

not give us pride of place among animals. The simple brain weight:bodyweight ratio of humans is 1:45, while it is 1:30 for a New World monkey (*Hapale rosalia*) and even higher (1:25) for common mice. Absolute size of elephant and whale brains exceeds by several-fold that of the human brain.^{7,8}

The relationship between brain size and 'intelligence', as measured by IQ tests or by socio-economic performance, within present-day humans is practically non-existent. Most studies find that brain size explains approximately 1% of the variance in variously measured 'intelligence' or mental aptitude.⁹⁻¹³ Recent studies using magnetic resonance imaging of the brain in individuals tested for IQ also find modest correlations between the size of cerebral structures and measures of intelligence.^{14,15}

FOSSIL RECORD OF HOMINID BRAIN EVOLUTION

Endocasts and cranial capacity

The ape-human comparison sets the limits for what comparative physiology and anatomy can reveal about our brain evolution. Between the ape and ourselves there are no living intermediate forms; the only possibility of revealing the specificity of human brain evolution is to study fossil material. Alas, brains, being very delicate, soft organs, do not fossilize. What, however, fossilizes well is the braincase, the bones of the skull. Living brain impresses itself onto the inner surface of the braincase due to intracranial bone remodelling. Therefore, the inner surface of the cranium bears impressions of cortical sulci, gyri and meningeal vessels. During the process of fossilization, some hominid skulls were filled, to varying levels, with minerals from the surrounding soil, producing natural endocasts. Those braincases that are found empty can be easily filled with latex to produce artificial endocasts. The first *Australopithecus* ever found, the Taung child, had a perfectly preserved natural endocast, including the entire right hemisphere and parts of the left hemisphere.¹⁶ Even as the impressions of sulci and gyri on the endocasts seem to be accurate, there are difficulties with interpretation of details; just one detail of the Taung's child brain endocast surface, the position of the lunate sulcus, has become the subject of a series of papers presenting competing views that the sulcus is either positioned in a human or in an ape's way.¹⁷⁻¹⁹ Many hominid cranial finds are fragmentary, thus preventing analysis of the details of the brain surface. It is, however, relatively easy to reconstruct from the size and shape of the fragments the total size of the braincase. Hence, the feature that can be most consistently and uniformly studied for a large number of hominid specimens is the total size of the brain (cranial capacity). Although the volume of the braincase is somewhat larger than that of the actual brain, with the specific gravity of the brain tissue being slightly above 1.0 g/mL,⁷ the volume of the endocast becomes an acceptable approximation of the actual size of the brain.

Avid searches of the fossil record of human ancestry over the past century have produced over 200 variously preserved hominid pre-Holocene crania whose capacity can be reconstructed. This fossil record shows a striking and rather gradual, three-fold increase in brain size over the past 4 million years from approximately 450 mL in the *Australopithecus*²⁰ to the modern human average of 1350 mL.²¹ This increase coincided with intellectual progress, as revealed by increasing complexity of the material remnants of

culture: tools, weapons, hearths, shelters, burials and rock art. This coincidence corroborates the hypothesis that mental capacity is related to brain size. The fact that brain size of equids increased 3.2-fold over the same period of time is often overlooked, although there are no known indicators of the change in equid intelligence.²²

Cranial capacity and body size

Numerous reconstructions of cranial capacities and body sizes are available in the literature. In the present paper, an updated version of the cranial capacity file compiled by Beals *et al.*²³ and the body size file compiled by Mathers and Henneberg²⁴ has been used. The file contains all estimates published until mid-1997. There are 276 estimates of cranial capacity, 297 estimates of body height and 626 estimates of bodyweight, covering the period from 5100 to 10 kaBP (thousands of years before present). Descriptions of exact methods used to produce various estimates included in the file are given elsewhere.²⁵⁻⁴⁴ Averages of brain size and body size of modern humans, based on some 10 000 individuals representing 122 populations worldwide,²¹ were also used.

Statistical analyses consisted of calculation of regressions and correlations between dates of fossils and their body and brain size estimates. Linear and exponential regression models were used. Significance of correlation coefficients was assessed by means of a *t*-test at the 0.01 probability level. The analysis was limited to cranial capacity and bodyweight because in all higher primates there is a strong and uniform relationship between bodyweight and height⁴⁵ and, thus, analyses using body height as a body size indicator yield results similar to those obtained using weight.

When the entire period of the past 5 million years of hominid evolution is considered, it is apparent that the increase in cranial capacity is accompanied by an increase in bodyweight (Fig. 1). The strength of correlation with date is larger for cranial capacity, which has a lower error of estimate than bodyweight. Both correlation coefficients are highly significant, indicating concurrence of brain and body size increase.

Despite the large number of cranial capacity and body size estimates for hominid fossils, we were able to find only 45 individuals

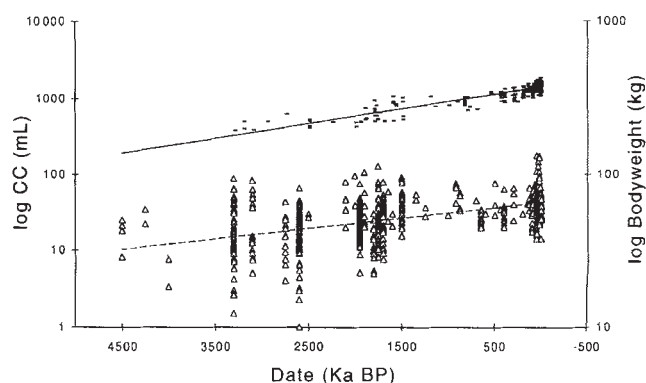


Fig. 1 Regression of fossil hominid cranial capacity (CC, dashes) and estimated bodyweight (open triangles) with date in thousands of years before present. Scales of CC and weight are logarithmic, exponential regressions were fitted to the data. Both correlation coefficients ($r = 0.91$ and 0.48 , respectively) are statistically significant ($P < 0.01$; d.f. > 200). Linear, logarithmic and power regressions all yield lower correlation coefficients for both variables than the exponential regressions shown.

for whom both bodyweight and cranial capacity are available. These include Al-288, Oh5, TM1517 and WT15000 hominids dated at between 3300 and 1500 kaBP plus a number of Late Pleistocene (90–10 kaBP) specimens listed in the Ruff *et al.* file.⁴⁰ A plot of cranial capacities of these hominids against their bodyweights yields an exponent of the allometric power curve practically equal to 1.0 (Fig. 2). The 95% confidence interval of the exponent is 0.889, 1.305. Therefore, the relationship between bodyweight and cranial capacity in hominids seems to be linear; that is, isometric rather than curvilinear, allometric. An isometric relationship is also obtained when average cranial capacities and bodyweights or heights of various hominid species are compared.^{21,46} In a large sample of brain size and bodyweight averages of modern human populations, a linear

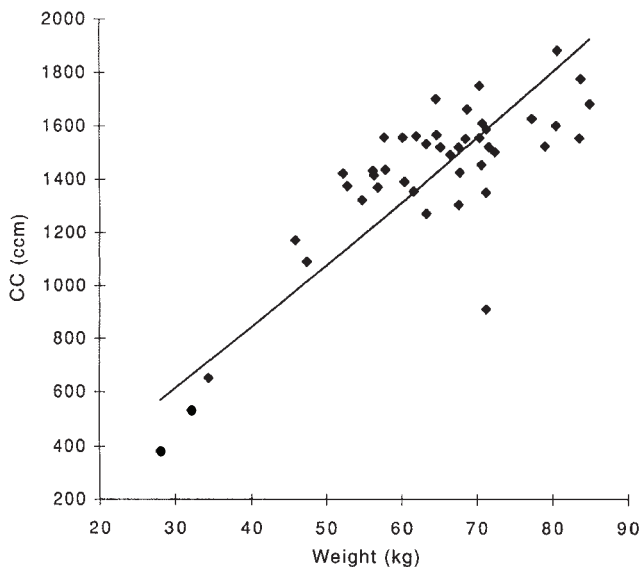


Fig. 2 Relationship between cranial capacity and bodyweight of fossil hominids dated between 3300 and 10 kaBP. A power curve has been fitted to the data. Note that the exponent is approximately 1.0, indicating a linear (i.e. isometric relationship). The correlation coefficient is significant at $P < 0.01$ (d.f. = 42; $y = 14.689x^{1.0971}$; $r^2 = 0.7299$).

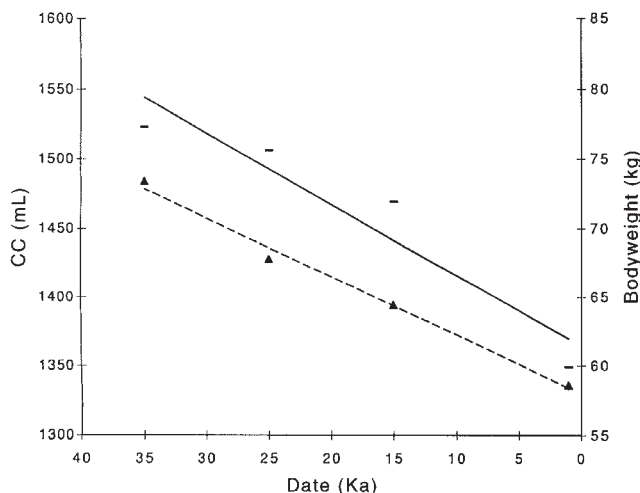


Fig. 3 Decrease of human cranial capacity (bars, solid line) and bodyweight (triangles, dashed line) since the Upper Pleistocene until modern times. Data points are averages based on 55 fossil cranial capacities, 119 weight estimates and samples from 122 modern human populations.²¹

relationship with $r = 0.63$ was observed.²³ This isometric relationship in hominids differs from negatively allometric relationships with exponents 0.67–0.75 recommended for calculation of mammalian encephalization quotients.^{4,5} When the standard allometric coefficient of 0.75 is applied to the data in Fig. 2, the squared correlation coefficient of 0.6604 is lower than that for the depicted isometric relationship (0.7299), while the confidence interval of the isometric exponent does not include 0.75, indicating a significant difference.

The decrease of human cranial capacity by approximately 10% of its average value (i.e. one standard deviation or approximately 100–150 mL) since the Late Pleistocene until the early 20th century has been documented on large samples from Europe and the Near East, Africa, Japan and Australia.^{40,47–50} This phenomenon of microcranialization⁴⁹ has been accompanied by a decrease in body size^{40,47} (Fig. 3). The averages depicted in Fig. 3 seem to suggest that the decline in brain size was inversely exponential while body size declined in a rather linear fashion. Detailed analysis of this disparity must await accumulation of more data on body size; at this stage, it is sufficient to point out that correlation coefficients of both body and brain size on time, as presented in Fig. 3, are -0.99 and -0.95 , respectively, and are both significant. It is worth noting that the reduction of human brain size during the past 10 kaBP coincides with the invention of agriculture, metal-based technologies, mass transport, urbanization, complex social and political systems and intellectual culture based on writing, mathematics and science. It can be argued that the recent decrease in average brain size is a result of the support provided by complex cultural systems for less intelligent and, thus, smaller-brained individuals.⁵¹ This would, however, produce a greater range of variation in modern human brain size in response to the postulated relaxation of selection. This is not the case as the variability of the modern human brain size is actually the same or smaller than that observed among fossil hominids.⁵²

Therefore, it seems that the hominid brain size tracks in its increase and decrease as well as in the individual variation the size of the body rather than the level of intellectual abilities. In samples of modern humans, correlation between brain size and bodyweight is weaker than that between brain size and body height,⁵³ probably due to large individual variation in the amounts of body fat. Brain size is most probably related to the lean body mass consisting of the musculoskeletal apparatus and the highly metabolically active tissues of the viscera, rather than to the overall bodyweight, which may incorporate a substantial proportion of inert adipose tissue.

Reduction of body size caused human encephalization

Irrespective of its close relationship to body size, the hominid brain constitutes a larger proportion of total bodyweight than the brains of apes.⁵⁴ Several authors have attempted to explain this greater encephalization of humans in terms of physiological factors unrelated to intelligence. Falk⁵⁵ proposed that the prime physiological 'releaser' of brain size in the genus *Homo* was an evolution of a network of cranial veins that allow cooling of the enlarged brain under conditions of hyperthermia, which affected hominids during foraging in Africa ('radiator theory'). Working from the similar premise of the need for thermohomeostasis in hominids hunting under the African sun, Fialkowski⁵⁶ argued that the enlarged hominid brain was a result of the application of von Neumann's rule, which states that a reliable system for information processing can consist of unreliable elements (neurons), provided the number of these

elements is increased. This would produce structural redundancy, resulting in physical enlargement of the human brain. Sacher⁵⁷ argued that the increased human brain size is related to our greater longevity as mammalian brain size is correlated with the length of life and the reproduction. Brain size of mammals seems to be scaling in proportion to their metabolic rates.^{58,59} This led Aiello and Wheeler⁵⁴ to ask how, in terms of energy supply, can humans afford to have large brains. They proposed 'the expensive tissue hypothesis' stating that the reduction in the size of the hominid gut offset the increased metabolic requirements of larger brains. Although interesting, this hypothesis is untestable because energy balances of hominids may have changed in numerous ways other than the trade-off between gut and brain.²²

The observation that, during hominid evolution, the relative size of the gastrointestinal tract decreased in comparison with apes⁵⁴ can be used to interpret human encephalization without speculation about the trade-off in metabolically expensive tissues. Since the Pliocene, the human gastrointestinal tract has evolved towards smaller relative size due to the ingestion of higher quality, partly extra-orally processed foods. This is a result of a combination of hominids turning to an increasing proportion of meat in their diets and to the use of tools and, later, fire to soften and chemically breakdown raw foods. These led to a reduction in the size of the teeth and masticatory skeleton as well as the muscles and size of stomach and the intestines. The basic cultural developments allowing this reduction to occur, use of weapons, tools and fire related to habitual consumption of meat, occurred well before 1 million years ago, at the time when hominid brain size was approximately one-half of its modern value.^{23,51} Hence, these cultural developments can hardly be considered a result of hominid brain expansion.

The change in hominid bodyweight during the Pliocene and the Pleistocene is a combination of two processes: (i) an overall increase resulting, like in many other mammals, from adaptive gains related to increased body size ('Cope's law'); and (ii) a decrease in the masticatory apparatus and gut size with a concomitant decrease in supporting musculoskeletal structures. It can be hypothesized that the variation in the size of the masticatory apparatus and gut is responsible for a sizeable portion of the variation in total body size, as this factor influences bodyweight directly and indirectly through the size of the locomotor apparatus required to carry around the gastrointestinal tract with its contents. Taking into account the three-fold increase in hominid brain size, hominid body size should increase from 35 kg in the Pliocene to 105 kg in modern humans. At the same time, however, the gut and the masticatory complex decreased to approximately 60% of their expected size.⁵⁴ Loss of approximately 40% of the gastrointestinal and masticatory complex size could be hypothesized to have caused an overall reduction of the body size by approximately one-third (a conservative estimate). This reduction would result from the direct loss of the mass of the gastrointestinal and masticatory structures, a related decrease in the size of the trunk and a reduction in the size of the musculoskeletal apparatus required to support a relatively smaller face and trunk. The reduction of modern human body mass predicted by the three-fold increase in brain size (105 kg) by one-third produces the figure of 70 kg, which was the actual Late Pleistocene estimated human bodyweight and which lies close to the bodyweight of many modern humans. With a full 40% reduction in body mass, the estimate for modern humans is 63 kg. Pliocene hominid brain size (450 mL) and bodyweight (35 kg) yield a brain size/body size ratio of 0.013.

Applying this ratio to the hominid body size that is expected without gut reduction (105 kg), one obtains a brain size of the late hominid of 1365 mL, which is similar to the average for modern humans (1350 mL).

CONCLUSIONS

The macro-evolutionary enlargement of the hominid brain in parallel with that of other mammals, its co-evolution with body size, the micro-evolutionary decrease in human brain size during the period of major intellectual and cultural achievements and the virtual lack of intraspecific correlation between brain size and variously measured human 'intelligence' lead to the conclusion that the special qualities of the human brain are not the result of its size or, probably, also not of its gross anatomical structure. The unusually high human encephalization may be more a result of the reduction in the relative body size than the increase in brain size.

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REFERENCES

1. Radinsky L. Primate brain evolution. *Am. Sci.* 1975; **63**: 656–63.
2. Haug H. Brain sizes, surfaces and neuronal sizes of the cortex cerebri: A stereological investigation of man and his variability and a comparison with some mammals (primates, whales, marsupials, insectivores and one elephant). *Am. J. Anat.* 1987; **180**: 126–42.
3. Stephan H. Evolution of primate brains: A comparative anatomical investigation. In: Tuttle R (ed.). *The functional and Evolutionary Biology of Primates*. Aldine-Atherton, Chicago. 1972; 155–74.
4. Jerison HJ. *Evolution of the Brain and Intelligence*. Academic Press, New York. 1973.
5. Martin RD. *Primate Origins and Evolution*. Princeton University Press, Princeton, NJ. 1990.
6. Radinsky L. Evolution of brain size in carnivores and ungulates. *Am. Naturalist* 1978; **112**: 815–31.
7. Mettler FA. *Culture and the Structural Evolution of the Neural System*. American Museum of Natural History, New York. 1956.
8. Lavelle CLB, Shellis RP, Poole DFG. *Evolutionary Changes to the Primate Skull and Dentition*. CC Thomas, Springfield, IL. 1997.
9. Pearson K. On the relationship of intelligence to size and shape of head and to other physical and mental characters. *Biometrika* 1906–7; **5**: 105–46.
10. Schreider E. Quelques correlations somatiques des tests mentaux. *Homo* 1968; **19**: 38–43.
11. Susanne C, Sporcq J. Etude de correlations existant entre des tests psychotechniques et des mensurations cephaliques. *Bull. Soc. R. Belge Anthropol. Prehist.* 1973; **84**: 59–63.
12. Passingham RE. Brain size and intelligence in man. *Brain Behav. Evol.* 1979; **16**: 253–70.
13. Henneberg M, Budnik A, Pezacka M, Puch AE. Head size, body size, and intelligence: Intraspecific correlations in *Homo sapiens sapiens*. *Homo* 1985; **36**: 207–18.
14. Willerman L, Schultz R, Rutledge JN, Bigler ED. *In vivo* brain size and intelligence. *Intelligence* 1991; **15**: 223–8.

15. Andreasen NC, Flaum M, Swayze VII *et al.* Intelligence and brain structure in normal individuals. *Am. J. Psychiatr.* 1993; **150**: 130–4.
16. Holloway RL. Australopithecinae endocast (Taung specimen, 1924): A new volume determination. *Science* 1970; **168**: 966–8.
17. Holloway RL. The Taung endocast and the lunate sulcus: A rejection of the hypothesis of its anterior position. *Am. J. Phys. Anthropol.* 1984; **64**: 285–8.
18. Falk D. Apples, oranges and the lunate sulcus. *Am. J. Phys. Anthropol.* 1985; **67**: 313–16.
19. Armstrong E, Zilles K, Curtis M, Schleicher A. Cortical folding, the lunate sulcus and the evolution of the human brain. *J. Hum. Evol.* 1991; **20**: 341–8.
20. Aiello LC, Dunbar RIM. Neocortex size, group size, and the evolution of language. *Curr. Anthropol.* 1993; **34**: 184–93.
21. Henneberg M. Brain size/body weight variability in *Homo sapiens*: Consequences for interpreting hominid evolution. *Homo* 1990; **39**: 121–30.
22. Henneberg M. Comment on Aiello and Wheeler's The Expensive Tissue Hypothesis. *Curr. Anthropol.* 1995; **36**: 212–13.
23. Beals KL, Smith CL, Dodd SM. Brain size, cranial morphology, climate and time machines. *Curr. Anthropol.* 1984; **25**: 301–30.
24. Mathers K, Henneberg M. Were we ever that big? Gradual increase in hominid body size over time. *Homo* 1995; **46**: 141–73.
25. Brown F, Harris J, Leakey R, Walker A. Early *Homo erectus* skeleton from west Lake Turkana, Kenya. *Nature* 1985; **316**: 788–92.
26. Carretero JM, Arsuaga JL, Lorenzo C. Clavicles, scapulae and humeri from Sima de los Huesos site (Sierra de Atapuerca, Spain). *J. Hum. Evol.* 1997; **33**: 357–408.
27. Coon CS. *The Origin of Races*. Knopf, New York. 1962.
28. Feldesman MR, Lundy JK. Statures estimates for some African Plio–Pleistocene fossil hominids. *J. Hum. Evol.* 1988; **17**: 583–96.
29. Feldesman MR, Kleckner JG, Lundy JK. Femur/stature ratio and estimates of stature in mid and late Pleistocene fossil hominids. *Am. J. Phys. Anthropol.* 1990; **83**: 359–72.
30. Hartwig-Scherer S. Body weight prediction in fossil *Homo*. *Cour. Forsch. Inst. Senckenberg* 1994; **171**: 267–79.
31. Johanson D, Edgar B. *From Lucy to Language*. Simon and Schuster, New York. 1996.
32. Jungers WL. New estimates in body size in australopithecines. In: Grine FE (ed.). *Evolutionary History of the 'Robust' Australopithecines*. Aldine de Gruyter, New York. 1988; 115–25.
33. Latimer B, Ohman JC, Lovejoy CO. Talocrural joint in African hominoids: Implications for *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* 1987; **74**: 155–75.
34. McHenry HM. How large were the australopithecines? *Am. J. Phys. Anthropol.* 1974; **40**: 329–40.
35. McHenry HM. Early hominid body weight and encephalization. *Am. J. Phys. Anthropol.* 1976; **45**: 77–84.
36. McHenry HM. New estimates of body weight in early hominids and their significance to encephalization and megadontia in 'Robust' australopithecines. In: Grine FE (ed.). *Evolutionary History of the 'Robust' Australopithecines*. Aldine de Gruyter, New York. 1988; 133–49.
37. McHenry HM. Sexual dimorphism in *Australopithecus afarensis*. *J. Hum. Evol.* 1991; **20**: 21–32.
38. McHenry HM. Femoral lengths and stature in Pliopleistocene hominids. *Am. J. Phys. Anthropol.* 1991; **85**: 149–58.
39. McHenry HM. Body size and proportions in early hominids. *Am. J. Phys. Anthropol.* 1992; **87**: 407–31.
40. Ruff CB, Trinkaus E, Holliday TW. Body mass and encephalisation in Pleistocene *Homo*. *Nature* 1997; **387**: 173–6.
41. Suwa G, Asfaw B, Beyene Y *et al.* The first skull of *Australopithecus boisei*. *Nature* 1997; **389**: 489–92.
42. Wolpoff MH. Posterior tooth size, body size and diet in South African gracile australopithecines. *Am. J. Phys. Anthropol.* 1973; **39**: 375–95.
43. Wolpoff MH. *Human Evolution*. McGraw-Hill, New York. 1996.
44. Wu X, Poirier FE. *Human Evolution in China. A Metric Description of the Fossils and a Review of the Sites*. Oxford University Press, Oxford. 1995.
45. Henneberg M, Hugg J, Townsend EJ. Body weight/height relationship: Exponential solution. *Am. J. Hum. Biol.* 1989; **1**: 483–91.
46. Henneberg M. *Evolution of human brain size. Pfizer Basic Medical Science Lectures, 8th Series*. University of Cape Town, Cape Town. 1988.
47. Henneberg M. Decrease of human skull size in the Holocene. *Hum. Biol.* 1988; **60**: 395–405.
48. Henneberg M, Steyn M. Trends in cranial capacity and cranial index in subsaharan Africa during the Holocene. *Am. J. Hum. Biol.* 1993; **5**: 473–9.
49. Henneberg M, Steyn M. Diachronic variation of cranial size and shape in the Holocene: A manifestation of hormonal evolution? *Riv. Antropol.* 1995; **73**: 159–64.
50. Brown P. Recent human evolution in East Asia and Australasia. *Phil. Trans. R. Soc. Lond.* 1992; **B337**: 235–42.
51. Tobias PV. *The Brain in Hominid Evolution*. Columbia University Press, New York. 1971.
52. Henneberg M. The problem of species in hominid evolution. *Perspect. Hum. Biol.* 1997; **3**: 21–31.
53. Holloway RL. Within-species brain–body weight variability: A re-examination of the Danish data and other primate species. *Am. J. Phys. Anthropol.* 1980; **53**: 109–21.
54. Aiello LC, Wheeler P. The expensive tissue hypothesis: The brain and the digestive system in human and in primate evolution. *Curr. Anthropol.* 1995; **36**: 199–221.
55. Falk D. Brain evolution in *Homo*: The 'radiator' theory. *Behav. Brain Sci.* 1990; **13**: 333–81.
56. Fialkowski K. A mechanism for the origin of the human brain: A hypothesis. *Curr. Anthropol.* 1986; **27**: 288–90.
57. Sacher GA. Maturation and longevity in relation to cranial capacity in hominid evolution. In: Tuttle RH (ed.). *Primate Functional Morphology and Evolution*. Mouton, The Hague. 1975; 417–41.
58. Armstrong E. Relative brain size and metabolism in mammals. *Science* 1983; **220**: 1302–4.
59. Martin RD. Relative brain size and metabolic rate in terrestrial vertebrates. *Nature* 1981; **293**: 57–60.