LETTERS

Insular dwarfism in hippos and a model for brain size reduction in *Homo floresiensis*

Eleanor M. Weston[1] & Adrian M. Lister[1]

Body size reduction in mammals is usually associated with only moderate brain size reduction, because the brain and sensory organs complete their growth before the rest of the body during ontogeny[1,2]. On this basis, 'phyletic dwarfs' are predicted to have a greater relative brain size than 'phyletic giants'[1,3]. However, this trend has been questioned in the special case of dwarfism of mammals on islands[4]. Here we show that the endocranial capacities of extinct dwarf species of hippopotamus from Madagascar are up to 30% smaller than those of a mainland African ancestor scaled to equivalent body mass. These results show that brain size reduction is much greater than predicted from an intraspecific 'late ontogenetic' model of dwarfism in which brain size scales to body size with an exponent of 0.35. The nature of the proportional change or grade shift[2,5] observed here indicates that selective pressures on brain size are potentially independent of those on body size. This study demonstrates empirically that it is mechanistically possible for dwarf mammals on islands to evolve significantly smaller brains than would be predicted from a model of dwarfing based on the intraspecific scaling of the mainland ancestor. Our findings challenge current understanding of brain–body allometric relationships in mammals and suggest that the process of dwarfism could in principle explain small brain size, a factor relevant to the interpretation of the small-brained hominin found on the Island of Flores, Indonesia[6].

Brain tissue is energetically expensive, and it has been suggested that a decrease in brain volume may be advantageous to an animal's survival under the environmental conditions associated with islands[4,7,8]. This phenomenon, if real, can be difficult to test because not only are most examples of dwarf island mammals extinct and known only from incomplete subfossil material, but knowledge of the founding ancestor can also be difficult to ascertain. The strongest case previously documented is that of a fossil bovid *Myotragus*, isolated on the Mediterranean island of Majorca for more than 5 Myr (refs 4, 9). The brain mass of *Myotragus* was decreased by up to 50% relative to those of extant bovids of equivalent body mass[4]. However, a link between the relatively small brain of *Myotragus* and the process of dwarfism has been disputed[10,11] in the light of the length of the bovid's isolation and its uncertain ancestry[9].

One aspect of the continuing debate[12–14] over whether the small-brained hominin discovered on the Island of Flores, Indonesia[6], evolved by insular dwarfism centres on scaling exponents between brain and body size[10,11]. For predicting the brain size of a mammal at a smaller body size, these 'intraspecific' scaling models are the most appropriate to accommodate the likely correlated effects of body size adjustment on brain size in closely related species[10,15,16] (see Supplementary Discussion). However, here we show that two species of extinct dwarf hippopotamus do not correspond to such dwarfing models because even though the same scaling exponents relating brain size to body size apply, large intercept shifts (grade shifts[2,5]) distinguish these 'phyletic dwarfs' from their mainland ancestor (Fig. 1, Supplementary Table 1 and Supplementary Discussion).

To model the dwarfing process, we took the extant large *H. amphibius*, a generalized representative of the genus *Hippopotamus*, to be the probable ancestor of two recently extinct dwarfed hippos, *H. lemerlei* and *H. madagascariensis*, from the island of Madagascar[17] (see Supplementary Discussion). These species can be unequivocally separated taxonomically[17] but both share apomorphies with the modern genus *Hippopotamus*[18]. The modern pygmy hippopotamus *Choeropsis liberiensis* represents a lineage distinct from all other hippopotamids, diverging from its closest relative before 5 Myr ago (ref. 18). Madagascar is a large island of diverse habitats that has prehistorically supported up to three species of hippopotamus[19], whose times of dispersal to Madagascar are unknown but whose remains persist to within the past 6,000 years[20].

Brain–body scaling trends in hippos can be inferred from the relationship of brain to cranial size, because the relation between a volumetric estimate of cranial size and a postcranial estimate of body mass across the two living hippos and the Madagascan dwarf species is approximately isometric (Supplementary Figs 3–7, Supplementary Table 4 and Supplementary Discussion). Predictions of decrease in brain size given in Table 1 are thus based on observed cranial size data and not on estimates of body mass (the latter are provided for contextual purposes only). In Table 1 we evaluate predictions of brain–body scaling in insular dwarf hippos and a dwarf elephant by considering

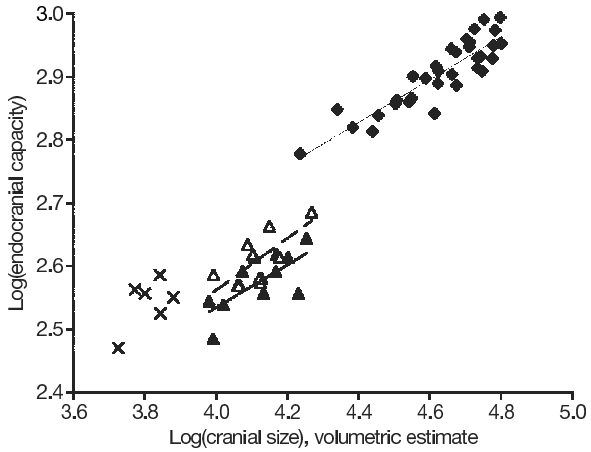

Figure 1 | Relationship between brain size and cranial size for an intraspecific 'late ontogenetic' model of dwarfing. Major axis slopes (95% confidence intervals): thin line, *H. amphibius*, 0.3482 (0.28–0.41); thick line, *H. lemerlei*, 0.369 (0.15–0.63); dashed line, *H. madagascariensis*, 0.4587 (0.20–0.79). Filled diamonds, *H. amphibius* ($n = 33$); filled triangles, *H. lemerlei* ($n = 12$); open triangles, *H. madagascariensis* ($n = 12$); crosses, *C. liberiensis* ($n = 6$). For statistical comparisons see Supplementary Table 1.

[1]Department of Palaeontology, Natural History Museum, London SW7 5BD, UK.

Table 1 | Estimates of brain size based on dwarfing models

Species	Body mass* (kg)	Endocranial capacity (cm^3)	Prediction of endocranial capacity†	
			Late ontogenetic scaling‡	Ontogenetic scaling§
Hippopotamus lemerlei	374 (25%)	380 (43%) [70%, 83%]	544 (62%)	456 (52%)
Hippopotamus madagascariensis	393 (26%)	421 (48%) [76%, 91%]	553 (63%)	465 (53%)
Choeropsis liberiensis	228 (ref. 19) (15%)	350 (40%) [83%, 105%]	421 (48%)	334 (38%)
Palaeoloxodon falconeri (scaled to cranial size)	200 (ref. 22) (2%)	1,800 (20%) [80%, 125%]	2,250 (25%)	1,440 (16%)
Palaeoloxodon falconeri (scaled to body mass)	100 (ref. 23) (1%)	1,800 (20%) [100%, 167%]	1,800 (20%)	1,080 (12%)

Values in parentheses are expressed as a percentage of the original mean value of the mainland ancestor (*H. amphibius* for the Malagasy hippos, and *P. antiquus* for *P. falconeri*) or, for *C. liberiensis*, the larger sister taxon (*H. amphibius*) (see Table 2). For endocranial capacity, numbers in square brackets indicate the observed values as a percentage of those predicted on the basis of the 'late ontogenetic' and 'ontogenetic' scaling models, respectively. For example, the endocranial capacity of *H. lemerlei* is decreased by 30% of the value predicted by the late ontogenetic model (endocranial capacity = 70% of predicted value), whereas the endocranial capacity of *H. madagascariensis* is decreased by 24% of the value predicted by the late ontogenetic model (endocranial capacity = 76% of predicted value). The scaling exponents (k) are modelled from *H. amphibius* postnatal cranial data (Supplementary Table 1). The Malagasy hippo body masses are estimated assuming isometry to cranial volume of the ancestor using an adult body mass of 1,495 ± 29.5 kg for *H. amphibius* (see Supplementary Discussion, and Table 2 for limb-bone estimates of body mass). *P. falconeri* brain size reduction is estimated from both cranial size (50-fold smaller than the ancestor[22]) and an estimate of body mass (100-fold smaller[23]) (*P. antiquus* has an approximate average mass of 10 tonnes, estimated from limb-bone data in ref. 25 and P. Davies, unpublished observations).
* Malagasy hippo estimates based on cranial size.
† Based on intraspecific dwarfing models using cranial size.
‡ k = 0.35: late phase of brain growth in the age range 2–40 years.
§ k = 0.47: early and late phases of brain growth in the age range 0–40 years.

two intraspecific dwarfing models: 'late ontogenetic' and 'ontogenetic'. In mammals that commonly dwarfed on islands, such as hippos, elephants and deer (see Supplementary Discussion), all of which have precocial young, there is generally thought to be a transition from rapid to slow growth of the brain that closely coincides with birth[2,15,16]. In *H. amphibius*, however, the rapid early phase of brain growth continues after birth for up to 2 years (Supplementary Fig. 1). The 'late ontogenetic' exponent (0.35) in this context is calculated from the late, slower phase of postnatal brain growth (2–40 years) and not just from static adult data. This distinction is important, because the 'growth' as opposed to the 'static adult' exponent will best characterize the size adjustments (developmental allometry) associated with the late phase of brain maturation[1]. However, because all late postnatal brain development in mammals typically involves a low exponent value (0.2–0.4 for intraspecific brain–body scaling)[5], 'late ontogenetic' exponents should be similar to, or only moderately higher than, those derived from static adult data (see Supplementary Discussion). The higher 'ontogenetic' exponent (0.47) is derived from a complete postnatal series from birth to adulthood in which rapid and slow growth phases are combined.

If the endocranial capacity of *H. lemerlei* scaled as (cranial size)$^{0.35}$ in accord with the 'late ontogenetic' model (Fig. 1 and Supplementary Table 1), an endocranial capacity of 544 cm^3 would be predicted; that is, 62% of the value of an ancestor four times its cranial size (Tables 1 and 2). The observed mean endocranial capacity of *H. lemerlei* is 380 ± 7.25 cm^3 (mean ± s.e.m.; Table 2), 30% smaller than that predicted from the 'late ontogenetic' model (Table 1). The observed mean endocranial capacity of *H. madagascariensis* is 421 ± 11.9 cm^3 (Table 2), 24% smaller than that predicted from the 'late ontogenetic' model (Table 1). The 'ontogenetic' model, in which the endocranial capacity of *H. lemerlei* would scale as (cranial size)$^{0.47}$ (Fig. 2 and Supplementary Table 1), predicts a endocranial capacity of 456 cm^3, 52% of the value of the ancestor, but the observed endocranial capacity is still 17% smaller than that predicted under this model, and in *H. madagascariensis* it is 9% smaller (Table 1).

The Malagasy dwarf hippos do not correspond to either 'intraspecific' scaling model (Figs 1 and 2 and Table 1), indicating that 'insular dwarfing' does not necessarily comply with predictions based on the ontogenetic scaling of the mainland ancestor. The Malagasy dwarf hippos are roughly equivalent in body mass to a 1–2-year-old *H. amphibius* (353–544 kg), a stage in development that marks the completion of the first rapid phase of brain growth. In contrast, the extant pygmy hippopotamus (*C. liberiensis*), with a body mass one-sixth to one-eighth that of *H. amphibius* (ref. 19 and Table 2), has a mean endocranial capacity of 350 ± 12.7 cm^3, approximately equal to the values predicted from the 'ontogenetic' scaling model (Table 1) but reduced by 17% relative to the values predicted from the 'late ontogenetic' model (Table 1). The extant pygmy hippopotamus is not an insular dwarf[21] and is phylogenetically more basal than *H. amphibius*, its only extant sister taxon[18] (see Supplementary Discussion). Adult *C. liberiensis* has a body mass equivalent to a 6-month-old *H. amphibius* (see Supplementary Discussion), a stage of development in which rapid early brain growth persists in the hippopotamus. In primates, too, a marked increase in relative brain size has been attributed to the prolongation of the rapid 'prenatal' phase of brain development[3]. In 'phyletic dwarfs' the opposite developmental adjustment, involving a decrease in the duration of rapid early brain growth, could potentially explain a 'grade shift' to a lower brain–body ratio, as demonstrated by the change in ratio of brain to cranial size in Fig. 1 (see Supplementary Discussion).

A further example is provided by *Palaeoloxodon falconeri*[22,23], the smallest insular dwarf elephant from Sicily and Malta, derived from the mainland *P. antiquus*[22,23]. The brain of a modern elephant grows relatively little after birth (the brain of a newborn elephant is 50% of its adult brain weight, whereas that of a common hippopotamus is 22% and that of a human is 25%)[24], indicating that rapid early brain growth is completed by the end of gestation. The adult *P. falconeri* is estimated to be approximately the size of a newborn modern elephant[23], and hence brain mass is expected to scale to body mass with a 'late ontogenetic' exponent typical of a precocial mammal. With brain size scaled as (body mass)$^{0.35}$, brain size matches the prediction of the 'late ontogenetic' model with a 100-fold estimated decrease in body mass (Table 1, second entry for *P. falconeri*; see also refs 10, 11). However, estimates of decrease in body mass in these elephants are imprecise,

Table 2 | Endocranial capacities, cranial sizes and body masses for species in Table 1

Species	Endocranial capacity (cm^3)	Adult cranial size (cm^3)	Body mass range (kg)
H. amphibius	882 ± 16 (n = 18)	52,533 ± 1,657 (n = 20)	1,210–2,001*
H. lemerlei	380 ± 7.25 (n = 24)	13,298 ± 810 (n = 12)	274–393
H. madagascariensis	421 ± 11.9 (n = 12)	13,948 ± 751 (n = 12)	310–642
C. liberiensis	350 ± 12.7 (n = 6)	6,524 ± 338 (n = 6)	180–275 (ref. 19)
P. antiquus	9,000 (ref. 22) (n = 1)	311,000 (ref. 22) (n = 1)	5,055–17,675 (ref. 25)
P. falconeri	1,800 (ref. 22) (n = 1)	6,120 (ref. 22) (n = 1)	80–200 (refs 22, 23)

The endocranial capacity and cranial size (volumetric estimate) data for all species of hippopotamus were collected as part of this study (see Methods). The elephant cranial data are from ref. 22. Observed ranges of adult body mass are given for the extant species (see Supplementary Discussion), and estimates based on postcrania are given for the extinct species (see Supplementary Table 4 for Malagasy hippo data, and Supplementary Discussion). Results are given as means ± s.e.m.
* See Supplementary Discussion.

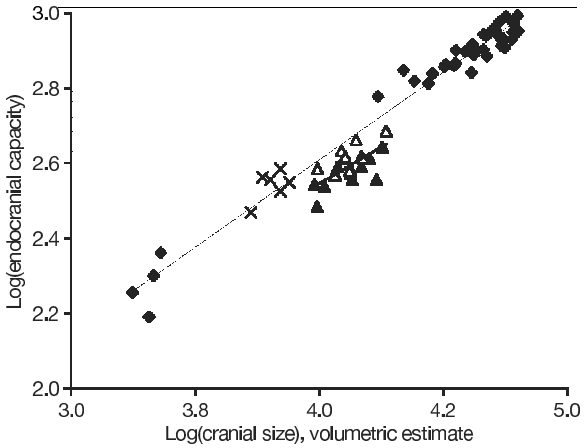

Figure 2 | Relationship between brain size and cranial size for an intraspecific 'ontogenetic' model of dwarfing. Major axis slopes (95% confidence intervals): thin line, *H. amphibius*, 0.468 (0.44–0.50); bold line, dwarf species pooled, 0.454 (0.27–0.67). Filled diamonds, *H. amphibius* ($n = 37$); filled triangles, *H. lemerlei* ($n = 12$); open triangles, *H. madagascariensis* ($n = 12$); crosses, *C. liberiensis* ($n = 6$). For statistical comparisons see Supplementary Table 1.

especially given the magnitude of the dwarfing (Table 2). Cranial volume, determined by direct measurement[22], is reduced only 50-fold, and when scaled as (cranial volume)$^{0.35}$, *P. falconeri* would have an endocranial capacity (2,250 cm^3) 25% of the original value of its ancestor (*P. antiquus*) 50 times its size (Tables 1 and 2). The actual endocranial capacity of *P. falconeri* is 1,800 cm^3 (ref. 22), 20% smaller than the value predicted from this 'late ontogenetic' model (Table 1, first entry for *P. falconeri*), in line with our results on the dwarf hippos. This discrepancy between the predictions based on cranial size[22] and those based on estimates of body mass[23,25] in these elephants gives grounds for caution in the use of the latter for the interpretation of brain-size scaling (see refs 7, 10, 11).

One argument put forward to rebut the idea that the small brain of *H. floresiensis* was linked to the process of insular dwarfism was that its small brain size could not be accommodated within predictions made from mammalian intraspecific brain–body scaling models[10,11]. Here we show empirically that it is mechanistically possible for dwarf mammals on islands to evolve significantly smaller brains in relation to their cranial size than would be predicted from models of dwarfing based on intraspecific scaling of the mainland ancestor. If the hippo model is applied to a typical *H. erectus* ancestor with a body mass of 60 kg (refs 10, 11, 26) and average endocranial capacity of 991 cm^3 (refs 10, 11, 27) that reduced its body mass by 62% to 23 kg (the median of the 16–29 kg estimated body mass of *H. floresiensis*)[6], an endocranial capacity of 704 cm^3 (71% of the original value) would be predicted from scaling as (body mass)$^{0.35}$. If the brain size were decreased by a further 30% of that value, as in the Malagasy hippo, *H. lemerlei*, an endocranial capacity of 493 cm^3 would result. This is still larger than the actual value of *H. floresiensis* (380–430 cm^3)[6,28], but if the ancestor had an endocranial capacity of 804 cm^3, as in the African *H. erectus* KNM-ER 3883 (ref. 27), scaling the body mass of the ancestor down to 23 kg and then decreasing the brain size by a further 30% of the scaled value gives an endocranial capacity of 405 cm^3, comparable to that of *H. floresiensis* (see Supplementary Table 5). By the same analogy, if the Dmanisi adult *Homo* remains (skull D3444 cf. *H. erectus*)[29], with an endocranial capacity 650 cm^3 (ref. 29) and body mass of 40 kg (ref. 30) are considered, an endocranial capacity of 378 cm^3 would result, a value close to that of *H. floresiensis* (see Supplementary Table 5). If cranial variables are used instead of body mass for scaling the endocranial capacity of these hominins, as in the hippo example, a similar result is obtained (see Supplementary Table 5).

Similar shifts in intercept to those illustrated in Fig. 1 have been reported from domesticated mammals that on average have smaller brains than their wild relatives[16]. Domesticated mammals provide proof of the developmental malleability of the brain among closely related species or within species, but there are some noteworthy distinctions between the phenomena of domestication and island dwarfism. The decrease in brain size of domestic mammals is not necessarily associated with decrease in body size, as it is in phyletic dwarfism, and domestication is usually associated with a decrease in the size of the sense organs[16]. *H. floresiensis*, unlike the bovid *Myotragus* and domesticated mammals, does not have reduced orbital dimensions[11], although such skeletal variation does not necessarily correlate with the actual size of the sense organ. This is also evident in the Malagasy hippos, in which orbit area is actually larger in the dwarf hippos relative to *H. amphibius* (Supplementary Fig. 2). A pathological explanation for this condition in the Malagasy species can be ruled out through the existence of more than 40 individual dwarf hippo specimens with intact braincases (Supplementary Table 2). Whatever the explanation for the tiny brain of *H. floresiensis* relative to its body size, the evidence presented here suggests that the phenomenon of insular dwarfism could have played a part in its evolution.

METHODS SUMMARY

A cross-sectional postnatal series of crania of *H. lemerlei*, *H. madagascariensis*, *H. amphibius* and *C. liberiensis* (see Supplementary Tables 2 and 3) was digitized with a MicroScribe G2 and inter-landmark distances were calculated to compute a volumetric measure of the entire cranium. Endocranial capacity was used as a surrogate for brain size. Exponents derived from brain–body allometric scaling relationships in mammals are widely applied in analyses of relative brain size[5], but here brain size has been regressed against cranial volume. Supplementary data are provided demonstrating that results generated from estimates of body mass are similar to those reported for cranial size (see Supplementary Figs 3–7 and Supplementary Discussion). The data and procedure used to determine body mass estimates from Malagasy dwarf postcrania are given in Supplementary Table 4 and in the Supplementary Discussion.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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1. Shea, B. T. Phyletic size change and brian/body allometry: a consideration based on the African pongids and other primates. *Int. J. Primatol.* **4**, 33–62 (1983).
2. Martin, R. D. *Human Brain Evolution in an Ecological Context: 52nd James Arthur Lecture on the Evolution of the Human Brain* (American Museum of Natural History, New York, 1983).
3. Gould, S. J. Allometry in primates with emphasis on scaling and the evolution of the brain. *Contrib. Primatol.* **5**, 244–292 (1975).
4. Köhler, M. & Moyà-Solà, S. Reduction of brain and sense organs in the fossil insular bovid *Myotragus*. *Brain Behav. Evol.* **63**, 125–140 (2004).
5. Martin, R. D. & Harvey, P. H. in *Size and Scaling in Primate Biology* (ed. Jungers, W. L.) 147–173 (Plenum, 1985).
6. Brown, P. *et al.* A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* **431**, 1055–1061 (2004).
7. Niven, J. E. Brains, islands and evolution: breaking all the rules. *Trends Ecol. Evol.* **22**, 57–59 (2006).
8. Richards, G. D. Genetic, physiologic and ecogeographic factors contributing to variation in *Homo sapiens*: *Homo floresiensis* reconsidered. *J. Evol. Biol.* **19**, 1744–1767 (2006).
9. Lalueza-Fox, C., Shapiro, B., Bover, P., Alcover, J. A. & Bertranpetit, J. Molecular phylogeny and evolution of the extinct bovid *Myotragus balearicus*. *Mol. Phylogenet. Evol.* **25**, 501–510 (2002).
10. Martin, R. D. *et al.* Comment on 'The brain of LB1, *Homo floresiensis*'. *Science* **312**, 999b (2006).
11. Martin, R. D., Maclarnon, A. M., Phillips, J. L. & Dobyns, W. B. Flores hominid: new species or microcephalic dwarf? *Anat. Rec.* **288A**, 1123–1145 (2006).
12. Köhler, M., Moyà-Solà, S. & Wrangham, R. W. Island rules cannot be broken. *Trends Ecol. Evol.* **23**, 6–7 (2008).
13. Argue, D., Donlon, D., Groves, C. & Wright, R. *Homo floresiensis*: microcephalic, pygmoid, *Australopithecus*, or *Homo*? *J. Hum. Evol.* **51**, 360–374 (2006).
14. Niven, J. E. Response to Köhler *et al.* Impossible arguments about possible species? *Trends Ecol. Evol.* **23**, 8–9 (2008).
15. Lande, R. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution Int. J. Org. Evolution* **33**, 402–416 (1979).

16. Kruska, D. C. T. On the evolutionary significance of encephalization in some eutherian mammals: effects of adaptive radiation, domestication and feralization. *Brain Behav. Evol.* **65,** 73–108 (2005).
17. Stuenes, S. Taxonomy, habits, and relationships of the subfossil Madagascan hippopoptami *Hippopotamus lemerlei* and *H. madagascariensis*. *J. Vertebr. Paleontol.* **9,** 241–268 (1989).
18. Boisserie, J.-R. The phylogeny and taxonomy of Hippopotamidae (Mammalia: Artiodactyla): a review based on morphology and cladistic analysis. *Zool. J. Linn. Soc.* **143,** 1–26 (2005).
19. Eltringham, S. K. *The Hippos: Natural History and Conservation* (Academic, 1999).
20. Burney, D. A. *et al.* A chronology for late prehistoric Madagascar. *J. Hum. Evol.* **47,** 25–63 (2004).
21. Weston, E. M. Evolution of ontogeny in the hippopotamus skull: using allometry to dissect developmental change. *Biol. J. Linn. Soc.* **80,** 625–638 (2003).
22. Accordi, F. S. & Palombo, M. R. Morfologia endocranica degli elefanti nani pleistocenici di Spinagallo (Siracusa) e comparazione con l' endocranio di *Elephas antiquus*. *Atti Accad. Naz. Lincei Rc.* **51,** 111–124 (1971).
23. Roth, V. L. Inferences from allometry and fossils: dwarfing of elephants on islands. *Oxf. Surv. Evol. Biol.* **8,** 259–288 (1992).
24. Shoshani, J., Kupsky, W. J. & Marchant, G. H. Elephant brain. Part I: Gross morphology, functions, comparative anatomy, and evolution. *Brain Res. Bull.* **70,** 124–157 (2006).
25. Christiansen, P. Body size in proboscideans, with notes on elephant metabolism. *Zool. J. Linn. Soc.* **140,** 524–549 (2004).
26. Kappelman, J. The evolution of body mass and relative brain size in fossil hominids. *J. Hum. Evol.* **30,** 243–276 (1996).
27. Stanyon, R., Consigliere, S. & Morescalchi, M. A. Cranial capacity in hominid evolution. *Hum. Evol.* **8,** 205–216 (1993).
28. Jacob, T. *et al.* Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalities. *Proc. Natl Acad. Sci. USA* **103,** 13421–13426 (2006).
29. Lordkipanidze, D. *et al.* A fourth hominin skull from Dmanisi, Georgia. *Anat. Rec.* **288A,** 1146–1157 (2006).
30. Lordkipanidze, D. *et al.* Postcranial evidence from early *Homo* from Dmanisi, Georgia. *Nature* **449,** 305–310 (2007).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions E.W. and A.L. designed the study. E.W. collected and analysed the data and drafted the paper. Both authors discussed the results and edited the manuscript.

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METHODS

Sample size. The number of specimens included in different analyses is not constant as a result of missing data (MD); all relevant landmarks were not preserved on every specimen studied, and endocranial capacity could not be measured accurately on some specimens as a result of braincase damage or poor state of preservation (see Supplementary Tables 2 and 3). Sample sizes were: *H. lemerlei*, $n = 29$ (17 with MD); *H. madagascariensis*, $n = 19$ (7 with MD); *H. amphibius*, $n = 50$ (13 with MD); *C. liberiensis* $n = 7$ (1 with MD).

Estimation of cranial volume. A volumetric measure of the entire cranium was computed from the product of three variables: cranial length (the posteriormost point of the nuchal crest to the mesialmost point of the first incisor socket), cranial width (zygion to zygion) and cranial height (akrokranion (the median dorsal point of the occipital region) to basion). The static adult samples used to derive values given in Table 2 include specimens from dental 'Age Group XI' and above (see Supplementary Tables 2 and 3 and Supplementary Discussion).

Estimation of endocranial capacity. Endocranial capacity, the volume of the endocranial cavity, was measured by pouring precision plastic (polypropylene) balls 5.5 mm in diameter into the braincase cavity (after the large foramina had been plugged with plastazote foam), and then decanting the balls into a measuring cylinder.

Analysis of relative brain size. Brain size in mammals scales allometrically with body size and is described by the bivariate power function

$$y = bx^k$$

or, after logarithmic transformation, by the linear equation

$$\log y = k \log x + \log b$$

where y and x are variables, and k (exponent expressing slope) and b (y intercept) are constants. Slopes were determined by major-axis and least-squares regression (see Supplementary Table 1), but major-axis values define k in Table 1. In view of the absence of associated data on body mass for a growth series of modern *H. amphibius* skeletons, an analysis of cranial size versus global skeletal size (an estimate of body mass determined from postcranial evidence) has been provided in Supplementary Material (see Supplementary Discussion). For the subfossil taxa, body mass values were estimated from crania or from unassociated skeletal elements (see Supplementary Table 4 and Supplementary Discussion). The endocranial cavity (used to represent brain size), forms part of the cranium; cranial size is therefore a conservative estimator of change that can be measured directly from both fossil and modern material, and in hippos it is a good proxy for body size (see Supplementary Discussion).