Primate brains, the 'island rule' and the evolution of *Homo floresiensis*

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Summary

The taxonomic status of the small bodied hominin, *Homo floresiensis*, remains controversial. One contentious aspect of the debate concerns the small brain size estimated for specimen LB1 (Liang Bua 1). Based on intraspecific mammalian allometric relationships between brain and body size it has been argued that the brain of LB1 is too small for its body mass and is therefore likely to be pathological. The relevance and general applicability of these scaling rules has, however, been challenged, and it is not known whether highly encephalised primates adapt to insular habitats in a consistent manner. Here, an analysis of brain and body evolution in seven extant insular primates reveals that although insular primates follow the 'island rule', having consistently reduced body masses compared to their mainland relatives, neither brain mass or relative brain size follow similar patterns, contrary to expectations that energetic constraints will favour decreased relative brain size. Brain:body scaling relationships previously used to assess the plausibility of dwarfism in *H. floresiensis* tend to underestimate body masses of insular primates. In contrast, under a number of phylogenetic scenarios, the evolution of brain and body mass in *H. floresiensis* is consistent with patterns observed in other insular primates.

Introduction

The remains of a small brained, small-bodied hominin from the Indonesian island of Flores (Brown et al., 2004) are still cause for much debate. Ascribed to a new species within our own genus, *Homo floresiensis*, the findings raise questions about the timings of early human migrations, how early human species co-existed, and the cognitive significance of brain size (Brown et al., 2004; Falk et al., 2005; Aiello, 2009; Wood, 2011). However, their status as a new species remains controversial with several studies reporting to show similarities between *H. floresiensis* and various pathological disorders in modern humans (Jacob et al., 2006; Martin et al., 2006; Hershkovitz et al., 2008; Oxnard et al., 2010). These suggestions have been consistently refuted (e.g. Martinez and Hamsici, 2008; Falk et al., 2009a, b; Brown, 2012) and no proposed pathology encompasses the full range of phenotypes observed in *H. floresiensis*, or satisfactorily explains how a diseased population could persist for over 50,000 years (Brown et al., 2004; Morwood et al., 2005). In a recent review of these arguments Aiello (2009) concluded that, although the debate can only be settled with the discovery of new specimens, the current level of evidence supporting a pathological explanation is not convincing. If not pathological, the small brain and body size of *H. floresiensis* requires an evolutionary explanation.

Two evolutionary hypotheses have been proposed to explain the origins of *H. floresiensis*. Either the small body (16-41kg; (Brown et al., 2004; Aiello, 2009) and small brain (417cc, Falk et al., 2005; 426cc, Kubo et al., 2013) of *H. floresiensis* is a product of insular dwarfism from a larger bodied ancestor, perhaps *H. erectus* (Brown et al., 2004; Kubo et al., 2013), or *H. floresiensis* is a descendent of an earlier, small bodied hominin that left Africa before *H. erectus* (Brown et al., 2004; Brown and Maeda, 2009). The latter hypothesis is controversial as the long supported 'Out of Africa 1' model posits that *H. ergaster/erectus* were

62 the earliest hominins to leave Africa (Wood, 2011). This model has, however, been challenged
63 by recent paleontological discoveries (Dennell and Roebroeks, 2005; Ferring et al., 2011) and a
64 number of morphometric and cladistic analyses have suggested *H. floresiensis* bears most
65 similarity to early African hominins, such as *H. habilis*, or the hominins discovered at Dmanisi,
66 Georgia (Tocheri et al., 2007; Gordon et al., 2008; Argue et al*,* 2009; Baab and McNulty, 2009;
67 Brown and Maeda, 2009), although not all studies agree with some providing evidence for
68 morphological affinities with early Javanese *H. floresiensis* (Kaifu et al., 2011).

69 Although descent from an unknown, similarly sized hominin remains possible, the insular
70 dwarfism hypothesis attracted the most attention immediately after the description of the remains
71 (Martin et al., 2006; Falk et al., 2006; Bromham and Cardillo, 2007) and continues to be
72 discussed in both the academic and popular press (e.g. Weston and Lister, 2009; Baab, 2012;
73 Kubo et al., 2013). This is in spite of the generality of the 'island rule' being strongly disputed
74 (Meiri et al., 2006, 2008, 2011). The 'island rule' suggests that large vertebrates generally
75 experience a reduction in body size on islands due, perhaps, to energetic constraints or changes
76 in predation rates (Foster, 1964; van Valen, 1973). Dwarfism on islands is not a general trend
77 found across mammals but has occurred in a limited number of groups (Meiri et al., 2006, 2008),
78 dependent upon the species' ecology and evolutionary history (McClain et al., 2013). One order
79 where the island rule may hold is primates (Bromham and Cardillo, 2007; Welch, 2009), support
80 for the island rule is found using inter-specific datasets (Bromham and Cardillo, 2007; Welch,
81 2009), but not with intra-specific datasets (Meiri et al., 2008; Schillaci et al., 2009) raising the
82 possibility that dwarfism in primates develops over longer time frames (Meiri et al., 2008).

83 Which one of the two evolutionary hypotheses is correct has implications for interpreting
84 the small brain size of *H. floresiensis*. Brain:body allometry between closely related species

85 closely follows intra-specific scaling relationships (Lande, 1979). Hence, if *H. floresiensis*
86 descended from a small-bodied hominin it is reasonable to expect that its brain size would be
87 predictable based on the degree of body size change and intraspecific allometry. However,
88 several notable examples suggest that during episodes of insular dwarfism selection can
89 dramatically reduce brain size in a non-allometric manner, both in absolute mass and relative to
90 body size (Roth, 1992; Köhler and Moyà-Solà, 2004; Weston and Lister, 2009). One suggested
91 explanation for this has been that in an environment with limited resources, energetically
92 expensive tissues, such as the brain (Aiello and Wheeler, 1995), are decreased in size in order to
93 balance energy expenditure (Köhler and Moyà-Solà, 2004). Hence, if *H. floresiensis* evolved
94 from a larger bodied ancestor in a resource-limited environment, additional selective pressures
95 may have driven the evolution of its small brain.

96 However, using both intraspecific scaling relationships between brain and body mass in
97 humans and other mammals, and an example of insular dwarfism, Martin et al. (2006) argued
98 that the estimated brain size for LB1 (*H. floresiensis*) is too small for its body mass. They
99 suggest this departure from expected patterns of brain:body allometry points towards a
100 pathological origin for the specimens (Jacob et al., 2006; Martin et al., 2006). The relevance of
101 these scaling relationships has, however, been questioned (Falk et al., 2006; Niven, 2007; Kaifu
102 et al., 2011) and some alternative scaling relationships are more accommodating of *H.*
103 *floresiensis*' small brain (Weston and Lister, 2009; Montgomery et al., 2010). Weston and Lister
104 (2009), for example, showed that the predicted decrease in *H. floresiensis'* brain size during
105 descent from African *H. erectus* is within the range observed in dwarfed Hippos, whilst
106 Montgomery et al. (2010) found it was within the range observed in primate genera in which
107 body mass decreased, if *H. floresiensis* was a descendent of either *H. habilis* or Dmanisi

hominins. These studies show that major phenotypic changes in brain size can occur during episodes of dwarfism. However, comparisons with *H. floresiensis* are not entirely straight forward. Comparing *H. floresiensis* with particular non-primate dwarfs assumes conservation in the genetic, developmental, physiological and behavioural constraints acting on brain size across large phylogenetic distances. The use of these examples to assert that extensive dwarfism and brain reduction is 'mechanistically possible' (Weston and Lister, 2009; Kubo et al., 2013) in hominins therefore has limitations. Likewise, comparing intergeneric patterns in non-insular primates assumes conservation in allometry between taxonomic scales and ecological niches.

Unfortunately our expectations of patterns of brain evolution on islands are based on only a handful of examples, and it remains unclear if there is a consistent pattern among insular dwarfs. Assessing whether or not *H. floresiensis* departs from expected evolutionary patterns of brain:body allometry relies on choosing taxa with which to compare the evolution of *H. floresiensis* to in a biologically meaningful way. In this respect a comparison with other insular primates is of direct relevance (Bromham and Cardillo, 2007). If primates follow the island rule for body mass (Bromham and Cardillo, 2007; Welch, 2009) examining how brain size evolved in these insular species arguably provides the best reference for contextualizing the small brain of *H. floresiensis* and assessing the arguments put forward against its taxonomic status, and different evolutionary hypotheses.

Based on a thorough analysis of 7 mainland/island pairs of extant primates, the present study examines patterns of brain evolution in insular primates and re-analyses predicted patterns of brain evolution during the origin of *H. floresiensis*. I first test whether or not there is an 'island rule' for brain size and then examine whether the patterns of brain:body allometry in extant insular primates are in line with scaling models previously used to assess the plausibility of the

dwarfism hypothesis for *H. floresiensis*. Finally I examine predicted patterns of brain evolution during the descent of *H. floresiensis* using both the observed allometric scaling among extant insular primates and typical intra-specific mammalian scaling. By doing so I aim to identify the phylogenetic scenarios under which the brain and body size of *H. floresiensis* is acceptable under either, or both, the hypotheses that it descended through insular dwarfism, or from a similarly sized hominin. These results are discussed in the context of morphological similarities between *H. floresiensis* and other hominins.

Materials and methods

Mainland/Island pairs

This study makes use of the dataset of mainland/island taxon pairs compiled by Bromham and Cardillo (2007) that was used to test the island rule for primate body size. Endocranial volume (ECV) and body mass data from wild individuals are available for 7 mainland/island primate pairs; all are catarrhines (Table 1, Isler et al., 2008). Although ECV is an indirect measure of brain size it is a more readily measurable trait and scales isometrically with brain mass (Isler et al., 2008). Data on cranial capacities were converted to brain mass by multiplication by the density of fresh brain tissue (1.036 g/cc) (Isler et al., 2008). Of the 14 species included in the analysis 3 were classed as 'data deficient' by the original authors (Isler et al., 2008) and are based on less than 3 individuals. Whilst poor sampling of intraspecific variation may introduce error in these cases, the data are included in the analysis in order to maximize an already small sample size. Comparisons involving these species are not outliers and the conclusions are robust to their exclusion.

153 Isler et al.'s data on species means are used throughout, but analyses using data from
154 each sex separately are also presented in the Supplementary Material and lead to the same
155 conclusions. In addition to low intraspecific sampling, variation in the sex ratios of the data and
156 the geographic distribution of the mainland species could introduce error into the analyses.
157 However, I assume this error affects both brain and body mass equally and would not bias the
158 results towards finding differences in the patterns of evolution between the two traits, or bias
159 estimates of brain:body scaling in any particular direction. Isler et al. (2008) suggest sample size
160 has a more important effect on parameter estimation than data quality so it is likely the size of
161 the dataset is the most limiting factor of this study.

162 Identifying the true ancestor of insular populations/species is challenging, and a potential
163 source of error in this study. For their study on primate body size Bromham and Cardillo selected
164 the closest mainland relative of each island population by taking into account published
165 phylogenies, taxonomies, species distribution data and consultation with experts. The divergence
166 times between most island/mainland pairs are unknown, however Bromham and Cardillo suggest
167 most of the islands in their dataset became separated from the mainland after the last glacial
168 maximum (<12,000 years ago) although divergence date estimates between species pairs, where
169 available, are typically older (Chatterjee et al., 2009; Perelman et al., 2011).

170 Recently several new species-level phylogenies have been published for primates based
171 on either a supermatrix approach (Bininda-Emonds et al., 2007; Chatterjee et al., 2009; Arnold et
172 al., 2010) or new, larger datasets that are likely to give more accurate phylogenetic
173 reconstructions but contain fewer species (Perelman et al., 2011). Unfortunately the relationships
174 among species, and occasionally genera, in these phylogenies do not always agree and none of
175 these phylogenies include all 14 taxa considered here. Discerning the species level relationships

within some genera of catarrhines is particularly troublesome given an apparently complex pattern of hybridization and gene flow between species (Chatterjee et al., 2009). Hence, whilst phylogenetics may ultimately confirm or revise which extant species is most closely related to each insular population, which may in turn prompt a revision of the analyses presented below, for the present study Bromham and Cardillo's mainland/island pairs are adopted as no new and robust evidence is available to support alternative pairs.

Tests of the island rule

Although it is generally assumed that brain size decreases on islands, this hypothesis has not been well tested (but see Mace and Eisenberg, 1982 for a test within *Peromyscus* mice). Although the dataset is limited, performing explicit tests of this hypothesis is preferable to assuming it is true. For the current analyses I take a broad view of an 'island rule' for brain size and simply search for consistent patterns among insular primates. If insularity has a consistent effect on brain size several patterns could be observed. First, brain mass could decrease coincidentally with body mass such that relative brain size remains constant. In this case, brain size would account for the same proportion of the species' energetic budget (Aiello and Wheeler, 1995). Alternatively, if energetically constrained, brain mass may decrease more rapidly than predicted by allometric scaling leading to a decrease in relative brain size. Finally, if brain mass remains relatively constant, perhaps due to cognitive or behavioural constrains (Deaner et al., 2007), but body mass decreases, relative brain size will increase.

There is considerable debate over how best to test the island rule (Lomolino, 1985; Bromham and Cardillo, 2007; Price and Phillimore, 2007; Meiri et al., 2008; Welch, 2009).

198 Welch (2009) reviewed the three main alternative tests of the island rule, their assumptions and
199 performance. Here I provide a brief overview of his conclusions.

200 1) 'Null hypothesis A' states that evolutionary size changes on islands do not depend on
201 the ancestral state. This hypothesis is tested using an Ordinary Least Squares (OLS) regression
202 between the island-mainland size ratio, R ($R = S_i/S_m$), and the size of the mainland species (S_m).
203 The null hypothesis is rejected when the slope is significantly negative (Lomolino, 1985).

204 2) 'Null hypothesis B' states that there are no differences between the patterns of
205 evolution of mainland and island species, and mainland relatives remain close to the ancestral
206 state. This is tested using a Standardized Major Axis (SMA) regression between the size of the
207 island species (S_i) and the size of the mainland species (S_m) (Price and Phillimore, 2007) where a
208 slope that is significantly less than one is consistent with the island rule. Welch (2007) proposed
209 an alternative permutation test for Null hypothesis B that can be implemented by generating all
210 possible combinations of the data where the island and mainland species are assigned randomly
211 within each pair and repeating the regression on these data to generate a null distribution. The p-
212 value is the proportion of tests with lower significance than the real data.

213 3) 'Null hypothesis C', states that insular evolution is characterized by a directional
214 change in size determined by a heritable trait. This is tested using phylogenetically controlled
215 regression between R and $\ln(S_m)$ (Meiri et al., 2008).

216 Using simulated datasets Welch found that the test of Null hypothesis A has an
217 unacceptable false positive rate when one of the other null models held and therefore
218 recommended against using this test. The tests of Null B and C were found to have acceptable
219 false positive rates and are recommended as tests of the island rule (Welch, 2009). I test the

island rule for body mass, brain mass and the encephalization quotient (EQ) (Jerison, 1973), a commonly used measure of relative brain size. The island rule has previously been shown to apply to body mass using the full Bromham and Cardillo dataset and different measures of body size (Bromham and Cardillo, 2007; Welch, 2009). The test is repeated here to confirm the pattern is detectable using only the 7 pairs for which brain mass data is available. Tests of Null A and B were performed using the SMATR package (Warton and Ormerod, 2007). The test for Null C was performed using Phylogenetic Generalized Least Squares (PGLS) regression between R and S_m as implemented in BayesTraits (Pagel, 1999). For this test it is necessary to include a phylogeny of taxon pairs (i.e. the relationships between mainland species). Following previous test of the island rule in primates I used the mammal supertree (Bininda-Emonds et al., 2007), but also accounted for phylogenetic uncertainty by repeating the regressions across a distribution of the 1000 most supported phylogenies from Arnold et al. (2010). In the latter not all mainland species were present in the phylogeny, so in some cases con-generics were used to generate the phylogeny. Note divergence date estimates between mainland/island pairs are not required for this analysis because the regression is between the mass ratio of the species pair and the mainland mass.

Scaling exponents and insular dwarfism in primates

In previous studies of *H. floresiensis* the scaling relationships between brain and body mass between mainland ancestors and insular dwarfs have been used to model expected degrees of body mass reduction in *H. floresiensis* given the estimated difference in brain size between *H. floresiensis* and a range of putative ancestors (Martin et al., 2006; Montgomery et al., 2010;

242 Weston and Lister, 2009). These models were applied to *H. floresiensis* to assess whether it
243 departs from expected patterns of brain:body allometry during insular dwarfism but no
244 consideration has been given to whether or not these models accurately predict patterns of
245 evolution in other insular dwarfs. Here, I assess how well these models are able to predict
246 observed patterns of body mass reduction in extant insular primates given the observed
247 difference in brain mass between the mainland and island taxa.

248 The following scaling exponents (b) were used to estimate the expected body mass of
249 each insular species given the observed decrease in body mass: Martin et al.'s (2006) Model A
250 (*Elphas antiquus* to *E. falconeri*; b = 0.32-0.35) and Weston and Lister's (2010) 'late ontogenetic
251 scaling' (b = 0.35) and 'ontogenetic scaling' (b = 0.47) models calculated from dwarfed, insular
252 hippopotami. Dwarfed hippos have smaller brains than predicted based on these models with
253 observed brain sizes up to 30% smaller than predicted by the 'late ontogenetic scaling' model
254 and up to 17% smaller than the 'ontogenetic scaling' model (2010). For these models, the
255 expected body mass was therefore also calculated within these bounds and are referred to as the
256 'late ontogenetic-plus scaling' and 'ontogenetic-plus scaling'. In many cases this results in the
257 island brain mass exceeding the mainland brain mass suggesting this model is not applicable to
258 some insular primates which show more modest differences in brain size, I only show the results
259 where this is not the case.

260

261 *Intraspecific scaling components*

262 In addition to scaling components from known cases of insular dwarfism, the brain and body
263 mass of *H. floresiensis* has also been assessed using intraspecific scaling components. The logic

of applying these models to cases of insular dwarfism derives from Lande's (1979) observation that the allometric scaling relationship between brain and body mass is the same within populations as between closely related species. If insular dwarfism is the product of phyletic evolution within populations they may therefore follow intraspecific scaling (see Weston and Lister, 2009 for further discussion). Across mammals brain mass typically scales with body mass allometrically with a slope of between 0.2-0.4 (Gould, 1975; Lande, 1979). Among non-human primates a similar range is observed, from 0.124-0.349 (Holloway, 1980), and Pilbeam and Gould (1974) derived a similar value (0.329) among australopithecines.

Martin et al. (2006) applied a 'typical mammalian' intraspecific model (Martin et al.'s Model B) with a scaling component of 0.25 to *H. floresiensis*, and three values of human intraspecific scaling components (Model C) for males (0.1), females (0.03) and both sexes combined (0.17). As noted by Kubo et al. (2013) these values are derived from a modern Danish sample (Holloway, 1980) and may not represent global patterns, although other regionally restricted datasets produce a similar range of scaling components (Peters et al., 1998).

I apply similar models here, but interpret them in a slightly different way. Intraspecific scaling may poorly predict patterns of brain:body allometry in insular dwarfs (Weston and Lister, 2009). Variation in life history and development is a potential explanatory factor if this causes a grade-shift between ancestor and descendent populations (Weston and Lister, 2009). However, another possible source of discrepancy is identified in Lande's original analysis of brain:body allometry (1979). Lande demonstrated that a scaling component of 0.2-0.4 is expected if the population evolved according to random genetic drift or directional selection acting only on body size. As discussed in the introduction, during episodes of insular dwarfism selection may not act solely on body size but may also have consequences for brain size and other traits. Directional

287 selection on both brain and body size could potentially lead to steeper allometric slopes (Lande,
288 1979). Hence, for the current purposes, intraspecific scaling components can effectively form a
289 null model which excludes the action of 'special' selective forces acting on both brain and body
290 mass.

291 Kubo et al. (2013) recently used an indirect measure of body mass, femoral head
292 diameter (FHD), to quantify brain:body scaling in humans and assess whether *H. floresiensis*
293 scales in a similar manner. Their data consists of geographically disperse populations, includes
294 both modern and ancient populations, and a number of modern human pygmy populations. For
295 completeness, in the Supplementary Material I derive body mass estimates from the FHD data to
296 discuss how their scaling relationships compare to other intraspecific datasets and the results
297 presented below. However, these results should be viewed with caution as converting the FHD
298 dataset to body mass may introduce a bias.

299

300 *Assessing* H. floresiensis, *insular dwarfism and intra-specific scaling*

301 The approach taken in the present study is to look for general patterns of brain evolution
302 in insular primates, to calculate a range of brain:body scaling components observed among
303 insular primates, and to use these to assess the evolution of *H. floresiensis* rather than to focus on
304 specific case studies (e.g. Köhler and Moyà-Solà, 2004; Martin et al., 2006; Weston and Lister,
305 2009). I argue this is preferable as there is a potential for taxon specific responses to selection
306 pressures experienced on islands, and variation in what those selection pressure may be could
307 cloud the interpretation of studies comparing *H. floresiensis* to one species/population, insular or
308 otherwise. By focusing on insular primates the response to island ecology is incorporated with

allometric effects in the comparison between the mainland and island taxa, it is therefore not necessary to invoke additional amounts of change observed in non-primate insular dwarfs in addition to observed changes (Weston & Lister, 2009; Kubo et al., 2013).

In the first set of analyses patterns of brain evolution in insular primates are compared to that of *H. floresiensis,* assuming recent common ancestry with one of a number of hominins previously proposed as possible ancestors or closely related species, and a range of body mass estimates for *H. floresiensis*. Kubo et al. (2013) recently published a revised estimate of LB1's ECV of 426cc, and this value is used throughout. Previous estimates have ranged from 380-430cc (Brown et al., 2004; Falk et al., 2005; Holloway et al., 2011). Estimating hominin body masses is a challenging exercise (Uhl et al., 2013) and estimates of *H. floresiensis'* body mass vary greatly, from 16-41.3kg (Brown et al., 2004; Aiello, 2009) but, unless otherwise stated, in the following analyses body mass is not assumed, being the trait estimated in the analyses. Where it is assumed a range of masses are used.

The phylogenetic affinities of *H. floresiensis* continue to be debated. Initially it was thought possible that *H. floresiensis* was a descendent of *H. erectus* (Brown et al., 2004) and some still favour this hypothesis (e.g. Lieberman, 2009; Kaifu et al., 2011; Kubo et al., 2013). However, several subsequent analyses of morphological similarity increasingly point towards a relationship with early *Homo* species (Morwood et al., 2005; Tocheri et al., 2007; Gordon et al., 2008; Argue et al., 2009). Here I assume a range of proposed ancestors in order to identify phylogenetic scenarios under which the brain:body scaling of LB1 is plausible:

- *H. erectus*: following Martin et al. (2006) I include *H. erectus* 'broadly defined' as well as the geographically localized Ngandong hominins from Java, and Dmanisi hominins from

Georgia which are (tentatively) assigned to *H. erectus*, but a primitive form (Vekua et al., 2002; Wood, 2011). I also include *H. ergaster*, a candidate African ancestor of *H. erectus* (Wood and Collard, 1999). Unfortunately limited post-cranial material are available from which to estimate body mass estimates for Javan *H. erectus*, including the Ngandong specimens. The body mass estimates are therefore uncertain and should be viewed with some caution. They are included here to allow direct comparison with previous studies (Martin et al., 2006; Montgomery et al., 2010; Kubo et al., 2013).

- *H. habilis* and *H. rudolfensis*: a cladistic analysis by Argue et al. (2009) suggested *H. floresiensis* was an early member of the genus *Homo* which emerged after *H. rudolfensis* and either before or after *H. habilis*. LB1 also shows some morphological similarities to *H. habilis* (Gordon et al., 2008; Martinez and Hamsici, 2008).

- *Australopithecus africanus* and *A. sediba*: finally I include two representatives of the australopithecines. *A. sediba* is proposed to be a descendent or close relative of *A. africanus* (Berger et al., 2010) and these species may be closely allied with early *Homo* and are two of the younger members of the genus (Irish et al., 2013 but see also Wood and Harrison, 2011; Kimbel, 2013). Some authors have argued descent from an australopithecine may be a possible explanation for the origin of *H. floresiensis* (Brown and Maeda, 2009)

Body and brain mass estimates for these species were taken from published sources (Table 2). ECVs were converted to mass as described above. Of course, both traits are estimates and are not known without error and there is debate surrounding the taxonomic classification of some named species, and their relationships to one another. The analyses should therefore not be viewed as

352 giving a precise description of the ancestor but a range of phylogenetic scenarios under which
353 the brain size of LB1 does not require special reasoning.

354 Each ancestor/descendant hominin pairing was used to calculate the expected *H.*
355 *floresiensis* body masses, given the observed decrease in brain mass, using the ratio of change in
356 Log_{10}(brain mass) and Log_{10}(body mass) for each extant, insular primate mainland/island pair
357 following Martin et al. (2006), and as described above.

358 Finally, as an alternative method of comparing *H. floresiensis* to insular primates, the
359 relationship between R_{brain} and R_{body} for *H. floresiensis* was compared to the extant
360 mainland/island pairs by assessing how the ratio for *H. floresiensis* fits the general primate
361 relationship across a range of assumed body masses. Specifically, for each ancestor I calculated
362 the R_{brain} and R_{body} for *H. floresiensis* across a range of body mass values for *H. floresiensis*
363 taking 1kg incremental increases between 0kg to 45kg. I then assessed the leverage of these sets
364 of *H. floresiensis* data points on the R_{brain}:R_{body} regression across the extant species pairs.
365 Leverage was measured using Cook's Distance (D_i) (Cook, 1977), which quantifies the effect on
366 a regression of deleting an observation. D_i values greater than $^4/_n$ indicate a data point has high
367 leverage (Bollen and Jackman, 1990). High leverage scores could be due to deviation from the
368 regression line or a large difference along either or both the x and y axis, i.e. either unexpected
369 deviation in brain:body allometry (x or y) or unexpectedly large phenotypic shifts (x and y). I
370 assume the regression for extant pairs represents the true relationship and interpret high leverage
371 scores for *H. floresiensis* as indicating that the data point departs from the expected relationship.
372 It is therefore possible to plot the leverage scores for a range of body masses for *H. floresiensis*
373 to identify the range of body masses that fit the pattern observed in extant insular primates for

each assumed ancestor. These can then be compared to the range of estimated body masses for *H. floresiensis*.

The analyses described above assume *H. floresiensis* was an insular dwarf and should therefore have brain:body scaling within the range of other insular primates. As a test the hypothesis that *H. floresiensis* was not a dwarf, but a descendent of an early species of *Homo* that left Africa as a small bodied, small-brained hominin, I apply the typical mammalian (b = 0.2-0.4), primate (b = 0.124-0.349) and Danish (b = 0.03-0.17) intraspecific scaling components described above.

Results

Primate brains do not follow an 'island rule'

For body mass, the SMA test of Null B is significant (p = 0.006, slope = 0.419) as is the permutation test of Null B (p = 0.016) and the PGLS test of Null C using both the mammal supertree (p = 0.014, R^2 = 0.734) and when accounting for phylogenetic uncertainty using the 10k Trees Project phylogenies (p = 0.008, R^2 = 0.782). This subset of data therefore reproduces support for the hypothesis that the island rule holds for primate body mass (Bromham and Cardillo, 2007; Welch, 2009).

In contrast, support for the applicability of an island rule to brain mass or EQ is not found. For brain mass the SMA test of Null B is not significant (p = 0.978, slope = 0.989) nor is the permutation test of Null B (p = 0.938). The test of Null C is also narrowly non-significant (mammal supertree: p = 0.055; 10K Trees: p = 0.056). Similarly for EQ the SMA test (p = 0.813,

slope = 0.966) and permutation test (p = 0.813) of Null B and the PGLS test of Null C (mammal supertree: p = 0.580; 10k Trees: p = 0.762) are not significant. Indeed, even the OLS test of Null hypothesis A, which has high false positive rates (Welch, 2009), fails to find support for the applicability of the island rule to brain mass (p = 0.226) or EQ (p = 0.571) despite the test being significant for body mass (p = 0.001). There is therefore no evidence for a consistent effect of insularity on primate brain size.

Brain:body allometry in insular primates does not fit either non-primate mammalian models of insular dwarfism or typical intraspecific scaling components

The ratio of brain and body masses between mainland/island pairs produce steeper allometric scaling relationships (b = 0.242-1.244, mean = 0.645) than would typically be predicted by intraspecific mammalian brain:body scaling (b = 0.2-0.4). Only two pairs fall within this range, one of which is the *Macaca fascicularis fascicularis/M. f. fusca* pair in which the insular species is larger than its mainland relative. On average, all the scaling components previously applied to model *H. floresiensis* underestimate the body mass of the insular species in the extant mainland/island pairs (Table 2) with average percentage errors from the observed body mass between 12.2% and 57.9%. Weston and Lister's (2010) 'late ontogenetic scaling' model has the lowest average percentage error, however there is substantial variation in the performance of all models.

In some cases the average error across models is substantial, with values over 15% for 4/7 pairs under the insular dwarfism models and even greater disparity under intraspecific scaling models. This suggests a lack of conservation in patterns of brain:body allometry

417 governing the evolution of primates and non-primate mammals on islands, and further refutes the
418 expectation that insular dwarfs should show patterns of brain:body evolution within the range
419 predicted by intraspecific allometry. The observation that these scaling exponents underestimate
420 the body mass of *H. floresiensis* (Martin et al., 2006) is therefore an unconvincing argument
421 against the status of *H. floresiensis* as a dwarfed hominin.

422

423 *Testing the insular dwarfism hypothesis in* H. floresiensis

424 The relationships between mainland and island primate species pairs were used to
425 provide a reinterpretation of the *H. floresiensis* data. When the brain:body scaling relationship
426 from each species pair was used to predict the body mass of *H. floresiensis* (Figure 1, Table S1)
427 the average body mass predicted is 12.9 kg based on descent from a Ngandong *H. erectus* like
428 population, and 16.2kg for generalized *H. erectus*. These values lie below the probable range of
429 body mass for *H. floresiensis* (Brown et al., 2004; Morwood et al., 2005; Aiello, 2009). In
430 contrast descent from earlier *Homo* produces estimates within the acceptable range. Descent
431 from Dmanisi hominins results in an average predicted body mass of 25.1kg, from *H. ergaster*
432 19.7kg, from *H. habilis* 21.8kg and from *H. rudolfensis* 20.7kg. If *H. floresiensis* is instead a
433 direct ancestor of an australopithecine, such as *A.africanus or A. sediba*, body mass estimates of
434 32.3kg and 34.3kg are predicted respectively, close to the values predicted from LB1's femoral
435 head diameter (Brown et al., 2004; Aiello, 2009). All of the scaling components from the 7 pairs
436 of primates predict body masses within the acceptable range for descent from either
437 australopithecines. Among *Homo*, the most consistent results are assuming ancestry with *H.*
438 *habilis*, for which 6/7 pairs produce acceptable body masses. In this case the pair that doesn't is

439 *M. f. fascicularis/M. f. fusca*. Descent from either Dmanisi hominoids or *H. rudolfensis* is
440 consistent with 5/7 pairs.

441 Across the extant species pairs the ratio of island/mainland brain mass (R_{brain}) and body
442 mass (R_{body}) are significantly associated ($p = 0.003$, $R^2 = 0.858$, Figure 2a). Assuming recent
443 common ancestry with a range of hominins, the fit of *H. floresiensis* to this regression was
444 assessed by calculating Cook's Distances across a range of body mass values for *H. floresiensis*,
445 from 1kg up to 45kg (Figure 2b), just above the upper end of the range of body mass estimates
446 derived from post-cranial morphology (Brown et al., 2004; Aiello, 2009). Cook's Distances
447 indicate that dwarfism of Ngandong *H. erectus*, or *H. erectus* more generally, is not consistent
448 with the relationship across primates unless *H. floresiensis* had a body mass of less than 3kg or
449 11kg respectively (Table 4; Figure 2b), outside the range of body mass estimates for *H.*
450 *floresiensis* (Brown et al., 2004; Aiello, 2009). Descent from *H. ergaster* requires a narrowly
451 permissible final body mass of <19kg. But the evolution of *H. floresiensis* is most consistent
452 with patterns of primate insular dwarfism ($D_i < 0.5$) if it had a body mass above 14kg and was a
453 dwarfed sister-lineage to Dmanisi hominins, above 8kg for *H. rudolfensis* or between 12kg and
454 38kg for *H. habilis*. These are well within the range of body mass estimates for *H. floresiensis*
455 (Brown et al., 2004). Similarly, descent from either *A. africanus* or *A. sediba* is acceptable if *H.*
456 *floresiensis* had a body mass between 22-42kg or 22-43kg respectively. For the
457 australopithecines, *H. habilis* and Dmanisi hominins the body mass at the lowest D_i values is
458 within the acceptable range. Figure 2 also illustrates that, depending on the final body mass for
459 *H. floresiensis*, some phylogenetic scenarios result in a proportional decrease in both brain and
460 body size within the range observed between the extant mainland/island pairs.

461

462 *Testing the descent without dwarfism hypothesis in* H. floresiensis

463 The analyses above show that insular primates deviate from typical intraspecific patterns
464 brain:body scaling, supporting previous evidence that insular dwarfs do not necessarily scale in
465 this manner (Weston and Lister, 2009). This deviation, which is presumably caused by shifts in
466 selection pressure or life history traits associated with insularity, permits the use of intraspecific
467 brain:body allometry as a model of descent without insular dwarfism, as these effects should be
468 absent. When the range of typical mammalian intraspecific brain:body scaling components are
469 applied to *H. floresiensis*, as described above, the range of body mass estimates for all scenarios
470 involving descent from a member of the genus *Homo* lie at the lower limit or below the
471 acceptable range (Table 5). Only if *H. floresiensis* descended from an australopithecine are the
472 body mass estimates reasonable. This pattern is even stronger if the range of intraspecific scaling
473 within extant primate species (b = 0.12-0.33), or within the Danish modern human population (b
474 = 0.03-0.17), is used.

475

476 **Discussion**

477 Despite generally being smaller than their mainland counterparts little evidence is found to
478 support the applicability of an island rule to primate brain size using formal statistical tests.
479 Although the dataset is limited in size it is sufficient to find strong statistical support for the
480 island rule holding for body mass in primates, as previously reported (Bromham and Cardillo,
481 2007; Welch, 2009). At the very least these results therefore suggests that the effects of insularity
482 on brain and body size differ. For EQ in particular there is little hint of any consistent affect of
483 insularity with increases being as common as decreases (Table 1). The scaling components

between brain and body mass vary greatly across pairs, from 0.24-1.24, this variability in response is a likely cause of the lack of an 'island rule' for relative brain size.

Although this conclusion may need to be revised when additional data is available, given the support for the island rule for body mass obtained using this dataset, the lack of support for the island rule for brain mass and EQ is perhaps surprising. Brain tissue is energetically expensive (Aiello, 2009) and it is expected that on islands resource limitation (Foster, 1964) will lead to an advantageous reduction in brain mass and relative brain size to reduce the total energy budget of the brain (Köhler and Moyà-Solà, 2004; Niven, 2007). This is observed in several insular dwarfs (Roth, 1992; Köhler and Moyà-Solà, 2004; Weston and Lister, 2009) and is further supported by evidence that food scarcity or seasonality in food abundance is associated with smaller relative brain sizes in strepsirhines (Taylor and Schaik, 2007; van Woerden et al., 2010). However, in primates, larger brains are associated with higher rates of innovative behaviour (Reader and Laland, 2002) and, in catarrhines, an ability to reduce the effects of food scarcity (van Woerden et al., 2012). Hence, one could hypothesize that for some insular primates the cognitive advantage of maintaining brain size on islands outweighs the energetic costs of doing so (Sol, 2009). The balance between these two selective forces is likely to depend on the environment of the island and the species' ecology and physiology (Navarrete et al., 2011; McClain et al., 2013) and it is clear from these results that the outcome is not necessarily consistent between species.

The range of responses observed in insular primates provides a meaningful framework within which to interpret the brain size of *H. floresiensis*. Assumptions surrounding the effects of insularity on brain size have had a major influence on the debate over the remains ascribed to *H. floresiensis* (Martin et al., 2006; Niven, 2007; Köhler and Moyà-Solà, 2008) despite being

507 largely untested. The poor performance of intraspecific brain:body scaling rules when applied to
508 extant insular primates implies that the application of these scaling relationships as a test of
509 whether or not the brain of *H. floresiensis* is too small to be non-pathological may be
510 uninformative. Based on the observed difference in brain size and expected brain:body scaling
511 relationship these models tend to underestimate the body mass of the insular species, just as they
512 do for *H. floresiensis* (Martin et al., 2006). The size of these errors are similar to most, if not all,
513 models applied to *H. floresiensis* (Martin et al., 2006). This discrepancy is caused by brain and
514 body mass scaling with a higher scaling exponent than is generally expected (Lande, 1979). It is
515 also notable that in many cases dwarfism models based on Hippopotamidae or *Elephas* also
516 produce large errors, again suggesting variability in the effects on insularity on brain size in
517 different mammalian taxa.

518 In contrast, when the scaling relationships between mainland and island primate species
519 pairs are used to predict the body mass of *H. floresiensis* assuming recent shared ancestry with a
520 range of hominin populations, the estimated mass is within the range predicted for *H. floresiensis*
521 (Brown et al., 2004) under a number of scenarios (Table S1; Figure 1, 2). Estimates for the body
522 mass of *H. floresiensis* vary and I here take the full range (16-41kg) as acceptable with the
523 following caveat. In the original description of LB1, Brown et al. (2004) derived a body mass
524 estimate of 16-28.7kg based on a stature of 106cm, and a mass of 36kg derived from femur
525 cross-sectional area. Based on femoral head diameters body mass is estimated to be between
526 31.4-41.3lkg (Aiello, 2009). Brown et al. initially favored the lower end of this range, but
527 subsequent finds have seen the consensus shift towards higher values (Morwood et al., 2005). A
528 body mass of around 30kg therefore seems more reasonable, but the intraspecific range requires
529 confirmation.

A close phylogenetic relationship with *H. erectus s.l.,* Ngandong *H. erectus* or *H. ergaster* would result in estimated body masses below, or at the very bottom of, the range of body masses for *H. floresiensis* (16.2kg, 12.9kg and 19.7kg respectively). In contrast, if *H. floresiensis* descended from an early *Homo*, represented here by *H. habilis*, *H. rudolfensis* or Dmanisi hominins, or an australopithecine-like hominin the predicted body mass is within the acceptable range. Within *Homo*, ancestry with *H. habilis* or Dmanisi hominoids produce the most consistent results with average estimated body masses for *H. floresiensis* of 21.8kg and 25.1kg respectively. Similar results are obtained from the Cook's Distance analysis, which provide an approximate range of body masses for *H. floresiensis* that would fit the relationship between changes in brain and body mass observed in extant insular primates. For *H. habilis, H. rudolfensis,* Dmanisi hominins and the australopithecines this range encompasses the higher estimates of body mass derived from postcranial morphology of *H. floresiensis.* These results provide a range of scenarios under which descent with insular dwarfism can explain the patterns of brain:body allometry in *H. floresiensis*. Across a range of body masses, descent from *H. habilis*, Dmanisi hominins or Autralopithecines would also result in proportional decreases in brain and body size within the range observed in insular primates (Figure 2).

Importantly, for the purposes of the present analysis, the fact that insular primates deviate from typical intraspecific scaling relationships permits the use of these models as a null hypothesis for descent without additional selection pressures such as those leading to insular dwarfing. When these intraspecific scaling components are used to model the descent of *H. floresiensis* the range of acceptable scenarios is much narrower. Essentially only descent from australopithecines produces body mass estimates consistent with those derived from post-cranial morphology of *H. floresiensis*, although descent from Dmanisi hominins or *H. habilis* produces a

553 range of estimates narrowly within the lowermost estimates. The convergence in results for
554 australopithecines using intraspecific scaling relationships and the relationship among extant
555 insular primates is due to the small differences in size between these species and *H. floresiensis*.

556 Unless *H. floresiensis* is a descendent of an australopithecine, the results suggest that that
557 both evolutionary hypotheses regarding the origin of *H. floresiensis* may be true; that is, *H.*
558 *floresiensis* descended from an early, small-bodied member of the genus *Homo* but its descent
559 was characterized, at least in part, by insular dwarfism. Whilst resolution of the characteristics of
560 the founding population is necessary to confirm that *H. floresiensis* was indeed an insular dwarf,
561 the earliest human artifacts on Flores suggest there was sufficient time for dwarfism to occur
562 (Bromham and Cardillo, 2007; Brumm et al., 2010) and the island fauna suggest environmental
563 conditions may have rendered dwarfism likely and advantageous for some species (Meijer et al.,
564 2010). Whilst equivocal, some features of *H. floresiensis* do point towards paedomorphic
565 dwarfism (van Heteren, 2008, 2012) and patterns of brain and body size evolution in *H.*
566 *floresiensis* are not inconsistent with other insular (this study) or otherwise dwarfed primates
567 (Montgomery et al., 2010; Montgomery and Mundy, 2013).

568 The phylogenetic scenarios suggested by these analyses are consistent with previous
569 reports of morphological similarities between *H. floresiensis* and early hominins. Several studies
570 of cranial shape and morphology have suggested a close relationship between *H. floresiensis* and
571 either Dmanisi hominins or *H. habilis* suggesting *H. floresiensis* was a descendent of an early
572 member of the genus *Homo* (Gordon et al., 2008; Martinez and Hamsici, 2008; Baab and
573 McNulty, 2009). Analysis of post-cranial morphology support this contention, with several
574 studies demonstrating the retention of traits typical of early *Homo*, including wrist morphology
575 (Tocheri et al., 2007), foot morphology (Jungers et al., 2009a), lower limb (Jungers et al., 2009b)

576 and shoulder morphology (Larson *et* al., 2007). A cladistic analysis of cranial and postcranial
577 characters also suggests *H. floresiensis* was most closely related to early members of the genus
578 *Homo* (Argue et al., 2009). Whether or not the immediate ancestry of *H. floresiensis* can be
579 traced back to the australopithecines is more contentious, with some studies directly refuting this
580 hypothesis (Gordon et al., 2008; Baab and McNulty, 2009; Kaifu et al., 2011) but others arguing
581 that it remains a possibility (Brown and Maeda, 2009).

582 The earliest evidence for *Homo* outside Africa comes from specimens found at Dmanisi
583 Gorge in Georgia, which extend back to c. 1.85 Ma and suggests primitive members of the genus
584 radiated out of Africa earlier than previously suspected (Ferring et al., 2011; Wood, 2011). The
585 Dmanisi remains have been preliminarily attributed to early *H. erectus* but they retain many
586 primitive characteristics and are smaller-bodied and have smaller brains than African *H. erectus*
587 leading some to associate them with *H. habilis* or a previously unnamed species (Vekua et al.,
588 2002; Rightmire et al., 2006; Lordkipanidze et al., 2007). The earliest evidence of *Homo* on
589 Flores date to c. 1 Ma (Brumm et al., 2010), which, assuming favorable climatic conditions,
590 leaves a reasonable time period for dispersal assuming *H. floresiensis* is closely related to the
591 Dmanisi hominins, and that these were the earliest non-African *Homo*. Characterizing this early
592 out-of-Africa migration is, however, at an early stage and in need of productive new sites
593 (Ferring et al., 2011; Wood, 2011). It remains possible that the Dmanisi hominins were not the
594 first Eurasians, and that an earlier lineage emerged from African and ultimately terminated with
595 *H. floresiensis* (Brown and Maeda, 2009).

596 However, not all authors agree that *H. floresiensis* has clear taxonomic affinities with
597 early *Homo.* Criticisms have been raised against some of the analyses (Trueman, 2009 and Kaifu
598 et al., 2011) and a reanalysis of cranial morphology using larger datasets of Indonesian *H.*

599 *erectus* which capture temporal variation in the population's morphology suggested *H.*
600 *floresiensis* may be derived from early Javanese *H. erectus* (Kaifu et al., 2011), a possibility not
601 rejected by previous studies (Baab and McNulty, 2009). Unfortunately the paucity of post-cranial
602 material associated with these crania has so far limited the potential for similar comparisons with
603 other anatomical traits, such as those indicating an affinity with early *Homo* (but see Kaifu et al.,
604 2011 for discussion.).

605 The goal of the present study was to identify the phylogenetic scenarios, and range of
606 body masses, under which patterns of brain and body size evolution in *H. floresiensis* does not
607 deviate from expected patterns. A recent analysis by Kubo et al. (2013) produced a wider range
608 of acceptable ancestors based on intraspecific scaling between brain size and femoral head
609 diameter (FHD) in modern humans. They suggest descent from *H. habilis* can be explained
610 solely by the allometric relationship between brain and body mass, whilst descent from early
611 Javanese *H. erectus*, which the authors favour (Kaifu et al., 2011; Kubo et al. 2013), requires a
612 similar decrease in brain mass beyond that predicted by allometry as observed in dwarfed Hippos
613 (Weston and Lister, 2009). This approach takes advantage of large datasets and avoids error
614 introduced when identifying ancestor/descendent relationships, but does not directly compare *H.*
615 *floresiensis* with other insular populations and, as discussed in the introduction, assumes
616 constraints on brain evolution are conserved between distantly related insular mammals.
617 However, the difference between the analysis of Kubo et al. and the results based on intraspecific
618 scaling in the present study must ultimately stem from differences in the estimated allometric
619 slope between brain and body mass. Indeed, when converted from FHD to body mass Kubo et
620 al.'s data give an intra-specific allometric slope of between 0.44-0.79, greater than typical
621 estimates for mammals (see Supplementary Material).

This raises two questions; first, how robust is this high allometric slope? And second, is it human-specific? Kubo et al.'s dataset contains means of different human populations that may not be phylogenetically independent; indeed some are likely descendents of others. Failing to correct for this non-independence could bias estimates of scaling components (Harvey and Pagel, 1991). The steep allometric slope therefore needs confirmation using phylogenetically controlled regressions. If confirmed, the question is then whether this high allometric slope is unique to humans and whether it can be applied to extinct hominins. The available data suggests extant primate populations scale within the range typical for other mammals (Holloway, 1980), as do australopithecines (Pilbeam and Gould, 1974). An upwards shift in intraspecific allometry within *Homo* is possible (Pilbeam and Gould, 1974), perhaps due to increased selection on brain mass, but further data and analysis are necessary to test this hypothesis.

Kubo et al.'s general conclusion however, that allometry can explain more of the reduction in brain size in *H. floresiensis* than previously thought, is in agreement with the current analysis. Where they have added variation in the estimated allometric slope by including global geographic human variation, here I have done so by examining allometry between insular primates and their mainland relatives. Although I reject descent from *H. erectus* as unlikely, descent from early Javanese *H. erectus* was not modeled here, as I know of no body mass estimates for this population. Given the lack of material for direct measurement Kubo et al. (2013) estimated FHD as 45-50mm based on size expectations and comparison with other hominins. Using this range, together with an ECV of 815cc (Kubo et al. 2013) as a model for the ancestral population of *H. floresiesnsis*, body mass estimates towards the lower end of the acceptable range for *H. floresiensis* are obtained (see Supplementary Material). I therefore

644 cannot rule out this scenario but, given the uncertainty in the body mass estimates, further data is
645 required to make firm conclusions.

646 In summary, I find that two evolutionary scenarios are plausible explanations for the
647 origin of *H. floresiensis* without the need to invoke an exceptional degree of phenotypic change.
648 If a contribution from insular dwarfism is rejected, patterns of brain size evolution are only
649 consistent with descent from an australopithecine-like ancestor. This would require a pre-*Homo*
650 radiation out of Africa. If instead, it is accepted that *H. floresiensis* is an insular dwarf, a wider
651 range of phylogenetic scenarios are consistent with descent from an early *Homo* species, similar
652 in morphology to *H. habilis* or Dmanisi hominins, being most consistent with both patterns of
653 brain size evolution, cranial (Gordon et al., 2008; Martinez and Hamsici, 2008; Baab and
654 McNulty, 2009) and post-cranial morphological analysis (Tocheri et al., 2007; Jungers et al.,
655 2009a, b; Larson et al., 2007). Of course, the taxonomic affinities of *H. floresiensis* are still
656 debated (Kaifu et al., 2011) and many interesting questions about *H. floresiensis* remain
657 unanswered (Aiello, 2009). What were the selection pressures favoring body mass reduction and
658 how rapid was this change? What were the behavioural consequences of decreasing brain size
659 and what neurological adaptations evolved to off-set size reduction (Falk et al., 2005, 2009)?
660 What path out of Africa did the lineage leading to *H. floresiensis* take, and what drove this early
661 migration (Brown and Maeda, 2009; Wood, 2011)? How much contact did this small bodied
662 hominin have with modern humans (Aiello, 2009)? And what level of hominin diversity remains
663 to be discovered? One can only hope further paleontological finds in Flores and elsewhere
664 provides further resolution to the evolutionary history, phylogenetic affinities and phenotypic
665 adaptations of *H. floresiensis.*

666

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Figure legends

Figure 1: Estimated body masses for *H. floresiensis* using the brain:body scaling relationship from each mainland/island primate pairs. The range of estimates is shown for each assumed ancestor, given along the x-axis. The lower grey box gives the range of body mass estimates for LB1 derived from femoral cross-sectional area, the upper grey box gives the range derived from the femoral head diameter (Brown et al., 2004; Aiello, 2009).

Figure 2:

A) Relationship between R_{brain} and R_{body} for extant mainland-island pairs. The regression line is shown with the range of minimum and maximum residuals from the extant data (grey area). The R_{brain} and R_{body} for each ancestral hominin is shown across a range of body mass estimates for *H. floresiensis*, from 16-41kg (colored horizontal lines). Color coding: black = *A. africanus*; red = *A. sediba*; orange = *H. rudolfensis*; yellow = *H. habilis*; fuchsia = *H. ergaster*; green = Dmanisi hominins; dark blue = Ngandong *H. erectus*; light blue = *H. erectus s. l.*.

B) Leverage of *H. floresiensis* on the Relationship between R_{brain} and R_{body}. Cook's Distances were calculated for the *H. floresiensis* data point across a range of *H. floresiensis* body masses (0-45kg). The dashed grey line is the cut-off threshold above which the *H. floresiensis* data point has high leverage. Color coding is the same as panel A. Note that for *H. erectus* s. l., Ngandong *H. erectus* and *H. ergaster*, after the curve's peak the D_i begins to fall again (dashed lines), however this is because these data so strongly influence the regression that the slope of the relationship flattens and significance is lost.

Table 1: Phenotypic data for 7 pairs of insular primates and their closest mainland relative[1]

	Species	Brain mass [g]	Body mass [g]	EQ	N Brain mass[2]	N body mass[2]
Mainland	*Macaca mulatta*	92.188	6792.766	2.080	103 (44/59)	83 (37/46)
Island	*Macaca cyclopis*	84.952	5470.000	2.216	2 (1/1)	11 (7/4)
Mainland	*Macaca radiata*	77.569	5084.083	2.125	9 (6/3)	9 (6/3)
Island	*Macaca sinica*	72.207	4440.000	2.166	13 (12/1)	78 (23/55)
Mainland	*Macaca fascicularis fasicularis*	64.297	3950.314	2.086	72 (45/27)	67 (44/23)
Island	*Macaca fascicularis fusca*	68.140	5017.875	1.883	11 (7/4)	11 (7/4)
Mainland	*Presbytis femoralis*	76.390	6847.878	1.714	14 (9/5)	14 (9/5)
Island	*Presbytis natunae*	59.254	5065.333	1.627	3 (0/3)	4 (04)
Mainland	*Nasalis larvatus*	95.627	14560.724	1.294	45 (24/21)	37 (10/17)
Island	*Simias concolor*	60.528	7975.000	1.226	6 (3/3)	6 (3/3)
Mainland	*Trachypithecus johnii*	87.646	11600.000	1.382	1 (1/0)	10 (7/3)
Island	*Trachypithecus vetulus*	63.499	6237.000	1.517	6 (3/3)	6 (3/3)
Mainland	*Hylobates moloch*	106.708	6577.000	2.460	1 (1/0)	1 (1/0)
Island	*Hylobates klossii*	91.159	5795.000	2.288	6 (2/4)	6 (2/4)

[1] species pairs from Bromham and Cardillo (2007), phenotypic data from Isler et al. (2008);

[2] total number and number of males/females in brackets

Table 2: Phenotypic data for the hominin taxa used to model the descent of *H. floresiensis*

Grouping	Species/taxa	Body mass (kg)	Brain mass (g)	Notes and references
Homo erectus and allies	*H. erectus s.l.* (broadly defined)	60.0	1026.7	Following Martin et al. (2006); Stanyon et al. (1993) and Kappleman et al. 1996
	H. erectus (Ngandong)	60.0	1190.4	Following Martin et al. (2006); Stanyon et al. (1993) and Kappleman et al. 1996
	Dmanisi homoids	50.0	687.9	Following Martin et al. (2006); Vekua et al. (2002) and Rightmire et al. (2006)
	H. ergaster	58.0	884.7	Wood and Collard (1999)
Early *Homo*	*H. habilis*	32.6	571.9	Kappelman et al. (1996)
	H. rudolfensis	50.0	779.1	Kappelman et al. (1996); Robson and Wood (2008)
Australopithecines	*A. sediba*	33.6	435.1	Wood and Collard (1999)
	A. africanus	36.0	473.5	Carlson et al. (2011)

Table 3. Application of scaling models to extant mainland/island species pairs[1]

a) Non-primate models of insular dwarfism

	Island body mass	Martin et al.'s Model A b = 0.32-0.35		Weston and Lister, late ontogenetic b = 0.35		Weston and Lister, late ontogenetic + 30%[2] b = 0.35	
Species pair	[g]	estimate	%age error	estimate	%age error	estimate	%age error
Macaca mulatta/M. cyclopis	5470	5260.9-5377.4	3.8-1.7	5377.4	1.7	-	-
Macaca radiata/M. sinica	4440	4064.7-4143.4	8.5-6.7	4143.4	6.7	-	-
Macaca f. fasicularis/M. f. fusca	5018	4735.0-4662.0	5.6-7.1	4662.0	7.1	-	-
Presbytis femoralis/P. natunae	5065	3095.5-3313.5	38.9-34.6	3313.5	34.6	-	-
Nasalis larvatus/Simias concolor	7975	3487.3-3941.8	56.3-50.6	3941.8	50.6	10921.3	-36.9
Trachypithecus johnii/T. vetulus	6237	4236.7-4618.7	32.1-25.9	4618.7	25.9	-	-
Hylobates moloch/H. klossii	5795	4020.5-4193.7	30.6-27.6	4193.7	27.6	-	-

a) cont'd

	Island body mass	Weston and Lister, early ontogenetic b = 0.47		Weston and Lister, early ontogenetic +17%[2] b = 0.47	
Species pair	[g]	estimate	%age error	estimate	%age error
Macaca mulatta/M. cyclopis	5470	5708.0	-4.4	-	-
Macaca radiata/M. sinica	4440	4365.6	1.7	-	-
Macaca f. fasicularis/M. f. fusca	5018	4468.8	10.9	-	-
Presbytis femoralis/P. natunae	5065	3988.2	21.3	5928.6	-17.1
Nasalis larvatus/Simias concolor	7975	5502.9	31.0	8180.2	-2.6
Trachypithecus johnii/T. vetulus	6237	5842.9	6.3	8685.7	-39.3
Hylobates moloch/H. klossii	5795	4704.3	18.8	-	-

b) Intraspecific scaling models

Species pair	Island body mass [g]	Typical mammalian (Martin et al.'s Model B) b = 0.2-0.4		Non-human primates b = 0.124-0.349		Human (Martin et al.'s Model C) b = 0.03-0.17	
		estimate	%age error	estimate	%age error	estimate	%age error
Macaca mulatta/M. cyclopis	5470	4512.9-5536.8	17.5--1.2	3512.4-5373.8	35.8-1.8	444.7-4198.7	91.9-23.2
Macaca radiata/M. sinica	4440	3554.0-4250.7	20.0-4.3	2853.8-4141.0	35.7-6.7	467.4-3336.5	89.5-24.9
Macaca f. fasicularis/M. f. fusca	5018	5279.0-4566.4	-5.2-9.0	6306.0-4664.2	-25.7-7.1	27308.8-5556.2	-444.2—10.7
Presbytis femoralis/P. natunae	5065	1922.3-3628.2	62.0-28.4	882.3-3306.6	82.6-34.7	1.4-1536.2	100.0-69.7
Nasalis larvatus/Simias concolor	7975	1479.4-4641.2	81.5-41.8	364.2-3927.1	95.4-50.8	0.0-988.1	100.0-87.6
Trachypithecus johnii/T. vetulus	6237	2315.0-5182.2	62.9-16.9	862.2-4606.5	86.2-26.1	0.3-1742.0	100.0-72.1
Hylobates moloch/H. klossii	5795	2992.4-4436.4	48.4-23.4	1846.8-4188.3	68.1-27.7	34.5-2604.2	99.4-55.1

[1] percentage errors: 100 – [(estimate/observed)*100]

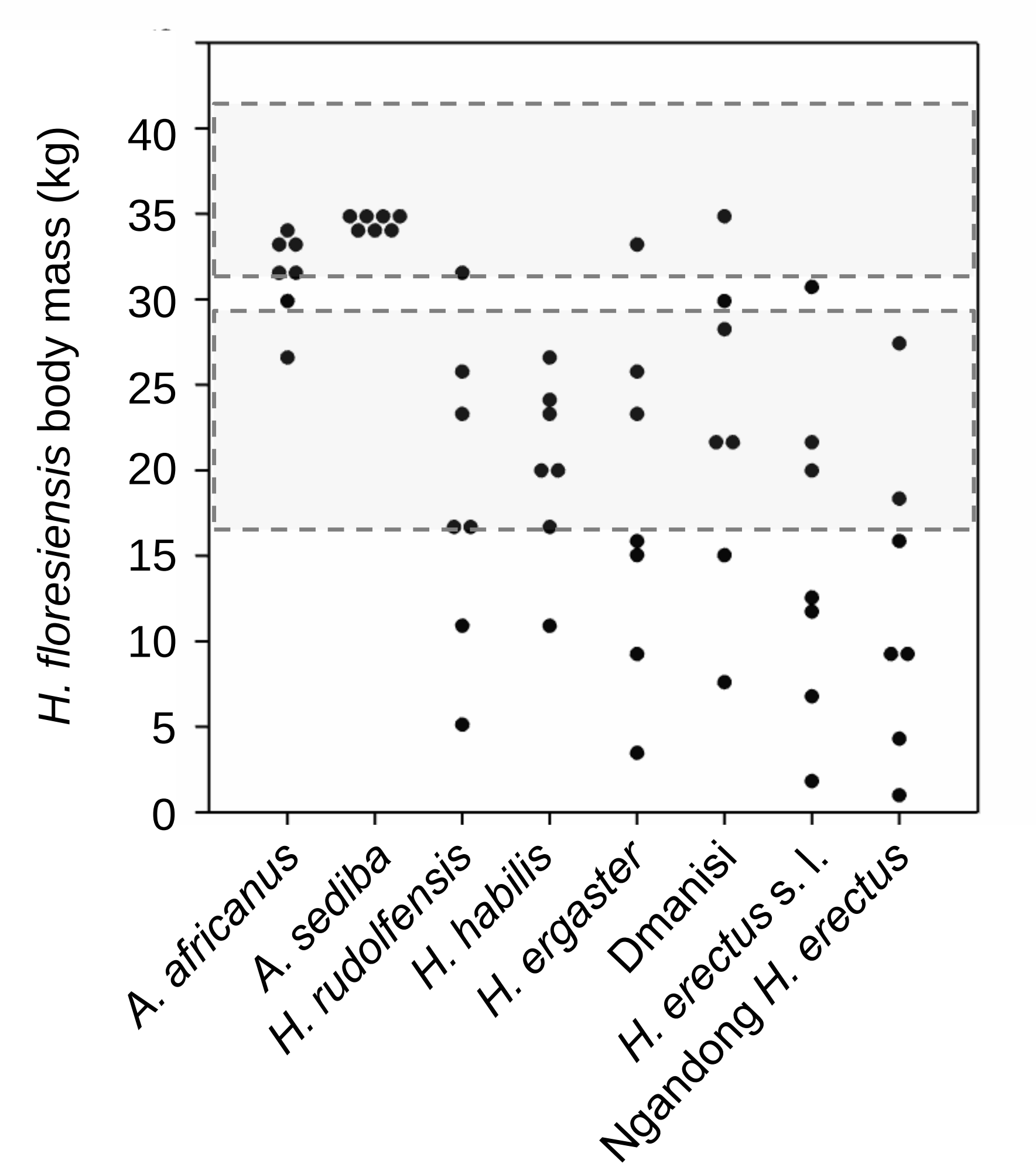
[2] results are only shown for pairs where the additional range does not result in the island species having a larger brain than the mainland species

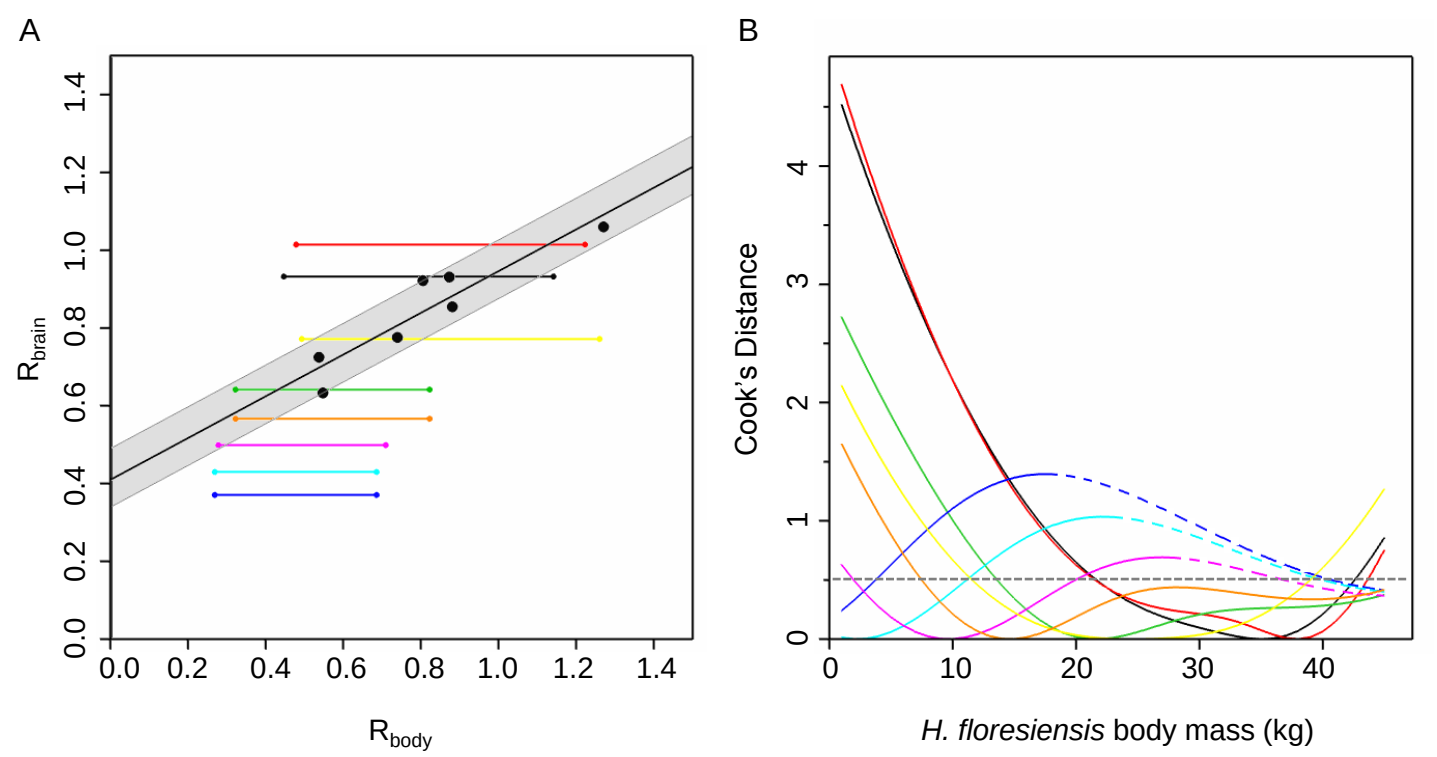
Table 4. Range of *H. floresiensis* body masses that produce low Cook's Distance values for each ancestor using the mean scaling component between mainland/island pairs of extant primates

	H. floresiensis body mass		
	Lower limit of range, $D_i < 0.5$	Upper limit of range, $D_i < 0.5$	Body mass at minimum D_i
Australopithecus africanus	22	42	35
Australopithecus sediba	22	43	38
Homo rudolfensis	8	>45	15
Homo habilis	12	38	25
Homo ergaster	<1	19	10
Dmanisi homoids	14	>45	22
Homo erectus s. l.	<1	11	2
Homo erectus (Ngandong)	<1	3	1

Table 5. Predicted *H. floresiensis* body masses that based on intraspecific scaling components and a range of ancestors

	Range of estimated body mass for *H. floresiensis* derived from scaling components (b)		
	Typical mammalian intraspecific scaling (b = 0.2-0.4)	Primate intraspecific scaling (b = 0.12-0.33)	Martin et al.'s human intraspecific scaling (0.03-0.17)
Australopithecus africanus	25.4 - 30.2	20.4 - 29.4	3.5 - 23.8
Australopithecus sediba	34.8 - 36.1	35.0-37.7	36.5 - 53.9
Homo rudolfensis	2.9 - 12.1	0.5 - 9.8	0.0 - 1.8
Homo habilis	8.9 - 17.1	4.0 - 15.5	0.0 - 7.1
Homo ergaster	1.8 - 10.2	0.2 - 7.9	0.0 - 1.0
Dmanisi homoids	5.4 - 16.5	1.4 - 14.0	0.0 - 3.7
Homo erectus s. l.	0.9 - 7.3	0.1 - 5.3	0.0 - 0.4
Homo erectus (Ngandong)	0.4 - 5.0	0.0 - 3.5	0.0 - 0.2


H. floresiensis body mass (kg)
0
5
10
15
20
25
30
35
40
A. africanus
A. sediba
H. rudolfensis
H. habilis
H. ergaster
Dmanisi
H. erectus s. l.
Ngandong H. erectus


A
B
R_{brain}
R_{body}
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
Cook's Distance
0
1
2
3
4
0
10
20
30
40
H. floresiensis body mass (kg)