The origin of *Homo floresiensis* and its relation to evolutionary processes under isolation

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Abstract   Since its first description in 2004, *Homo floresiensis* has been attributed to a species of its own, a descendant of *H. erectus* or another early hominid, a pathological form of *H. sapiens*, or a dwarfed *H. sapiens* related to the Neolithic inhabitants of Flores. In this contribution, we apply a geometric morphometric analysis to the skull of *H. floresiensis* (LB1) and compare it with skulls of normal *H. sapiens*, insular *H. sapiens* (Minatogawa Man and Neolithic skulls from Flores), pathological *H. sapiens* (microcephalics), Asian *H. erectus* (Sangiran 17), *H. habilis* (KNM ER 1813), and *Australopithecus africanus* (Sts 5). Our analysis includes specimens that were highlighted by other authors to prove their conclusions. The geometric morphometric analysis separates *H. floresiensis* from all *H. sapiens*, including the pathological and insular forms. It is not possible to separate *H. floresiensis* from *H. erectus*. *Australopithecus* falls separately from all other skulls. The Neolithic skulls from Flores fall within the range of modern humans and are not related to LB1. The microcephalic skulls fall within the range of modern humans, as well as the skulls of the Neolithic small people of Flores. The cranial shape of *H. floresiensis* is close to that of *H. erectus* and not to that of any *H. sapiens*. Apart from cranial shape, some features of *H. floresiensis* are not unique but are shared with other insular taxa, such as the relatively large teeth (shared with Early Neolithic humans of Sardinia), and changed limb proportions (shared with Minatogawa Man).

Key words: LB1, Minatogawa Man, geometric morphometrics, *Homo erectus*, *Australopithecus africanus*

Introduction

The dramatic change in size that can be observed in many insular mammalian taxa is certainly the best-known adaptation to isolated conditions. However, this size change, however spectacular it may be, is not the only evident modification of island species. Generally, adaptations of island species are reflected in their craniodental anatomy, as a response to changes in diet and defensive systems, and their postcranial anatomy, as a response to changes in locomotion (Sondaar, 1977). These morphological changes are often so extensive that it is not easy to trace with certainty their direct mainland ancestry. In a few cases, such as the dwarf hippopotamuses and dwarf elephants of the Mediterranean islands, this is relatively easy because of the very limited number of mainland candidates. *Homo floresiensis*, the small-bodied hominid from Flores, could provide such a case as well, because here also there are only a very few known species that could be its direct ancestor.

However, since the description of this new species (Brown et al., 2004) several papers have appeared expressing different opinions about its origin. In the original description of the species, Brown et al. (2004) suggested that *H. floresiensis* is a descendant of *H. erectus* and explained its small size as an evolutionary adaptation to the insular environment of Flores. Later works gave further support to this theory (e.g. Falk et al., 2005, 2007; Argue et al., 2006; Baab et al., 2007; Gordon et al., 2008). The inclusion of postcranial elements in the phylogenetic analysis, however, leaves open the possibility that *H. floresiensis* originated from *H. habilis* or another, as yet unknown, early *Homo* (e.g. Morwood and Van Oosterzee, 2007). This hypothesis has not been contradicted by further studies of the cranial (Gordon et al., 2008), postcranial (Tocheri et al., 2007) and endocranial (Falk et al., 2005) anatomy of *H. floresiensis*. A completely different path to explain the origin of *H. floresiensis* was followed by other researchers who considered the small hominid from Flores as a modern human, suffering from some kind of pathology or disorder (Henneberg and Thorne, 2004; Weber et al., 2005; Jacob et al., 2006; Martin et al., 2006; Hershkovitz et al., 2007; Obendorf et al., 2008).

In this contribution, we analyze the cranial morphology of *H. floresiensis*, applying geometric morphometrics in order to further clarify its phylogenetic position. To test the hypothesis that *H. floresiensis* is a pathological *H. sapiens*, we first compare *H. floresiensis* with both microcephalic and normal *H. sapiens*. To test the hypothesis that *H. floresiensis* is similar to, or a pathological form of, the Neolithic small

people of Flores, we compare *H. floresiensis* with the Liang Togé subfossil remains. To test the hypothesis that *H. floresiensis* originates from *H. erectus* or another early hominin, we compared *H. floresiensis* with *H. erectus*, *H. habilis*, and *Australopithecus africanus*. We further discuss some particular features of its cranial and postcranial anatomy within the scope of evolutionary processes observed in insular mammals, by comparing these features with those of insular mammals known from the fossil record, including the endemic Minatogawa people from Okinawa Island, Japan.

Materials and Methods

For the comparison of *H. floresiensis* with other hominins we used material from the collections of the Nationaal Natuurhistorisch Museum, Leiden, the Netherlands (NNML), National Archaeological Museum of Athens, Greece (NAMA), and Berliner Medizinhistorisches Museum der Charité, Berlin, Germany (CMPA).

The sample of modern humans (*H. sapiens*) comprises 32 skulls, all from NNML (Table 1), including skulls originating from other islands of the Malay Archipelago.

We further included two microcephalic modern humans in our analysis. The first comes from Cave Malakari of Crete (Greece; NAMA–Malakari–1962), generally referred to as 'Minoan' (e.g. Poulianos, 1975; Argue et al., 2006), though in reality it belongs to the Protogeometric period, dated at about 3,000 BP (Platon, 1966). This particular skull is the specimen used by Henneberg and Thorne (2004) to demonstrate that *H. floresiensis* is a microcephalic modern human. The second microcephalic skull comes from the Netherlands (NNML). This skull was used by Dubois to disprove the claim of Lydekker (1895, in Dubois, 1896) that the skull cap of *H. erectus* from Trinil 2 (Java) belonged to a 'microcephalic idiot'.

In addition, we analyzed two skulls (NNML) from archaeological sites on Flores, excavated in the 1950's (Maringer and Verhoeven, 1970). The first skull originates from the Liang Togé cave and has been dated to 3550 ± 525 BP (Jacob,

Table 1. Skulls of non-pathological recent humans (*H. sapiens*) in alphabetical order of provenance.

Ambon	NNML–B8E, NNML–B8D
Belgium	NNML–B13D
China	NNML–B7D, NNML–B7E, NNML–B7F, NNML–B7B.
Congo	NNML–Efe–Pygme
Germany	NNML–B13F
Greenland	NNML–B10D
Indonesia	NNML–B9A (Java), NNML–B5A (Sulawesi), NNML–B5B (Sulawesi)
Japan	NNML–B10C, NNML–B10A, NNML–B10B, NNML–B10E
Netherlands	NNML–anat.r.n.155, NNML–anat.r.n.159
New Caledonia	NNML–B34A
New Zealand	NNML–B9C
Nigeria	NNML–B11C
Papua–New Guinea	NNML–B18A, NNML–B31A, NNML–B30B, NNML–B29A, NNML–B28F, NNML–B26A
South Africa	NNML B11B, NNML B11A
Thailand	NNML–B8F
United Kingdom	NNML–B13F

1967). The second skull was excavated in Liang Momer and, based on the artifacts found in the site, has been dated to about 5000–3000 BP (Jacob, 1967). The small stature of the individual from Liang Togé was highlighted by Henneberg and Thorne (2004) as proof that *H. floresienis* was not a dwarf.

The following specimens of fossil hominids were analyzed and digitized: a stereolithographic replica of the skull of *Homo floresiensis* (LB1) from Liang Bua (Flores), a first-generation cast of *H. erectus* (Sangiran 17) from Sangiran (Java), a cast of *H. habilis* (KNM–ER 1813) from Koobi Fora (Kenya) and a cast of *A. africanus* (Sts 5) from Sterkfontein (South Africa) (all four from the collections of NNML).

The landmarks used in this study were collected with the use of a Microscribe G2 (multijoin 3D digitizer) and are presented in Figure 1. Due to the absence of most vault sutures
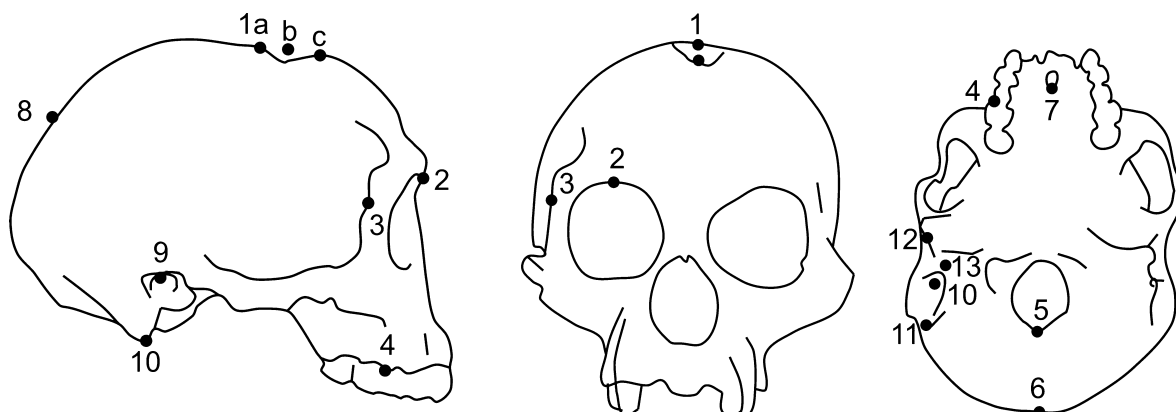

Figure 1.   Sketch of *Homo floresiensis* LB1 skull with the measured landmarks. (1) bregma, (2) mid-torus inferior (point on the inferior margin of the supraorbital torus roughly at the centre of the orbit), (3) Frontomalare temporale (where the frontozygomatic suture crosses the lateral edge of the zygoma), (4) M1–2 contact point (laterally projected onto the alveolar margin), (5) opisthion, (6) inion, (7) incisivion, (8) lambda, (9) porion, (10) mastoidale, (11) lateral end of the mastoid notch, (12) deepest point of the lateral margin of the articular eminence, (13) stylomastoid foramen. Landmark 1 has three different alternatives (a, b, c: see also Materials and Methods section).

in *H. floresiensis* LB1 (Brown et al., 2004), most of the standard landmarks could not be digitized on the dorsal part of the neurocranium. In addition, the region around the bregma is missing (Figure 2A). In order to describe that part of the skull, three points were digitized along the mid-sagittal plane: one at the rostral end, one at the caudal end, and one at the centre of the damaged region. The position of the central point is estimated by reconstructing the missing part. Subsequently, we ran the analysis three times, each time assuming that the bregma coincides with a different one of these three positions. The differences between these three analyses appear to be negligible. This means that the exact anteroposterior position of the bregma is not so important. For our analysis, we take the reconstructed central position for the bregma.

To compare the overall cranial shape of *H. floresiensis* LB1 with that of the other hominids we performed a principal component analysis and a cluster analysis of the shape, as represented by the digitized landmarks. For the morphometric analysis we performed a generalized least-squares superimposition. Based on the mean Procrustes coordinates for each specimen, we calculated the Euclidean distances among specimens. According to Lockwood et al. (2004), al-

though these Euclidean distances are not identical to true Procrustes distances, they are a close approximation. The specimens were clustered by a weighted pair-group method of arithmetic means cluster analysis based on squared Euclidean distances between specimens for all the principal components (Sneath and Sokal, 1973). For the general Procrustes analysis, principal component analysis, and visualization of shape variation along principal components we used Morphologika (O'Higgins and Jones, 1997, 1998; Strand Viarsdóttir et al., 2002). For the cluster analysis we used the statistical software SPSS.

In addition to the skulls that were analyzed with geometric morphometrics, we used three more hominid specimens for a conventional comparison of their morphology: a microcephalic modern human (CMPA 8934/1842), the type specimen of *H. erectus* (NNML Trinil 2) from Java, and a first-generation cast (NNML) of the best-preserved skull (Minatogawa No. 1) of the Late Pleistocene endemic Minatogawa people (early *H. sapiens*) of Okinawa (Ryukyu Islands), Japan. Radiocarbon dates of 18250 ± 650 to 16600 ± 300 years BP were obtained from charcoal fragments from the lower deposit of the Minatogawa site (Kobayashi et al., 1974), while direct gamma-ray spectro-
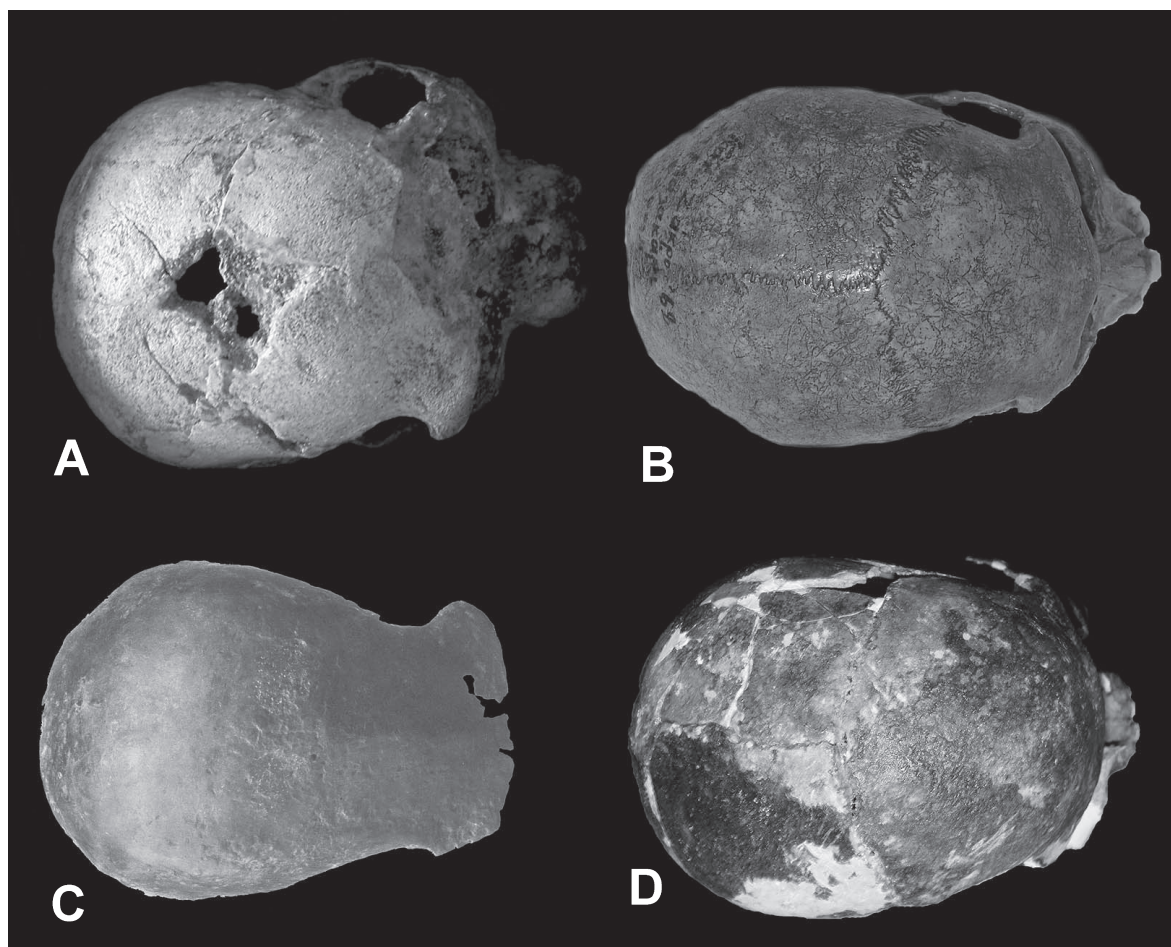

Figure 2. Dorsal view of (A) *H. floresiensis* (LB1), (B) Microcephalic *H. sapiens* from Crete (NAMA–Malakari–1962), (C) *H. erectus* (NNML–Trinil–2), and (D) *H. sapiens* from Liang Momer (NNML–Momer skull E). All specimens are scaled to the same anteroposterior length.

metric uranium series dating gives an age of 19200 ± 1800 years BP (Yokoyama, 1992). However, the relation of the charcoal to the human remains is not certain and there are many uncertainties in the uranium-series dating of fossil bone (Matsu'ura, 1999). The morphology of this skull differs essentially from that of the later Neolithic Jomon people, who replaced the Minatogawa people (Suzuki, 1982; Baba and Narasaki, 1991). The original is stored in the Department of Anthropology and Prehistory, University Museum, Tokyo University.

Results

Overall shape analysis of the cranial morphology

Shape differences among the studied specimens clearly indicate that *H. floresiensis* is distinct from modern humans, including microcephalic specimens, Neolithic specimens from Flores, and Melanesian specimens.

The first principal component (PC1) separates all measured modern humans on the one side from *H. floresiensis* (as represented by LB1), *H. habilis* (as represented by

KMN–ER 1813), *H. erectus* (as represented by Sangiran 17), and *A. africanus* (as represented by Sts 5) on the other side (see Figure 3). The separation of the groups along PC1 is qualified by the height of the cranial vault, the degree of prognathism, and the development of the supraorbital region. This is partly the result of the landmarks that correspond to the position of the incisivion and bregma (see Figure 1). The exact anteroposterior position of bregma appears not to affect the results of our analysis as was already noted in the Materials and Methods section. However, the same is not true for its vertical position. This landmark lies much higher in modern humans than in the fossil *Homo* specimens and *A. africanus*. Modern humans have a much higher arched skull and a less prognathic face than the extinct hominids. In this respect, *H. floresiensis* cannot be separated from *H. erectus*. A similar low vault in combination with a more prognathic face is seen in the microcephalic specimen from Crete. However, although this specimen may superficially look like *H. erectus*, it lies at the boundary of the modern human range, but within the range, and is far removed from *H. erectus* and the other extinct hominids.

LM: Skull E of *Homo sapiens* from Liang Momer
LT: Skull of *Homo sapiens* from Liang Toge

micro-NL: Microcephalic man from the Netherlands
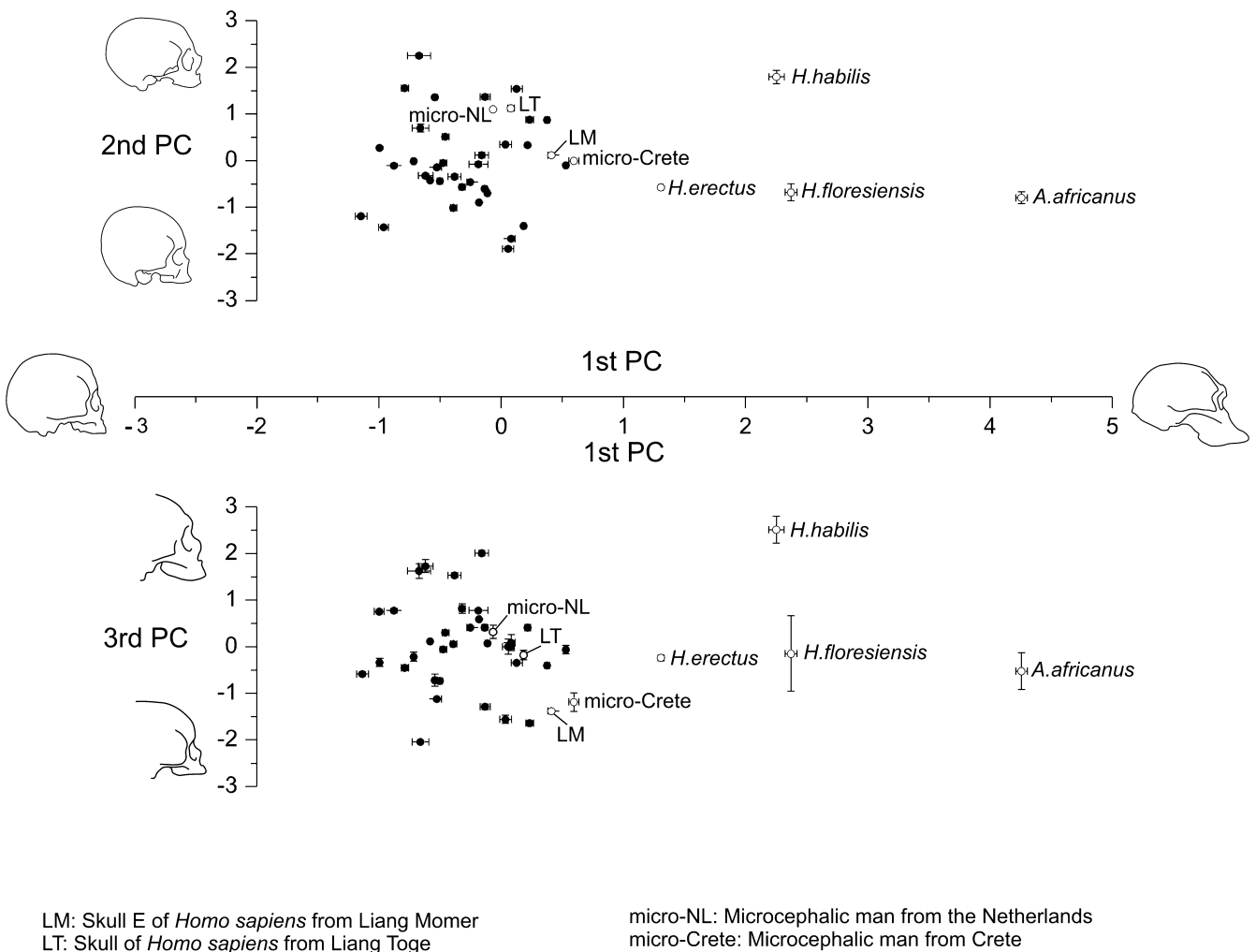micro-Crete: Microcephalic man from Crete

Figure 3.   Plot of the first three principal components of the principal component analysis. The error bars explain the uncertainty concerning the exact location of the bregma (landmark 1 of Figure 1; see Materials and Methods).

The second principal component (PC2) describes the changes in the midsagittal contours of the neurocranium, mainly the elongation of the vault. In this respect, *H. floresiensis* is similar to *H. erectus*. The Cretan microcephalic is somewhat similar to *H. floresiensis*, whereas the other microcephalic has a longer vault. The third principal component (PC3) mainly describes facial length. *H. habilis* has a much longer face than *H. floresiensis*. This is due to a more ventrally placed incisivion, and the contact point between the alveoli for M1 and M2 at the lingual side.

Based on the first three principal components, *H. floresiensis* is morphologically closest to the *H. erectus* and *H. habilis* specimens and far removed from *Australopithecus*. The microcephalic modern humans and the Neolithic Flores specimens cluster with *H. sapiens*.

When taking all principal components into account with the use of Euclidean distances (see Figure 4), *H. floresiensis* clusters only with *H. erectus*. The distance between these two taxa and modern humans, based on the branch length, is too large to assume a morphological similarity between these two groups. The similarity between *H. habilis* and *H. floresiensis* is significantly less than between the latter and *H. erectus*, from which it cannot be separated.

To conclude, the overall morphology of the skull of *H. floresiensis* is more similar to *H. erectus* than to modern humans and *H. habilis*.

Other aspects of cranial morphology

Seen from above (Figure 2), the skulls of *H. floresiensis* (Figure 2A) and *H. erectus* (Figure 2C) both show a clear postorbital constriction, whereas this is only minimally so in the Neolithic microcephalic skull from Crete (Figure 2B) and practically absent in the Neolithic small skull from Flores (Figure 2D). Seen from the side, the skulls of the small Neolithic people of Flores differ from microcephalic skulls, as their foreheads are similar to those of all modern humans. The same is not true for the microcephalic modern humans. Figure 5 presents the skulls of three microcephalics of different brain size compared to the small Neolithic Flores skulls. Despite the differences in size, the three microcephalics share the same basic shape. They have a posteriorly sloped frontal bone with respect to normal *H. sapiens*, they are prognathic, and they have relatively large orbits. These features become even more evident as the skull gets smaller. The skull of Minatogawa is very different from all other *H. sapiens*, due to its low, long, and wide skull vault, and it shows no similarity with LB1 in that respect. In general, *H. floresiensis* differs from all *H. sapiens* (microcephalic or not) by virtue of its relatively low vault, a feature that it shares with the extinct species of *Homo*.

Discussion

Comparison with pathological forms

A number of researchers have considered *H. floresiensis* as a microcephalic *H. sapiens* (e.g. Hennenberg and Thorne, 2004; Weber et al., 2005; Martin et al., 2006; Jacob et al., 2006). In contrast, others have demonstrated that the skull of LB1 cannot be assigned to a modern microcephalic human, whether based on its endocranial (Falk et al., 2005, 2007) or cranial (Argue et al., 2006) anatomy. Although variable morphotypes correspond to microcephaly (Falk et al., 2007), in most cases, the skulls of microcephalic modern humans are not just smaller in size, but are also different in morphology, characterized by a somewhat more 'primitive' look, and thus are particularly interesting for our study. However, they remain different from small-sized normal humans (Figure 5). A decrease in skull size due to pathological pro-
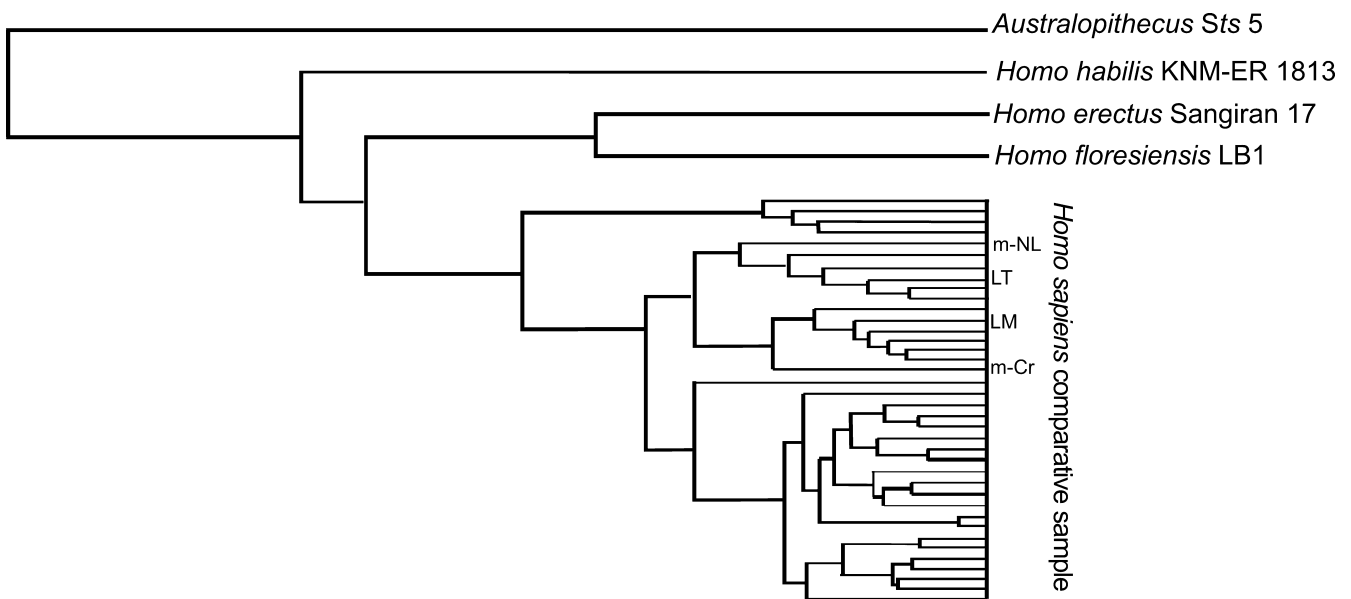

Figure 4. Weighted pair-group method of arithmetic means cluster analysis based on squared Euclidean distances of all specimens used in the principal component analysis. m-NL: microcephalic man from the Netherlands; m-Cr: microcephalic man from Crete; LT: skull from Liang Togé; ML: skull from Liang Momer.
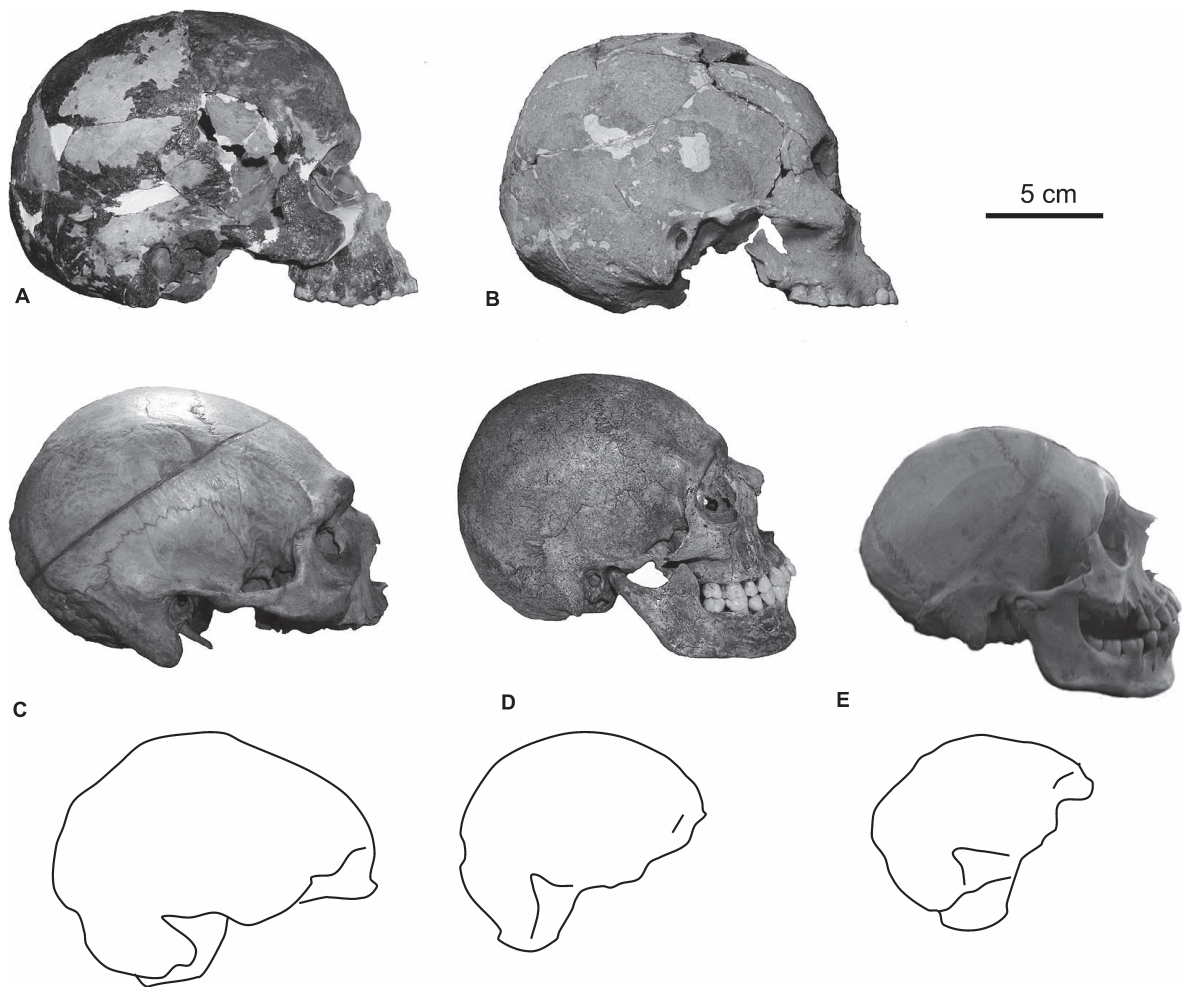
Figure 5.   Lateral views of the two prehistoric skulls from Flores, three microcephalics and outlines of their endocranial casts. (A) Skull E from Liang Momer (NNML); (B) Liang Togè (NNML); (C) microcephalic from the Netherlands (NNML); (D) microcephalic from Malakari Cave, Crete, Greece (NAMA); (E) microcephalic from Kiwittsblott, Germany (CMPA 8934/1842).

cesses apparently yields a different morphology than due to evolutionary processes.

In this contribution we compared the skull of *H. floresiensis* to the skulls of two microcephalics, using geometric morphometrics. Due to their particular anatomy, these two microcephalics fall on the edge of the *Homo sapiens* morphospace (see Figure 3). Nevertheless, their overall cranial shape still corresponds to the modern human morphology, which easily distinguishes them from extinct species of *Homo* (*H. erectus*, *H. floresiensis*, and *H. habilis*). The microcephalics have thin supraorbital ridges, similar to those of *H. sapiens* (see Figure 2) and unlike those of extinct human species. Their supraorbital ridges are more pronounced than in normal modern humans, because their eyes are less affected by the reduction in brain size (Figure 5). However, these ridges are thin and similar in absolute size to those of modern humans, unlike those of extinct *Homo* species. In addition, their foreheads, although relatively low for *H. sapiens*, are much higher than those of both *H. floresiensis* and *H. erectus*. Taking all these differences together, we conclude that the material from Liang Bua cannot be considered a mi-

crocephalic modern human. An alternative hypothesis, that LB1 is a microcephalic *H. erectus*, cannot be dismissed entirely, because such microcephalics would cluster with *H. erectus* just as microcephalic *H. sapiens* cluster with the rest of *H. sapiens*; see, however, the end of this section.

Recently, Hershkovitz et al. (2007) explained the small stature and unique anatomical features of *H. floresiensis* as the result of primary growth hormone insensitivity, known as Laron syndrome. However, the development of the supraorbital ridges that is seen in patients with Laron syndrome (see Figure 2 in Hershkovitz et al., 2007) is far too small for *H. floresiensis*. Furthermore, these patients have delicate faces, marked chins, and thin vaults (Obendorf et al., 2008), none of which is the case in *H. floresiensis*. Hershkovitz et al. (2007) admitted that several differences in cranial anatomy exist between patients with Laron syndrome and *H. floresiensis*, but considered these differences as entirely due to the different basic cranial anatomy of the populations of Southeast Asian islands compared to those of the Mediterranean region from where their sample came. The two prehistoric skulls from Flores indeed have more project-

ing faces and more sloped frontal bones than most modern humans of our sample (Figure 4 and Figure 5). However, these prehistoric skulls still fall within the modern human morphology, whereas LB1 does not.

Obendorf et al. (2008) describe the hominin fossils from Liang Bua as possible myxoedematous endemic cretins, a form of congenital hypothyroidism resulting in a dwarf-like stature with a small brain induced by a low iodine intake during pregnancy and early development. Their basic argument concerns the size of the pituitary fossa, and consequently that of the hypophysis, which they consider much larger than usual, befitting a patient with a primary hypothyroidism. This, however, stands in sharp contrast to the opinion of Dean Falk, a member of the team that produced and described the virtual endocast of *H. floresiensis* LB1, who clearly stresses that the pituitary fossa of LB1 is of a normal size (Culotta, 2008). Another feature highlighted is the primitive wrist morphology of LB1, but this can be explained in various ways (see below). Finally, iodine deficiency is not a likely factor on an island surrounded by seawater, which is naturally rich in iodine, and iodine-rich flora and fauna.

To conclude, from the above it is evident that the skull of *H. floresiensis* LB1 does not belong to a modern human who suffered from one of the above-mentioned disorders (microcephaly, Laron syndrome, cretinism). Naturally, other disorders that mimic the morphology of *H. floresiensis* may be described in the future, resulting in more publications interpreting the fossils as pathological. In fact, the attribution of newly discovered species of insular mammals to pathological forms of already established species is nothing new. The unusual morphology of the fossils of insular mammals has regularly been explained as the result of degeneration due to a high degree of inbreeding (for discussion, see Sondaar, 1977), even as late as the 1960s (e.g. Kuss, 1965) when the idea of adaptations of island mammals was already widely accepted.

The reason behind the reluctance to accept *H. floresiensis* as a new human species might very well be different. Two very important human fossils in the history of palaeoanthropology were also discarded as pathological forms when they were announced. This fate first befell the Neandertal, the first distinct fossil human known. The discoverers (Fuhlrott, 1856, 1859; Schaaffhausen, 1858) recognized the remains as those of a robust ancient race, but others concluded that their Neandertal Man was an idiot, or suffering from hydrocephalus or rickets (Moerman, 1977). The next victim was Java Man (*Pithecanthropus erectus*, now *H. erectus*), presented as the supposed missing link between apes and humans (Dubois, 1894). Its remains were initially received with scepticism, and even considered by some to be a pathological modern human, a pygmoid *H. sapiens* (Buyssens, 1937), a small Neandertal Man (Mair, 1922), a giant gibbon (Krause, 1895: *Hylobates giga*; Bumüller, 1899: *H. giganteus*), or even a bastard form of a human and ape (Mahaudeau, 1909). The main problem was that if the skullcap belonged to the femur, than the size of the individual was of a normal human being (Manouvrier, 1895). However, a normal human being with such a small brain size cannot be other than an idiot or a microcephalic (Cunningham, 1895; Lydekker, in Dubois, 1896).

A third early human was not considered pathological, but equally not accepted as a new human-like species. This happened to *A. africanus*, hailed as our ancestor by its describer (Dart, 1925), but dismissed as a fossil ape, again based on its small brain size. *H. floresiensis* falls into both categories, that of the dwarfed insular mammals, and that of the extinct human species. It is thus not surprising that *H. floresiensis* is regularly interpreted as a pathological form.

Comparison with mainland hominins

Researchers who consider *H. floresiensis* to be the outcome of evolutionary processes (Brown et al., 2004; Falk et al., 2005, 2007; Argue et al., 2006; Baab et al., 2007; Morwood and Van Oosterzee, 2007; Tocheri et al., 2007; Gordon et al., 2008) propose that it could be either a dwarfed descendant of an early *H. sapiens*, of *H. erectus*, or even of an earlier hominin, such as *H. habilis*. It is still unclear which of these extinct human species is the closest to the ancestry of *H. floresiensis*.

In our analysis we compared LB1 with examples of the three proposed ancestors: *H. sapiens*, *H. erectus* from Java (Sangiran 17), and *H. habilis* (KMN–ER–1813). The overall cranial shape of LB1 appears to be very distinct from that of modern humans and closer to that of *H. erectus*. The difference from *H. habilis* is much smaller, but clearly larger than that between *H. erectus* and *H. floresiensis*. Therefore, based on the available data, we may conclude that *H. floresiensis* is morphologically closest to *H. erectus* from Sangiran. Further evidence is needed to determine the degree of similarity with any other *H. erectus*, because we could only include one specimen of Asian *H. erectus* in our analysis, due to the fragmented nature of the fossil record of *H. erectus*. Sangiran 17 is the most complete specimen of Asian *H. erectus*, except for the Dmanisi material, which unfortunately is unavailable to us. However, since these forms are conspecific or at least phylogenetically close to the Sangiran 17 specimen, the conclusion that *H. floresiensis* is related to *H. erectus* remains basically the same. Such a close relationship was already suggested in the initial paper by Brown et al. (2004), who pointed out a series of morphological similarities with *H. erectus*. In addition, they suggested that the latter species should have arrived on Flores by about 800,000 years ago, based on the findings of a primitive lithic industry (Maringer and Verhoeven, 1970; Morwood et al., 1998; Sondaar, 1998, 2000; Brumm et al., 2006) and biostratigraphical data (Van den Bergh, 1999) that support this time of arrival.

Argue et al. (2006) used linear cranial measurements to explore the affinities of *H. floresiensis*. They confirmed that the hominin from Flores has a quite distinct morphology and that it should be a species of its own. In their analysis too, *H. floresiensis* is very different from *H. sapiens* and has many similarities to *H. erectus*, which supports our conclusions. They further conclude that *H. floresiensis* is particularly close to *H. ergaster*, but we could not confirm this because several landmarks could not be taken on *H. ergaster* material, due to missing parts.

Gordon et al. (2008) explored the affinities of *H. floresiensis* using linear measurements of the cranial vault, and concluded that *H. floresiensis* is morphologically similar to *H. erectus*, in particular to the specimen from Dmanisi, to *H.*

ergaster (KMN–ER 3733) and to *H. habilis* (KMN–ER 1813). Our results differ from theirs in the sense that *H. floresiensis* is in our view morphologically closer to *H. erectus* from Sangiran than to *H. habilis*. The differences between our results and those of Argue et al. (2006) and Gordon et al. (2008) are best explained by the fact that we used geometric instead of traditional morphometrics. The only other published work containing results of a geometric morphometric analysis of *H. floresiensis* LB1 is that of Baab et al. (2007), which is only an abstract, and hence without much detail. Their results, like ours, indicate a close similarity between *H. floresiensis* and Asian *H. erectus*.

To conclude, the outcome of our analysis is that *H. floresiensis* is morphologically similar to *H. erectus*. The stratigraphic record of Flores indicates that humans arrived on the island at least 800,000 years ago, and it seems thus reasonable to assume that the ancestor of *H. floresiensis*, an Asian type of *H. erectus*, is precisely this colonizer.

Comparison with insular taxa

In the above paragraphs we supported the idea that *H. floresiensis* is morphologically similar to *H. erectus* and is its descendant. However, as many authors have already pointed out, there are several differences between the two species. Morwood et al. (2005) noted that the skull and mandibles of *H. floresiensis* present a combination of primitive and derived features. They also pointed out that its body proportions are similar to those of *Australopithecus*. Furthermore, though its brain has many similarities with that of *H. erectus*, its size is considerably smaller (Brown et al., 2004; Falk et al., 2006, 2007; Martin et al., 2006; Richards, 2006).

According to us, these differences partly reflect adaptational changes to the island environment. In general, insular large mammals evolve morphologies that present a mixture of derived and primitive features in response to a change in habitat and diet (Van der Geer, 2005). A number of derived features which were vital for survival on the mainland are no longer advantageous and are lost, resulting in an apparent return to the primitive condition, whereas a number of other features are secondarily derived in order to survive under the changed circumstances. The overall outcome is a mixture of derived and primitive features.

Similar processes are to be expected in insular humans as well, but such remains are extremely scarce. With the exception of Flores, there are only a few well-studied cases of endemism in island humans: Late Palaeolithic-Early Neolithic human remains from Sardinia (Spoor and Sondaar, 1986), Neolithic remains from the Palau Islands (Berger et al., 2008), and Late Palaeolithic remains from Okinawa Island, Japan (Suzuki and Hanihara, 1982). The fossils from Sardinia show an unusual morphology and might thus represent evidence of endemism. However, the material is limited to two cranial fragments, a phalanx and a proximal ulna, which is insufficient to draw any certain conclusions, though the robustness of the zygomatic process and the large size of the alveoli are striking (Spoor and Sondaar, 1986). The preliminary report of the human remains from the Palau islands notes several differences from present-day inhabitants of the islands, such as a small stature and some primitive traits, for example a reduced chin (Berger et al., 2008). The latter are explained as primitive traits due to pleiotropic or epigenetic correlates of development programmes for a small body size.

Much better documented are the Late Pleistocene Minatogawa people of Okinawa Island, Japan. These people exhibit a different morphology compared to the Neolithic Jomon people who replaced them (Suzuki, 1982; Baba and Narasaki, 1991). The typical features are considered partly phylogenetic (retention of archaic features), and partly environmental (adaptation to the island), which are not easy to distinguish (Baba, 2000). In any case, the most prominent differences in the skull that can be explained phylogenetically are the thick cranial bones, the lateral projection of the supramastoid region, and the projection of the glabella, whereas those that are explained as environmental are the smaller stature (150–155 cm: Baba and Endo, 1982), the extraordinarily strong development of the masticatory muscles, the deep temporal fossae with flared zyogmatic arches, the wide and high position of the attachment of the masseter muscles in the zygomata, and the thick alveolar bones. All these changes are interpreted as adaptations to a different diet with increased chewing stress (Baba, 2000), further evidenced by the high degree of tooth wear. Unfortunately, our geometric landmarks describe the shape of the skull and cannot be used to detect the above-mentioned masticatory adaptations. The primitive or phylogenetic features define the Minatogawa people as archaic *H. sapiens*, not as *H. erectus*. The Minatogawa skull differs essentially from modern *H. sapiens*, probably as a result of long-term evolution in isolation. What makes the Minatogawa skull unique is its long and low skull vault which at the same time is wide.

The small stature of *H. floresiensis* is considered an adaptation to the island environment as well (Brown et al., 2004). Dwarfism is frequently observed in island mammals, and is explained as advantageous because of the smaller amount of food needed and the more efficient thermal regulation of this body type (Sondaar, 1977, 1986). What seems to be more difficult to explain is its smaller brain size. Martin et al. (2006) compared the brain size of *H. floresiensis* with that of other insular animals and concluded that, if it would have followed the patterns seen in other insular animals, the human from Flores should have had a much lower body mass than was calculated by Brown et al. (2004). There is only one other case of an insular mammal with a considerably smaller brain in comparison with its mainland ancestor. The mouse goat *Myotragus balearicus* (Mallorca, Pleistocene to Holocene) has a much smaller brain than *Gallogoral*, which is supposed to be its closest mainland relative (Palombo et al., 2008). All other documented insular mammals have a brain of the same relative size as their mainland relatives: the Cretan dwarf deer *Candiacervus* (Palombo et al., 2008), the Sardinian dog *Cynotherium* (Palombo and Giovinazzo, 2004), the Cypriot pygmy *Hippopotamus minutus* (unpublished data), or even relatively larger, as in the Sicilian pygmy elephant *Elephas falconeri* (Palombo and Giovinazzo, 2005). It appears that what is observed in *H. floresiensis* and *Myotragus* is rather the exception and not the rule in island evolution.

A recent study indicated that there is an association between food scarcity and small brain size in *Pongo* (Taylor

and van Schaik, 2007). It is therefore also possible for a primate to evolve under particular ecological conditions towards a form with a smaller brain size. On the other hand, some may argue that larger brains have certain advantages, and in the case of humans, the ability to make tools is one of them. However, the brain of *H. floresiensis* is not only smaller than that of *H. erectus*, but also has certain derived features (Falk et al., 2005), indicating an evolutionary case not seen in mainland hominids.

Apart from the small stature of *H. floresiensis*, shared with the above mentioned other insular humans, its limb proportions are also considered primitive, resembling those of *Australopithecus* (Morwood et al., 2005). In addition, its humeral torsion is significantly less than seen in other *Homo* and in *Australopithecus* (Morwood et al., 2005). Furthermore, the morphology of its wrist differs from that of modern humans (Tocheri et al., 2007). These differences in postcranial morphology indicate a different locomotion and use of the hands by *H. floresiensis* compared to modern humans and to some other members of the genus *Homo*. At first sight, a human with limb proportions similar to those of *Australopithecus* might sound strange, but it is no stranger than a deer with goat-like limbs or a dwarf hippo that was able to live in the mountains. There are several examples of such animals, e.g. the dwarf deer *Candiacervus* (Crete), *Hoplitomeryx* (Gargano), and *Cervus astylodon* (Ryukyu Islands) (Van der Geer, 2005), and the pygmy hippopotamuses *Hippopotamus creutzburgi* (Crete) and *H. minutus* (Cyprus) (Spaan et al., 1994). These cases clearly demonstrate that a radical change in limb proportions and morphology is a common trend in insular large mammals. The Minatogawa people are no exception with their large and stout foot bones, extremely short heels (tuber calcanei), large and thick wrist bones, short tibiae, and broad fibulae (Baba and Endo, 1982).

The teeth of *H. floresiensis* are also relatively large. Brown et al. (2004) noted that LB1 is megadont relatively to *H. sapiens* and *H. erectus*, but not to *H. habilis*. The large teeth of *H. floresiensis* cannot be raised as an argument against an origin from *H. erectus*. Relatively large teeth are a common feature in dwarfed insular mammals (Maglio, 1973; Gould, 1975), indicating that teeth might show the tendency to reduce in size at a slower rate than the rest of the skull. This is further evidenced by the negative allometry of molar size relative to skull size found in African and Philippine pygmies compared to normal-sized Africans and Filipinos, respectively (Shea and Gomez, 1988). Thus if *H. floresiensis* is a dwarfed *H. erectus*, then its teeth are expected to be relatively large. In the Minatogawa people, however, the teeth are of normal size, in contrast to their well-developed masticatory muscles. On the other hand, the Late Pleistocene maxilla of Sardinian hominins have large alveoli, strongly suggesting the presence of relatively large teeth.

Conclusion

The overall cranial morphology of *H. floresiensis* (LB1) when compared with that of Asian *H. erectus* (Sangiran 17), *H. habilis* (KMN–ER 1813), *A. africanus* (Sts 5) and a sample of normal as well as microcephalic modern *H. sapiens*, is most similar to that of *H. erectus*. On the ground of this morphological similarity we agree with the phylogenetic schemes that suggest a close relationship between the Flores hominin and *H. erectus*. Furthermore, our results are not in conflict with stratigraphic data indicating that humans arrived on the island of Flores by about 800,000 years BP.

Some researchers questioned the initial affinity suggested between *H. floresiensis* and *H. erectus*, mainly on the ground of its supposedly primitive limb proportions, which are reminiscent of those of the australopithecines, and its unexpectedly small brain size. However, postcranial proportions cannot be used as a valid character in phylogenetic analyses, because all known insular dwarf mammals evolved secondarily derived changes in their limb anatomy and proportions. Endemic Palaeolithic humans, such as the Minatogawa people of Okinawa Island, Japan, are no exception. Furthermore, the relatively much smaller brain size of *H. floresiensis* can be explained in the light of insular evolution as well, because there is another well-documented example of such a decrease in brain size in an insular mammal (*M. balearicus*). However, this latter case appears to be an exception rather than a rule, as brain size in other insular mammals remains constant during the process of dwarfing. Further study of *H. floresiensis* in relation to its ancestor, an Asian branch of *H. erectus*, is thus needed to shed light on this enigmatic case.

References

Argue D., Donlon D., Groves C., and Wright R. (2006) *Homo floresiensis*: microcephalic, pygmoid, *Australopithecus*, or *Homo*? Journal of Human Evolution, 51: 360–374.

Azzaroli A. (1961) Il nanismo dei cervi insulari. Palaeontographia Italalica, 46, Paleontologia ed ecologia del Quaternario, 4(1): 1–32.

Baab K.L., McNulty K.P., and Brown P. (2007) Allometric scaling of craniofacial shape: implications for the Liang Bua hominins. PaleoAnthropology A2.

Baba H. (2000) Physical adaptation of the Minatogawa People to island environments. Tropics, 10(1): 231–241.

Baba H. and Endo B. (1982) Postcranial skeleton of the Minatogawa Man. In: Suzuki H. and Hanihara K. (eds.), The Minatogawa Man: The Upper Pleistocene Man from the Island of Okinawa. University Museum Bulletin 19, The University of

Tokyo, pp. 61–159.

Baba H. and Narasaki S. (1991) Minatogawa Man, the oldest type of modern *Homo sapiens* in East Asia. Quaternary Research, 30: 221–230.

Berger L., Churchill S., De Klerk B., and Quinn R. (2008) Small-Bodied Humans from Palau, Micronesia. PLoS ONE, 3(3): e1780.

Brown P., Sutikna T., Morwood M.J., Soejono R.P., Jatmiko, Wayhu Saptomo E., and Awe Due R. (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature, 431: 1055–1061.

Brumm A., Aziz F., van den Bergh G.D., Morwood M.J., Moore M.W., Kurniawan I., Hobbs, R.D., and Fullagar R. (2006) Early stone technology on Flores and its implications for *Homo floresiensis*. Nature, 441: 624–628.

Bumüller J. (1899) Das menschliche Femur, nebst Beiträgen zur Kenntnis der Affen-Femora. Dissertation München, Augsburg.

Buyssens P. (1937) Le Pithécanthrope était-il un Pygmée? Brüssel.

Culotta E. (2008) Were the Flores hobbits really cretins? ScienceNOW, March 2008.

Cunningham D.J. (1895) A paper on *Pithecanthropus erectus*, the man-like transitional form of Dr. Eug. Dubois. Journal of Anatomy and Physiology, 29, NS, 9: xviii–xix.

Dart R. (1925) *Australopithecus africanus*: the man-ape of Southern Africa. Nature, 115: 195–199.

Dubois E. (1894) *Pithecanthropus erectus*, eine Menschenaehnliche Uebergangsform aus Java. Landesdruckerei, Batavia.

Dubois E. (1896) On *Pithecanthropus erectus*: a transitional form between Man and the Apes. Transactions of the Royal Dublin Society, 6(1): 1.

Falk D., Hildebolt C., Smith K., Morwood M., Sutikna T., Brown P., Jatmiko E., Saptomo W., Brunsden B., and Prior F. (2005) The brain of *Homo floresiensis*. Science, 308: 242–245.

Falk D., Hildebolt C., Smith K., Morwood M.J., Sutikna T., Jatmiko, Saptomo E.W., Brunsden B., and Prior F. (2006) Response to comment on "the brain of LB1, *Homo floresiensis*." Science, 312: 999c.

Falk D., Hildebolt C., Smith K., Morwood M.J., Sutikna T., Jatmiko, Wahyu Saptomo E., Imhof H., Seidler H., and Prior F. (2007) Brain shape in human microcephalics and *Homo floresiensis*. Proceedings of the National Academy of Sciences of the USA, 104: 2513–2518.

Fuhlrott C. (1856) Der fossile Mensch aus dem Neanderthal und sein Verhältniss zum Alter des Menschengeschlechts. Verlag von B. Kalf und Bolmer, Duisburg.

Fuhlrott C. (1859) Menschliche Ueberreste aus einen Felsengrotte des Düsselthals. Verhandlungen des Nationales Verein des Preusisches Rheinlandisches und Westfalens, 16. Bonn.

Gordon A.D., Nevell L., and Wood B. (2008) The *Homo floresiensis* cranium (LB1): size, scaling, and early *Homo* affinities. Proceedings of the National Academy of Sciences USA, 105(12): 4650–4655.

Gould S. (1975) On scaling of tooth size in mammals. American Zoologist, 15: 351–362.

Henneberg M. and Thorne A. (2004) Flores human may be a pathological *Homo sapiens*. In: Barham L. (ed.), Some initial informal reactions to the publication of the discovery of *Homo floresiensis* and replies from Brown & Morwood. Before Farming, 4: 2–4.

Hershkovitz I., Kornreich L., and Laron Z. (2007) Comparative skeletal features between *Homo floresiensis* and patients with primary growth hormone insensitivity (Laron syndrome). American Journal of Physical Anthropology, 134: 198–208.

Jacob T. (1967) Some Problems Relating to the Racial History of the Indonesian Region. Drukkerij Neerlandia, Utrecht.

Jacob T., Soejono R.P., Hsü K., Frayer D.W., Eckhardt R.B., Kuperavaga A.J., Thorne A., and Henneberg M. (2006) Pygmoid Australomelanesian *Homo sapiens* skeletal remains from Liang Bua, Flores: population affinities and pathological abnormalties. Proceedings of the National Academy of Sciences USA, 103: 13421–13426.

Kobayashi H., Hirose Y., Sugino M., and Watanabe N. (1974) TK-99 Minatogawa. Radiocarbon, 16: 100.

Krause W. (1895) Besprechung von *Pithecanthropus erectus*, eine menschenähnliche Uebergangsform aus Java von E. Dubois. Zeitschrift für Ethnologie, 27: 78–81.

Kuss S.E. (1965) Eine pleistozäne Säugetierfauna der Insel Kreta. Berichte der Naturforschenden Gesellschaft zu Freiburg im Breisgau, 55(2): 271–348.

Lockwood C.A., Kimbel W.H., and Lynch J.M. (2004) Morphometrics and hominoid phylogeny: support for a chimpanzee-human clade and differentiation among great ape subspecies. Proceedings of the Royal Society, 101(13): 4356–4360.

Maglio V.J. (1973) Origin and evolution of the Elephantidae. Transactions of The American Philosophical Society of Philadelphia, NS, 63: 1–149.

Mahaudeau P.G. (1909) L'Origine de l'homme au poit de vue experimental. Revue Ecologie d'Anthropologie, 19.

Mair R. (1922) Über die Bregmagegend und die Lage des Bregma mit besonderer Berücksichtigung des *Pithecanthropus*. Zeitschrift für Morphologie und Anthropologie, 22: 435–480.

Manouvrier L. (1895) Discussion du '*Pithecanthropus erectus*' comme précurseur présumé de l'homme. Bulletin de la Société d'Anthropologie de Paris, 6: 12–47.

Maringer J. and Verhoeven T.H. (1970) Die Steinartefacte aus der Stegodon-Fossil-Schicht von Mengeruda auf Flores, Indonesien. Anthropos, 65: 229–247.

Martin R.D., MacLarnon A.M., Philips J.L., and Dobyns W.B. (2006) Flores hominid: new species or microcephalic dwarf? The Anatomical Record A, 288A: 1123–1145.

Matsu'ura S. (1999) A chronological review of Pleistocene human remains from the Japanese Archipelago. In: Omoto K. (ed.), Interdisciplinary Perspectives on the Origins of the Japanese, International Symposium 11-B. International Research Center for Japanese Studies, Kyoto, pp. 181–197.

Moerman P. (1977) Op het spoor van de Neanderthal mens. De Boekerij, Baarn.

Morwood M. and Van Oosterzee P. (2007) The Discovery of the Hobbit. The Scientific Breakthrough that Changed the Face of Human History. Random House, New York.

Morwood M.J., O'Sullivan P.B., Aziz F., and Raza A. (1998) Fission-track ages of stone tools and fossils on the east Indonesian island of Flores. Nature, 392: 173–176.

Morwood M.J., Brown P., Jatmiko, Sutikna T., Wahyu Saptomo E., Westaway K.E., Awe Due R., Roberts R.G., Maeda T., Wasisto S., and Djubiantono T. (2005). Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. Nature, 437: 1012–1017.

Obendorf P.J., Oxnard C.E., and Kefford B.J. (2008). Are the small human-like fossils found on Flores human endemic cretins? Proceedings of the Royal Society, B, DOI:10.1098/rspb.2007.1488 (in press).

O'Higgins P. and Jones N. (1997) HYMS functional morphology and evolution. Available on-line at: http://hyms.fme.googlepages.com/downloadmorphologica.

O'Higgins P. and Jones N. (1998) Facial growth in *Cercocebus torquatus*: an application of three- dimensional geometric morphometric techniques to the study of morphological variation. Journal of Anatomy, 193: 251–272.

Palombo M.R. and Giovinazzo C. (2004) Brain weight versus body mass in Late Pleistocene *Cynotherium sardous* studiati, 1847 from Dragonara Cave (north-western Sardinia). Giornate di Paleontologia 2004, Bolzano, 21–23 Maggio, p. 44. Societa Paleontologica Italiana.

Palombo M.R. and Giovinazzo C. (2005) *Elephas falconeri* from Spinagallo Cave (South-Eastern Sicily, Hyblean Plateau, Siracusa): a preliminary report on brain to body weight comparison. Monografies de la Societat d'Historia Natural de les Balears, 12: 255–264.

Palombo M.R., Kohler M., Moya-Sola S., and Giovinazzo C. (2008) Brain versus body mass in endemic ruminant artiodactyls: a case studied of *Myotragus balearicus* and smallest *Candiacervus* species from Mediterranean Islands. Quaternary International, 182: 160–183.

Platon N. (1966) N. Anaskafi Zakrou. Praktika tis Archaeologikis Eterias tou etous, 1962: 142–168 (in Greek).

Poulianos A.N. (1975) An early Minoan microcephale. Anthropos, 2: 40–47.

Richards G. (2006) Genetic, physiologic and ecogeographic factors contributing to variation in *Homo sapiens*: *Homo floresiensis* reconsidered. Journal of Evolutionary Biology, 19: 1744–1767.

Schaaffhausen H. (1858) Zur Kenntniss der ältesten Rassenschädel. Archiv für Anatomie, Physiologie und wissenschaftliche Medicin, 25: 453–478.

Shea B.T. and Gomez A.M. (1988) Tooth scaling and evolutionary dwarfism: an investigation of allometry in human pygmies. American Journal of Physical Anthropology, 77: 117–132.

Sneath P.H.A. and Sokal R.R. (1973) Numerical Taxonomy. W.H. Freeman and Company, San Francisco.

Sondaar P.Y. (1977) Insularity and its effect on mammal evolution. In: Hecht M.K., Goody P.C., and Hecht B.M. (eds.), Major Patterns in Vertebrate Evolution. Plenum, New York, pp. 671–707.

Sondaar P.Y. (1986) The island sweepstakes. Natural History, 95(9): 50–57.

Sondaar P.Y. (1998) Paleolithic Sardinians: paleontological evidence and methods. In: Balmuth M.S. and Tykot R.H. (eds), Sardinian and Aegean Chronology, Studies in Sardinian Archaeology, 5: 45–43.

Sondaar P.Y. (2000) Early Human Exploration and Exploitation of Islands. Tropics, 10(1): 203–230.

Spaan A., Sondaar P.Y., and Hartman W. (1994) The structure of the evolutionary process. Geobios, 27(3): 385–390.

Spoor F. and Sondaar P.Y. (1986) Human fossils from the endemic island fauna from Sardinia. Journal of Human Evolution, 15: 399–408.

Strand Vilarsdóttir U., O'Higgins P., and Stringer C. (2002) A geometric morphometric study of regional differences in the ontogeny of the modern human facial skeleton. Journal of Anatomy, 201: 211–229.

Suzuki H. (1982) Skulls of Minatogawa Man. In: Suzuki H. and Hanihara K. (eds.), The Minatogawa Man: The Upper Pleistocene Man from the Island of Okinawa. University Museum Bulletin, 19: 123–206. The University of Tokyo.

Suzuki H. and Hanihara K. (eds) (1982) The Minatogawa Man: the Upper Pleistocene Man from the Island of Okinawa. University Museum Bulletin 19. The University of Tokyo.

Taylor A.B. and van Schaik C.P. (2007) Variation in brain size and ecology in *Pongo*. Journal of Human Evolution, 52: 59–71.

Tocheri M.W., Orr C.M., Larson S.G., Sutikna T., Jatmiko, Wahyu Saptomo E., Awe Due R., Djubiantono T., Morwood M.J., and Jungers W.L. (2007) The primitive wrist of *H. floresiensis* and its implications for hominin evolution. Science, 317: 1743–1745.

Yokoyama, Y. (1992) Quest for the origins of modern humans. Kagaku, 62: 195–196 (in Japanese).

Van den Bergh G.D. (1999) The late Neogene elephantoid bearing fauna of Indonesia and their paleozoogeographic implication. A study of the terrestrial fauna succession of Sulawesi, Flores and Java, including evidence for early hominid dispersal east of Wallace's line. Scripta Geologcia, 117: 1–419.

Van der Geer A.A.E. (2005) Island ruminants and the evolution of parallel functional structures. In: Cregut E. (ed.), Les ongulés holarctiques du Pliocène et du Pléistocène. Actes Colloque International Avignon, 19–22 septembre. Quaternair, 2005 hors-série 2: 231–240.

Weber J., Czarnetzki A., and Pusch C.M. (2005). Comment on the brain of LB1, *Homo floresiensis*. Science, 310: 236.