



Brains, islands and evolution: breaking all the rules

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The announcement in 2004 that a small-brained hominin, *Homo floresiensis*, had been discovered on the island of Flores, Indonesia, was hailed as a major scientific breakthrough because it challenged preconceptions about the evolution of our closest relatives. Now, just over two years later, questions raised by the interpretation of the fossil abound. In a series of recent papers, critics have questioned the interpretation of the small brain volume of the fossil as that of a new hominin species, suggesting instead that it was due to microcephaly. The arguments raised by critics and advocates alike prompt a re-examination of ideas about what is possible during the evolution of the brain.

Is *Homo floresiensis* special?

In 2004, Brown *et al.* reported a fossil find from the island of Flores, in Indonesia, that of a ~1-m tall hominin, with a brain volume of ~380 cm³ [1] (revised subsequently to 417 cm³ [2]). The fossils, which they classified as *Homo floresiensis*, suggest that this hominin lived as recently as 18 000 years ago. Therefore, *H. floresiensis* might have overlapped geographically and encountered *H. sapiens* as they dispersed across South East Asia ~60 000–40 000 years ago [3,4]. Both in stature and absolute brain volume, *H. floresiensis* is smaller than any other known hominins, including *Homo erectus*, *Homo habilis* and australopithecines (e.g. *Australopithecus africanus*). *Homo floresiensis* might have evolved these features after becoming isolated from a larger mainland hominin species on Flores [1], a process known as insular dwarfing, which has occurred repeatedly when mammals more than 1 kg in weight, such as hippopotami (e.g. *Phanourios minutus*) or elephants (*Elephas falconeri*) have become isolated on islands [5]. However, the hominin from which *H. floresiensis* was derived remains unclear; the fossils share some characters with *H. erectus* [1], but not others, making their phylogenetic relationship uncertain [2].

Recently, four independent studies have re-examined the evidence and concluded that *H. floresiensis* is unlikely to be a distinct species [6–9]. Here, I review the main arguments of these four studies and assess them in the context of what we know (or do not know) about the evolution of the vertebrate brain to determine whether they are indeed sufficient for us to now dismiss the claims of the authors of the original study.

Re-examining the evidence

The four independent papers construct distinct arguments, many of which (although by no means all) focus upon two of

the most surprising features of *H. floresiensis*: its small brain volume and short stature.

Weber *et al.* [6] analyzed the morphology of 19 microcephalic brains (Box 1) and argued that the brain morphology of *H. floresiensis* is not sufficiently different to exclude the possibility that it is that of a microcephalic. Martin *et al.* [7] used a series of scaling models to argue that the relative brain volume of *H. floresiensis* is too small to be the result of insular dwarfism. Specifically, they examined the scaling relationships observed in the insular dwarfing of *Elephas falconeri* (a fossil pygmy elephant found on Mediterranean islands that evolved from a larger elephant found on continental Europe), the intraspecific scaling observed in most mammals and the intraspecific scaling observed in *H. sapiens* [7]. By applying these models to different hominin fossils (*H. erectus* and Dmanisi hominids), the authors predicted unrealistically small body weight estimates for *H. floresiensis* at the correct brain volume. Instead, they proposed that the small-brained *H. floresiensis* is a microcephalic, either from a small-bodied hominin population or of an individual with combined microcephaly and growth retardation from a normal-sized human population [7].

Jacob *et al.* [8] re-examined dental, cranial and postcranial skeletal features and compared them with those of modern human populations, including those of pygmies, from a range of geographical locations. From these re-examinations and demographic arguments, the authors also suggested that *H. floresiensis* is an individual from a pygmoid *H. sapiens* population with microcephaly. Richards [9] compared a range of skeletal features from *H. floresiensis* with those of *H. sapiens*, including pygmoid and microcephalic individuals. Reviewing a wide range of evidence, he suggested that *H. floresiensis* is an individual from a local population of *H. sapiens* that had acquired non-pathological mutations in genes causing pygmoid stature and microcephaly [9].

Is there an alternative viewpoint?

Based on these recent studies [6–9], should we now be consigning *H. floresiensis* to a new status as a pygmy *H. sapiens* (or other hominin) with microcephaly? The authors of the original study continue to support their original conclusion that *H. floresiensis* is a new hominin species, a view shared by another recent independent study that compared the cranial and postcranial morphology of *H. floresiensis* with that of fossil hominins (*H. erectus*, *H. habilis* and australopithecines), extant apes and a wide range of *H. sapiens*, including pygmies and two microcephalics [10].

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Box 1. Microcephaly and *Homo floresiensis*

Four groups of researchers have suggested that the fossil skull (LB1) of *H. floresiensis* is that of a microcephalic from a pygmy human or hominin population [6–9]. Microcephaly is a clinical condition in which the occipital-frontal head circumference (and hence brain volume) is severely reduced [17]. It can be caused by decreased brain size at birth or by impaired brain growth after birth, known as primary and secondary microcephaly, respectively. Although both can be caused by genetic factors, they can also be caused by environmental factors, such as maternal nutrition [17]. Although human microcephalics can live for 30 years or more, they often have severely impaired cognitive function and suffer from seizures. Recent studies have suggested that two genes in which mutations are associated with primary microcephaly (microcephalin, MCPH1, and abnormal-spindle-like, microcephaly associated, ASPM) were important in the expansion of the human brain. The roles of other genes linked to microcephaly in the evolution of the human brain are less clear.

The range of brain volumes in microcephalic modern humans (280–591 cm³ [6]) is significantly smaller than the average brain volume of modern humans (1296 ± 149 cm³ [1]). Thus, the range of brain volumes of human microcephalics encompasses the volume of the *H. floresiensis* brain (417 cm³). Microcephalic brains often show distortions in the size of different brain regions. For example, the shape of the neocortex is often distorted and it can be reduced in volume relative to other brain regions. The fossil skull of LB1, *Homo floresiensis*, shows enlargement of the prefrontal cortex, a region that is implicated in higher cognitive functions in modern humans [2]. Such enlargement has been suggested to account for the creation and use of tools found near the fossils. However, Weber *et al.* [6] have suggested that such enlargement also occurs in some microcephalic individuals.

In addition, the authors of the original study have questioned whether the morphologies of microcephalic brains are similar to that of *H. floresiensis* [11]. They have also questioned whether the scaling relationships applied by Martin *et al.* [7] are appropriate because they had previously ruled out *H. erectus* as a possible ancestor of *H. floresiensis* [2] (although this was suggested in their original paper [1]).

Both the original papers and the recent re-examinations of the evidence force us to question what we know about the potential for and the causes and consequences of reduction in brain volume in island vertebrates.

The evolution of small brains on islands

In their response to Weber *et al.* [6] and Martin *et al.* [7], Falk *et al.* [11] point out that the relative brain volume of *H. floresiensis* is consistent with that of apes and australopithecines. In doing so, they highlight an important point: the lowest body weight estimates (16 kg) suggest that *H. floresiensis* had a large relative brain volume (or brain weight) for a mammal; even the highest body weight estimates (36 kg) suggest that the relative brain weight of *H. floresiensis* was greater than that of most primates (Figure 1) [1,12]. Relative brain weight is thought to be a more meaningful measure than absolute brain weight because the relative (but not the absolute) brain weight of humans exceeds that of other vertebrates [13,14]. Numerous studies show that mammals and birds with large relative brain weights (or specific brain regions) often display behaviours that are considered to be ‘complex’, such as tool use or food caching [13,14]. Although it is tempting to suggest that the large relative brain weight of

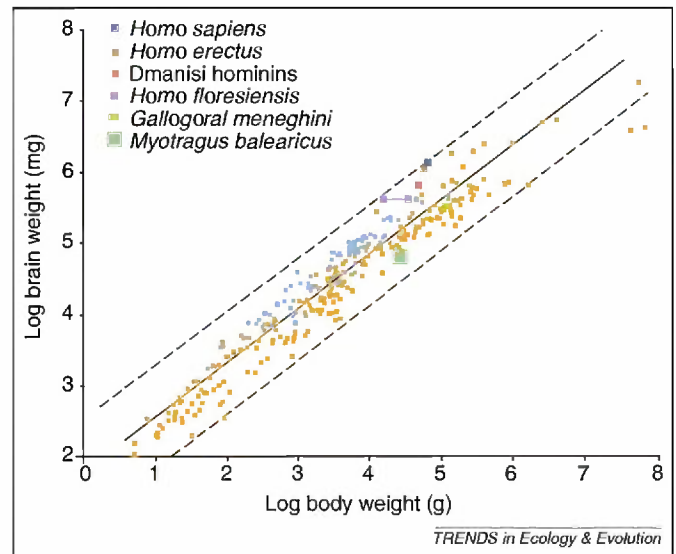


Figure 1. Allometric scaling of brain weight (mg) with body weight (g) for 309 extant placental mammals including humans (orange squares, mammals except primates; blue squares, primates). Additional data are given for three extinct hominins (*Homo erectus*, *H. floresiensis*, Dmanisi hominins) and two extinct bovids (*Myotragus balearicus* and *Gallogoral meneghini*). Although the Dmanisi hominins share characters with *H. ergaster*, they are not assigned a species name as their affiliations remain unclear. The solid line represents the best fit linear correlation, the dashed lines represent fivefold variation above and below this line. The figure is adapted from [12]. Additional data for hominins were taken from Refs [1,7] and data for *Myotragus balearicus* and *Gallogoral meneghini* were taken from Ref. [15].

H. floresiensis could explain the presence of tools found near the fossils, little is known about the interaction between absolute brain weight, relative brain weight and behaviour. For example, pocket mice have relatively larger brain weights than do elephants, but much smaller absolute brain weights [13], yet the impact of relative and absolute brain weight on their respective behaviour is unknown.

Given the arguments of Martin *et al.* [7], the scaling of brain and body weight that occurred during the proposed insular dwarfing of *H. floresiensis* from an ancestor of the genus *Homo* would have to be particularly extreme. It is unclear, however, the extent to which scaling between brain weight and body weight (either inter- or intraspecific) should be viewed as a constraint on brain evolution. The presence of mutations in the human population (such as microcephalin, MCPH1) that cause a dramatic reduction in brain volume might be taken as evidence that there is ‘potential’ within hominin genomes for reductions in brain volume.

Richards [9] has suggested that *H. floresiensis* represents the remains of a *H. sapiens* group that acquired both dwarfed stature and microcephaly. This scenario could lead to the evolution of a new species of hominin with similar proportions to *H. floresiensis*. Moreover, as Martin *et al.* [7] point out, an example of such an extreme reduction in brain weight does occur in *Myotragus balearicus*, an extinct bovid whose fossils are found on two islands in the Mediterranean [15]. Following its isolation, *M. balearicus* underwent a dramatic reduction in brain weight; 44–50% compared with living bovids of similar body mass, such as Thomson’s gazelle *Gazella thomsoni* (Figure 1). *Gallogoral meneghini*, the putative ancestor of

M. balearicus from continental Europe, has a relative brain weight that is similar to that of other fossil and living bovids [15]. The substantial deviation of *M. balearicus* from this scaling relationship suggests that dramatic reductions in brain weight in island forms are indeed possible. Although why the reduction in the brain weight of *M. balearicus* is greater than in *E. falconeri* (a fossil pygmy elephant) remains unclear, but might reflect differing selective pressures during their insular dwarfing.

Islands, behaviour and resources

Islands are often depauperate ecosystems compared with the mainland, lacking large predators, although Flores certainly had at least one large predator, the Komodo dragon *Varanus komodoensis*. Nevertheless, a depauperate island ecosystem might have reduced the number and possibly the 'complexity' of behaviours required for survival, although there are exceptions to this argument. For example, as a population, Cocos finches *Pinaroloxias inornata* show a range of feeding behaviours that encompass those of several families of mainland bird species [16]. Although each individual bird adopts a specialized feeding strategy, they are thought to do this by learning [16]. By most measures, this would suggest that the complexity of the behaviour of the Cocos finches has increased relative to mainland bird species.

Resources on Flores might have been limited as the population of an invasive hominin species, free of mainland predators, increased. Indeed, Flores might have only been able to support between 570 and 5700 individuals with requirements similar to human hunter-gatherers [8]. This would potentially increase selection for efficient energetic expenditure, thereby favoring a reduction in the size of energetically expensive brain tissue [14]. A reduction in brain volume might be advantageous, despite its effects on behaviour, if there are sufficient benefits from reduced energetic costs, as might occur under the environmental conditions found on some islands.

Conclusion

Any discussion of brain evolution, irrespective of the scenario being proposed, is replete with assumptions. Although many of these assumptions appear reasonable, it is usually possible to find species that are exceptions.

Given this, it seems too early to dismiss fully the original claims that *H. floresiensis* is a new small-brained hominin species. For many researchers, however, this will remain in doubt until additional proof for this remarkable claim is found.

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