HOMO FLORESIENSIS AS AN ISLAND FORM

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ABSTRACT

Homo floresiensis is a small bodied hominin from the Indonesian island Flores. The type specimen, LB1, is believed to be a female of approximately 1 m or a bit more than 3 feet in length with a cranial capacity of around 400 cc. There is still no agreement on the cause of the small stature and small cranial capacity of LB1 and the associated individuals. *Homo floresiensis* displays several island adaptations, which also have been observed among the members of other typical island faunas, indicating that *Homo floresiensis* might very well have been an endemic island form. *Homo floresiensis* has morphology similar to that of a *Homo erectus* juvenile, since it has a high orbital, dental and brachial index, low humeral torsion, low tibial torsion and a high gonial angle. Additionally *Homo floresiensis* has shortened lower limbs. The features displayed by *Homo floresiensis* give an indication of the manner of dwarfing by paedomorphosis, which was by truncating growth through increase in the rate of skeletal ossification, possibly caused by hormonal changes.

Introduction

Homo floresiensis is a small bodied hominin from the Indonesian island Flores. The type specimen, LB1, is believed to be a female of approximately 1 m in length with a cranial capacity of around 400 cc (Brown *et al.*, 2004; Falk *et al.*, 2005). There is still no agreement on the cause of the small stature and small cranial capacity of LB1 and the associated individuals. It is believed by some that *Homo floresiensis* is a descendant of *Homo erectus* or some other primitive hominin and derived the small stature and small cranial capacity by endemic island dwarfing (Brown *et al.*, 2004; Morwood *et al.*, 2005). Others believe that *Homo floresiensis* is a population of microcephales, or that LB1 is a microcephale from a population of pygmies (Richards, 2006; Jacob *et al.*, 2006).

That LB1 is a strange looking hominin from the island of Flores is agreed upon by the scientific community. However, whether his peculiarities are best described by island adaptations or pathology is currently the main focus of the scientific discussion.

LB1 could either have been a sick individual or a dwarfed descendant of *Homo sapiens*, or a dwarfed descendant of *Homo erectus*, or a descendant of an earlier hominin. The cranium of LB1 displayed many archaic features, such as a sloping forehead, browrides, the absence of a bony chin and the fact that the skull is widest at the level of the mastoids. Although these features are occasionally displayed by single individuals, there is not a single recorded case which reports all of these features combined in one *Homo sapiens*. This suggests that the combination of archaic features in LB1 is highly unlikely to have evolved from an endemic population of *Homo* sapiens or to have developed due to a disease in an individual of the species *Homo sapiens*. This suggests that the features found in *Homo floresiensis* are not due to having a *Homo sapiens* ancestry or being a sick individual of the species. Of the other two possibilities, the *Homo erectus* ancestry seems the most likely, because *Homo erectus* was the only known hominin in Southeast Asia around 800 ka, the time when Flores was first colonised (Brumm *et al.*, 2006).

Island adaptations of *Homo floresiensis*

If *Homo floresiensis* is indeed an island form we would expect it to display similar adaptations to other island animals. If LB1 is a pathological individual, we would expect it to display features characteristic of *Homo sapiens*, but also features characteristic of a certain disease. However, I have not been trained to adequately assess pathologies, so I will focus on the hypothesis that *Homo floresiensis* is an island form. Up until now no consistent pattern for island adaptations has been observed. This is due to the fact that each species adapts to different circumstances on different islands. However, what all island forms do have in common is that they adapted to their new environment by means of heterochrony and, in the case of large animals dwarfing, paedomorphism. So, all island animals look like the juveniles of the ancestral species. *Homo floresiensis* is hypothesised to have adapted to the island conditions of Flores by paedomorphism, just like the other island animals.

Research conducted on *Elephas cypriotes* (Bromage *et al.*, 2002) has revealed that this species of dwarfed elephant had approximately the same growth rate as its large relatives, but the growth was truncated at an earlier absolute age leaving the elephant smaller than its mainland counterparts. These conclusions are based on the striae of Retzius, which are caused by near-weakly periods of growth, and the cross-striations, which are daily periods of growth, in the molars. The distance between the striae of Retzius and the cross-striations are similar in *Elephas cypriotes* and *Elephas recki*, an indication of similar growth rates and an indication of paedomorphism. Because only a cast of the cranium and mandible of LB1 was available for this research, the striae of Retzius and the cross-striations could not be measured, since they are internal features of the enamel. Let us hypothesise that *Homo floresiensis* had increased the rate of bone development compared to its normal sized ancestor, thereby truncating growth, just like *Elephas cypriotes*, and see how that explains the features described below.

Methods

In order to investigate this several measurements have been taken and observations have been made from the cast of LB1 and photographs of LB1 and associated individuals. The

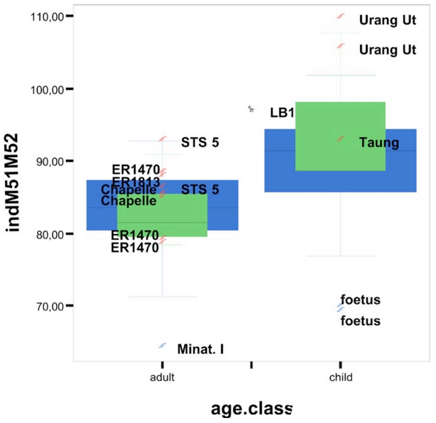

Figure 1: Boxplot of the right orbital index of *Homo floresiensis* and the combined left and right orbital indices of all other individuals. When *Homo floresiensis* is compared with *Homo erectus*, it falls within the middle 50% of children, but outside the range of adults. When *Homo floresiensis* is compared with *Homo sapiens*, it falls outside the range of adults but is clearly within the range of children. The ranges of children and adults overlap, but in general the orbital indices of children are higher than the orbital indices of adults. *Homo sapiens* is indicated in blue (wide), *Homo erectus* is indicated in green (narrow), all other species in red and the black dot is *Homo floresiensis* LB1.

measurements were made with a sliding caliper and with a combination of a protractor and a setsquare. Statistical analyses have been performed with SPSS. All the comparative material is stored in the National Museum of Natural History Naturalis in Leiden, the Netherlands.

Measures taken include orbital breadth, orbital height and mandibular angle (measurements 51, 52 and 79 from Martin, 1914). The cranial base length is the direct distance between the basion and the projected midpoints of the orbits on the orbit border on both sides. The dental length P3-M2 is the direct distance between the medial border of P3 and the distal border of M2. The orbital index has been calculated according to Martin (1914) and the dental index has been calculated as follows:

$$\text{dental index} = \frac{\text{dental length} * 100}{\text{cranial base length}}$$

Boxplots have been created in SPSS to assess whether the ranges of the data overlap and how the spread is. Furthermore, Student's t-tests have been performed to assess whether LB1 is significantly different from the comparative material. In the case of the mandibular angle the comparative sample has been assumed to be too small to conduct any valid statistical analyses.

Results

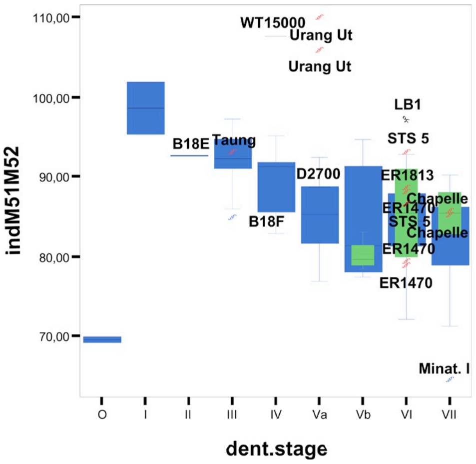

Figure 2: Boxplot of the right orbital index of *Homo floresiensis* and all other combined left and right orbital indices with an estimated age specification. *Homo floresiensis* falls within the ranges of the children of all age classes, but just outside the range of adults. The foetus forms an exception compared to the other children. *Homo sapiens* is indicated in blue (wide), *Homo erectus* is indicated in green (narrow), all other species in red and the black dot is *Homo floresiensis* LB1.

	age.class	N	Mean	Std. Deviation	Std. Error Mean
indM51M52	adult	72	832229	566520	66765
	child	46	905284	786752	116000
	Homo floresiensis	1	968454	-	-

Table 1: Group statistics of the orbital index per age class.

	age.class	adult	child	*Homo floresiensis*
indM51M52	adult	-	0.000	20
	child	-	-	431
	Homo floresiensis	-	-	-

Table 2: Significance of the 2-tailed independent samples T-test using the data of table 1. The hypothesis that *Homo floresiensis* has the same orbital index as children cannot be rejected, implying that *Homo floresiensis* has a pedomorphic orbital index

Cranial adaptations

The orbital index of *Homo floresiensis* clearly indicates that *Homo floresiensis* is more childlike than adultlike compared to its ancestor *Homo erectus.* A comparison can be made between the right orbital index of *Homo floresiensis* and the orbital indices of adults and children (figure 1). The right orbital index of *Homo floresiensis* falls within the middle 50% of *Homo erectus* children, but outside the range of *Homo erectus* adults for this sample. When *Homo floresiensis* is compared with *Homo sapiens,* it falls outside the range of adults and in the upper quartile of children. *Homo floresiensis*' orbital index is also closer to the median orbital index of children for both *Homo erectus* and *Homo sapiens,* than to the median orbital index of adults for both species in this sample. The orbital index of children in this sample is higher than of adults in this sample, but the ranges do overlap for a large part. According to this figure *Homo erectus*' median orbital index of this sample is lower than *Homo sapiens*' median orbital index of this sample, but their ranges overlap. The group statistics for the independent sample T-test are displayed in table 1, the results are displayed in table 2. Statistically the adults and children in this sample do not have the same orbital index, nor does *Homo floresiensis* have the same orbital index as adults. However, it is very well possible that *Homo floresiensis* does have a similar orbital index as children, because the hypothesis that they do, cannot be rejected. In this sample the highest orbital indices belongs to a baby with dental stage I, followed

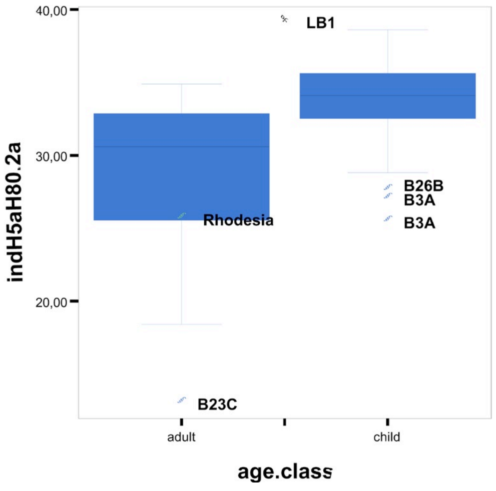

Figure 3: Boxplot of dental index 80(2)a. The mean of the dental index of *Homo floresiensis* lies closest to the mean of children, but does not fall within the range of children. It is, however much closer to the range of children, than to the range of adults. *Homo sapiens* is indicated in blue (boxplot), *Homo erectus* is indicated in green (Rhodesia), all other species in red and the black dot is *Homo floresiensis* LB1.

by a toddler with dental stage II, children with dental stages III and IV and adolescents with dental stage Va and the lowest orbital indices go with adults (figure 2). The right orbital index of *Homo floresiensis* falls within the range of the baby, children and adolescents, but outside the range of adults, the foetus or the baby B18E. The right orbital index of *Homo floresiensis* lies closest to the median orbital index of the baby with dental stage I.

The mandibular angle of *Homo floresiensis* ranges between 109° and 113°. This is much more comparable to juvenile *Homo erectus* than to either adult *Homo erectus* or juvenile or adult *Homo sapiens* (table 5).

Comparisons can be made of the endocast of *Homo floresiensis* with the endocasts of both healthy and microcephalic *Homo sapiens*, *Pan troglodytes* (chimpanzee), *Homo erectus*, as depicted in Falk *et al.* (2005, figure 1B) and with Mojokerto child (*Homo erectus* juvenile), as depicted in Balzeau *et al.* (2005, figure 7). LB1 lacks the occipital expansion over the cerebellum of the adult *Homo erectus* and its endocast is more brachycephalic. Mojokerto child also misses this occipital expansion, as do the healthy *Homo sapiens*, the microcephalic *Homo sapiens* and *Pan troglodytes*. The occipital lobes of healthy *Homo sapiens* are less posteriorly expanded than in *Homo erectus* and in *Pan troglodytes*, because of the relatively large development of the parietal lobes. This feature is absent in adult and juvenile *Homo erectus* and *Pan troglodytes* and also in LB1. LB1 has cerebellar lobes in a posterior position, under the occipital lobes, as is the case in *Homo erectus* and *Pan troglodytes*, whereas they are more anterior, under the parietal lobes, in *Homo sapiens*, both healthy and microcephalic. LB1's cerebellar lobes are separated by a large depression as in *Homo erectus*, but contrary to *Homo sapiens* and *Pan troglodytes*. The shape of the cerebellar lobes of LB1 is closer to *Homo erectus* than to *Homo sapiens*. Summarizing, the endocast of LB1 is more similar to *Homo erectus*, than to healthy or microcephalic *Homo sapiens*, or *Pan troglodytes*. And, the endocast of LB1 looks more like juvenile *Homo erectus* than adult *Homo erectus* with respect to the occipital expansion.

The sutures of the cranium of LB1 are highly obliterated compared to its dental age. Another feature of the cranium of LB1 also indicates retention of juvenile characteristics; the *canine fossa* is relatively deep, as is normally the case in juveniles (Kennis & Kennis, pers. comm.).

Palombo (2001) describes the paedomorphic features of the skull of *Elephas falconeri*. The brains are relatively large to maintain a minimal functional volume of the brain when the size of the skull is very reduced, because the brain size of normal sized elephants is relatively small already. Therefore the respiratory axis has a forward and downward inclination. *Elephas falconeri* has a proportional reduction

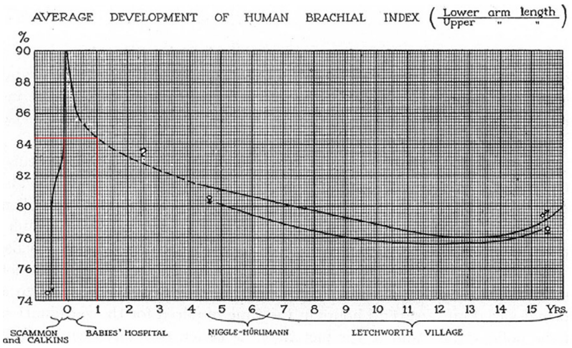

Figure 4: Development curve of brachial index from intrauterine life to puberty. Data have been taken from various sources as named. 0.5 to 5 years, data sparse. After Davenport (1934). The red lines indicate the position of *Homo floresiensis*. Using the data of Morwood *et al.* (2005) the brachial index of *Homo floresiensis* can be calculated by:

$$\frac{\text{length ulna} * 100}{\text{length humerus}} = \frac{205 * 100}{243} = 84.4.$$

	age.class	N	Mean	Std. Deviation	Std. Error Mean
indH5aH80.2a	adult	39	291478	558656	89457
	child	19	330728	341166	78269
	Homo floresiensis	1	391608	-	-

Table 3: Group statistics of the dental index per age class.

	age.class	Adult	Child	*Homo floresiensis*
indH5aH80.2a	adult	-	7	85
	child	-	-	99
	Homo floresiensis	-	-	-

Table 4: Significance of the 2-tailed independent samples T-test using the data of table 3. The hypothesis that *Homo floresiensis* has the same dental index as children cannot be rejected, but nor can the hypothesis that *Homo floresiensis* has the same dental index as adults.

of the facial region. Juvenile contemporaneous elephants exhibit skull morphology very similar to that of adults of *Elephas falconeri*. The orbital cavities of *Elephas falconeri* are very large and the zygomatic arches are very arched according to Palombo (2003). The adult specimens of *Elephas falconeri* display great similarity to the juveniles of contemporary elephants.

Sus nanus n. sp. from Northeast Sardinia is an endemic island species, which was described by Van der Made (1988). Its most probable ancestor is *Sus arvernensis*. *Sus nanus* is a little smaller than its ancestor, it is more hypsodont, its anterior premolars are reduced, its snout is shortened and the milk dentition is replaced at an earlier stage. The shortened snout of *Sus nanus* is a paedomorphic feature, because juveniles of mammalian species tend to have shorters snouts than their parents.

Both *Elephas falconeri* and *Sus nanus* display paedomorphic features in their skull morphology, just as *Homo floresiensis* does. The adaptations are not necessarily the same, but the patterns of cranial paedomorphic features should become clear from these examples.

Dental adaptations

The dental index of *Homo floresiensis* is closer to the range, median and mean of children than to the range, median and mean of adults (figure 3). The statistics displayed in tables 3 and 4 are not conclusive as to which group *Homo floresiensis* could belong to. *Homo sapiens* juveniles have statistically significantly different dental indices than adults. When *Homo floresiensis* is compared with adults and juveniles, *Homo floresiensis* has a statistically similar dental index to both juveniles and adults of *Homo sapiens*. Both dental indices of *Homo floresiensis* resemble the dental indices of children most. So the dental index gives the same result as the other features dealt with above and also indicates heterochrony.

Other island animals also have dental paedomorphic features, take for example *Myotragus*. In addition to its small size, *Myotragus* had only one incisiform dention with constantly growing incisors in both jaws obtained through a neotenic process, furthermore he had the eyes in a frontal position (Bover & Alcover, 1999b).

Postcranial adaptations

The most obvious change in the skeleton of *Homo floresiensis* compared to *Homo erectus* is the decrease in body size. Whereas *Homo erectus* had body sizes comparable to modern *Homo sapiens*, *Homo floresiensis* reached heights of around one meter.

Island dwarfing and island gigantism are biological phenomena by which the size of animals isolated on islands shrinks or increases dramatically over generations. It is a form of natural selection in which smaller or larger size provides a survival advantage. The underlying mechanism causing these changes in size is probably a tendency toward an energetically ideal surface content relation in mammals. On the mainland it is often not possible to possess this ideal surface content relation, because the presence of predators forces the animal to be larger or smaller than energetically ideal. On islands large endothermic predators are usually absent and the faunal assemblage is unbalanced, which opens up possibilities for animals to evolve towards the ideal size. Several examples are discussed below.

The Flores giant rat (*Papagomys armandvillei*) occurs on the island of Flores in Indonesia. Head and body length is 41-45 cm and tail length is 33-70 cm, making the Flores giant rat at least twice the size of an average brown rat (*Rattus norvegicus*) with a 25 cm long body and 15 cm long tail. The Flores giant rat is the only species in the genus *Papagomys* (Musser, 1981).

Dwarf elephants, mammoths and stegodonts are pre-historic members of the order *Proboscidea*, which, through the process of allopatric speciation, evolved to a fraction of the size of their modern relatives. Skeletal remains of dwarf elephants or mammoths have been found on the Mediterranean islands Cyprus (Bate, 1903; 1904a,b; Simmons, 1999), Malta (Falconer, 1868), Crete (Poulakakis *et al.*, 2002) and Sicily (Ambrosetti, 1968). Other islands where dwarf elephants or mammoths were found are Sulawesi (Van den Bergh, 1999), Flores (Van den Bergh, 1999; Van den Bergh *et al.*, 2001), Timor (Van den Bergh, 1999) and the Channel Islands of California (Agenbroad, 2003; Tikhonov *et al.*, 2003).

On Sulawesi and Flores there is a succession of distinct endemic island faunas with dwarfed Elephants and stegodonts until the Middle Pleistocene, which is described by Van den Bergh (1999). Around the early Middle Pleistocene new immigrants of large to intermediate size replaced the first population of dwarfed elephants. The present understanding of the succession of *Stegodon* species on Flores is that endemic dwarfs, represented by the Early Pleistocene species *Stegodon sondaarii* became extinct around 840.000 years ago. These dwarf forms were then replaced by the medium to large sized *Stegodon florensis*, a species closely related to the *Stegodon trigonocephalus* group found in Java and the Wallacea islands.

Evidently it is quite common for large endothermic species to become smaller as soon as they end up in an island environment. Hominins are no exception in this respect and when *Homo erectus* ended up on Flores the same could have happened to those individuals leading to *Homo floresiensis*. Apart from this change, more changes took place.

Age	**Angle (in °) of Homo sapiens**	**Angle (in °) of Pan troglodytes**	**Angle (in °) of Homo erectus**
Early embryo	130	No data	No data
Birth	140-145	No data	No data
Juvenile	128-133	121-129	107-113
Adult	120-127	108-120	97-108
Old age	117-124	No data	No data
After loss of teeth	124-131	No data	No data

Table 5: The ontogeny of the mandibular angle of *Homo sapiens, Pan troglodytes* and *Homo erectus*. *Homo sapiens* data from Moore and Lavelle (1974). *Pan troglodytes* data measured from specimens from the National Museum of Natural History Naturalis in Leiden, The Netherlands. Juvenile *Homo erectus* data consist of the following specimens: *Sinanthropus* BI: 107°; *Sinanthropus* FI: 112° (Weidenreich, 1936), KNM-ER820: 111°; D2735: 110° (estimated from photographs) and KNM-WT15000: 113° (measured from photograph). Adult *Homo erectus* data consist of the following specimens: *Sinanthropus* GI: 97°; *Sinanthropus* HI: 108° (Weidenreich, 1936) and KNM-ER992: 108° (estimated from photograph).

The right humerus of LB1 has relatively limited degree of humeral torsion according to Morwood *et al.* (2005). The humeral torsion is approximately 110°, which is less than in large bodied apes and humans (141-178°) and other known hominins (Evans & Krahl, 1945; Larson, 1988). In *Homo sapiens* juveniles also have lower humeral torsion than adults, so this feature could also be an indication of paedomorphism.

The tibial torsion of *Homo floresiensis* is 14°. This is rather low for an adult. The normal tibial torsion for adults lies between 18° and 23°, for newborns this torsion angle lies at 0° (http://www.univie.ac.at/cga/faq/torsion.html). The 14° tibial torsion of LB1 then clearly lies in the juvenile range. Of course this is compared with *Homo sapiens*, but *Homo erectus* had a very similar postcranial skeleton to *Homo sapiens* and no data were available for *Homo erectus*.

In other island animals there are also features of neoteny in the postcranial skeleton. A lack of humeral and femoral torsion in *Elephas falconeri* has been described by Palombo (2003). This is exactly the same adaptation as *Homo floresiensis* displays, indicating the same evolutionary pattern of heterochrony.

The brachial index of *Homo floresiensis* is similar to that of a child at birth or at the age of 1 year (figure 4). Morwood *et al.* (2005) already stated that the humerofemoral index is outside the range of (adult) *Homo sapiens*. Following the statement of Martin (1914) that during foetal life the arms are longer than the legs, at birth the arms and legs have approximately the same length, between the sixth and the ninth year the legs become longer than the arms and during adulthood the relation between arms and legs is 4:5; the intermembral index of *Homo floresiensis* is similar to children.

This same adaptation is not uncommon among island animals and has been encountered in among others *Myotragus,* which had modified limb bones that most likely restricted it to slow locomotion (Alcover *et al.*, 1981; Quetglas & Bover, 1998; Sondaar, 1977). *Myotragus* also had very robust extremities according to Alcover & Bover (2002).

LB1 has relatively thin cortical bone in the long bones according to Jacob *et al.* (2006). This feature is also present in people with osteoporosis type II (senile osteoporosis).

Discussion

This model of heterochrony due to increased ossification fits the data well. If it is assumed that this scenario is true then this essentially means that growth in *Homo floresiensis* was stopped at an absolutely earlier age, just like in the pygmy elephants of Cyprus (Bromage *et al.*, 2002) . This phenomenon is not unique and can actually be expected to occur in an island situation. In fact, all island forms display heterochronic or paedomorphic features, indicating that island animals adapt by means of heterochrony. The fact that *Homo floresiensis* also displays paedomorphic features, even though the features themselves do not necessarily need to be the same, lends support to the hypothesis that *Homo floresiensis* is indeed an island form.

Judging from the fact that *Homo floresiensis* had a relatively aged body in relation to true age compared to *Homo erectus*, *Homo floresiensis* probably became sexually mature relatively early as well, because otherwise it would not have had enough time to reproduce sufficiently. Thus the life history traits of *Homo floresiensis* must have been very different from the life history traits of *Homo erectus*, all the milestones were passed much sooner in absolute time.

The purpose of this heterochrony is fairly simple. Endemic island faunas are generally unbalanced, meaning that they lack mammalian predators and other animals such as birds and reptiles take over this ecological niche. However, fossil evidence suggests that the predation pressure of birds and reptiles does allow endemic island animals to change size and shape in contrast to mammalian predation pressure. Therefore, small body size is not only advantageous for *Homo floresiensis* energetically, but also ecologically possible due to the lack of mammalian predators. Furthermore relatively short legs are also advantageous in mountainous areas, such as Flores. The easiest way to obtain these two characteristics through only one adaptation is by making the rate of ossification increase. The increase in the rate of bone development would cause the sutures of the cranium to start closing at a younger absolute age, but also obliteration of the sutures would occur with increased speed. This would result in abnormally, at least compared to its ancestor, obliterated sutures in relation to the dental development. An increase in ossification would have given the humerus and tibia their permanent shapes before the muscles would have had time enough to induce the full amount of torsion. The relative lengths of the upper extremities and the lower extremities and the relative lengths of the upper arms and legs and the lower arms and legs also indicate paedomorphism. The bones have ossified before the legs were able to catch up with the arms or the upper arms and legs with the lower arms and legs. Furthermore an increase of ossification suggests that an increase of dissolution of bone might also occur, explaining the thin cortical bone in the long bones.

Burness *et al.* (2001) have made estimations of body mass of endothermic and ectothermic top herbivores and top carnivores. The top carnivore at the time of *Homo floresiensis* was the 70 kg *Varanus komodoensis* (komodo dragon). The top herbivore was a small *Stegodon*. The position of *Homo floresiensis*, likely omnivorous, is not dealt with directly in this article. However, the expected body mass of an endothermic top omnivore can logically be predicted to lie somewhere in between the values for endothermic herbivores and endothermic carnivores. Using the regression equations of Burness *et al.* (2001) *Homo floresiensis* should have a weight between 4.5 kg (carnivore) and 67.7 kg (herbivore) on an island the size of Flores. However, being an omnivore, *Homo floresiensis* is expected to have a weight approximately halfway these two values, which is close to 36 kg. Brown *et al.* (2004) have estimated LB1 to have had a weight between 16 and 36 kg. These values are very compatible with each other, making it likely that *Homo floresiensis* was about the right size for an omnivore on Flores.

There are several features of LB1, which are considered to be pathologies by some researchers. However, these features can all be explained in alternative ways.

Jacob *et al.* (2006), the most important opponents, have tried to make a case for the possible pathology of LB1. One of their arguments is that LB1 is very asymmetrical. Apart from the fact that most crania, which have been buried, are asymmetrical due to taphonomy, it is actually quite normal for crania to be asymmetrical (Martin, 1914). The asymmetries in the femora cannot be readily explained by deformation during burial, but the problem with these femora is that it is not proven that they belong to the same individual. It is likely that in any other situation the two femora would have been assigned to different individuals based on the different size and different morphology, which should also have been done in this case. Jacob *et al.* (2006) raise the question of contact between the populations of *Homo floresiensis* and *Homo sapiens*. It is highly likely that *Homo floresiensis* and *Homo sapiens* have had contact with each other; however, this does not imply that there was also sexual intercourse and if so, that they had fertile offspring. It is not unlikely that *Homo floresiensis* and *Homo sapiens* were different to such a great extent that they may not have recognised each other as potential sexual mates. This of coarse does not consequently mean that *Homo floresiensis* might not have learned from the habits of *Homo sapiens*, explaining cultural similarities. Physical similarities on the other hand can better be explained by analogous evolution, than by interbreeding. Both *Homo floresiensis* and *Homo sapiens* in that region have adapted to the same environment. The claim that the first *Homo erectus* individuals to live on the island would have been a highly isolated inbred population and that they would have been adaptively constrained by a consequently narrow gene pool, is not valid. *Stegodon* migrated to Flores as well, so they too must have had a very small population in the beginning, but they managed very well to adapt to their environment. Many other animals, which have migrated to islands, all started out as a small population, but they all adapted very well. The statement of Jacob *et al.* (2006) that Flores is too small to sustain a viable population is based on the following. They state that the conventional figures for population densities at hunter-gatherer subsistence level is one person per 25-2,5 km^2, however they do not give any reference for this. However, Binford (2001) cites 19 hunter-gatherer populations with more than one person per 1 km^2, so other figures that the one mentioned by Jacob *et al.* (2006) are clearly possible. In fact equatorial hunter gatherer population with semisedentary settlements that do not move as part of a groups positioning strategy throughout the year and from which subsistence activities are launched, and which are mainly dependent on terrestrial plants have a mean population density of one person per 2.0 km^2 (Binford, 2001), which is also higher than the figures mentioned by Jacob *et al.* (2006). Using the figure of one person per 25-2,5 km^2 Jacob *et al.* (2006) come up with a one-generation total census population size of 570-5700 people, which is lower than the minima estimated for survival of vertebrate populations over 40 generations (5816-7316; Reed *et al.*, 2003). However, the difference is only 116 persons, which does not seem to be a very large difference, especially not in the light of the fact that Jacob *et al.* (2006) only quote the figures by Reed *et al.* (2003) for estimates of minimum population size, whereas other studies have given estimates of minimal population sizes varying between 2000 and 5500 individuals (Franklin, 1980; Newmark, 1987; Thomas, 1990; Schultz & Lynch, 1997; Reed & Bryant, 2000; Whitlock, 2000). Using any one of these other estimates would result in the conclusion that *Homo floresiensis* was indeed capable of sustaining a viable population on Flores. Furthermore, the small size of *Homo floresiensis* and its small brain size would have lowered its energy requirements and allowed it to sustain higher population densities than normal sized *Homo sapiens*.

The statement of Jacob *et al.* (2006) that it is impossible for *Homo erectus* to have reached Flores only once, because members of the genus *Stegodon* have reached the island at least twice, is an illogical consideration. The first migration of *Stegodon* to Flores occurred before the presence of *Homo erectus*, or any other known hominin, in the region (Van den Bergh, 1999). In the period in which *Homo erectus* was present in the region and migration was possible, *Stegodon* only migrated once, making it very plausible that *Homo erectus* also only migrated once.

Martin *et al.* (2006) compare the skull and endocast of *Homo floresiensis* with two microcephales. They conclude that the size and shape of the cranium of *Homo floresiensis* is very similar to one of these individuals. Therefore they think it is likely that LB1 also suffered from this disease. However, the way they make this comparison is not unambiguous. They compare the right side of the cranium of LB1 with the left side of a microcephalic cranium and with two endocasts. It is hardly possible to compare a cranium with an endocast, because the two are clearly not the same.

If LB1 would have been a case of pathology we would at least expect it to display the features characteristic of *Homo sapiens*. However, LB1 and LB6 both do not display a bony chin. Furthermore LB1 has a receding forehead, characteristic of *Homo erectus* and other ancient hominins, not *Homo sapiens*. LB1 has widest width of the skull at the level of the mastoid process and brow ridges, both features which have disappeared in *Homo sapiens*. LB1 has a very thick cranium, but no occipital bun. The face is slightly prognathic. Additionally, *Homo floresiensis* has a shoulder morphology comparable to that of Nariokotome boy (Larson *et al.*, 2007). All these features indicate that LB1 and associated individuals do not belong to the species *Homo sapiens*, but physically resemble *Homo erectus* or perhaps another earlier hominin.

Conclusion

Under the assumption that *Homo floresiensis* is indeed a descendant of *Homo erectus* and has adapted to the island environment on Flores, nearly all morphological features of *Homo floresiensis* can be explained, at least the ones that are claimed to be evidence of pathology. The process responsible for these island adaptations is heterochrony, resulting in paedomorphic features.

So, in conclusion it can be stated that *Homo floresiensis* is most likely a case of adaptation to the island environment of Flores by means of heterochrony. The rate of ossification is increased, thereby giving *Homo floresiensis* paedomorphic features. *Homo floresiensis* was a bipedal, healthy individual and probably a descendant of *Homo erectus*.

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