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Perspectives

Five Years of *Homo floresiensis*

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ABSTRACT Since *Homo floresiensis* was first described in October 2004 there has been a lively debate over its status. Is it a late surviving species of early *Homo* or merely a modern individual afflicted with disordered growth and one of the many syndromes resulting in microchephaly? Recently the discovery team has published a series of articles providing detailed descriptions of the hominin material, its geomorphological context, and the associated archaeology and faunal material (Morwood and Jungers: J Hum Evol 57 (2009) 437-648). In addition, other researchers have put forward new hypotheses for possible pathologies including Laron's Syndrome and Myxoedematous Endemic (ME) Cretinism. Here I review this new information and conclude that the evidence supports the hypothesis that *Homo floresiensis* is a late-surviving species of early *Homo* with its closest morphological affinities to early African pre-*erectus*/*ergaster* hominins. Although this hypothesis requires fundamental paradigm changes in our understanding of human evolution, it provides a more economical explanation for *H. floresiensis* than do the alternatives. None of the current explanations for microcephaly and disordered growth account for the range of features observed in *H. floresiensis*. Neither do they provide explanations for why a pathological condition in modern humans would mimic so closely the morphology observed in earlier hominins. This conclusion is based on the current evidence for *H. floresiensis* and on the particular pathological explanations that have appeared in the literature. There is no doubt that controversy over *H. floresiensis* will continue until new and conclusive evidence is available to settle the debate one way or another. Am J Phys Anthropol 142:167–179, 2010. ©2010 Wiley-Liss, Inc.

We are currently in the middle of a debate in human evolution that is similar in many respects to controversies that surrounded the discovery of the Neanderthals, *Pithecanthropus erectus* or the Taung child. What all of these have in common is a fossil discovery that is fundamentally inconsistent with prevailing notions about the course of human evolution. Did the new material represent a paradigm-changing chapter in human evolution or was it just a diseased modern human (or simply another ape in the case of Taung)?

The current debate is over the taxonomic status and evolutionary position of the hominin material known as *Homo floresiensis* (Brown et al., 2004; Morwood et al., 2004, 2005). The fossil record for *H. floresiensis* comprises a relatively complete skeleton (LB1) and other material representing a total of at least nine (Morwood et al., 2005) and possibly as many as 14 individuals (Morwood et al., 2009) discovered at the cave site of Liang Bua on the Island of Flores between 2003 and 2004 (Brown et al., 2004; Morwood et al., 2005, 2009). The material represents individuals who were small in stature (~106 cm) (Brown et al., 2004) and who occupied the cave from ~95 to 74 to 17[1] ka (Roberts et al., 2009; Morwood et al., 2009). The one cranium that is currently known (LB1) has an unusually small cranial capacity of 385–417 cm^3 (Brown et al., 2004; Falk et al., 2005a; Holloway et al., 2006) and is reminiscent of African early *Homo erectus* in a number of features. The LB1 skeleton also has limb proportions that resemble *A. afarensis* with short legs relative to arms, and other postcranial features that individually are most similar either to apes, or to australopithecines, or to *Homo erectus* or are totally unique such as its unusually large feet (Jungers et al., 2008, 2009a). The *H. floresiensis* fossil material is also associated with what have been described as relatively advanced stone tools and other cultural activities including butchering and the use of fire. Critics remind us, however, that caves are complicated depositional environments, and that this must be kept in mind when drawing inferences from these apparent associations.

Context of the material

The Liang Bua cave is located ~14 km north of the regional capital of Ruteng in western Flores (Fig. 1). The cave is 30 m wide, 25 m high at the entrance, and 40 m deep and overlooks the Wae Racang river valley (Morwood et al., 2004). Liang Bua was formed as an underground chamber ~600 ka and was exposed by action of

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[1] The previously published date for the disappearance of *H. floresiensis* and *Stegodon* at Liang Bua of about 12 ka (Morwood et al., 2004) has been revised to ~17 ka on the basis of more recent excavation and analysis (Morwood et al., 2009; Roberts et al., 2009).

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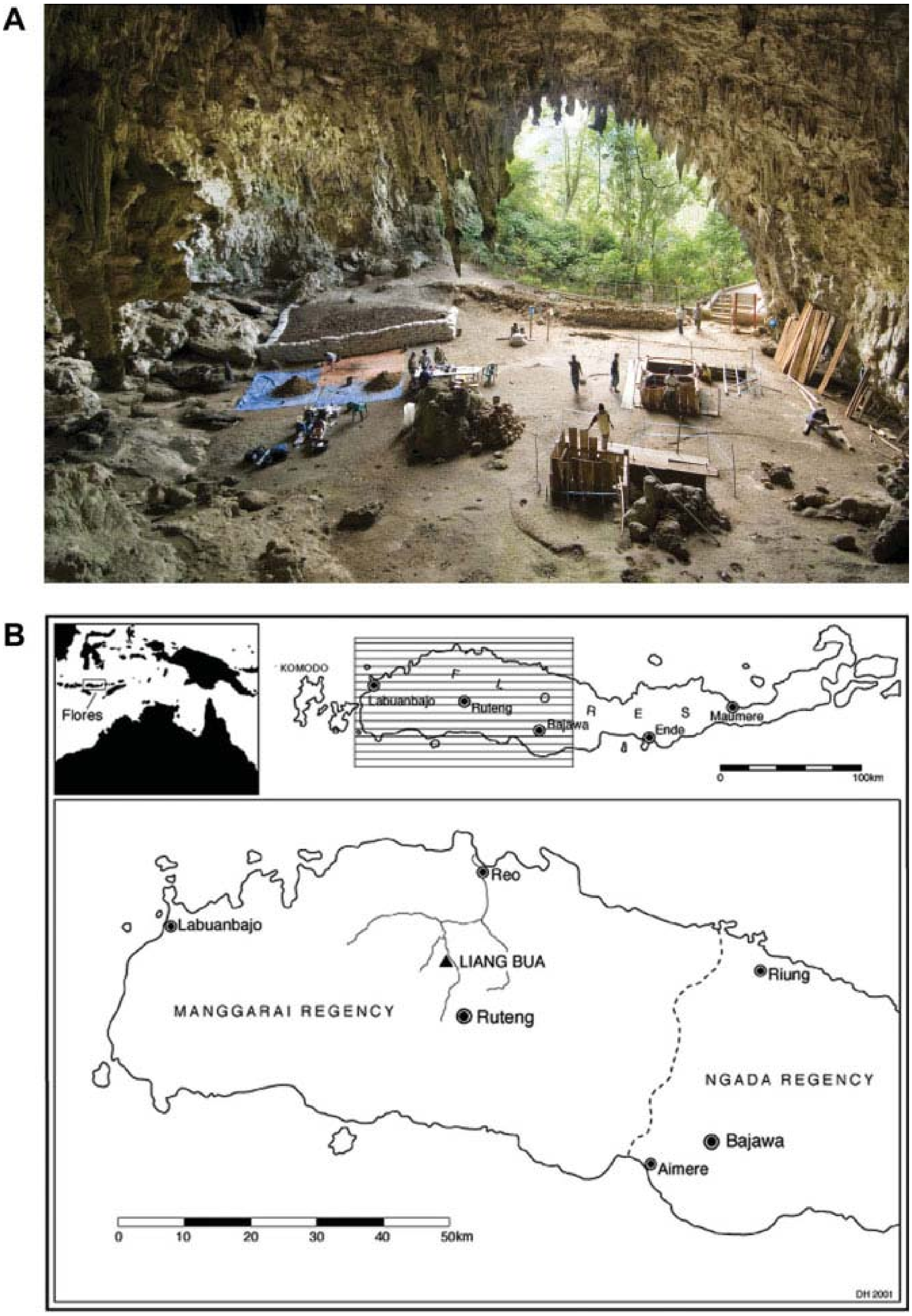

Fig. 1. **A**: Liang Bua during the archaeological excavations in 2007. (Photo: Djuna Ivereigh/ARKENAS). **B**: Map of Southeast Asia showing the location of Flores and of Liang Bua. (Map credit: Mike Morwood). [Color figure can be viewed in the online issue, which is available at www.interscience.wiley.com.]

the Wae Racang river ~190 ka. At that time, a conglomerate containing artifacts was deposited at the rear of the cave, indicating the presence of hominins in the area (Westaway et al., 2009a,b).

There are two known major periods of occupation in the cave associated with *H. floresiensis*. The earliest dates between ~74 and 61 ka and is located near the west wall and in the center of the cave. The more recent dates between ~18 and 16 ka and is located by the east wall (Roberts et al., 2009; Westaway et al., 2009b). The environment around the cave was influenced by the glacial phases and changed from humid forest to grassland. The remains of *H. floresiensis* are variously associated with stone tools and with *Stegodon*, the only other large mammal on the island, the Komodo dragon, giant rats, bats, and birds including the giant carnivorous marabou stork, *Leptoptilos sp*. that stood 1.8 m tall (Van den Bergh et al., 2009).

The uppermost of the two layers containing *H. floresiensis* remains is capped by deposits that reflect a massive volcanic eruption ~17 ka. Morwood et al. (2009) speculate whether this caused the extinction of *H. floresiensis* and *Stegodon* or whether the disappearance of both is related to climate change, to the arrival of modern humans or to a combination of events. Modern humans and their cultural remains are found in higher levels of the cave beginning ~11 ka.

The majority of the *H. floresiensis* remains are found in the levels of the cave dating between ~18 and 16 ka. The LB1 type skeleton dating to ~18 ka was found against the eastern cave wall in a situation suggesting that it was rapidly covered in a standing pool of water. There is no evidence of intentional burial. Other *H. floresiensis* material was found in the center of the cave in association with charred bone and clusters of reddened fire-cracked rocks suggesting the use of fire. There are also neonatal and juvenile *Stegodon* bones and some of these show cut marks (Morwood et al., 2005).

A brief history of *H. floresiensis'* first year

Homo floresiensis was announced on October 28, 2004, to wide media attention fueled by fascination with a new species of human that lived recently in time and had an entirely unexpected morphology (Brown et al., 2004; Morwood et al., 2004). Lahr and Foley (2004) stated that "... finds don't get better than this" and other senior anthropologists described it as "jaw dropping" (Wood cited in Gibbons, 2004). The skull of *H. floresiensis* has been portrayed as one of paleontology's most iconic recent images and has even been immortalized in a painting by Damien Hurst, one of the world's best-known contemporary artists (Hopkin, 2005).

Although initially resisted by at least some of the discoverers, the nickname "Hobbit" for *H. floresiensis* proved to be irresistible. The third fantasy epic film in the Lord of the Rings trilogy (*The Return of the King*) had appeared the preceding year after eight years of filming in New Zealand. Public attention was focused on little people and on Australasia to the extent that some on the discovery team were considering naming the new species *Homo hobbitus* (Morwood and van Oosterzee, 2007).

Because of the unexpected mosaic of features, the describers originally proposed a new genus for the material, *Sundanthropus floresianus* (Sunda Man from Flores). However, reviewers for the original description of the material in *Nature* (Brown et al., 2004) pointed out that the cranium was clearly *Homo* despite the unusually small brain size. As a result, the material was referred to the genus *Homo* (Gee, 2007; Morwood and van Oosterzee, 2007).[2]

Brown et al. dismissed pathological explanations (including microcephaly and dwarfism) for *H. floresiensis* (Brown et al., 2004). On the basis of the general facial and dental similarities of *H. floresiensis* with large-bodied Pleistocene *Homo* (Fig. 2), they favored insular dwarfing as an explanation for the small size of *H. floresiensis*. *H. erectus* is well known from Indonesia (e.g. Dubois, 1924, 1926; Weidenreich, 1951; Jacob, 1973; Von Koenigswald, 1975; Santa Luca, 1980; Antón, 2003; Kaifu et al., 2008). Furthermore archaeological evidence from the Soa Basin site of Mata Menge suggests that hominins (presumably *H. erectus*) were present on Flores as long ago as 800–880 ka (Morwood et al., 1998; Brumm et al., 2006; Moore and Brumm, 2007). The logical assumption was that an isolated *Homo erectus* population had dwarfed over the ensuing years in a fashion similar to many other relatively large bodied mammals in island situations. However, Brown et al. (2004) did not reject the alternative hypothesis that the ancestors of *H. floresiensis* could have been an unknown small-bodied and small-brained hominin who arrived on the island from the Sunda Shelf.

From the beginning, there was some unease over *H. floresiensis* in general and the insular dwarfism hypothesis in particular. Insular dwarfism meant that a relatively nonencephalized descendant had evolved from a more encephalized ancestor. In addition, the tools found together with the new species apparently also are found elsewhere in Southeast Asia with modern humans (Lahr and Foley, 2004). Could a species of small-bodied and small-brained hominin survive alongside modern humans who are known elsewhere in Indonesian from ~50 ka? Others asked whether a small-brained hominin would be capable of making the stone tools, hunting and using fire as suggested by the archaeological context (Hennenberg and Thorne, 2004). These are all legitimate questions.

Hennenberg and Thorne (2004) in an early critique of the material argued that microcephaly combined with dwarfism could not be rejected as an explanation for *H. floresiensis*. In their view, such an explanation was more consistent with the context of the site, its age, and artifacts. This was met by a strong reply from Brown and Morwood who dismissed the suggestion as poorly informed and based on an ill designed piece of nonrefereed "research" [quotes theirs] (Brown and Morwood, 2004). This unfortunately has been the tone of much of the ensuing debate surrounding the status of *H. floresiensis*.

The months following the publication were taken up by what was described in the popular and scientific press as a tug-of-war over the analysis of the bones. This tug-of-war resulted from culture and generation clashes over Indonesian paleontological tradition (Indriati, 2007). The senior Indonesian team-member, Radien Soejono of the Indonesian Centre for Archaeology in Jakarta, agreed that the Liang Bua hominins be transferred to Gadjah Mada University in Yogyakarta and studied by his long-term collaborator, Teuku Jacob. The events are documented in Morwood and Oosterzee (2007), Henneberg and Schofield (2008) and in the pages of *Nature* (Dalton, 2005), *Science* (Balter, 2004a,b; Culotta, 2005a) and other journals (Powledge, 2005). Tensions were fueled by Jacob's belief that *H. floresiensis* was a pathological modern human and not a new species. He also invited others who shared this belief including Hennenberg and Thorne to study the material, gave samples to the Max

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[2] The species name, *floresianus*, also became *floresiensis* because of the fear that generations of students would refer to it as "flowery anus" (Gee, 2007; Morwood and van Oosterzee, 2007).

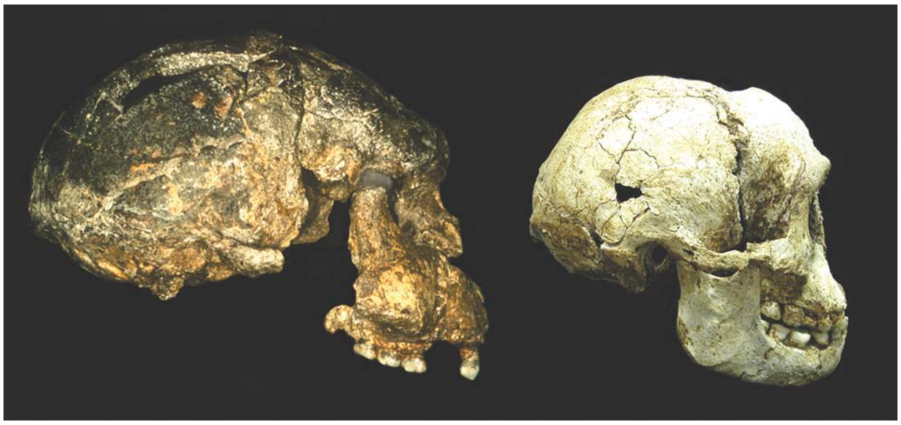

Fig. 2. Sangiran 17 (left) and LB1 (right). (Photo: Peter Brown).

Planck Institute for Evolutionary Anthropology in Leipzig for DNA analysis and returned the bones late and in a damaged condition. This fueled further controversy over whether the damage occurred while under Jacob's care or, as he claimed, in transit back to Jakarta (Culotta, 2005c).

While this drama occupied the media, research on the endocranial cast of LB1 was underway. Falk et al. (2005a) concluded that the brain of *H. floresiensis* had its closest similarities with *Homo erectus* and rejected the microcephalic hypothesis based on a comparative analysis of a single microcephalic endocranial cast. They argued that the *H. floresiensis* brain was derived in the frontal and temporal regions and in the position of the lunate sulcus, features that are associated with advanced cognitive function. Their conclusion was that *H. floresiensis* would have been capable of cultural behaviors inferred for it from the associated archaeological material in spite of its small brain size. This set in motion a still continuing debate over the interpretation of the LB1 endocranial cast (Weber et al., 2005; Falk et al., 2005a,b, 2006, 2007a,b,c, 2009b; Holloway et al., 2006; Martin et al., 2006a,b; Martin, 2007).

In October 2005, just less than one year after the description of the original material further evidence was published in *Nature* (Morwood et al., 2005). This material included the right arm bones of LB1, which confirmed the nonhuman limb proportions of the hominin. Morwood et al. argued that this together with the lateral flare of the LB1 ilium provided strong evidence against a pathological explanation for *H. floresiensis* because hormone related dwarfism and microcephaly in modern humans resulted in normal limb and pelvic proportions. A newly discovered complete mandible (LB6) similar to LB1 but slightly more recent in age (∼17 ka) also suggested that LB1 was not unique but was a member of a longer lived population with dental features that were most reminiscent of early *H. erectus* from Africa or *H. georgicus* from Dmanisi, Georgia.

Critics were quick to point out that there was still only one cranium and that other individuals may have had normal brain sizes. In addition, postcranial skeletons of microcephalics are virtually unknown in museum collections and it is unclear whether any of the many syndromes resulting in microcephaly might produce a similar postcranial morphology. The debate was far from settled by the new material (Culotta, 2005b; Lieberman, 2005).

Fig. 3. The LB1 skeleton. (Photo: Djuna Ivereigh/ARKENAS).

Where do we stand now?

Jacob et al. published the results of their research on the original *H. floresiensis* material in 2006 (Jacob et al., 2006). Their main conclusion was that some aspects of the cranial and postcranial morphology showed direct evidence of developmental pathologies that would have seriously impaired function (e.g., facial asymmetry resulting in inefficiency in mastication, weak muscle development, extremely thin cortical bone, etc.). Otherwise, *H. floresiensis* fell within the range of variation of small-bodied Australasian peoples (Jacob et al., 2006).

Other scientists remain divided. Some agree that the weight of the evidence supports a pathological explanation (Weber, 2005; Martin et al., 2006a,b; Martin, 2007; Richards, 2006; Henneberg, 2007; Hershkovitz et al., 2007; Tuttle and Mirsky, 2007; Rauch et al., 2008; Obendorf et al., 2008). Others equally strongly support the "new species hypothesis" (e.g. Argue et al., 2006, 2007; Brumm et al., 2006; Falk et al., 2005a,b, 2006, 2007a,b,c; Larson 2007; Larson et al., 2007a,b; Tocheri et al., 2007; Zeitoun et al., 2007; Van Heteren and de Vos, 2007; Gordon et al., 2008; Jungers et al., 2008, 2009a; Lyras et al., 2009; see also Jungers and Morwood, 2009 and the papers therein).

Indriati (2007) has observed that scientists with broad backgrounds dealing with modern human variation (e.g., geneticists, clinicians and human biologists) tend to favor a pathological explanation. Alternatively, those with backgrounds concentrating more narrowly in palaeoanthropology tend to favor the "new species hypothesis." Some argue that the pathological explanation cannot be rejected "... until medically informed scientists eliminate all possible pathological explanations ..." (Tuttle and Mirsky, 2007, pg. 6) while others are equally adamant that the "new species hypothesis" cannot be rejected until a pathological explanation can account for the morphology observed in *H. floresiensis* (e.g. Falk et al., 2009a). One of the major challenges in the current controversy is to bridge this divide.

The following discussion will summarize what is currently known about the biology and context of *H. floresiensis* and assess the various debates relating to insular dwarfism and possible pathologies involving microcephaly.

The cranium and dentition

The cranium of LB1 has been interpreted in two different ways. In the original description, Brown et al. (2004) highlighted the extremely small size of the cranium but also emphasized the fact that its shape was similar to *H. erectus* (Fig. 2). The greatest breadth is across the inflated supramastoid region and the vault is broad in relation to its height. The similarity with *H. erectus* was supported by a principal components analysis of five linear height and breadth measurements that positioned LB1 closest to ER-3883, ER-3733, and Sangiran 2. The morphology of the face is similar to members of the genus *Homo*. The facial height and prognathism are reduced in relation to australopithecines and in lateral view the infraorbital region is oriented posteriorly. The mandible lacks a chin, has a developed alveolar planum and a symphysis most similar to LH4 (*A. afarensis*) with a developed superior transverse torus, a deep digastric fossa and a low, rounded inferior transverse torus. The total morphological pattern was interpreted by Brown et al. as being unlike modern *H. sapiens* and represented a mosaic of features unobserved in any other hominin.

Jacob et al. (2006) on the other hand argue that marked asymmetries in the cranium indicated abnormal growth and development. Aside from the abnormalities, 94 qualitatively assessed features on the cranium (and 46 features on the mandible) individually do not lie outside of the range of variation found in modern Australo-Melanesian humans. On this basis, they proposed that that LB1 was a member of a modern pygmy *H. sapiens* population and suffered from growth abnormalities including microcephaly.

Other researchers have confirmed that asymmetry does exist (Baab and McNulty, 2009; Kaifu et al., 2009; Falk et al., 2009a) but that it is within the range of variation found in modern humans, extant African apes and fossil hominins (Baab and McNulty, 2009). Although Baab and McNulty suggest that this is postmortem deformation, Kaifu et al. (2009) convincingly argue against postmortem distortion and suggest that the deformation is consistent with posterior deformational (positional) plagiocephaly (PDP).

PDP is a common syndrome which results in an asymmetrical (parallelogram) shape of the skull that frequently develops after birth from repeatedly positioning an infant supinely with its head in the same position on a flat surface. In the case of LB1, the deformation manifests as left occipital flattening and a slight anterior shift of the left face associated with a rotation of the maxillary body and a leftward shift of the maxillary and mandibular dentition. The main point is that the asymmetries do not lie outside of the normal range of variation and would not have impaired masticatory function as originally suggested by Jacob et al. (2006). There is no reason to suggest that the asymmetries indicate any type of developmental abnormality.

Jacob et al. (2006) also suggest that qualitative features of the cranium may individually be found in modern humans. However, other researchers repeatedly emphasize that the total morphological pattern of the cranium is different from modern humans, including microcephalics. It is most similar to early *Homo* (variously *H. habilis, H. georgicus* or *H. erectus* from Africa or Asia) (Argue et al., 2006; Zeitoun et al., 2007; Gordon et al., 2008; Martinez and Hamsici, 2008; Lyras et al., 2009; but see Thorne and Henneberg, 2007 for a methodological critique).

Baab and McNulty (2009) carried out an extensive geometric morphometric analysis and conclude that LB1 best fits the predictions of a small representative of fossil *Homo* and not a small modern human. They go on to conclude that because of the small size of LB1 the allometries in facial morphology converge on what has been interpreted as a more modern face. This suggests that the facial morphology of LB1 most probably does not indicate any particularly close relationship with modern humans.

Arguments that the mandibular morphology can be matched in modern Australo-Melanesian people (Jacob et al., 2006; Richards, 2006) or in pathological modern humans (Martin et al., 2006a; Hershkovitz et al., 2007, 2008) have been refuted in detail by Brown and Maeda (2009). Morphological and metrical aspects of the symphyseal, corpus, and ramus morphologies are distinct from both *H. sapiens* and *H. erectus*. Mandibular morphology, together with premolar morphology, is reminiscent of African early *Homo* or *Australopithecus* (see

Brown and Maeda, 2009, Table 3, for a trait list of mandibular features for LB1 and LB6 and other hominins).

Absolute tooth size is most similar to a large global sample of modern humans (Brown et al., 2004) and the molar size ratio for both the mandibular and maxillary teeth is $M1 \geq M2 > M3$. Relative tooth size is dependent on the estimate of body mass that is employed (Brown and Maeda, 2009). Using the original body mass estimate for LB1 (16–29 kg based on estimated stature and on the femoral cross-sectional area) and the megadontia quotient of McHenry (1988), LB1 is megadont (1.26-2.11) in relation to both *H. sapiens* (0.9) and *H. erectus* (0.9) and is equivalent to *H. habilis* (1.9) (Brown et al., 2004; Brown and Maeda, 2009). If body mass is estimated on the basis of femoral head breadth (35.9 kg; range, 31.4–41.3 kg), relative postcanine tooth size is similar to that expected for an Australian Aborigine of LB1's body mass (Brown and Maeda, 2009). Mandibular morphology and tooth wear (occusal and interstitial) are consistent with powerful chewing of a tough fibrous diet.

On the basis of this work there is no direct evidence from the cranium that LB1 is pathological or (except for dental size) has a particularly close relationship to any modern humans. The closest phenetic similarities lie with earlier hominins and particularly with early *Homo*.

The endocranial cast

One of the most vigorously debated features of *H. floresiensis* is the endocranial cast and inferences that can be made from brain size and shape.

Martin et al. have argued that the degree of brain size reduction is simply too much to be explained by insular dwarfism (Martin et al., 2006a,b; Martin, 2007). Hominin body size could have reduced significantly as has been the case in many other mammalian species in island situations. However, brain size is another thing. The great majority of dwarfed mammals, including humans (Schoenemann and Allen, 2006), have relatively large brain sizes because the brain does not reduce in a one-to-one relationship with body size reduction. Exceptions to the contrary such as the fossil bovid, *Myotragus*, from the island of Majorca, have been fiercely debated (Kohler and Moya-Sola, 2004; Martin et al., 2006a; Niven, 2007, 2008; Köhler et al., 2008). On the basis of intraspecific scaling Martin et al. argue that the *H. floresiensis* body size would have to be unrealistically small to achieve a *H. floresiensis* brain size from either an ancestor similar in size to the Javanese *H. erectus* from Ngandong or the smaller-bodied *H. georgicus* from Dmanisi (Martin et al., 2006a,b; Martin, 2007).

The question is whether brain size reduction in *H. floresiensis* would have been constrained by this scaling trend. On the basis of the analysis of two species of extinct dwarf hippos (*Hippopotamus lemerlei* and *H. madagascariensis*) from the island of Madagascar, Weston and Lister (2009) demonstrate that *H. floresiensis* may not have been so constrained. They argue that ontogenetic allometry rather than the static adult allometry employed by Martin et al. may be the more relevant scaling relationship particularly in species like hippos and humans that have altricial young with a rapid period of brain growth early in ontogeny. If *H. floresiensis* had dwarfed along a trajectory similar to that of *H. lemerlei*, hominins with brain sizes similar to or smaller than the African *Homo erectus*, KNM-ER 3883, (endocranial capacity = 804 cm^3; body mass = 59.2 kg) could have represented the ancestral population (Weston and Lister, 2009, supplementary information, Table 5). This work is currently the best evidence that insular dwarfism could have played a part in the evolution of *H. floresiensis* and its small brain size, particularly in an environment where energetic efficiency may have been a highly important constraint.

However, for those who cannot accept that insular dwarfism could result in the small *H. floresiensis* brain and/or that *H. floresiensis* arose from an unknown small-bodied small-brained ancestor, the only alternative is that it represents an individual afflicted with dwarfism together with one of the many different syndromes or causations resulting in microcephaly. To address this argument, Falk et al. have argued that there are fundamental differences between normal human endocranial casts and all known microcephalic endocranial casts available for study (Falk et al., 2007a). Their conclusion is that *H. floresiensis* falls clearly with modern humans. On the other hand Weber et al. (Weber et al., 2005) and Martin et al. (Martin et al., 2006a,b; Martin, 2007) argue that microcephalic endocranial casts are highly variable and that the *H. floresiensis* cast can be matched in some microcephalics.

The debate revolves around the availability and appropriateness, or not, of the material and of the comparisons used to argue the respective interpretations. The main issue is that there are relatively few microcephalic endocranial casts available for study to settle the debate one way or another. In addition, many different syndromes can result in microcephaly. However if Falk proves to be correct and the morphology of the *Homo floresiensis* endocranial cast is not compatible with microcephaly, there are interesting implications for hominin brain evolution. Falk recognizes seven derived features of the LB1 endocranial cast, suggesting that that neurological reorganization occurred independently of an increase in brain size (Falk et al., 2009b). The overall shape of the endocranial cast is also most similar to *H. erectus* (Falk et al., 2005a). Not only does this contribute to long-standing controversies about the relative importance of brain size increase versus neurological organization in hominin brain evolution but also it suggests that *H. floresiensis'* cognitive capacity could have been compatible with cultural abilities inferred for it.

Falk has been accused of "the most outlandish form of special pleading" in this conclusion (Martin, 2007, pg. 14); however, she is not arguing that *H. floresiensis* was capable of the totality of modern human behavior. She is simply arguing that the brain is derived in the direction of modern humans (also contra Conroy and Smith, 2007) and that *H. floresiensis* would have had a cognitive ability greater than observed in modern apes or inferred for the australopithecines with similar brain sizes.

The postcranial skeleton

A similar controversy surrounds the interpretation of the postcranial skeleton of *Homo floresiensis* (Fig. 3).

Recent studies of the hand, foot and shoulder provide evidence that features found in *H. floresiensis* are similar to the morphology of earlier hominins (Tocheri et al., 2007, 2008; Larson, 2007; Larson et al., 2007a,b, 2009; Jungers et al., 2008, 2009a,c). The main question is whether these indicate phylogenetic relationship with earlier hominins. Alternatively, are they convergences resulting from pathological developmental?

Analyses of the trapezoid, scaphoid, and capitate show that these *H. floresiensis* wrist bones have a primitive morphology for the African ape-human clade that predates the wrist morphology found in Neanderthals and modern humans and also *Homo antecessor* (evidence from the capitate) (Tocheri et al., 2007, 2008). The morphology therefore predates 800 ka. Wrist morphology emerges early in embryonic growth while developmental pathologies tend to appear later. This significantly reduces the probability that developmental pathologies could result in the primitive condition of the LB1 carpals (Tocheri et al., 2007).

The morphology of the LB1 shoulder also appears to predate the appearance *Homo antecessor* (Larson, 2007; Larson et al., 2007a). The two key features are the short clavicle and a humerus with a low torsion angle. Both features are shared with early *Homo erectus* (Nariokotome and *H. georgicus* from Dmanisi). The first appearance of a more derived shoulder morphology (a longer clavicle) is found in *H. antecessor*. In modern humans a short clavicle can occur as the result of a pathological condition known as hypoplastic clavicle syndrome and a humero-clavicular index approaching that found in LB1 is found variably in some Australians and Sami (the indigenous people from Sápmi, which today encompasses parts of Sweden, Norway, Finland and the Kola Peninsula of Russia). However, it is not parsimonious to explain *H. floresiensis* morphology as the combination of these two factors (Larson et al., 2009). The main reason is the presence of this morphology in the much earlier geographically dispersed hominins.

The foot also has a number of features that are primitive for the genus *Homo* based on our current understanding of the evolution of pedal morphology (Jungers et al., 2009a,c). Prime among these is the morphology of the navicular, which suggests that it was weight-bearing. This would imply that LB1 did not have a transverse arch that is typical in modern human feet. The foot is also long in relation to the length of the tibia and femur, and the forefoot is particularly long in relation to the tarsal skeleton with proximal pedal phalanges that have a moderate curvature, resembling some australopithecines. Jungers et al. (2009b) suggest that the pattern of weight transfer through the foot during the stance phase and toe-off and the kinematics of the swing phase (resulting from clearance problems of the long foot) would be different from modern humans in both walking and running.

Other features of the postcranium such as the morphology of the pelvis and femur show a mix of features (Jungers et al., 2009c). For example, the iliac blade of the pelvis flares strongly beyond the rim of the acetabulum and the size of the acetabulum is relatively small as in the australopithecines, but the superior portion of the acetabular lunate surface is broader than the posterior horn, which distinguishes it from these earlier hominins. The femur is shorter than found in any normal modern human and is different from femora excavated in more recent (modern human) sites on Flores. It has a small head and long anterior-posteriorly compressed neck as in the australopithecines but differs from them in the laterally flaring greater trochanter and the strongly developed intertrochanteric crest (Jungers et al., 2009c; Culotta, 2008; Richmond and Jungers, 2008).

These new analyses do not support Jacob's earlier suggestion that the skeleton showed direct evidence of disordered growth based on marked asymmetries as well as inflated circumferences of the long bones, very thin cortical bone and weak muscle markings (Larson et al., 2009; Jungers et al., 2009c). As with the cranium, the asymmetries are demonstrated to be within normal ranges of variation and direct measurement has shown the cortical bone to be of normal thickness. Any suggestion that weak muscles relate to the lower humeral torsion also has been effectively refuted by Larson et al. (2009).

Richards (2006) argues that features such as the wide pelvis and the short legs relative to arms can be found in modern human pygmy populations. However, this also has been disputed. The *H. floresiensis* pelvic morphology is unknown in modern humans and is consistent with a small-bodied hominin with a very small cranial capacity (Jungers et al., 2009c) and there is no evidence that any modern humans (normal or pathological) have limb proportions similar to those found in *H. floresiensis* (Argue et al., 2006).

However, *H. floresiensis* is smaller in size than modern humans and the effects of this magnitude of size reduction on morphology and limb proportions are not fully understood. Holliday and Franciscus (2009) argue that the femur is negatively allometric in African apes and is either isometric or positively allometric in a large, geographically mixed sample of modern humans. Femur length relative to body size in both groups would converge in the size range of *H. floresiensis*. Hominins of the body size of *H. floresiensis* (or *A. afarensis* as represented by AL 288-1), would therefore be expected to have short lower limbs merely as a function of this scaling relationship.

Although this work suggests that small apes would have longer femora than larger apes and small hominins possibly would have shorter femora than larger hominins, it does not address the issue of interlimb proportions. The humerus is isometric in hominoids, including humans (Jungers, 1994), and there is no evidence that interlimb proportions (either the humerofemoral or the intermembral indices) increase with decreasing body size in modern humans (Jungers, 2009; Sylvester et al., 2008).

The analysis of femoral and humeral strengths (cf. Ruff, 2009) will be important in determining whether limb usage in *H. floresiensis* was similar to that in modern humans. This work is currently in progress (Jungers, 2009, pers. comm.). Evidence from the postcranial morphologies mentioned above suggests that this might not be the case. For example, the foot and shoulder morphologies are inconsistent with endurance running (e.g. Bramble and Lieberman, 2004) and the shoulder and wrist morphologies are inconsistent with more advanced tool-related manipulative behaviors (throwing for the shoulder morphology and more efficient tool making and manipulation for the hand) (Tocheri et al., 2007, 2008; Larson, 2007; Larson et al., 2007a).

Could *Homo floresiensis* be pathological?

These detailed palaeoanthropological analyses of *H. floresiensis* highlight its similarity to earlier hominins in many aspects of its morphology. Cladistic analysis of 60 cranial, mandibular and postcranial character states results in two equally parsimonious cladograms supporting this interpretation (Argue et al., 2009; see supplementary material for the character states and their distribution). The first cladogram places *H. floresiensis* between *Homo rudolfensis* and the clade including

H. habilis and all later hominins. The second places *H. floresiensis* between *H. habilis* and the clade including *H. georgicus* (Dmanisi) and all later hominins. We must be mindful of the gaps in our knowledge about the morphology of early *Homo*. However, this analysis suggests that *H. floresiensis* may well be a later surviving species of early *Homo* that first evolved in either the late Pliocene or early Pleistocene.

The possibility remains, however, that the distinctive morphology observed in *H. floresiensis* is pathological and only by chance mimics the morphology observed in earlier hominins (Hennenberg and Thorne, 2004; Weber et al., 2005; Richards, 2006; Jacob et al., 2006; Martin et al., 2006a; Hershkovitz et al., 2007, 2008; Rauch et al., 2008; Obendorf et al., 2008). Of those who have studied the original fossil material in detail, Jacob et al. (2006) are the only research group who support this point of view. As demonstrated above, the evidence put forward by these authors in support of disrupted growth in *H. floresiensis* has not been confirmed by further analyses. It has been shown either to have been misinterpretations of the preserved morphology (e.g. thin-walled, "tublated bone" or weak muscles) or to fall within the range of variation of normal humans or apes (e.g. asymmetry) (Baab and McNulty, 2009; Larson et al., 2009; Kaifu et al., 2009; Jungers et al., 2009c).

Other researchers who have not had the opportunity to study the original fossil material have suggested that *H. floresiensis* suffered from one of a variety of syndromes resulting in severe growth retardation and microcephaly as well as in selected additional *H. floresiensis* features. These syndromes include a combination of growth hormone-insulin-like growth factor I axis modification and mutation of the MCPH (Microcephalin) gene family (Richards, 2006), Laron Syndrome (Hershkovitz et al., 2007, 2008), Microcephalic Osteodysplastic Primordial Dwarfism Type II (MOPD II) (Rauch et al., 2008), and Myxoedematous Endemic (ME) Cretinism (Obendorf et al., 2008). However, these syndromes have not stood up to scrutiny as explanations for *H. floresiensis* morphology.

The most comprehensive treatments have concerned Laron Syndrome and ME Cretinism. Laron Syndrome is a growth hormone insensitivity associated with extremely small stature, reduced cranial volume and relatively normal intelligence (Hershkovitz et al., 2007, 2008). The argument in favor of Laron Syndrome as an explanation for *H. floresiensis* morphology is based on data for 64 LS patients followed over 45 years by Zvi Laron. Hershkovitz et al. (including Laron) provide a table of 34 diagnostic features for LS all but one of which are shared in common between LS patients and *H. floresiensis*. At face value, this might be taken as strong evidence that LB1 suffered from LS. However, critics point out that the large clinical literature on Laron's Syndrome does not support the trait list put forward by Hershkovitz et al. (Falk et al., 2008; Falk et al., 2009a). They also note that many of the claimed similarities between LS patients and LB1 are not supported by direct observation of LB1 (Falk et al., 2008; Brown and Maeda, 2009; Falk et al., 2009a; Jungers et al., 2009c). Information is not available in LS patients for important *H. floresiensis* features, such as the wrist, foot and shoulder morphologies.

A similar situation holds true for ME Cretinism. ME cretins are born without a functioning thyroid due to environmental factors including iodine deficiency (Obendorf et al., 2008). Obendorf et al. (2008) claim that LB1 has an enlarged pituitary fossa, which is one of the diagnostic features of ME cretinism. Examination of the original material, however, shows conclusively that this is not the case. Furthermore, many of the other features claimed to be in common between LB1 and ME cretins do not hold up to close scrutiny (Falk cited in Dalton, 2008; Jungers et al., 2009a). These features include among others a persisting bregmatic fontanelle, a depressed nasal bridge, absence of a frontal sinus, and a bipartite trapezoid (Jungers et al., 2009b).

The examples of both Laron Syndrome and ME Cretinism underscore the vital importance to test rigorously any hypothesis that claims a pathological explanation for LB1 against the original fossil material (cf. Rauch et al., 2008).

The fact that existing hypotheses postulating pathological explanations for LB1 can be falsified by the available evidence does not falsify all potential hypotheses. Although as time goes on and more is known about the morphology and context of the *H. floresiensis* material, the mere assertion that that there are syndromes that result in both microcephaly and severe growth restriction in modern humans becomes less and less convincing as an explanation for this material.

To settle the argument one way or another will take the discovery of new evidence as convincing as that which settled the Neanderthal, *Homo (Pithecanthropus) erectus* and Taung (*Australopithecus africanus*) controversies in the 19th and early 20th Centuries. Alternatively, it would take the recognition of a pathological condition that presents all of the features observed in *H. floresiensis* and not merely short stature and reduced brain size.

Important questions

Until new information becomes available, the existence of *H. floresiensis* as a surviving species of early *Homo* poses a number of questions about its origin and survival.

1. When and how did *H. floresiensis* arrive on Flores?
2. Is *H. floresiensis* an insular dwarf derived from a larger bodied form of *Homo erectus* or is it derived from a smaller bodied form of early *Homo*?
3. Is the small brain size of *H. floresiensis* incompatible with the behavioral capabilities that have been inferred from the associated cultural material?
4. How could *H. floresiensis* have survived when modern humans are known to have been present in Australasia from ~50 ka?

When and how did *H. floresiensis* arrive on Flores?

There are a few clues that suggest *H. floresiensis* may have been on the island for a considerable length of time. The first of these is the archaeological record, itself. Skeletal evidence attributed to *H. floresiensis* dates to ~74 ka at Liang Bua (Roberts et al., 2009; Morwood et al., 2009). However, there are stone tools dating to ~190 ka that were washed into the cave. This material suggests that hominins were in the vicinity at this time. The next earliest evidence is from the Soa Basin site of Mata Menge where archaeological evidence documents the presence of hominins as early as 800–880 ka (Morwood et al., 1998; Brumm et al., 2006).

Could *H. floresiensis* also have been present at the time of the earlier Liang Bua deposits and the yet earlier Mata Menge deposits? There is continuity between the tool technologies at Mata Menge and Liang Bua (Brumm et al., 2006; Moore and Brumm, 2007; Moore et al., 2009 and below) but perhaps the most interesting evidence comes from the faunal remains. Van den Bergh et al. (2009) report evidence of a major faunal turnover in the Soa Basin of Flores around 900 ka that also is associated with the first evidence for stone artifacts and with the first appearance of *Stegodon florensis*, which is closely associated with another stegodon species known from Sulawesi. There is evidence of a massive volcanic eruption at this time and van den Bergh et al. (2009) suggest that hominins may have arrived on Flores as the result of a tsunami-like occurrence with Sulawesi as the probable source. The predominant currents are north-to-south, which would facilitate such a sweepstakes event.

There is no evidence of any new mammalian colonizers on Flores between the 900 ka turnover and a subsequent faunal turnover a ~17 ka resulting from another volcanic event (Van den Bergh et al., 2009). This, together with the impoverished and endemic nature of the non-hominin fauna and the strong oceanic currents between adjacent islands, is the best evidence that *H. floresiensis* might be a direct descendent of the much earlier Soa Basin hominins. Of course, more data are needed to test this hypothesis; however, at present it appears to be the most consistent with the available evidence.

Is *H. floresiensis* an insular dwarf derived from a larger bodied form of *Homo erectus* or is it derived from a smaller bodied form of early *Homo*?

The original idea that *H. floresiensis* evolved as the result of the insular dwarfism of an ancestral population of larger-bodied *Homo erectus* (Brown et al., 2004) was logical in that it was based on the known existence of *H. erectus* in island southeast Asia. However, does it stand up to scrutiny?

Although Köhler et al. (2008) claim that *H. floresiensis* breaks too many of the "rules" to fit the island pattern, objections for the most part have been convincingly challenged. For example, primates do follow the "island rule" at least in reduction of body size (Bromham and Cardillo, 2007) and insular dwarfism and/or ecological factors can result in significant brain size reduction (Taylor and van Schaik , 2007; Weston and Lister 2009). Furthermore, based on analogies with modern human pygmies, small body size in *H. floresiensis* could have been an adaptation for energetic efficiency and reproductive success under conditions of reduced resource availability and/or increased mortality rate (Migliano et al., 2007). This may have been a particular issue for *H. floresiensis* because of the contemporaneous carnivorous Komodo dragon and giant marabou stork, *Leptoptilos sp*.

In addition, many of the features that Köhler et al. drew from Jacob et al. (2006) to demonstrate that *H. floresiensis* was not compatible with natural selection on islands (e.g. weak muscle development, extremely thin cortical bone, etc.) have been shown to be based on incorrect interpretation of the fossil evidence (e.g. Jungers et al., 2009c; Larson et al., 2009). Likewise their belief that the island of Flores could not have been totally isolated during the period of *H. floresiensis* occupation or that it was too small to support a long-term, viable population of hominins has been questioned by further analysis. This work confirms long-term isolation, phylogenetic continuity, and impoverishment of the island fauna (Van den Bergh et al., 2009) as well as potential viability of a small-bodied hominin population on Flores (Van den Herteren, 2008).

If, as this research suggests, insular dwarfism is a plausible explanation for *H. floresiensis*, is there any direct evidence that it actually occurred? Dental scaling suggests that dwarfed or pygmoid humans have relatively larger teeth than their normal-sized counterparts (Shea and Gomez, 1988); however, as noted above, it is unclear whether LB1 is megadont in relation to either *H. erectus* or modern humans (Brown and Maeda, 2009). Van Heteren et al. suggest that certain aspects of *H. floresiensis* morphology point towards size reduction through paedomorphosis (van Heteren and de Vos, 2007; van Heteren, 2008; Van Heteren and Sankhyan, 2009). These features include among others the orbital index and the size of the dentition in relation to cranial base length. However more comparative work needs to be done to provide conclusive evidence that these features demonstrate dwarfing.

Although current gaps in the fossil record, particularly in relation to early *Homo*, limit the inferences that can be made, many features of *H. floresiensis* appear to be similar to pre-*erectus* hominins. These include mandibular morphology, limb proportions, skeletal robusticity, wrist and foot morphology and brain size (Falk et al., 2005a; Tocheri et al., 2007, 2008; Jungers et al., 2008; Brown and Maeda, 2009; Jungers et al., 2009b,c). These similarities suggest that *H. floresiensis* separated from the mainstream hominin line before the evolution of *H. erectus* in Africa (or Dmanisi).

If the ancestral *H. floresiensis* arrived on Flores ~900 ka as suggested by the faunal evidence (Van den Bergh et al., 2009), there would be ample time for the evolution of its own unique morphology, even if it were larger in body size. There is direct evidence that stegodon reduced in size from the larger-bodied *Stegodon florensis florensis* to the dwarfed *Stegodon florensis insularis* (associated with *H. floresiensis*) during this period (Morwood et al., 1998; Van den Bergh et al., 2009). The specific nature of the *H. floresiensis* ancestor awaits future fossil discovery. However, the possibility remains that it was a pre-*erectus* hominin that arrived on Flores with both a small body and a small brain, as is currently favored by Brown (Brown and Maeda, 2009) and is the consensus opinion of the discovery team (Morwood and Jungers, 2009; see also Sankhyan and Rao, 2007; Van Heteren and Sankhyan, 2009).

Is the small brain size of *H. floresiensis* incompatible with the behavioral capabilities that have been inferred from the associated cultural material?

One of the main early criticisms of *H. floresiensis* was that the associated stone tools also were found across island Southeast Asia in association with modern humans (e.g. Martin et al., 2006a). However, Morwood et al. argue that it is "just plain wrong" that the Liang Bua artifacts are so sophisticated that they must have been made by modern humans (Culotta, 2006).

On the basis of the recovery and analysis of artifacts from the site of Mata Menge (800–880 ka) in the Soa Basin of Flores, Moore, Morwood et al. argue for technological continuity with the archaeological material from Liang Bua (Brumm et al., 2006; Moore and Brumm, 2007; Moore et al., 2009). Similarities include the use of volcanic/metavolcanic fluvial cobbles as raw materials, core reduction strategies, and the maximum dimensions of flake scars. There are some minor differences separating the sites that span the long length of time between Mata Menge, the first artifacts at Liang Bua (190–130 ka) and the *H. floresiensis* associated material (74–95 ka to 16.6–19.7 ka). However, major differences in the Liang Bua assemblage occur only after the disappearance of *H. floresiensis* and the appearance of modern humans after 11 ka. These changes include an increased emphasis on the use of chert, new artifact types and the first evidence of symbolic behavior in the form of personal ornaments, pigments, and burial of the dead (Bowdler, 2007; Moore et al., 2009).

This interpretation is against the background of paradigm changing work on the archaeology of island Southeast Asia, which dispenses with the dichotomy between core tool technologies presumably associated with *H. erectus* and flake tool technologies associated with modern humans (Moore and Brumm, 2007). The argument is that both "technologies" are part of a continuous reduction series and were present from the early Pleistocene. By inference early hominins (*H. erectus* and/or *H. floresiensis*) and *Homo sapiens* used similar basic stone tool production techniques, which provided the basis for technological "add-ons" particularly in later *sapiens*-associated assemblages.

Although this interpretation remains controversial, the major point is that the stone tool technology associated with *H. floresiensis* is not as advanced and sophisticated as assumed by some critics. Moore et al. (Moore and Brumm, 2007; Moore et al., 2009) argue that the basic reduction sequence is similar to the African Oldowan and was used not only on Flores but across island Southeast Asia by both earlier and later hominins including *Homo sapiens* (O'Connor, 2007). It is difficult to miss the fact that the Oldowan was produced by hominins with absolute and relative brain sizes only slightly larger than those found in *H. floresiensis*.

How could *H. floresiensis* have survived when modern humans are known to have been present in Australasia from ~50 ka?

One remaining problem is how *H. floresiensis* could have survived on Flores up until their disappearance (together with *Stegodon*) at about 17 ka (Roberts et al., 2009; Morwood et al., 2009). Modern humans are known to have arrived in Australia between 50 and 60 ka and have been present in other areas of the Sunda Shelf, Wallacea and the Sahul Shelf by 30–40 ka (O'Connor, 2007). If modern humans took the northern route from Borneo through Sulawesi to Papua New Guinea that bypasses Flores there would have been no problem. The strong ocean currents between islands along the southern route (from Sumatra, through Java, Bali, Lombok, Flores, and East Timor) may have restricted access until well into the Holocene when there is clear evidence that humans were moving between these islands.

However, the issue of migration through Australasia has become more interesting with the publication of dates in excess of 42,000 cal BP for the archaeological site of Jerimalia on East Timor (O'Connor, 2007). These are the earliest dates for modern human occupation in island Southeast Asia east of the Sunda Shelf. O'Connor (2007) argues that they provide evidence that the southern route to Australia through Sumatra, Java, Bali, Lombok, Flores, and East Timor remains a viable alternative which would have taken modern humans past Flores.

There is always the possibility that the early inhabitants of East Timor could have come from the north following the prevailing currents. Faunal evidence from the introduction of non-endemic species suggests that modern humans may not have been moving freely among the islands on the southern route until well into the Holocene (Van den Bergh et al., 2009). Hypothesis about the early habitation of East Timor and any contact between *H. floresiensis* and modern humans will have to remain just that until more data are forthcoming.

CONCLUSION

The continuing debate over the status of *Homo floresiensis* began almost immediately after it was first published in 2004. It is unlikely that the debate will be settled until conclusive evidence is forthcoming. Such evidence would need to demonstrate that LB1 is characteristic of a long surviving species of hominin on Flores (and perhaps on surrounding islands) or that it was a pathological modern human.

What can be concluded at this stage is that the current evidence for pathologies in the form of microcephaly and disordered growth is not convincing. This is not because syndromes do not exist that result it small stature and small brain sizes in modern humans. It is simply because the pathological explanations for *H. floresiensis* that have been suggested to date do not account for the complete morphology recognized in *H. floresiensis*. It is up to those who support a pathological explanation for *H. floresiensis* to provide evidence that falsifies the "new species hypothesis." It is not sufficient to simply point out that pathologies exist in some fossil hominins (e.g. Tuttle and Mirsky, 2007) or to note perceived deficiencies in palaeoanthropological methodologies (e.g. cladistic analysis) that obscure continuities between populations and "... direct attention away from more dynamic aspects of evolutionary process" (Eckhardt, 2007; p. 107).

There is no doubt that a pathological explanation for *H. floresiensis* is, at face value, a simpler and more comfortable solution to the many questions raised by the discoveries at Liang Bua. The argument has been used many times in the past to account for unexpected fossil discoveries that do not fit with preconceived notions for human evolution. However, when pathological explanations are not supported by the available evidence it is time to examine the preconceived notions that we hold.

The Flores situation has forced paradigm-changing research in a number of areas. These include the relationship between the evolution of brain size, brain reorganization and cognitive ability (Falk et al., 2009b) and the evolution of the shoulder girdle and its relationship to locomotion and tool using behavior (Larson, 2007). They also include the succession of stone tool traditions in South East Asia and the core/flake tool tradition dichotomy (Moore and Brumm, 2007), the time of extinction of *Stegodon* and the general question of survival of mammals on islands (Morwood et al., 2009; Van den Bergh et al., 2009).

It also has raised a number of questions that remain to be answered that include (1) when and how *H. floresiensis* got to Flores, (2) how it survived and evolved for perhaps ~800 ka on the island, (3) its relationship with modern *Homo sapiens* in island Southeast Asia, and (4) its physiology, life history, locomotion, and lifestyle.

The biggest question raised by this material, however, is the role of eastern Asia in hominin evolution (Dennell and Roebroeks, 2005). If *H. floresiensis* is indeed a surviving representative of early *Homo* it questions the traditional "Out of Africa 1" model for the first colonization of Eurasia by *Homo ergaster* (early African *Homo erectus*). If *H. floresiensis'* closest affinities are with pre-*ergaster/erectus* hominins as suggested by the current research, the logical conclusion is that earlier and more primitive hominids (than *H. ergaster/erectus*) were the first to leave Africa.

The discovery of *H. floresiensis* (as well as many other prior discoveries in Africa and Eurasia) clearly demonstrates that we are naïve to believe that we already know the full picture of human evolution including all of the species of hominins that ever existed. As Dennell and Roebroeks (2005) suggest, we may be on the threshold of a major transformation in our understanding of human evolution that will have profound and far-reaching implications. We need to remember that discoveries like *H. floresiensis* are what move science and our understanding of human evolution forward.

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