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The hominins of Flores: Insular adaptations of the lower body

Les hominins de Flores : adaptations du corps aux conditions insulaires

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ABSTRACT

The fossil remains of *Homo floresiensis* have been debated extensively over the past few years. This paper will give a brief summary of the current debate, which can be summed up in three main competing explanations for the morphology of the type specimen: pathology, descendent of an early australopith-like hominin, or insular descendent of *H. erectus*. This paper will make a case for island dwarfing being the most plausible scenario, with *H. erectus* as the mainland ancestor. Additionally, the morphology of the pelvis and lower limbs are compared to other insular vertebrates and interpreted in terms of function and adaptation to the island environment of Flores.

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RÉSUMÉ

Les restes fossiles d'*Homo floresiensis* ont été abondamment discutés au cours de ces dernières années. Cet article présente un bref exposé du débat actuel qui peut se résumer par trois principales explications sur la morphologie du spécimen-type: la pathologie, la descendance d'un homininé proche des premiers australopithèques, la descendance d'*Homo erectus* sous des conditions insulaires. Cet article traitera particulièrement du nanisme insulaire considéré comme le scénario le plus plausible avec *Homo erectus* pour ancêtre continental. La morphologie du pelvis et des membres inférieurs sont également comparée à celle des autres vertébrés insulaires et interprétée en termes de fonction et d'adaptation à l'environnement insulaire de Flores.

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1. Introduction

Everybody knows what hobbits are. Whether you have read or seen *Lord of the Rings*, followed the scientific debate on *Homo floresiensis*, or both, we all agree they

are small. And that is exactly where the agreement stops and the discussion begins. LB1, the type specimen, has too many interesting, or even unexpected, features to be easily explained (Fig. 1).

LB1 was found in Liang Bua, a cave on western Flores, together with the remains of several other individuals. In the Middle and Late Pleistocene Flores was inhabited by pygmy and dwarfed *Stegodon*, giant rats, and Komodo

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Fig. 1. The skeleton of LB1, type specimen of *Homo floresiensis*, courtesy of W. Jungers.

Fig. 1. Le squelette LB1, spécimen type d'*Homo floresiensis*, avec l'aimable autorisation de W. Jungers.

dragons (Meijer et al., 2010; van den Bergh, 1999; van den Bergh et al., 2009) in addition to the hominins. The type specimen of these hominins was approximately 1 m tall and 25–40 years old at the time of death 18 ka (Brown et al., 2004; Jacob et al., 2006). Although this is small for modern human standards, LB1 was actually relatively large compared to the other individuals from Liang Bua. The endocast shows a particularly small brain and the limb proportions are unlike those of any modern human (Brown et al., 2004; Morwood et al., 2005). Additionally, the wrist and ankle bones show a mixture of derived and primitive features (Jungers et al., 2009b; Tocheri et al., 2007).

As is generally the case with island animals in unbalanced island faunas, an overall confusion characterises the scientific communications on *H. floresiensis*. All possible explanations, hypotheses, and theories can be summed up in three main categories: pathology, descendant of an early australopith-like hominin, or insular descendent of *H. erectus*. In this article, the available fossil material is summarised, the three possibilities are assessed, and new interpretations of the morphology of the lower body are given.

2. Fossil evidence

Elaborate descriptions of the fossil material recovered from Liang Bua and its stratigraphical context have been given in a special issue of the *Journal of Human Evolution* (Brown and Maeda, 2009; Falk et al., 2009; Jungers et al., 2009a; Larson et al., 2009; van den Bergh et al., 2009; Westaway et al., 2009a, 2009b). The skeleton of LB1 is depicted in Fig. 1 and a brief summary is given below.

Only one cranium has been found in Liang Bua cave so far, belonging to LB1. According to its craniodental morphology it is most likely a member of the genus *Homo* (Brown et al., 2004). LB1 has a short and relatively orthognathous face with small cheek teeth compared to *Australopithecus*. LB1 lacks both upper third molars, the right congenitally and the left premortem, and shows rotation of the fourth upper premolars on both sides of the jaw. Additionally, it has a long and low cranial profile, mound-like occipital torus, mastoid fissure, and the maximum cranial breadth is in the supramastoid region. The frontal bone is rather narrow with a relatively great constriction across the frontotemporale. Furthermore, the cranial vault bone is relatively thick, but lies within the range of both *H. erectus* and *H. sapiens*, and is thickened posteriorly and in areas of pneumatization in the lateral cranial base (Brown et al., 2004). LB1 has a narrow foramen magnum. The canine fossae of LB1 are relatively deep with large infra-orbital foramina, and the canine juga are pronounced. LB1 has a sloping forehead and brow ridges that arch over the orbit. The orbits have a particularly arched superior border. LB1 has a projecting occipital, but no occipital bun. The masticatory apparatus is similar to that of the members of the genus *Homo*. Some asymmetry occurs in the LB1 cranium (Jacob et al., 2006). However, the degree is not beyond what might be expected in an archaic hominin population, especially when taphonomic processes are taken into account, which are more likely to be the cause than developmental processes (Baab and McNulty, 2009). The LB1 cranium shows several pathologies, which have been described elaborately elsewhere (Jacob et al., 2006).

Since only one skull has been found in Liang Bua so far, there is also only one cranial endocast. The small cranial capacity of LB1 and relative brain size are similar to those found in apes and australopiths (Falk et al., 2005). However, the endocast resembles that of *H. erectus* in its relative height, the relative widths of its caudal and ventral surfaces and its long, low lateral profile (Falk et al., 2005). LB1's endocast is extremely brachycephalic because of lateral expansion of the caudal part of the temporal lobes. LB1's frontal lobes lack the ape-like orbitofrontal

sulci (Falk et al., 2009). Its relative frontal breadth and lack of cerebellar protrusion are more similar to healthy *H. sapiens* than microcephalic *H. sapiens* (Falk et al., 2007). LB1's virtual endocast shows a highly convoluted cerebral cortex with a unique combination of derived features (Falk et al., 2005, 2009). In LB1, the occipital lobe extends caudally relative to the cerebellum without the presence of an occipital expansion. In this respect, the endocast of LB1 resembles the endocast of juvenile *H. erectus* more than that of adult *H. erectus* (van Heteren, 2008). LB1 has a laterally expanded prefrontal region. Two distinct gyri that border the midline in the rostral prefrontal cortex at the tip of LB1's frontal poles, which are identified as Brodmann's area 10, are expanded too (Falk et al., 2005).

Two mandibles have been found to date, belonging to LB1 and LB6. The mandibular angle of *H. floresiensis* ranges from 109° to 113° (van Heteren, 2008; van Heteren and de Vos, 2007; van Heteren and Sankhyan, 2009). The averaged mandibular angle for LB1 is 111°, whereas LB6 has a mandibular angle of 112° (van Heteren, 2008; van Heteren and Sankhyan, 2009). The mandibular angle is more comparable to juvenile *H. erectus* than adult *H. erectus* or *H. sapiens* (van Heteren, 2008). Both mandibles lack a mental tuberosity, and they are relatively robust relative to their body mass. The bifurcated mandibular third premolars (Brown et al., 2004) have also been suggested to be deciduous molars (Obendorf et al., 2008).

The skeleton of LB1 includes a partial clavicle and a nearly complete humerus. The scapula of LB6 is also available. The right humerus of LB1 has a relatively limited degree of humeral torsion (Larson et al., 2007b; Morwood et al., 2005). Estimates of the humeral torsion vary between 110° and 120° (Larson et al., 2009; Morwood et al., 2005). The clavicle of LB1 appears to be relatively short (Larson et al., 2007b). The scapula might have been more protracted than in modern humans, resulting in an anteriorly facing glenoid fossa. A low humeral torsion in this configuration would have resulted in a 'normal' position of the arm.

Portions of both the left and the right ulnae of LB1 are preserved. The right ulna is nearly complete. The shaft displays an anteroposterior curve, which is anteriorly concave, and has a rounded contour (Larson et al., 2009). The left ulna of LB6 is missing the distal end (Larson et al., 2009). A radius of LB6 has also been recovered from the sediments. The distal end is highly distorted and probably the result of a fracture (Larson et al., 2009; Morwood et al., 2005). Five carpals belonging to the type specimen have been recovered, all from the left wrist (Tocheri et al., 2007). A three-dimensional quantitative comparative analysis of the scaphoid, trapezoid and capitates showed that these carpals display a symplesiomorphic pattern of features similar to African apes, *H. habilis* and australopiths (Tocheri et al., 2007).

The left os coxae of LB1 is relatively complete, the right is more fragmentary. The ilium exhibits comparatively much lateral flare relative to the acetabulum (Brown et al., 2004; Jungers et al., 2009a). The width of the greater sciatic notch falls in the range of modern human females (Jungers et al., 2009a), but is relatively narrow compared to australopiths (Häusler and Schmid, 1995). The iliac blade is relatively

short and wide, and the ischial spine is not very pronounced (Brown et al., 2004).

Both left and right femora of LB1 have been preserved, the left being more complete. The shafts of the femora are relatively robust. The collodiaphysal angle is approximately 128–130° (Brown et al., 2004; Jungers et al., 2009a). The femoral bicondylar angle is 14° (Brown et al., 2004).

The tibial torsion of *H. floresiensis* has been measured to be 14° (van Heteren, 2008); this is not confused with the femoral bicondylar angle as Jungers et al. (2009a) state, which could have been clear from the subsequent reference. The tibial torsion measurement was taken from proximal and distal photographs with a horizontal reference line, but admittedly could have been influenced by image distortion or measurement error. However, at the time of publication (van Heteren, 2008), the data of Jungers et al. (2009b) were not yet available, and this was as good an approximation as possible at that time. Although Jungers et al. (2009a) only mention that the "Angular torsion of the distal articular surface relative to the proximal end in LB1/13 appears positive but very low compared to most modern humans (cf. Wallace et al., 2008)", Jungers et al. (2009b) state in an earlier publication that the tibial torsion is 5–7°. Wallace et al. (2008) in turn refer to Le Damany (1909) and Bello y Rodriguez (1909). It was impossible for the author to verify the angles and references (Bello y Rodriguez, 1909; Le Damany, 1909) mentioned by Wallace et al. (2008), but based on other more recent data available to the author (Kristiansen et al., 2001; <http://www.univie.ac.at/cga/faq/torsion.html>), it seems that these ranges (Bello y Rodriguez, 1909; Le Damany, 1909) are inclusive of children, and as such unsuitable for comparison with an adult fossil individual like LB1. Thus, tibial torsion in *H. floresiensis* (Jungers et al., 2009b; van Heteren, 2008) is rather low compared to modern humans (Kristiansen et al., 2001; <http://www.univie.ac.at/cga/faq/torsion.html>), but comparable to Dolí Věstonice 13 (Trinkaus, unpublished data, in Wallace et al., 2008). The tibial shafts are oval in cross section, which also suggests a very small torsion angle.

The skeleton of LB1 includes a relatively complete left foot and parts of a right foot (Jungers et al., 2009b). The feet of LB1 clearly are very different from modern feet. The feet are approximately 70% of the femur length (Jungers et al., 2009b). This is relatively large compared to modern humans (54%) and comparable to bonobos (*Pan paniscus*) (74%) (Jungers et al., 2009b). The first metatarsal is relatively short compared to the other metatarsals and without sesamoid grooves (Jungers et al., 2009b). The metatarsals of LB1 are long relative to tarsal length, and the proximal phalanges are long relative to the metatarsals (Jungers et al., 2009b).

3. Competing theories

3.1. Diseased *Homo sapiens*

Theoretically, it would be possible that the distinctive morphology observed in LB1 is pathological and many different possibilities and arguments have been given over time. A very exhaustive and one of the first opponents of

the new species theory, [Jacob et al. \(2006\)](#), have tried to make a case for the possible pathology of LB1 and many have followed after them (e.g., [Martin et al., 2006b](#); [Oxnard et al., 2010](#)). One of their arguments is that LB1 is very asymmetrical, which may be an indication of growth anomalies. Aside 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](#)).

Another one of their arguments is that the neurocranium and the face of LB1 have archaic features which are all encountered routinely among Australomelanesians ([Jacob et al., 2006](#)). Their research ([Jacob et al., 2006](#)), for example, shows that 93.4% of the Rampassassa pygmies, which live on Flores close to Liang Bua cave, where *H. floresiensis* was found, have a neutral or negative chin. However, this was determined from photographs of living humans on which the bony structures cannot be seen, because they are covered with flesh. And, although each archaic feature may separately be encountered amongst modern populations, there is no record of one individual having all the reported archaic features.

They also note possible pathologies on the postcranial remains ([Jacob et al., 2006](#)). The right humerus shaft reportedly has very weakly marked muscle attachment sites and the deltoid tuberosity is nearly absent ([Jacob et al., 2006](#)). [Morwood et al. \(2005\)](#) have reported that the humeral torsion of 110° falls below the hominin range, and [Jacob et al. \(2006\)](#) conclude from this that the low humeral torsion of *H. floresiensis* is caused by a lack of muscle development. The tibial shafts are oval in cross section, suggesting to them ([Jacob et al., 2006](#)) a compromise between the need to support and move body mass and generally weak muscle development. CT scans of diaphyses have been reported to show thin cortical bone and very large marrow cavities ([Jacob et al., 2006](#)), used as further evidence that LB1 was abnormal. However, the arguments of [Jacob et al. \(2006\)](#) concerning the postcranial and cranial material from Liang Bua are based on several misconceptions about the postcranial skeleton, such as the degree of left/right asymmetry and the cortical bone thickness ([Larson et al., 2007a](#)).

A disease like microcephaly has been proposed as an explanation for the small brain size of LB1. [Henneberg and Thorne \(2004\)](#) have used measurements of a 4000-year-old Minoan microcephalic cranium and LB1 to make a statistical comparison of the two. They conclude that it cannot be rejected that LB1 and the Minoan microcephalic belonged to the same microcephalic population. Additionally, [Weber et al. \(2005\)](#) state that they find it possible that LB1 was a microcephalic, based on a comparison of the endocast of LB1 with the endocasts of 19 modern microcephalics. [Martin et al. \(2006a, 2006b\)](#) compare the skull and endocast of *H. floresiensis* with microcephalics, and they also come to the conclusion that the size and shape of the cranium of *H. floresiensis* is very similar to one of these individuals. Therefore, they think it is likely that LB1 suffered from this disease as well. However, these assessments are mainly based on absolute dimensions, and ratios of dimensions, whereas the morphology of the endocast and the cranium are at least as important. For example, the maximum cranial breadth may be similar in size for LB1 and a microcephalic individual, but if they occur at a differ-

ent position on the skull there is actually no similarity at all.

Laron Syndrome has also been proposed as a possible pathology for LB1 by [Herschkovitz et al. \(2007\)](#). The morphology of patients with Laron Syndrome has been compared with LB1 both quantitatively and qualitatively leading to the conclusion “that LB1 is but a local individual in a highly inbred, probably pygmy-like population (of *Homo sapiens*) in whom a mutation of the GH receptor had occurred”. However, [Herschkovitz et al. \(2007\)](#) write that “for comparative purposes we used photographs of “normal” sized skulls of LS individuals, not the microcephalic cases”. A comparison between LB1 and a microcephalic LS patient would have been more appropriate, since this is the affliction they propose. The current comparison casts doubt on whether both microcephaly and the other reported cranial features are actually encountered in the same individuals. In addition to this, they mention several other similarities between LB1 and patients with Laron Syndrome that do not match clinical literature. They write that patients with Laron Syndrome have abnormal limb proportions with disproportionately short legs ([Herschkovitz et al., 2007](#)). [Rosenbloom et al. \(1996\)](#) have, however, determined that adults with the syndrome have relatively short arms. [Herschkovitz et al. \(2007\)](#) also state that the maximum cranial breadth is in the mastoid region, whereas radiographs [[Laron et al., 1996](#), p. 14, fig. 11] show that the maximum cranial breadth is at the parietals, which is comparable to healthy *H. sapiens*. And, there are also several features displayed by LB1, which are not mentioned by [Herschkovitz et al. \(2007\)](#), that also do not fit the diagnosis of Laron Syndrome. In LB1, the sutures are almost completely obliterated ([Brown et al., 2004](#)), whereas in Laron Syndrome patients, microcephaly is accompanied by delayed closure of the sutures ([Kornreich et al., 2002](#); [Laron et al., 1996](#)). A craniofacial feature of LB1 is that it has a sloping forehead ([Brown et al., 2004](#)), Laron Syndrome patients on the other hand have a very prominent forehead ([Rosenbloom et al., 1996](#)). Another feature of LB1 is that it has a relatively short first metatarsal and relatively large feet ([Jungers et al., 2009b](#)), whereas malformations of patients with Laron Syndrome include a short fourth metatarsal and relatively small hands and feet ([Laron et al., 1996](#)). The diagnosis of Laron Syndrome, thus, does not match the morphology of *H. floresiensis*.

Yet other researchers have proposed hypothyroid or myxoedematous cretinism as the disease from which LB1 suffered ([Obendorf et al., 2008](#); [Oxnard et al., 2010](#)). According to them, the cause for cretinism on Flores is the lack of iodine and they support this by stating that no marine food remains have been found in Liang Bua. Although this is true ([van den Bergh et al., 2009](#)), research on Pleistocene caves has shown that caves may only be used seasonally (e.g., [Marín Arroyo and González Morales, 2007](#); [de Lumley et al., 2004](#)) and a lack of marine fossils in Liang Bua does not necessarily mean a lack of marine resources in the diet of the occupying hominins; only further zooarchaeological research will be able to determine whether Liang Bua was used as a long duration habitat, a temporary seasonal habitat, or a hunting stopover. LB1 groups with ME cretins in the morphometric analysis of [Obendorf](#)

et al. (2008). However, the three other fossil hominins included in their analysis also consistently group with the microcephalics even though they are not considered to be unhealthy. This clearly shows that their analysis is not suitable for distinguishing between healthy and unhealthy hominins. All their study indicates is that LB1 does not resemble a healthy *H. sapiens*. And there are several other problems with the cretinism hypothesis. The main argument for the hypothyroid cretinism hypothesis is that the pituitary fossa of LB1 is relatively large (Oxnard et al., 2010), which is not true. Although the area is damaged (Jungers et al., 2009c), the pituitary fossa is small if anything (Holloway in Wong, 2008). The authors (Oxnard et al., 2010) also cannot convincingly explain the small brain size of LB1. They make an educated guess that cretins derived from an endemic pygmy population might have brain sizes as small as that of LB1, but they fail to provide a single example. Oxnard et al. (2010), furthermore fail to take allometry into account in all their calculations. They use ratios, which eliminate size, but not allometry, which might influence the results greatly when the analyses deal with such a large range of sizes. One of the postcranial features which is supposed to support the cretin hypothesis is that the wrist bones of LB1 resemble those of cretins (Oxnard et al., 2010). However, their main argument that the trapezoid is bipartite is, again, false (Jungers et al., 2009c; Tocheri et al., 2007). Additionally Oxnard et al. (2010) write that Professor Alan Cooper has stated that “So far, however, only modern human DNA sequences have been found, consistent with handling of the specimens by multiple individuals prior to sampling”, they continue to write that it is likely that the modern human DNA sequences found, actually did belong to the fossil specimens and that this may be an indication that the fossils belong to pathological *Homo sapiens* instead of a new species. Another enquiry with Professor Alan Cooper (pers. comm.), however, resulted in the following statement: “The situation for any ancient specimen that has been handled by excavators, archaeologists, museum curators etc. is that it is expected to be contaminated with modern human DNA, which will generally be in relatively good condition (in comparison to the trace amounts of short, damaged fragments of ancient DNA). Hence, finding modern human DNA sequences in the hobbit material is totally expected, as no explicit steps were taken to limit contamination of the material. Furthermore, because we detected multiple modern human sequences in the samples, they are clearly due to contamination. This result says nothing about the hobbit being an extinct hominin, or otherwise.”

There are also several issues surrounding the (a)symmetry of the LB1 cranium. Most authors acknowledge some degree of asymmetry (Baab and McNulty, 2009; Brown et al., 2004; Eckhardt and Henneberg, 2010; Eckhardt et al., 2010; Jacob et al., 2006; Kaifu et al., 2010), which is sometimes ascribed to antemortem developmental problems and sometimes to postmortem deformation. Falk et al. (2010) give an elaborate description of the conditions under which the cranium of LB1 was found, from which it is clear that postmortem deformation is most likely responsible for at least some of the asymmetries found in the cranium of LB1. Additionally, they point out

severe weaknesses in the methodology for assessing the degree of asymmetry of Jacob et al. (2006).

So far, all proposed pathologies for LB1 have been refuted based on the skeletal evidence available (Argue et al., 2009; Brown and Maeda, 2009; Jungers et al., 2009c; Tocheri et al., 2007). It therefore seems highly unlikely that LB1 suffered from any currently known disease and one of the new species hypotheses should be accepted as being most likely.

The claim that the first *H. 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 (Jacob et al., 2006), is not valid either. *Stegodon* migrated to Flores as well (van den Bergh, 1999; van den Bergh et al., 2009); they too were a very small population in the beginning, but they adapted to their new environment. Many other animals that have migrated to islands started out as small populations, but they all adapted (van der Geer et al., 2010). There is no reason why hominins would not also be capable of adaptation. In fact, the small genetic variation expected in such a founder population increases the probability of evolution taking a different course than on the mainland.

3.2. Early hominin ancestry

A currently popular alternative is that *H. floresiensis* is a new species derived from some early australopith-like hominin. At present, there is no evidence for such a hominin in Asia, but its presence has been hypothesised by several authors on the basis of the Flores finds (Argue et al., 2009; Brown and Maeda, 2009; Jungers et al., 2009c). Recently, an elaborate review of the current debate has led to the conclusion that the most economical explanation for the morphology of *H. floresiensis* is that it is a descendent of an early australopith-like hominin (Aiello, 2010). *H. floresiensis* possesses both derived and primitive characters, and the presence of primitive characters mainly drives the hypothesis that *H. floresiensis* could not have been a descendant of *H. erectus*, but must have had an earlier, more primitive ancestor. The morphology of the wrist and foot bones also supports this view according to some (Jungers et al., 2009b; Tocheri et al., 2007).

Although there is not a complete *H. floresiensis* pelvic girdle available, the morphology of the parts which are available suggests great similarity with australopiths. This, together with other evidence, has contributed to the idea that *H. floresiensis* is a direct descendent of an australopith (or very early *Homo*) (Aiello, 2010). The pelvis, however, is not very suitable for phylogenetic investigations, because it has an important function in locomotion and child-birth, and as such is likely to be under high selection pressures.

Brown and Maeda (2009) believe that, considering the mandibular morphology, relative limb proportions, skeletal robusticity, wrist function and brain size, it is unlikely that *H. floresiensis* is an insular dwarf that is descended from *H. erectus*. LB1 has the limb proportions and endocranial volume of an African Pliocene *Australopithecus* (Morwood et al., 2005). And the two mandibles of *H. floresiensis* share

symplesiomorphic characters with *Australopithecus* and early *Homo* (Brown and Maeda, 2009), which are at least uncommon in *H. erectus*. Reversals to a more ancestral state, however, are often encountered among island animals, as will be detailed below. The high robusticity of the lower limb bones of *H. floresiensis* is a functional adaptation, which is also explained below, and commonly seen in island animals. The wrist of *H. floresiensis* is more primitive than that of modern humans or Neanderthals as well. This eliminates the possibility that LB1 was a pathological modern human, but does not provide much insight into the ancestry of *H. floresiensis*, because no wrist bones of *H. erectus* have been found so far apart from one partial lunate. The morphology of the wrist of *H. floresiensis* can thus be consistent with both a *H. erectus* and an early hominin ancestry.

Cladistic analyses (Argue et al., 2009) suggest that *H. floresiensis* may have evolved in the Late Pliocene or Early Pleistocene, and was a descendent of an early species of *Homo*. Brown and Maeda (2009) argue that *H. floresiensis* arrived on Flores in the Middle Pleistocene and remained there relatively unaltered until its extinction. Insular artiodactyls exhibit sharp reversals to ancestral characteristics, which troubles cladistic analyses, as it groups islanders closer to less derived forms of the same taxon, rather than their own ancestors (van der Geer, 2005b). The same situation may be occurring for *H. floresiensis*, which is grouped with australopiths by cladistic analyses (Argue et al., 2009, 2010), rather than *H. erectus*.

Whereas the morphology of LB1 may seem strange, or even impossible, when compared to other hominin fossils, it is not at all unexpected when compared to palaeontological finds from Flores and other islands (Meijer et al., 2010; Niven, 2007; van Heteren and de Vos, 2007). The strangest case of endemism is arguably *Hoplitomeryx*. Its most striking characteristic is the presence of five horns, of which one is positioned between the eyes and the other four in pairs above the orbits. In spite of having horns, *Hoplitomeryx* is considered cervoid based on a cervid morphology of the molars, a distally closed metatarsal gully and the presence of a double lacrimal orifice on the rim of the orbit. *Hoplitomeryx*, thus, is a deer-like creature that developed horns instead of antlers. Compared to this animal, the 'strange' features displayed by LB1 seem relatively minor adaptations compared to a *H. erectus* base line. Appendix A gives a quantitative overview of changes undergone by other endemic animals. *H. floresiensis* is not any more different from *H. erectus* than the other endemics are from their ancestors or close relatives.

3.3. Island dwarfing of *Homo erectus*

Initially, Brown et al. (2004) wrote that the most likely explanation for *H. floresiensis* "is long-term isolation, with subsequent endemic dwarfing, of an ancestral *H. erectus* population". Although most researchers now accept an earlier ancestry, this is a very plausible idea. It has been shown that the environment on Flores during the Pleistocene was very suitable for insular dwarfs and giants to evolve and

H. floresiensis may have been one (van den Bergh et al., 2009; Lucas, 2006; Meijer et al., 2010).

It has been argued that it is improbable that all plesiomorphic traits of *H. floresiensis* were a consequence of island dwarfing, because some modern pygmies have greatly reduced body size without any evidence of evolutionary reversals (Jungers et al., 2009b). Modern pygmies, however, have large *H. sapiens* as ancestors, unlike *H. floresiensis*, and the different starting point would naturally result in a different end product. Furthermore, modern human pygmies belong to the same species as large *H. sapiens*, whereas *H. floresiensis* may have been a different species from *H. erectus*, although the possibility of a subspecies cannot be excluded at present. And because of seafaring, modern pygmies are much less genetically isolated than *H. floresiensis* was. Furthermore, island animals regularly show such reversals to a more primitive condition (van der Geer, 2005b; van der Geer et al., 2010). *Phanourios*, a pygmy hippopotamus, evolved a more lophodont dentition than its ancestor, which is a return to a more primitive condition (van der Geer et al., 2010). Hooijer (1954) describes *Archidiskodon* (= *Elephas*) *celebensis* as a dwarfed descendent of *A. planifrons*, but as being more primitive mostly based on the dentition. And the Japanese *Hemimastodon* (= *Gomphotherium*) *annectens* has molars which resemble those of the primitive genus *Phiomia* (van der Geer et al., 2010). *Gymnesicolagus* aff. *gelaberti* has a short diastema, which is a primitive character shared with continental ochotonids and insular leporids (Quintana and Agusti, 2007). Another good example is *Hoplitomeryx*. The orbital position of the horns of *Hoplitomeryx* is a return to a more primitive configuration (Leinders, 1983). The absence of 'pogo-stick' locomotion is characteristic of more primitive ruminants, but it is also found in *Hoplitomeryx*. This is characterised by a primitive astragalus, which can be found in both *Hoplitomeryx* and *Myotragus* (van der Geer, 1999, 2005b; van der Geer et al., 2010). And *Hoplitomeryx* has patellae which have returned to the primitive condition as well (van der Geer, 2005b). Primitive ruminants are very small compared to the derived forms. Island ruminants are also very small and have developed some features that are similar to the primitive ruminants. Analogously, australopiths are small compared to later members of the genus *Homo*, and *H. floresiensis*, similar in size to australopiths, has secondarily evolved primitive features as well. So, the presence of reversals to a more primitive condition should not be viewed as evidence against island dwarfing of *H. floresiensis*, but can be seen as supportive of this theory.

The external morphology of the LB1 cranium is significantly different from that of modern humans and similar to that of archaic *Homo* (Baab and McNulty, 2009), in particular *H. erectus* (Gordon et al., 2008; Lyras et al., 2009). This similarity with *H. erectus* indicates that *H. erectus* is a very likely large-sized ancestor for *H. floresiensis*. Many of the features which are considered to be australopith-like can be explained as paedomorphic features relative to *H. erectus*. *H. floresiensis* has a high orbital, dental and brachial index, low humeral torsion, low tibial torsion and a high gonial angle, in addition to shortened lower limbs (van Heteren, 2008; van Heteren and de Vos, 2007; van Heteren

and Sankhyan, 2009). Of course, being adapted to the particular environmental challenges of Flores, *H. floresiensis* is not an exact copy of a *H. erectus* child. Neither are other island animals, which display paedomorphic features relative to their ancestors, exact copies of their ancestors' young. In fact, descendents of the same ancestor evolved differently on different islands due to local circumstances or display radiation on the same island (van den Bergh, 1999; van der Geer, 2005a, 2008; de Vos and van der Geer, 2002). The paedomorphic features found in *H. floresiensis* merely indicate the mode of dwarfing, but specific environmental adaptations have also occurred.

For example, contrary to the paedomorphic pattern described above, the head of *H. floresiensis* is relatively small, not relatively large, compared to the body. This is a specific energy-saving adaptation (Taylor and van Schaik, 2007) also reported for *Myotragus* (Köhler and Moyà-Solà, 2004). As the brain is a particularly expensive tissue (Aiello and Wheeler, 1995), any mutations reducing the cost of the brain without decreasing chances of survival, such as reorganisation in combination with reduced size (Falk et al., 2005), will be beneficial and carried into the next generation. The feet of *H. floresiensis* also do not follow the paedomorphic pattern, because they are relatively large, not relatively small. This is a specific locomotory island adaptation, which is explained further below.

H. floresiensis has been found to be megadont compared to *H. sapiens* and *H. erectus* (Brown et al., 2004; Lucas, 2006). This is expected in the case of island dwarfing (e.g., elephants) (van den Bergh, 1999), as teeth tend to diminish in size more slowly than the rest of the skeleton, which has been shown in *H. sapiens* (Shea and Gomez, 1988).

That *H. floresiensis* is likely a descendant of *H. erectus* has led to the expectation that the earliest fossils on Flores, if they exist, should look more like *H. erectus* and be larger than the Liang Bua specimens, and in the case of gradual evolution, intermediate forms should be found; this would be proper evidence of the island dwarfing theory to be true (Lieberman, 2005). However, so far, no intermediate forms or large ancestors have been found on islands for any of the other island species apart from *Myotragus* (van der Geer et al., 2010). *Myotragus*, however, has been isolated on Mallorca for more than 5 million years. And the different *Myotragus* species are not examples of intermediate forms, each better adapted to the island than its ancestor. Rather, each species is adapted to the changing circumstances on Mallorca over time. And each species is a fully evolved island form in its own right. Insular dwarfing is a relatively rapid process and the odds of an individual from one of the first generations to be preserved in the fossil record are so small that, although not impossible, it is highly unlikely it will ever be uncovered. The conclusion of whether *H. floresiensis* is a result of insular dwarfing should, therefore, not depend on such evidence, but on palaeontological and palaeoanthropological comparisons with other insular taxa. Thus, as explained above, a very plausible explanation for the morphology of LB1 and associated specimens is that this population is derived from *H. erectus* and underwent insular dwarfing.

4. The gender of LB1 and reproduction in *Homo floresiensis*

Several researchers have proposed or assumed that LB1 was most likely a female based on the morphology of the pelvis (Brown et al., 2004; Falk et al., 2005, 2007; Jungers et al., 2009a). Although they acknowledge that the pelvic morphology of LB1 is very similar to australopiths, or even propose a pre-*H. erectus* ancestry, they systematically compare the pelvis of LB1 with modern humans in order to establish its gender. This comparison, however, is not a valid one.

First, *H. floresiensis* is much smaller than modern humans, even pygmies. Allometric scaling is likely to have an influence on the morphology of the pelvis and should be taken into account when a comparison with a much larger species is made.

Second, and most importantly, the main reason for sexual dimorphism in the pelvic area in modern humans is the function of the female pelvis as a birth canal for babies with relatively large heads. The balance between locomotor efficiency and successful childbirth in modern humans is different from that of a species with a smaller body and much smaller head. LB1 has an adult brain and body size comparable to australopiths, therefore neonatal brain and body size are also expected to be similar following the equations of Leutenegger (1987). The overall morphology of the pelvis is more comparable to australopiths than to modern humans as well. So, a comparison with australopiths is much more appropriate than with modern humans for gender determination. The form of the greater sciatic notch of australopiths lies outside the range of modern human males and females, being much wider (Häusler and Schmid, 1995). Based on the pelvic and relative brain size similarities between LB1 and australopiths *H. floresiensis* might have had a different range than modern humans as well. If anything, the fact that the form of the sciatic notch of LB1 falls within the range of modern females (Jungers et al., 2009a) means it is relatively narrow for a creature with such small body and brain sizes, leading to the tentative conclusion that LB1 was male, not female. The relatively large size of LB1 compared with the other individuals from Liang Bua also supports this view.

Nelson et al. (2011) claim that sexual dimorphism of *H. floresiensis* approaches that of *H. sapiens*. However, their reference (Brown and Maeda, 2009, p. 583) states "nothing is known about the expression of sexual dimorphism in *H. floresiensis*". This is very true, because not only is there not more than one reasonably complete skeleton and cranium available, the skeleton and cranium that are available are of unconfirmed gender. Until LB1 and the other specimens have been reliably sexed, caution should be taken concerning the determination of sexual dimorphism in *H. floresiensis*.

5. Locomotion in *Homo floresiensis*

Hoplitomeryx displays reversals to a more ancestral state for biomechanical reasons, as is explained above. The same principle applies to *H. floresiensis*. Its primitive appearance

provides it with biomechanical benefits similar to early hominins.

The relatively wide pelvis and the short legs of LB1 are very similar to those of *Australopithecus afarensis* AL 288-1, aka Lucy (Brown et al., 2004; Kramer and Eck, 2000; Rak, 1991). The large iliac flare (Brown et al., 2004) would have led to an increase of the abductor moment arm about the hip and as a consequence a reduction in the abductor force necessary (Ruff, 1995). And, although the distance between the acetabula of LB1 cannot be assessed quantitatively without an associated sacrum, it appears from the general morphology and resemblance with australopithecines that the acetabula were likely relatively far apart. This is supported by the high bicondylar angle, which has also been found to be associated with a large interacetabular distance, particularly in a short lower limb (Tardieu and Preuschoft, 1996). Interacetabular distance has the potential to contribute to stride length through rotation of the pelvis (Gruss et al., 2007; Kramer, 1999; Rak, 1991). Furthermore, Gruss et al. (2007) have determined that pelvic rotation has relatively much influence on stride length in individuals with short limbs. Moreover, short legs decrease the energy required for walking (Kramer and Eck, 2000). The lower body configuration of *H. floresiensis* and australopithecines, therefore, makes them more efficient walkers at low speeds than modern humans. However, their preferred transition speed from walking to running is also lower and they would have walked at lower absolute speeds, therefore, they would have had a smaller daily walking range. Kramer and Eck (2000) explain how this is a functional adaptation for australopithecines. *H. floresiensis* acquired the same adaptation independently and for a different reason. As Flores is relatively small and no mammalian predators are present, high gear locomotion is unnecessary for survival and low gear locomotion provides valuable energy savings. The adaptation to low gear locomotion is not unique for *H. floresiensis*, but is frequently seen in island taxa, such as *Hoplitomeryx* (van der Geer, 2005b), Cervidae (Caloi and Palombo, 1995) and *Myotragus* (Köhler and Moyà-Solà, 2001).

Jungers et al. (2009a) use a different definition of robusticity than Jacob et al. (2006). Whereas Jacob et al. (2006) base the conclusion of 'weak development' on the oval shape of the cross section of the tibia, Jungers et al. (2009a) base their conclusions on the transverse diameter relative to the length of the bone. The definition used by Jungers et al. (2009a) is adopted in this part of the discussion. The adaptation to low gear locomotion of *H. floresiensis* is not only visible in the pelvis, but also in the long bones of the lower body. The femora and tibiae of *H. floresiensis* have been found to be relatively robust (Brown et al., 2004; Jungers et al., 2009a). The increased robusticity and shortening of the limb elements compared to its ancestor *H. erectus* resulted in the centre of gravity being closer to the ground, which increases stability during stance and locomotion. Island fauna also often exhibit robust limbs and the distal limb segments are relatively shortened (van der Geer, 2005b). The intermembral index of *H. floresiensis* resembles that of australopithecines more than that of *H. sapiens* (Donlon et al., 2006; Morwood et al., 2005), and LB1 is sometimes said to have relatively long arms (Lieberman, 2005). In

fact, the arms (and feet) of *H. floresiensis* are not relatively long, but the legs are relatively short. Other island fauna exhibit the same feature with dwarfing being due for the most part to a shortening of the locomotory limbs. Changes in body proportions are also observed in endemic insular pigs. Short-leggedness is seen in the extant Sulawesi warty pig (*Sus celebensis*) and the two Pleistocene Sulawesi pigs (*Celebochoerus heekereni*, *Celebochoerus* sp.), and the Sardinian island pig (*Hyotherium insularis*) had shortened phalanges (van der Geer et al., 2010). As *H. floresiensis* is not quadrupedal, shortening is expected mostly in the legs and indeed this is the case. Although it may seem that the distal limb elements in *H. floresiensis* are elongated and not shortened, because it has such large feet, from a functional perspective this should be viewed as an increase in robusticity of the most distal part of the limb rather than an elongation. This has been brought about by shortening of the lower limbs without proportionate associated shortening of the foot bones (Jungers et al., 2009b).

The short straight toes of modern humans are adapted for running, but for walking the length of the toes does not make an energetic difference (Rolian et al., 2009). Running was not very important for the survival of *H. floresiensis* and long toes may have helped *H. floresiensis* with stability, possibly in the way a gymnast curls her toes around the edge of a balance beam. Relatively low talar torsion is associated with flat-footedness (Rothbart, 2004), which is also suggested by Jungers et al. (2009a) based on the navicular and cuboid. The first metatarsal is relatively short and is lacking sesamoid grooves (Jungers et al., 2009a). A relatively short hallux has been reported to be common among people with flat feet (Rothbart, 2004), but does not normally cause foot disability (Harris and Beath, 1949). Flat-footedness results in extra mobility in the transverse tarsal joint (Elftman and Manter, 1935), which may be adaptational. The lack of sesamoid grooves on the hallux implies there were no sesamoid bones present in life. This is, however, not an indication of a difficult toe-off mechanism. In modern humans, the congenital absence of both sesamoids is rare, but when it occurs it is usually asymptomatic (Anwar et al., 2005; Scheuer and Black, 2004). However, as the only available talar remains come from one individual, it is currently impossible to determine whether this is a population-wide adaptation, or whether LB1 was a single flat-footed individual.

6. Conclusions

Of the three possible explanations for the morphology of LB1 and associated specimens, it is very unlikely that *H. floresiensis* was a pathological modern human. And, although it is at present still difficult to completely disprove the hypothesis that *H. floresiensis* evolved from an early hominin, the parallels with other island animals are so striking that the most parsimonious solution seems that *H. floresiensis* evolved from *H. erectus* in an island environment. The dwarfing process has resulted in paedomorphic features, but additional adaptations have also occurred. The brain is relatively small to lower the daily energy requirements. The legs are relatively short and robust and the pelvis relatively broad as an adap-

tation to low gear locomotion and to increase stability on uneven terrain. Additionally, the morphology of the pelvis suggests that LB1 was more likely male than female.

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Appendix A. Body measurements of endemic and comparative species. The difference is indicated in percentages in the last column. Negative percentages indicate the endemic species is a dwarf, positive percentages indicate the endemic species is a giant. *Homo floresiensis* is given in the first row and is no exception compared to the other species.

Taxon	Island	Endemic species	Comparative species	Measurement	Endemic	Comparative	%
Human	Flores	<i>Homo floresiensis</i>	<i>Homo erectus</i>	Height (cm)	106 ^a	162 ^b	–35
				Weight (kg)	32 ^a	54 ^b	–41
Rat	Ryukyu	<i>Rattus legatus</i>	<i>Rattus norvegicus</i>	Body length (cm)	27.5 ^c	22 ^d	25
	Flores	<i>Papagomys armandvillei</i>	<i>Rattus norvegicus</i>	Body length (cm)	38 ^e	22 ^d	73
				Tail length (cm)	33 ^e	18 ^d	83
Moon rat	Gargano	<i>Deinogalerix</i>	<i>Echinosorex</i>	Body length (cm)	56 ^f	36 ^f	56
				Weight (kg)	5.4 ^f	0.9 ^f	500
Ochotonid	Menorca	<i>Gymnesicolagus aff. gelaberti</i>	extant ochotonids	Weight (kg)	5.4 ^g	0.2 ^g	2600
Fox	Channel Islands	<i>Urocyon littoralis</i>	<i>Urocyon cinereoargenteus</i>	Head-to-tail length (cm)	69 ^h	96 ⁱ	–28
				Tail length (cm)	20 ^h	36 ⁱ	–44
Solenodon	Cuba	<i>Solenodon arredondo</i>	extant solenodon	Weight (kg)	1.75 ^c	1.75 ^c	75
Stegodon	Flores	<i>Stegodon sondaari</i>	<i>Stegodon trigonocephalus</i>	Weight (kg)	300 ^j	1365 ^j	–78
	Flores	<i>Stegodon florensis</i>	<i>Stegodon trigonocephalus</i>	Weight (kg)	652 ^j	1365 ^j	–52
	Sulawesi	<i>Stegodon sompoensis</i>	<i>Stegodon trigonocephalus</i>	Weight (kg)	650 ^j	1365 ^j	–52
Mammoth	Channel Islands	<i>Mammuthus exilis</i>	<i>Mammuthus columbi</i>	Shoulder height (cm)	172 ^c	375 ^c	–54
	Sardinia	<i>Mammuthus lamarmorae</i>	<i>Mammuthus columbi</i>	Shoulder height (cm)	140 ^c	375 ^c	–63
Stork	Flores	<i>Leptoptilos robustus</i>	<i>Leptoptilos crumeniferus</i>	Weight (kg)	16 ^k	9 ^l	78
				Height (cm)	180 ^k	152 ^l	18
		<i>Leptoptilos falconeri</i>	<i>Leptoptilos crumeniferus</i>	Weight (kg)	20 ^l	9 ^l	122
				Height (cm)	200 ^l	152 ^l	32
Pigeon	Mauritius	<i>Raphus cucullatus</i>	<i>Calounas nicobarica</i>	Weight (kg)	12 ^m	0.6 ⁿ	1900
Eagle	Cuba	<i>Buteogallus borra</i>	<i>Buteogallus urubitinga</i>	Humerus length (mm)	178 ^o	123 ^o	45
				Femur length (mm)	119 ^o	87 ^o	37
				Tarsometatarsus length (mm)	164 ^o	117 ^o	40

^a Brown et al. (2004).

^b Walker and Leakey (1993).

^c van der Geer et al. (2010).

^d Verts and Carraway (1998).

^e Musser (1981).

^f Butler (1980).

^g Quintana and Agusti (2007).

^h Wayne et al. (1989).

ⁱ Jansa (1999).

^j van den Bergh (1999)

^k Meijer and Due (2010).

^l Louchart et al. (2005).

^m Anonymous (1993).

ⁿ McNab (2000).

^o Suarez and Olson (2007).

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