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Size and Scaling in Human Evolution

Homo sapiens is a peculiar large primate; however, all australopithecines are versions of the "same" animal.

David Pilbeam and Stephen Jay Gould

Human paleontology shares a peculiar trait with such disparate subjects as theology and extraterrestrial biology: it contains more practitioners than objects for study. This abundance of specialists has assured the careful scrutiny of every bump on every bone. In this context, it is remarkable that the most general character of all—body size (the difference in absolute size among fossil hominids, and the clear phyletic trend toward larger bodies)—has been rather widely neglected.

Increase in body size has played an especially important role in evolution for two reasons.

1) It is so common. Several evolutionary phenomena are encountered so frequently that their canonization as "law" has been widely accepted. "Cope's law" of phyletic size increase is the best known and most widely touted of these statistical generalizations (*1*).

2) It has such important and ineluctable consequences. Galileo (*2*) recognized that a large organism must change its shape in order to function in the same way as a smaller prototype. The primary law of size and shape involves unequal scaling of surfaces and volumes (*3*), but other differential increases have their potent effect as well (*4*). As a terrestrial vertebrate evolves to larger size, its limb bones become relatively thicker, the ratio of brain weight to body weight decreases, and digestive and respiratory surfaces become more complex.

We cannot begin to assess the nature of adaptation in lineages obeying Cope's rule until we establish "criteria of subtraction" for recognizing the changes in shape that larger size requires. A simple description of changing shape will not suffice, for some changes merely compensate for increased size and reproduce the "same" animal at a larger scale, while others represent special adaptations for particular conditions. Yet such a separation is rarely attempted.

We make such an attempt in this article and use it to argue a simple thesis about human evolution. We try to demonstrate that the three generally accepted species of australopithecines (*5*) represent the "same" animal expressed over a wide range of size. In other words, size increase may be the only independent adaptation of these animals, changes in shape simply preserving the function of the smaller prototype at larger sizes. In evolving toward modern man, on the other hand, hominids also increased steadily in size, but they developed adaptations of brain and dentition that cannot be attributed to the mechanical requirements of larger bodies. In other words, the extinct branch of australopithecines did little more than increase in size during its evolution; the thriving branch of hominids increased in size and developed special adaptations as well.

Hominid Phylogeny

The hominids we discuss, known informally as Plio-Pleistocene hominids, come from African deposits ranging in age from a little less than 6 million to perhaps less than 1 million years (*5*). The first early hominid from South

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Africa, an infant specimen of *Australopithecus africanus*, was discovered in 1924 at Taung. Many more specimens were recovered in South Africa during the decades that followed, and collecting continues today. Large to moderate samples are known from Swartkrans, Sterkfontein, and Makapansgat; a handful of hominids come from Kromdraai; Taung is still represented by the original specimen alone. Those from Sterkfontein, Makapansgat, and Taung are frequently described as gracile, because they were apparently lighter in average body weight than the "robust" forms from Kromdraai and Swartkrans (*6*).

Many workers have emphasized the similarities between South African forms by classifying them in one genus, generally as two species: *Australopithecus africanus* (Taung, Sterkfontein, Makapansgat) and *A. robustus* (Kromdraai, Swartkrans) (*7, 8*). Apart from probable differences in body size, there are other contrasts between these two forms, including differences in tooth size and shape, in cranial proportions, and (possibly) in postcranial anatomy. Brace (*9, 10*) has argued for some time that the larger *A. robustus* was in many respects an allometric variant of the smaller form (although he has not quantified his argument).

Robinson (*6*), however, has long advocated a very different explanation of variability in the South African hominids. He placed the robust material from Kromdraai and Swartkrans in a genus, *Paranthropus*, distinct from *Australopithecus*, in order to emphasize what he saw as important morphological differences between robust and gracile specimens. *Paranthropus* had larger cheek teeth and smaller anterior teeth than *Australopithecus*, which was therefore more like later *Homo* in dental size and proportions. Robinson (*11*) cited these contrasts as evidence for a major dietary difference between the two forms, with *Australopithecus* being an omnivore and carnivore and *Paranthropus* a herbivore. Cranial morphology also differed, the graciles having higher, more rounded calvariae, with more vaulted frontals. In these features, again, Robinson saw *Australopithecus* as significantly more like *Homo* than *Paranthropus*. Postcranially, according to Robinson and others, the two forms differed, the graciles being more like *Homo*. Recently, Robinson (*6, 12*) has reclassified *A. africanus* as *Homo africanus* to emphasize his view that this gracile form is ancestral to later *Homo*.

Early hominids were little known in East Africa until 1959, when Leakey (*13*) described *Zinjanthropus boisei*, a very large (cheek) toothed form, from Olduvai in Tanzania. Subsequently, more dental, cranial, and postcranial remains of this "hyper-robust," large-bodied animal have been recovered elsewhere in East Africa (Olduvai and Lake Natron in Tanzania, East Rudolf in Kenya, Omo in Ethiopia) from well-dated sites (*14–18*). Most workers now prefer to regard *A. boisei* as an *Australopithecus* (*7, 8*); however, Robinson (*6*) allies it to his *Paranthropus*, calling it *P. boisei*. These disagreements have centered around interpretations of dental and cranial anatomy, Robinson seeing *A. boisei*, with its relatively enormous cheek teeth, small brain, and low vaulted skull with massive browridges, as a form far removed from the smaller and more manlike *A. africanus*.

In 1964, Leakey *et al.* (*19*) described another hominid from Olduvai Gorge, *Homo habilis*. The species is now reasonably well represented by cranial and dental remains from Olduvai, East Rudolf, Omo, and a few other sites (*14–18*). *Homo habilis* differs from the *Australopithecus* species in having smaller cheek teeth and larger anterior teeth, an enlarged brain, and a postcranial skeleton (in the parts preserved) more like that of *Homo* in a number of features (*20–22*). The two East African hominids, *H. habilis* and *A. boisei*, are less similar to each other than are the South African species *A. africanus* and *A. robustus*. Most material from East Africa can be assigned to *A. boisei* or *H. habilis*; a few specimens may, however, be closer to the smaller *Australopithecus* species.

These East African hominids are, in the main, well dated radiometrically, especially at Olduvai, East Rudolf, and Omo, where they span the period between 3 million and about 1 million years (*14–18*). A couple of older hominid sites, Kanapoi and Lothagam in Kenya, go back to about 4 million and 5.5 million years, respectively (*15, 23*).

Unfortunately, there are no radiometric age determinations for South African sites. Some relative age estimates have been made, based mainly on faunal comparisons (*15*). There is general agreement that the site of Swartkrans is younger than Sterkfontein and Makapansgat, possibly much younger, although there is disagreement about whether it is older or younger than 2 million years; the Kromdraai hominids may well be undatable. The type specimen of *A. africanus*, the infant from Taung, has long been considered as equivalent in age to Sterkfontein, although Butzer (*24*) believes it to be younger.

Most workers regard *A. robustus* and *A. boisei* as closely related subspecies or species, or ancestor and descendant species (*25*). Postcranially, they seem to be similar, the main difference being the greater mean body size of *A. boisei*, with its consequence of increased dental and cranial robustness (*5, 26*).

The relationship between *A. africanus* and *H. habilis* has been vigorously debated. Many see them as closely similar, even conspecific (*6*). Others would separate them at the species level, on the basis of differences in tooth size and proportions, endocranial volume, and postcranial anatomy (*5*). Whether they are different genera (that is, whether *habilis* is a *Homo* or an *Australopithecus*) is largely a matter of taste. In tooth proportions and brain volume, *H. habilis* is intermediate between *A. africanus* and *Homo erectus* (*20–22*). The postcranial evidence is sparse, and equivocal, but what there is suggests that *H. habilis* is closer to *H. erectus*.

There certainly are resemblances between *A. africanus* and *Homo*. The question is, to what extent are these due to the small body size of *A. africanus*? For our purposes, we will follow most workers in placing *A. africanus, A. robustus*, and *A. boisei* in one genus, and retaining *H. habilis* in *Homo*, a scheme that we believe is further justified by the work reported here. [Brace (*10*), Wolpoff (*27*), and others have included all these forms in a single lineage.]

Various views, including our own, on the most probable phylogeny for hominids are outlined in Fig. 1. Precise temporal relationships are uncertain for the South African sites, but our general thesis is that Plio-Pleistocene hominids can be clustered into two major groups. One consists of *A. africanus, A. robustus*, and *A. boisei*, animals that are, in a number of characters, allometric variants of each other. Since they are scaled versions of the "same" animal, precise temporal sequence becomes less important in evaluating evolutionary relationships. The other group consists of *H. habilis, H. erectus*, and *H. sapiens*, species that form a reasonable ancestor-descendant sequence showing increase in body weight through time. It seems probable that the ancestor of

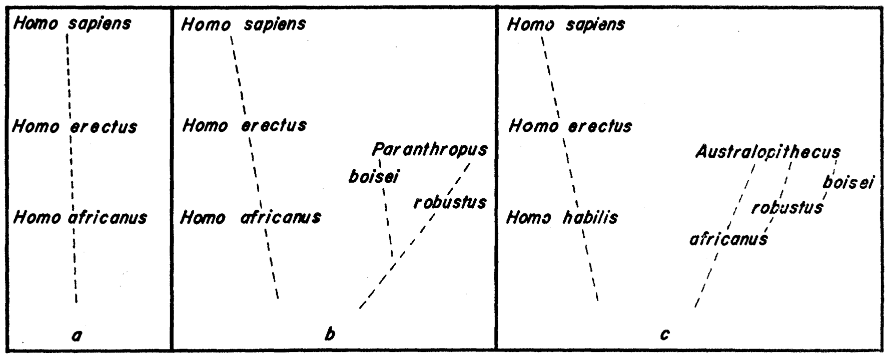

Fig. 1. Three hypothetical schemes for Pliocene and Pleistocene human evolution. (a) The single-species hypothesis (*10, 27*); *H. africanus* includes all Plio-Pleistocene hominids. (b) Views of Robinson (*6*) and many others [(*5*), for example]; *H. africanus* includes gracile South and East African forms only. (c) Our current best estimate; a suitable hypothetical common ancestor would be *A. africanus*.

H. habilis resembled *A. africanus*, and so this form can be included in our second group as well, as a (perhaps hypothetical) ancestor. However, we believe that *A. africanus* exhibits "advanced" dental and cranial features primarily because it is small. Thus, resemblances between it and other *Australopithecus* species have often been obscured because the size-related differences were not seen as such. We believe that *H. habilis* was probably the first animal to exhibit a shift away from the basic australopithecine adaptive pattern.

These conclusions have important consequences. *Australopithecus africanus* has been popularly advertised as a carnivorous, hunting form, the "killer ape" (*28*). On the contrary, we believe there are no good reasons for assuming that *A. africanus* was any less a vegetarian than *A. robustus* or *A. boisei*. However, *H. habilis* does show a shift in the direction of later hominids; yet, the evidence for large-scale bloodletting on its part is meager, to say the least.

Table 1 lists our estimates for body weight, cranial capacity, and tooth size in pongids and hominids (*29*). Tooth areas are calculated by summing the products of lengths and breadths of individual teeth. Although this is not a very satisfactory measure of masticatory function, we prefer it to length, breadth, or module, and it is easy to calculate. Mandibular dentitions are used for hominids to increase sample size; maxillary areas are calculated for pongids (because their third lower premolar is sectorial) and considered equivalent to mandibular areas for comparison with the hominid data.

Table 1. Estimates of mean body weights, cranial capacities, and tooth areas for great apes and hominids. Body weight estimates for fossils are considered accurate within about 20 percent. For hominids, tooth areas are for third lower premolar to third lower molar (posterior) and first lower incisor to lower canine (anterior). For great apes they are for third upper premolar to third upper molar (posterior) and first and second lower incisors (anterior). The area ratio is calculated as anterior/posterior.

Animal	Body weight (g)			Cranial capacity (cm^3)			Tooth area (mm^2)		Area ratio × 100
	Male	Female	Combined	Male	Female	Combined	Posterior	Anterior	
				Hominids					
A. africanus			32,000			450	860	170	19.8
A. robustus			40,500			500	970	150	15.5
A. boisei			47,500			510	1140	140	12.3
H. habilis			43,000			725	750	185	24.7
H. erectus (Choukoutien)			53,000			1050	630	170	27.0
H. sapiens (Australian aborigines)	60,000	54,000	57,000			1230	560	145	25.9
				Great apes					
Pygmy chimp	38,500	32,000	35,250	355	330	343	415		
Chimp	49,000	41,000	45,000	410	380	395	480	145	30.2
Gorilla (lowland)	140,000	70,000	105,000	550	460	505	1030	155	15.0
Orangutan	69,000	37,000	53,000	415	370	393	730	175	24.0

Some of the estimates are quite accurate, while others are little more than educated guesses. Most have been rounded to avoid spurious appearances of high accuracy. Those for apes come from a variety of sources (*10, 30, 31*). *Homo sapiens* is represented by a group of hunter-gatherers, the Australian aborigines. Body weights are from Martin and Saller (*32*), cranial capacity estimates from Ashton and Spence (*31*), and tooth areas from Campbell (*33*). The *H. erectus* weight estimate is very approximate and is based on work by Weidenreich (*34*), as are estimates of endocranial volume and dental size. We have selected this sample because it is the most complete for *H. erectus*. Of particular interest is the fact that body weight estimates are lower than samples from most *H. sapiens* groups.

For earlier hominids, there are many more problems in estimating population parameters (*29*). Body weights for *A. africanus* apparently ranged from some 22 kilograms to no more than about 40 kilograms (*6, 29*). Holloway (*21*) has estimated the *A. africanus* endocranial volume at about 440 cubic centimeters; this may be an underestimate if a disproportionate number of the better specimens are females. Accordingly, we suggest a mean volume of 450 cm^3. Estimates of tooth area are approximate, but we believe not too inaccurate (*35*). [Since complete dentitions are hard to come by, we have taken the mean area of each tooth and summed the averages. Where there is reason to suspect that a disproportionate number of large (male?) or small (female?) specimens have been preserved, we adjusted our estimates accordingly. We doubt that the values have more than about 5 percent error, and we are satisfied with their relative magnitudes.]

Estimates of body weight for *A. boisei* range from more than 70 kg to a little more than 20 kg, based mainly on published postcranial material (*26*). An average of 45 to 50 kg seems acceptable. Brain volume estimates are from Holloway (*21*). *Australopithecus robustus* body weights almost certainly fall between those of *A. africanus* and *A. boisei* and probably overlapped both (*26*); our best estimate is around 40 kg. The only complete *A. robustus* brain cast (from Swartkrans) yields a volume of 530 cm^3 (*36*). However, crushed and fragmentary crania from Swartkrans are clearly smaller than the larger *A. boisei* crania (*8, 31, 37*), so we think that our estimate of 500 cm^3 is reasonable; it may even be a little high. Tooth areas are based mainly on material from Swartkrans (*35, 38*).

Body weight estimates for *H. habilis* are difficult to make. It seems unlikely, on the basis of presumed *H. habilis* femora, that this species was, on average, lighter than *A. robustus* or heavier than *A. boisei* (*18, 22*). An estimate of between 40 and 45 kg seems reasonable. Brain volume estimates for *H. habilis* specimens have ranged between 600 and 800 cm^3 (*18, 21*) although the smaller values come from specimens that are fragmentary or that may not represent *H. habilis*. The complete braincase of hominid 1470 from East Rudolf has a volume of 775 cm^3. Hominid 7 (the type specimen) and hominid 16, both from Olduvai, probably had volumes of 700 cm^3 or more (*39*). We have used a mean of 725 cm^3, which may be conservative, realizing that this estimate is subject to error. Tooth area estimates are fairly reliable (*16, 17, 20, 40*).

Scaling of Cranial Capacity

Cuvier (*41*) recognized that large animals have relatively small brains—that brain weight, in other words, increases more slowly than body weight as we progress from small to large species in a coherent taxonomic group. The treatment of relative brain weight with the equation

$$\text{brain weight} = b(\text{body weight})^a$$

(where a is the slope and b the y-intercept of a log-log plot) dates to work of Snell (*42*) and Dubois (*43*) in the 1890's and anticipates by more than 30 years the generalization of power functions in the allometric method of Huxley (*44*). Jerison (*45*) has amassed all previous data and gathered much new information into an impressive synthesis of allometric studies on relative brain size. He proves that the slope of the power function for mammals—and for all vertebrate classes for that matter—is very close to 0.66 in static, mouse-to-elephant plots, where each point represents an average adult of a single species. (A slope of 2/3 implies that brain weight does not keep pace with body weight but increases only as fast as nonallometric body surfaces.)

The 0.66 slope for static, interspecific plots of major taxonomic groups does not exhaust the variety of brain-body relationships. Less than 10 years after Snell and Dubois determined the interspecific values, Lapicque (*46*) (for birds and mammals) and Dubois (*47*) himself (for man) found that intraspecific plots (for adults within a species, races of a species, or very closely related species displaying the "same" body plan over a wide range of size) produced slopes ranging between 0.2 and 0.4. (Lapicqué, in fact, referred to this observation as a law, citing a "universal" value of 5/18 or 0.28). In Lapicque's argument, 5/18 represents a brain that enlarges old neurons without adding new ones; 2/3 would then mark a brain that adds just enough neurons to serve the increased body bulk. Any scaling in excess of 2/3 must indicate an increase in cephalization. Confirmation of the range 0.2 to 0.4 has been abundant; these values for very closely related adults are as firmly established as the 2/3 slope for larger taxonomic groupings. Scholl (*48*), for example, calculated 0.18 for several species of macaques; Bertalanffy and Pirozynski (*49*) cited 0.20 for adult rats; and we have computed 0.23 for Lapicque's data on races of domestic dogs (*50*) and 0.33 for Pilleri and Busnel's (*51*) data on adults of the cetacean *Delphinus delphis*. [Further citations can be found in Rohrs (*52*), Frick (*53*), and Bahrens (*54*)].

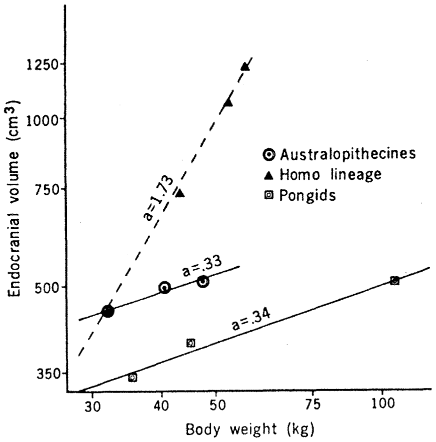

Fig. 2. Scaling of endocranial volume in pongids and hominids. We believe that estimates for hominid body weights are accurate within about 20 percent. The criterion for intraspecific functional equivalence is $a = 0.2$ to 0.4.

These generalities of scaling lead to a set of predictions: a sequence of closely related animals differing in size but not in function or "grade" of evolution should yield a brain-body plot with a slope between 0.2 and 0.4. The highest slope that can be justified in making a claim of functional equivalence is 0.66. If a mammal evolves to larger sizes with cranial capacity scaling at greater than 0.66, we must affirm an increase in cephalization, for descendants will have larger brains than mammals of the same size living at the time of their ancestors. Ironically, a phyletic slope of 1 (signifying no change in shape) reflects a pronounced increase in cephalization, since growth of the brain along a slope of 0.66 marks the maximum rate of increase for functional equivalence.

Figure 2 and Table 2 present the data for cranial capacity and body size of pongids and hominids listed in Table 1. We have used the standard power function and report the parameters of both least squares (y on x) and major axis fits. Least squares is the oldest and most popular technique, but it is inappropriate in cases (such as these) where both variables are subject to error and extrapolative prediction is not the purpose of plotting. Jolicoeur (*55*) has argued persuasively that the major axis should be preferred among lines that consider errors in both variates. (Readers who prefer the reduced major axis may calculate it by dividing the least squares slope by the correlation coefficient.) When correlation coefficients get much below .95, different techniques yield markedly different

Table 2. Scaling of cranial capacity of great apes and hominids.

Sequence	Correlation coefficient	Least squares slope	Major axis slope	Intercept of major axis
		Great apes		
Pygmy chimp–chimp–gorilla				
Combined	.988	0.338	0.339	10.16
Males only	.988	0.321	0.322	12.30
Females only	.993	0.412	0.415	4.55
Pigmy chimp–chimp–orangutan–gorilla				
Combined	.984	0.339	0.340	9.94
		Australopithecines		
A. africanus–A. robustus–A. boisei	.965	0.327	0.329	14.93
		Lineage of Homo sapiens		
A. africanus–H. habilis–H. erectus–H. sapiens	.999	1.73	1.73	7.3×10^{-6}

slopes; the choice of a proper method is no trivial affair. We shall use the major axis fits as our primary reference. Zar (*56*) has argued that statistical fits should be made directly, but Jolicoeur (*57*) and Sacher (*58*) have defended the conventional logarithmic transformation used here.

Giles (*59*) and others have advanced the idea that gorillas and chimpanzees are different expressions of the "same" body design for different sizes—or, to put it crudely, that gorillas are allometrically enlarged chimps. The addition of *Pan paniscus*, the pygmy chimpanzee, increases the size range for a claim of similar brain design. The slope of the power function is 0.339, comfortably within the range 0.2 to 0.4 for closely related forms. Addition of the orangutan changes the slope insignificantly ($a = 0.340$).

When australopithecines are plotted, we obtain a line of the same slope ($a = 0.329$), lying above the pongid regression. The australopithecines occupy a higher level of cephalization than pongids, for the ratio (australopithecine brain/pongid brain) is nearly constant for any common body weight. But, as with pongids, australopithecines scale among themselves with the predicted value for a series of animals differing only in size, but not in design. Large *A. boisei* is neither more nor less cephalized than its small prototype; it is, in fact, the very creature that we would predict if asked to build *A. africanus* at 1.5 times its average body weight. No one appreciates more than we the biometrical hazards of basing claims on three points; in a field as important yet as bereft of data as this, one must work with what one has. We do draw some comfort from the fact that very different estimates for brains and bodies of hominids yield the same form of scaling. Using Tobias's estimates (*60*), the brain-body slope for australopithecines is 0.26 ($r = .984$) [while that for the sequence *A. africanus* to *H. sapiens* is 1.17 ($r = .994$)].

The story of our own lineage is quite different. The sequence *A. africanus–H. habilis–H. erectus–H. sapiens* yields a slope of 1.73. This value is far in excess of any that could be justified in asserting a claim of similar cephalization with increasing size. As we argued previously, even a slope of 1 (with the preservation of a constant brain-body ratio) would mark a pronounced improvement over the strong negative allometry of functional equivalence ($a = 0.66$). In fact, the brain increased with marked positive allometry during the evolution of our species.

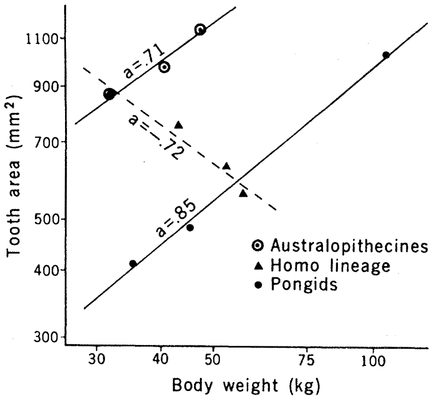

Fig. 3. Scaling of surface area for cheek teeth in pongids and hominids. We believe that estimates for hominid body weights are accurate within about 20 percent. The criterion for geometric similarity is $a = 0.66$.

Holloway (*61*) has noted, in a qualitative way, the tight correlation of cranial capacity and body weight during the evolution of *H. sapiens* (*r*, from our data, is .999). This strong correlation, he suggests, might mean that an essentially human level of brain function had been attained by *A. africanus*, and that further increase in brain size could be ascribed to increasing body size. We point out, however, that the strength of a correlation is a very different issue from the form of a regression. It is the parameters of regression that must determine functional claims in allometric studies. A slope greater than 1, no matter how tight the correlation, indicates a remarkable rise in cephalization with increasing size. The tightness of correlation need only reflect the strength of selection for mental traits grounded on increasing brain size.

These results show that all australopithecines had brains equally expanded beyond the ape grade. As Holloway (*62*) demonstrated, robust australopithecines had brains that were as much (or more) like those of later hominids in external morphology as those of gracile forms. According to Holloway, the brains of *A. africanus* and *A. robustus* differ from each other in external morphology no more than those of chimp and gorilla do. Thus, Robinson (*6*, p. 220) is incorrect in stating that the gracile brain was "significantly larger" than that of robusts, and that the robust forms had not "embarked upon the hominid brain expansion."

In the lineage leading to *H. sapiens*, brain volume does increase dramatically, but *A. africanus* was not the ancestor that first showed brain expansion beyond the australopithecine level; that honor must go to *H. habilis*, one reason for placing this species in *Homo*.

Scaling of Postcanine Tooth Size

Relative to body weight, the surface area of cheek teeth is greater in robust than in gracile australopithecines. Robinson (*11*) used this difference as a primary argument for his dietary hypothesis, claiming that robust forms needed massive molars to support a herbivorous diet, while gracile forms, as partial carnivores, had less use for grinding teeth. This hypothesis has received an extraordinarily wide press, particularly in Ardrey's (*28*) fanciful ideas about the biological basis of human violence and moviemaker Stanley Kubrick's depiction of killer apes as human antecedents (the twirling weapon of Pliocene bone transforms to the space station in *2001* as Richard Strauss's "Zarathustra" yields to Johann's "Blue Danube").

Yet our experience with the scaling of brains should forestall any immediate ascription of functional significance to differences in shape among species of varying sizes. Could large animals require larger teeth than their smaller ancestors just to maintain functional equivalence? Grinding, after all, is a function of tooth surfaces; yet the ground food must feed a body that increases in weight as the cube of length. Differential increase of surfaces and cross-sectional areas in large animals is the most fundamental allometry in nature. Haldane (*63*) once wrote that "comparative anatomy is largely the story of the struggle to increase surface in proportion to volume."

The allometry of the brain has been thoroughly examined for more than 80 years; yet no one, as far as we know, has studied the relationship between the surface area of teeth and body size in a quantitative way. Watson (*64*) and many others have presented qualitative arguments linking increased tooth height (hypsodonty) to body size (*65*). A relationship between relative area and body weight is implicit in the observation that large ungulates (*66*) and rodents (*67*) often molarize their posterior premolars. Still, we can find no systematic, quantitative data in the literature. Consequently, we shall first report our data for pongids and hominids, and then present the results of our own study on the scaling of relative tooth area in several orders of mammals.

Table 3. Scaling of postcanine tooth area in great apes and hominids.

Sequence	Correlation coefficient	Least squares slope	Major axis slope	Intercept of major axis
	Great apes			
Pygmy chimp–chimp–gorilla	.998	0.85	0.85	0.054
Pygmy chimp–chimp–orangutan–gorilla	.953	0.84	0.88	0.044
	Australopithecines			
A. africanus–A. robustus–A. boisei	.981	0.70	0.71	0.552
	Lineage of Homo sapiens			
A. africanus–H. habilis–H. erectus–H. sapiens	−.974	−.712	−0.725	1.64×10^6

Figure 3 and Table 3 display our data for plots of postcanine surface area against body weight. When areas (L^2) are plotted against weights (L^3), a slope of 2/3 is the expected value of geometric scaling for constant proportions throughout the size range. Any value higher than 2/3 indicates that large animals have relatively larger postcanine teeth than smaller members of the series.

The data for our own lineage (*A. africanus* to *H. sapiens*) reaffirm the conclusion already established for scaling of the brain. The correlation of tooth area and body size is very high, but the parameters of regression preclude any claim of functional equivalence during phyletic increase in size. The slope of the regression is − 0.725; the teeth not only became relatively smaller, they evolved to absolutely smaller sizes! No hypothesis of functional equivalence could entertain the expectation that large animals require absolutely small cheek teeth. The reduction of cheek tooth size in human evolution is a special adaptation not related to the mechanical requirements of an enlarging body.

The australopithecines show a very different pattern; the correlation is equally good, but the slope of 0.71 indicates positive allometry, with relatively larger teeth in larger animals. Great apes display the same trend. Major axis slopes are 0.85 for the sequence *Pan paniscus–Pan troglodytes–Gorilla gorilla* and 0.88 with the addition of the orangutan. We must now recall two earlier conclusions: (i) the pongid brain scaled according to predictions for functional equivalence, and (ii) the chimp-gorilla series may represent, on other grounds, a group of animals differing fundamentally only in size. All great apes are herbivores, the smaller ones being more frugivorous and the larger more folivorous (*68*). None of them include meat as more than a minute fraction of their diet. These differences in herbivory can be ascribed to differences in body size. The similar patterns of australopithecines and great apes might support a hypothesis of functional equivalence. We clearly need more data.

We have no sure mechanical basis for a prediction and seek merely to test the plausibility of positive allometry on empirical grounds. The 0.75 scaling of basal metabolism versus body weight is among the most stubborn facts of mammalian organization; it has survived numerous attempts as disproof, and may now be receiving its first adequate explanation (*69*). We are intrigued with the idea that a positive allometry of teeth might reflect a functional link with metabolism, but can advance no sure argument for how the basal rate should scale with total energetic requirements. Rensberger (*67*) has offered another suggestion from qualitative observations of increasing tooth area in large rodents. He argues that small rodents may feed selectively on more succulent plants while large relatives use more abundant but less rich sources; this would parallel the situation in pongids. Although this is a "dietary" hypothesis, it bears no relationship to Robinson's claim for australopithecines (*11*).

To test the hypothesis that tooth area increases with positive allometry, we chose several groups of mammals with a wide range of size among species, and no systematic variation in design or habitus that could not be ascribed to differences in absolute size (Table 4). Each pair of tooth and body measures represents a single individual of a single species; we used only one species per genus (the type species when available). All material comes from the collection of skulls in the Department of Mammalogy of the Museum of Comparative Zoology, Harvard University. We do not require that specimens be representative of their species or genera; we are merely constructing a "quasi-random" system for sampling a size range—that is, we seek to avoid the potential bias of taxonomic specialization by selecting one sample from each discrete unit and sampling as many units as possible. We choose a specimen per genus, not per species, to avoid replication of a diverse generic design at the expense of genera containing only a single species.

We measured the surface area of postcanine teeth by summing the product (maximum length × maximum width) of the first upper premolar to the third upper molar for all teeth, and avoided specimens with teeth worn past their largest dimensions. Ideally, this summed area would be regressed against body weight, but this favored estimate of body size is rarely provided in museum collections of dry bones.

Table 4. Scaling of postcanine tooth area in selected mammalian groups. Abbreviations: S.L., skull length; B.W., body weight; F.L., femur length; *F*, *F*-value for one-sided test of difference from isometric slope; d.f., degrees of freedom.

Group	Criterion	*N*	Correlation coefficient	Least squares slope	Major axis		*F*	d.f.
					Slope	Intercept		
South American hystricomorph rodents	S.L.	34	.967	2.26	2.40	0.0032	17.04	1,32
	B.W.	14	.971	0.70	0.72	0.2941	1.07	1,12
Suine artiodactyls	S.L.	9	.953	2.14	2.31	0.0029	1.62	1,7
Deer	F.L.	17	.962	2.04	2.17	0.0083	1.35	1,15
Primates								
Lemuroids								
Males	S.L.	11	.945	1.99	2.18	0.0155	0.61	1,9
Ceboids								
Males	S.L.	14	.975	2.09	2.18	0.0132	1.71	1,12
Cercopithecoids								
Males	S.L.	14	.953	1.81	1.95	0.0348		
Males	B.W.	10	.971	0.78	0.80	0.1796	3.89	1,8
Females	S.L.	11	.931	1.95	2.19	0.0173	0.56	1,9

We decided not to use average body weights as reported in the literature, for these must be drawn from incommensurate sources and do not, in any case, bear much relationship to the actual specimens used in calculating surface areas. We preferred to use an estimate of body size taken directly from the specimens measured for tooth areas. In most cases this was basicranial skull length. We tried to assess the allometry of skull length itself by regression against long-bone lengths for specimens with complete skeletons and, when allometry was detected, used another criterion of body size (these are discussed below, case by case). Since we are plotting tooth area against a measure of length, slopes significantly greater than 2 will indicate positive allometry. If tooth area increases as metabolism at the 0.75 power of body weight, we predict a slope of 2.25 (0.75 × 3.0).

Our procedure is consciously biased against our prediction to produce a conservative test. The major (or at least the most discussed) ways of increasing relative area are not included in our measure of tooth area: (i) hypsodonty [which permits the use of an unchanged area for a much longer time by increasing tooth height and thus prolonging the period of wear—many mammals die when their teeth are completely worn (*65*)], and (ii) changes of shape to produce squarer teeth in larger species (the premolars of many groups are triangular in small species and square in large; the increase in area attained by converting a triangle into a square is not captured by measures of length × width).

1) South American hystricomorph rodents [ranging in size from *Mesomys ecaudatus* (skull length 30.4 mm) to the giant capybara (skull length 190.5 mm)]. For 34 genera the slope of the major axis in a plot of tooth area against skull length is 2.40 (Fig. 4); this is significantly different from 2 at $P < .01$ ($F = 17.04$ at 1 and 32 degrees of freedom for a one-sided test). Skull length seems to be a good estimate of body size since the slope in a plot of skull length against femur length for 22 specimens with complete skeletons is 1.00. For 14 species with mean body weights recorded in Walker (*70*), the slope for tooth area versus body weight is 0.72.

2) Suine artiodactyls (peccaries, pigs, and hippopotamuses). The slope of tooth area versus skull length is 2.31 for nine genera. That of skull length versus femur length is 0.99 for six genera.

3) Deer (from *Moschus moschiferus* at skull length 131 mm to the American moose at 533 mm). Deer skulls display a well-known positive allometry to body size (*71*); the slope for skull length versus femur length is 1.16 for 17 genera (*F* for a difference from 1 is 13.45 at 1 and 15 degrees of freedom; $P < .01$). We therefore plotted tooth area against femur length (mixing males and females together because we could detect no differences between the sexes when they were plotted separately). For 17 genera, the slope for tooth area versus femur length is 2.17.

4) Primates (males only). (i) Lemuroids. For all genera, ranging from 23.8 (*Microcebus murinus*) to 85.1 mm (*Indri indri*) in skull length, a plot of tooth area against skull length yields a slope of 2.18. (ii) Ceboids. For 14 genera, ranging from 24.0 (*Cebuella pygmaea*) to 106.0 mm (*Alouatta seniculus*) in skull length, the slope for tooth area versus skull length is 2.18. (iii) Cercopithecoids. For 14 genera, ranging from *Miopithecus talapoin* (skull length 48.9 mm) to *Mandrillus leucophaeus* (skull length 157.2 mm), plotting tooth area against skull length yields a slope of 1.95.

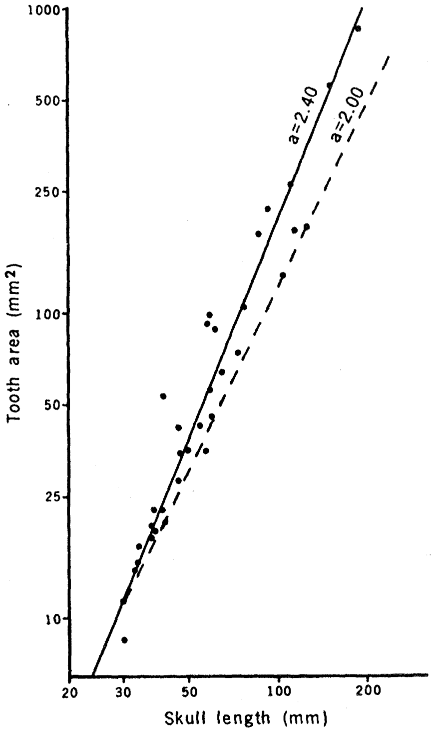

Fig. 4. Scaling of surface area for cheek teeth in South American hystricomorph rodents. The criterion for geometric similarity is $a = 2.00$. The major axis which best fits our data has $a = 2.40$; a line of $a = 2.00$, passed through the average value of tooth area/skull length for a small hystricomorph, misses the trend for larger species.

It is ironic that, of all groups tested, only the Old World monkeys show no positive allometry, for these are the closest phyletic relatives of hominids and pongids. Yet, without special pleading, we claim that this result is spurious. The skull length criterion is inappropriate because all large species in our sample are baboons, and no group displays a more marked positive allometry of skull length. Huxley (*44*) and Freedman (*72*) calculated slopes in excess of 4.0 for plots of muzzle length against calvaria length in the ontogeny of several baboon species; interspecific slopes are lower, but also markedly allometric. Thus, large skulls in our sample yield too high an estimate of general body size and depress the slope in a plot of tooth area versus estimated body size below its actual value. We therefore plotted our tooth areas against mean body weights for males of ten species (*73*). We now find positive allometry with a slope of 0.80 for tooth area plotted against body weight. To test this claim further, we plotted tooth areas against skull length for female cercopithecoids. Female baboons also display positive allometry of skull length, but the relative elongation is far less pronounced than in males. For 11 genera, the plot of tooth area against skull length for females yields a major axis slope of 2.19.

We do not think we have proved our case. Only one group yields a slope significantly in excess of the isometric value of 2.00 (South American hystricomorphs); sample sizes of other groups are too small to produce significance for predicted values so little in excess of 2.0. Nonetheless, the best estimates for slopes in all six groups are greater than 2.0. The individual items are not statistically significant, but the pattern begins to convince by its unerring repetition. We have at least established a plausible case that positive allometry of postcanine tooth area is the expected situation in sequences of related mammals that vary in size but not in basic design. We therefore conclude that the positive allometry of tooth area in australopithecines affords no evidence for differences in diet or behavior. As for cranial capacity, again australopithecines may simply represent the "same" animal displayed over a wide range of body size.

Differences in degree of premolar molarization between gracile and robust forms are presumably no more significant than in the other groups of mammals surveyed. Robinson's claim (*74, 75*) that the cheek teeth of robusts were more chipped than those of graciles because of differences in diet has been challenged (*8, 76*); chipping occurs about equally in all South African hominid populations.

Differences in Anterior Tooth Size and the Dietary Hypothesis

The dietary hypothesis is based not only on differences in cheek tooth size but on differences in the anterior dentition as well (*6*). The incisors and canines (which, in hominids, are rather incisiform morphologically and functionally) of *A. africanus* are on average slightly larger than those of *A. robustus*; thus the ratio of anterior to posterior tooth size is higher in *A. africanus*. Robinson (*6*) has used this difference to argue for the close relationship of graciles to later hominids, the aberrant nature of robust australopithecines, and a marked dietary difference between a tool-making, omnivorous-carnivorous protohuman (*A. africanus*) and an acultural herbivore (*A. robustus*).

In Table 1 we have estimated anterior tooth size in hominids (lower incisors and canine areas) and pongids (lower incisors only) and compared this measure to cheek tooth size. *Australopithecus africanus* has an anterior/posterior tooth area ratio of about 20, while *A. robustus* yields a value of 15.5. Thus, graciles are indeed closer to *H. erectus* (27.0) and *H. sapiens* (almost 26), but by no means very close. Since the mid-1960's, new data have become available for the East African forms. *Homo habilis* yields a ratio of almost 25, and is therefore similar to later *Homo* but not to *A. africanus*. *Australopithecus boisei*, on the other hand, has anterior teeth that are absolutely smaller than those of *A. robustus*, yielding a ratio of about 12.

Thus, as body size and cheek tooth size increase in *Australopithecus*, anterior teeth become absolutely somewhat smaller; the anterior/posterior tooth area ratio steadily falls with increasing body weight. The opposite is true in the presumed *A. africanus–H. habilis–H. erectus* lineage.

What does this mean? Similar shifts in correlation with body size are also found among pongids (see Table 1). Robinson's (*77*) log ratio diagrams show a greater difference between chimpanzee and gorilla than between South African gracile and robust *Australopithecus* in tooth proportions. Shifts also occur in hylobatids, where the smaller and more frugivorous gibbon has relatively larger incisors than the somewhat larger and more folivorous siamang (*78*); the ratios are 17 and 12.5, respectively. Jolly (*79*) has studied living and extinct species of *Theropithecus*, the gelada baboon, of widely differing body sizes. He notes that absolute incisal breadth is, if anything, somewhat less in *T. oswaldi mariae*, as big as a female gorilla, than in the much smaller living *T. gelada*. This parallels the situation seen in orangutan and gorilla, for example. *Australopithecus boisei* and *A. robustus* were probably herbivores; on the basis of absolute and relative anterior tooth size, it seems improbable to us that *A. africanus* was significantly less herbivorous. However, *H. habilis* may have been, like *H. erectus* and *H. sapiens*, more omnivorous (possibly a hunter-gatherer in a more human fashion).

Accordingly, we support the dietary hypothesis in comparisons between East African *H. habilis* and *A. boisei*, but not between *A. boisei* or *A. robustus* and *A. africanus*. We believe that the three australopithecines were all herbivores of one kind or another. As others have noted (*80*), they had relatively enormous cheek teeth, markedly larger than those of pongids. They were probably ground feeders, eating a variety of plant food, including small tough objects such as seeds, roots, tubers, small animals, and so forth (*6, 80*). For an adequate analogy we should probably search outside the pongids (*80*), perhaps even outside Primates as well (peccaries and other suines; *Ailuropoda*).

Cranial Allometry

Cranial anatomy differs among the australopithecines. *Australopithecus africanus* has a relatively small face and large, rounded braincase, while the robust forms have larger faces with lower calvaria, flatter frontals, bigger browridges, more robust zygomatic arches, better developed ectocranial structures (crests, ridges), and so forth (*5*). Robinson (*6*) has argued that the more spherical braincase and smaller face of *A. africanus* is an "advanced" feature, indicating an elusive relationship with later hominids; again, he sees the larger australopithecines as aberrant.

Many others (*5, 8–10*) have suggested that these cranial differences are allometric. From our foregoing discussion of brain and tooth scaling, it seems highly likely that this is so. Again, skulls of African pongids—ranging from the delicately built, rounded cranium of the pygmy chimpanzee to that of the gorilla, large-faced and massively constructed (*50*)—provide us with an analog. An exact quantitative solution is hard to derive since sufficient complete and undistorted material has not been found for African hominids. Robinson (*75*) has argued that allometry cannot be invoked to explain the difference in cranial morphology between, for example, the Sterkfontein and Swartkrans samples because a single robust cranium from Swartkrans (SK 48) is supposedly smaller than a gracile one from Sterkfontein (Sts 5). Apart from the fact that comparisons should be between samples, and that it is clear from the data [SK 46 (*81*) and SK 1585 (*36, 38*)] that there are larger crania at Swartkrans than at Sterkfontein, it should be emphasized that SK 48 is a damaged specimen.

The nearly universal trend both of primate ontogeny and of static series of closely related adults is toward negative allometry of the brain and positive allometry of the face (*82*). Most features enumerated above are simply the consequences of one of these primary allometries—lower calvaria and flatter frontals reflect the relatively smaller brain of large primates, while a sagittal crest supports the massive musculature that a relatively large face and jaw requires. Both the australopithecine and the chimpanzee-gorilla sequence display this set of allometric consequences; larger forms are scaled-up replicas of their smaller prototypes. *Homo sapiens* provides the outstanding exception to this trend among primates, for we have evolved a relatively large brain and small face, in opposition to functional expectations at our size. We retain, as large adults, the cranial proportions that characterize juvenile or even fetal stages of other large primates; partial neoteny has probably played a major role in human evolution. *Australopithecus africanus* has a rounded braincase because it is a relatively small animal; *H. sapiens* displays this feature because we have evolved a large brain and circumvented the expectations of negative allometry. The resemblance is fortuitous; it offers no evidence of genetic similarity.

We have not analyzed postcranial remains, although this is a potentially fruitful area. Although Napier (*83*) and Robinson (*6*) see major differences between South African graciles and robusts in postcranial anatomy, other workers (*26, 29, 84, 85*) have pointed out the similarities between the samples. Robinson has emphasized strong similarities between *A. africanus* and later hominids, although these resemblances are undetected by others (*84, 86*).

Conclusions

Our general conclusion is simply stated: many lineages display phyletic size increase; allometric changes almost always accompany increase in body size. We cannot judge adaptation until we separate such changes into those required by increasing size and those serving as special adaptations to changing environments.

In our view, the three australopithecines are, in a number of features, scaled variants of the "same" animal. In these characters, *A. africanus* is no more "advanced" than the larger, more robust forms. The one early hominid to show a significant departure from this adaptive pattern toward later hominids—cranially, dentally, and postcranially—is *H. habilis* from East Africa. The australopithecines, one of which was probably a precursor of the *Homo* lineage, were apparently a successful group of basically vegetarian hominids, more advanced behaviorally than apes (*87*), but not hunter-gatherers.

The fossil hominids of Africa fall into two major groupings. One probable lineage, the australopithecines, apparently became extinct without issue; the other evolved to modern man. Both groups displayed steady increase in body size. We consider quantitatively two key characters of the hominid skull: cranial capacity and cheek tooth size. The variables are allometrically related to body size in both lineages. In australopithecines, the manner of relative growth neatly meets the predictions for functional equivalence over a wide range of sizes (negative allometry of cranial capacity with a slope against body weight of 0.2 to 0.4 and positive allometry of postcanine area with a slope near 0.75). In the *A. africanus* to *H. sapiens* lineage, cranial capacity increases with positive allometry (slope 1.73) while cheek teeth decrease absolutely (slope − 0.725). Clearly, these are special adaptations unrelated to the physical requirements of increasing body size. We examined qualitatively other features, which also seem to vary allometrically. Of course, many characters should be studied quantitatively, but we think that the scheme outlined here should be treated as the null hypothesis to be disproved.

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NEWS AND COMMENT

Scientific Manpower Employment: So Far, It Seems to Be Holding Up

How hard hit by the recession are scientists and engineers? The information now available indicates that they haven't been affected as adversely as other categories of workers. So far—and that "so far" is emphasized by almost everyone who follows scientific and engineering manpower trends—the impact of the current slump has been less severe for scientists and engineers than the big layoffs of the early 1970's. At the same time, there are reports of hard times for some specialties and for some age groups and also increasing signs that the cycle of surplus and shortage of technical manpower is going to continue.

A major caveat about the reasonably steady employment readings for professionals, obviously, is that the layoffs in the automobile industry and the coal strike could presage a further serious downtrend in the economy. During periods of recession since World War II, the percentage of unemployment among scientists and engineers has been consistently lower on a national basis than that of production workers, but that generalization has not been tested by economic dislocations of prewar dimensions.

Currently, demand is strong for engineering graduates entering the job market. This is also true for science graduates with degrees marketable in the energy sector, such as geology, geophysics, and materials science. Government hiring of engineers is up substantially. Much less encouraging are the prospects for middle-aged engineers and scientists with experience in industry now looking for jobs. And competition for faculty jobs in colleges and universities in most science and engineering disciplines is now so fierce that higher education can hardly be considered a major job market, at least for the time being.

One catch in attempting to appraise unemployment trends is the absence of national data on scientists and engineers in industry, where 70 percent of these professionals are employed. Between 1950 and 1970, the Labor Department's Bureau of Labor Statistics (BLS) carried out regular surveys on the employment of scientists and engineers in industry which, although imperfect, did provide an informative general picture of employment of professionals. Support for the surveys came from the National Science Foundation (NSF), which has a statutory responsibility for this sort of manpower data. In 1970 these surveys were discontinued because of plans for a new, comprehensive survey that would include other categories of industrial workers and involve cooperation with individual states in collecting and promulgating data. This super survey immediately ran into trouble with funding, data gathering, and arrangements with the states, and so far only a few pilot surveys have been produced. The upshot is that there are no hard data on employment of scientists and engineers during the recession of the early 1970's and, consequently, there is not much of a basis for judging the present situation. There are plans to carry out a survey of the employment of scientists and engineers in industry next year with NSF sponsoring and the Census Bureau carrying out the survey, but the interregnum has been, at the least, unfortunate.

If employment among scientists and engineers today appears relatively stable, the perspective of the past 5 years should be applied. Starting in 1969, thousands of scientists and engineers lost their jobs in what for these professionals was the worst economic reversal since World War II. The root cause was the cut in federal funding of a wide range of programs which employed scientists and engineers through government contracts. At the same time the general economy was suffering from a combination of stagnation and inflation. The aerospace industry was hit particularly hard, and the chemical industry also had problems that were reflected in the relatively high rate of unemployment for chemists and chemical engineers. One side effect of the shake-out of professionals was a drop of enrollments in engineering and the sciences in universities at both undergraduate and graduate levels.

Now as a consequence the number of degree holders entering the job market is down from previous years and competition to hire them is up. In shortage categories salaries have jumped this year, and the bidding for the ablest graduates is hot.

What seems to be hardening into a cyclical pattern is the interaction between employment and scientific and engineering enrollments which pro-