cranial capacity of 450 cc (Asfaw et al. 1999). These later gracile *Australopithecines* thus also overlap with, but extend significantly beyond, the range of modern chimpanzee cranial capacities. Body size estimates again suggest that they were smaller than modern chimpanzees, and hence would have had higher EQs than modern apes (though again, the behavioral significance is unclear).

At this point, there is a divergence of at least two different lineages in hominin evolution. One resulted in the robust australopithecines, while the other resulted in the genus *Homo*. Although brain size increase was most dramatic in *Homo*, it is curious that the robust lineage apparently also experienced a moderate increase. The presumed ancestor of later robusts (at least in East Africa), *Paranthropus aethiopicus*,

had a cranial capacity of 410 cc (Holloway et al. 2004; see Chapter 3 by Strait, and Chapter 23 by Wood and Schroer, this volume). The later robust form in East Africa, *Paranthropus boisei*, had cranial capacities ranging from 475 to 545 cc (specimens date from 1.85–1.4 Ma), and appear to have increased over time (Elton et al. 2001). The later South African robust form, *Paranthropus robustus*, had cranial capacities ranging from 450 to 530 cc (specimens from 1.5 Ma). Thus, an independent trend of increasing cranial capacity is suggested in the robust lineage. It is not known whether this was because of increased competition with contemporary *Homo* species, use of stone tools, increased group sizes, or perhaps interbreeding with larger-brained *Homo*.

The *Homo* lineage shows a more dramatic increase in cranial capacity, beginning sometime between 3 and 2 Ma (Figure 8.1b). This is not surprising, since larger-brained fossil hominins are invariably placed in the *Homo* genus. Only one *Homo habilis* specimen, KNM-ER 1813 (at 509 cc), has a cranial capacity in the range of contemporary robust australopithecines. All other specimens range from 582 cc (KNM-ER 1805) to 687 cc (OH 7). These specimens date between 1.88 and 1.50 Ma. A second putative early *Homo* taxon, *H. rudolfensis*, dating between 1.88 and 1.85 Ma, has cranial capacities ranging from 752 cc (KNM-ER 1470) to 825 cc (KNM-ER 1590). *Homo ergaster* specimens (which curiously overlap with both *H. habilis* and *H. rudolfensis*, being found from 1.88–1.57 Ma) range from 750 cc (KNM-ER 3732) to 848 cc (KNM-ER 3733). Regardless of whether these taxonomic groupings are truly valid, a significant number of specimens demonstrate cranial capacities outside the range for modern apes of similar body sizes.

From early *Homo* on, a reasonably steady increase is evident in cranial capacity up to Neanderthals, ranging from 1172 to 1740 cc (La Quina 5 and Amud, respectively), and anatomically modern *Homo sapiens*, ranging from 1090 to 1775 cc (Minatogawa 4 and Grotte des Enfants 4, respectively). Ignoring the inherently problematic question of individual specimen species assignment, the overall trend shows no obvious punctuated, step-like changes (Figure 8.1b). A smooth transition over time is also seen for EQs of individual specimens (where body size is estimated from eye orbit size; Kappelman 1996). If taxonomic placement is valid, it is possible to see punctuated changes, but too much depends on the correct species identification for individual fossils. Given the range of cranial capacities at any given time point is approximately the same as seen in extant *Homo sapiens* (Figure 8.1b), the most likely interpretation is a reasonably constant increase.

These increases in hominin brain size are not matched by increases in the size of the brains of monkeys over the same period (Elton et al. 2001), suggesting that there was something special about hominin niches, that either specifically selected for increasing brain size, or allowed for brain sizes to increase because of an increase in the ability to extract resources from the environment (thereby providing the metabolic resources necessary to support such large brains), or both.

## REORGANIZATION

Although overall brain size is the easiest neuroanatomical feature to measure in fossils (via cranial capacity), brains are not simple, single functional units. As discussed above, comparative anatomical studies show that different parts of our brain evolved to

different extents. The timing of these changes is the matter of some debate. One possibility, long championed by Ralph Holloway, is that important changes in the internal organization of the brain (which he calls “reorganization”) occurred *before* brain size increased. He believes that it was specifically these early changes that spurred later brain evolution. Holloway points to the relatively small size of the primary visual cortex (VI) in modern humans (discussed above; Holloway 1992). Though this could have been the result of VI lagging behind increases in other areas, Holloway believes that several fossil endocasts indicate the boundary of VI is in a more posterior (human-like) position in australopithecines, as judged from likely positions of the lunate sulcus, which marks the boundary of VI in hominoids (Holloway 2008). However, another leading paleoneurologist, Dean Falk, favors a model in which reorganization occurred simply through the differential enlargement of some areas over others (Falk 1980, 2007). Holloway et al. (2003) reported on two chimpanzees who have human-like lunate positions, which they point out show it is theoretically possible for early australopithecines to have evolved in the human direction (before any dramatic increase in overall brain size). However, this also demonstrates that the change can have no behavioral implications, thereby undermining the significance of such a change. Furthermore, if the hypothesized change occurred in australopithecines because more elaboration was needed in anterior regions, this implicitly suggests a *decrease* in visual processing ability, since neural tissue devoted to visual processing (or at least VI) would have decreased (at least initially) under Holloway’s model. This seems unlikely, but cannot be ruled out at present.

Suggestive evidence of elaboration in Broca’s area, which in modern humans plays a key role in language production, appeared in early *Homo*. This has been inferred from the development of Broca’s Cap, which is a raised area (bump) overlaying Broca’s area on endocasts. Qualitative studies suggest that Broca’s Cap is larger on the left than the right even in early *Homo* species (Holloway 1983). Falk (1983) also argues that a *Homo rudolfensis* specimen (KNM-ER 1470, 1.8 Ma) shows modern-human-like sulcal impressions where Broca’s area would be.

Another feature that appears during hominid evolution is asymmetrical protrusions known as petalias. Modern humans typically display a left occipital/right frontal petalial pattern. Other apes sometimes display petalias, but the majority do not show the combination very commonly seen in humans (Holloway and de la Coste-Lareymondie 1982). Further, this pattern is common in *Homo erectus* and Neanderthals, and is suggested in australopithecines (Holloway and de la Coste-Lareymondie 1982). Exactly what this means behaviorally is unfortunately not known. Language is typically lateralized to the left hemisphere, but why this would lead to left occipital but not left frontal protrusion is not obvious. The right frontal plays a key role in prosody (the patterns of stress and intonation in a language), but the left frontal contains the language-functional Broca’s area for most people. In addition, the typical modern human pattern is found in some individual apes. All of this confounds a clear functional explanation for left occipital/right frontal petalias.

Studies of *Homo erectus*, Neanderthal, and *Homo sapiens* endocasts also suggest that parietal regions have expanded to a greater extent than other regions (Bruner 2004). Parietal regions are known to mediate a variety of spatial analysis tasks, many of which appear to be important for motor sequences involved in manipulation of the hands, suggesting a role for tool-making (Bruner 2004).

## BRAIN AND BEHAVIOR

The behavioral implications of these evolutionary changes hinge on the extent to which neural volume truly predicts ability. First, note that increasing neural resources come at an evolutionary cost, which must be paid every generation. In addition to very high metabolic rate, larger brains take longer to mature (Harvey and Clutton-Brock 1985), so their possessors have fewer offspring per unit time. Larger brains are also problematic for childbirth in bipedal primates, since this form of locomotion selects for narrow hips (minimizing the lateral displacement of the hip joint from the center of gravity; Lovejoy 1988; see Richmond and Hatala, this volume Chapter 10). Thus, increasing brain size must have substantial counterbalancing benefits wherever it occurs (Smith 1990).

It is generally assumed that the benefits relate to some sort of behavioral advantage, because of the brain's central function. Darwin himself suggested: "As the various mental faculties gradually developed themselves the brain would almost certainly become larger. No one, I presume, doubts that the large proportion which the size of man's brain bears to his body, compared to the same proportion in the gorilla or orang, is closely connected with his higher mental powers." (Darwin 1871:145.) But exactly which "higher mental powers" explain increasing brain size in hominins? Clear candidates for this are behaviors unique or highly elaborated in humans: language, manufacturing and use of tools, extraordinary levels of social complexity, and high emphasis on learned behaviors. Intelligence is also frequently assumed to be relevant, though defining "intelligence" has proved to be contentious (both within and between species).

Comparative studies in primates have demonstrated significant correlations among various components of brain and social complexity, tool use, and behavioral innovation (Reader and Laland 2002; Dunbar 2003). Absolute brain size actually correlates more highly than EQ with general cognitive abilities (Deaner et al. 2007). Larger-brained primates appear to conceptually understand tasks, not just learn associations, and are therefore more behaviorally flexible (Gibson et al. 2001). The behavioral relevance of EQ is in fact unclear, even though it is commonly assumed to be centrally important. At the level of entire mammalian orders, average EQ does correlate strongly with average ethogram size (i.e., number of different behaviors displayed; Changizi 2003).

The general explanatory model for brain evolution is that selection for some adaptive behavioral characteristic(s) led to changes in brain anatomy. There are a number of assumptions here:

1. individual differences in the relevant behavioral abilities must have had reproductive consequences within each generation, on average;
2. there must be a genetic correlation (not just a phenotypic correlation) connecting brain structure size with behavioral ability; and
3. the genetic correlations must be due to genetic influences on brain anatomy causally influencing behavior, or vice-versa (Schoenemann 2006).

Each of these assumptions is at least partially testable, in principle. For a given hypothesis about brain evolution to be more than an idle guess, specific research on these questions is crucial.

While it is impossible to demonstrate that a particular behavioral ability always had positive consequences for reproduction, it has at least been shown that fertility was positively associated with educational attainment in one community at one time (Bajema 1966), and negatively associated with overt schizophrenia (Laursen and Munk-Olsen 2010), for example. Most models of brain evolution simply assume that it would always be adaptive to be more intelligent.

Few studies have actually estimated *genetic* correlations between brain anatomy and behavior, with most focusing on general cognitive ability. There is a significant *phenotypic* correlation between IQ and brain size (meta-analysis suggesting  $r$ =approximately 0.40; Rushton and Ankney 2009). However, phenotypic correlations can result both from non-genetic influences as well as from a non-random distribution (through cross-assortative mating) of independent genetic influences on brain and behavior. Phenotypic correlations of this sort would not support an evolutionary model. Only three studies have effectively controlled for such effects, and their results suggest the actual genetic correlation is significantly weaker: somewhere between 0 and 0.2 (Schoenemann et al. 2000; Posthuma et al. 2002; Gignac et al. 2003; reviewed in Schoenemann 2006).

Furthermore, because enriched environments cause measurable increases in brain volumes in rats (Diamond 1988), some (presumably small?) portion of the association in humans could be due to similar effects. The actual evolutionarily-relevant genetic correlation between brain size and general cognitive ability is therefore likely smaller than 0.2, though probably not zero.

This might seem to be too low for selection on greater general cognitive ability to conceivably cause hominin brain size increases. However, an increase of approximately 1000 cc over an estimated approximately 125,000 generations translates to only approximately 0.8 cc/generation. This means the necessary brain-behavior genetic correlation can actually be very small (though not zero) for selection on the hypothesized behavior to cause this change (Schoenemann et al. 2000).

It is also likely that selection acted on other abilities besides those tapped by modern IQ tests. Some studies have reported associations between cognitive tasks and specific brain regions. Holloway et al. (1993) suggest that apparent sex differences in corpus callosum morphology (e.g., Smith 2005) might in turn be explained by sex differences in spatial (Halpern 1987) and/or social abilities. Variation in corpus callosum morphology may be associated with such abilities, though studies have not yet been published.

The ability to manipulate information in short-term memory to solve particular problems or goals (so-called “working memory”) correlates with measures of brain size (Posthuma et al. 2003). Because prefrontal cortex is known to mediate such abilities, it may be that the association is even stronger for that region. The ability to focus on particular stimuli in the face of distractors, as indexed by the Stroop test (Stroop 1935), has been shown to be moderately correlated with the size of the prefrontal cortex (Schoenemann et al. 2000). The prefrontal has also been implicated in temporal and serial order information processing (Fuster 1985; Petersson et al. 2004).

Because language relies on a wide array of circuits located in the temporal, parietal and prefrontal lobes, as well as subcortical circuits involving basal ganglia and the cerebellum (Schoenemann 2009), it is likely that disproportionate increases in these

areas are at least partly due to selection for language, though direct empirical studies connecting neuroanatomical variation and language ability in humans are lacking.

The disproportionate increases in cerebellar components in apes and humans outlined above may also have important behavioral implications, as the cerebellum has been implicated in a number of higher cognitive functions, including aspects of memory and learning, attention, visuo-spatial processing, modulating emotional responses, goal organization and planning, and even language (MacLeod et al. 2003; Baillieux et al. 2008). Conversely, the relatively small motor, premotor, primary visual, and olfactory bulb areas may well indicate no behavioral differences between apes and humans, since absolute size is more important than relative size for many behavioral dimensions. In absolute terms, premotor and V1 areas are actually larger in humans than in apes. The study of brain-behavior associations with respect to gross anatomy is in its infancy right now, however, and future studies will be needed to fully explore the possibilities.

## INTERPRETING BRAIN EVOLUTION

In light of the evidence regarding functional implications of neuroanatomical differences, it is possible to outline likely behavioral implications of neuroanatomical evolution in apes and humans. First, changes in ape brains – particularly increased absolute brain size and elaboration of cerebellar areas with respect to body size – suggest a significant enhancement of general cognitive ability, behavioral flexibility, learning, and planning compared with monkeys. Further changes during human evolution suggest even greater enhancement of these same abilities in our lineage. Increases in brain areas relevant to language, particularly in temporal, parietal, and prefrontal areas, also suggest a key evolutionary role for communication, and by implication social interaction generally (Deacon 1997; Schoenemann 2009). Elaboration of prefrontal areas also suggests an important increase in planning and causal reasoning (Schoenemann 2006), both of which are central not only to technological innovation but also reasoning about social relationships.

## NOTE

- 1 Brain size does not correlate with metabolic resources when statistically controlling for body size (McNab and Eisenberg 1989), but this also removes approximately 95 percent of the variation in brain size – exactly the variation the model is trying to explain.

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