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Homo floresiensis: Microcephalic, pygmoid, *Australopithecus*, or *Homo*?

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Abstract

The remarkable partial adult skeleton (LB1) excavated from Liang Bua cave on the island of Flores, Indonesia, has been attributed to a new species, *Homo floresiensis*, based upon a unique mosaic of primitive and derived features compared to any other hominin. The announcement precipitated widespread interest, and attention quickly focused on its possible affinities. LB1 is a small-bodied hominin with an endocranial volume of 380–410 cm^3, a stature of 1 m, and an approximate geological age of 18,000 years. The describers [Brown, P., Sutikna, T., Morwood, M.J., Soejono, R.P., Jatmiko, Wayhu Saptomo, E., Awe Due, R., 2004. A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. Nature 431, 1055–1061] originally proposed that *H. floresiensis* was the end product of a long period of isolation of *H. erectus* or early *Homo* on a small island, a process known as insular dwarfism. More recently Morwood, Brown, and colleagues [Morwood, M.J., Brown, P., Jatmiko, Sutikna, T., Wahyu Saptomo, E., Westaway, K.E., Awe Due, R., Roberts, R.G., Maeda, T., Wasisto, S., Djubiantono, T., 2005. Further evidence for small-bodied hominins from the Late Pleistocene of Flores, Indonesia. Nature 437, 1012–1017] reviewed this assessment in light of new material from the site and concluded that *H. floresiensis* is not likely to be descended from *H. erectus*, with the genealogy of the species remaining uncertain. Other interpretations, namely that LB1 is a pygmy or afflicted with microcephaly, have also been put forward.

We explore the affinities of LB1 using cranial and postcranial metric and non-metric analyses. LB1 is compared to early *Homo*, two microcephalic humans, a 'pygmoid' excavated from another cave on Flores, *H. sapiens* (including African pygmies and Andaman Islanders), *Australopithecus*, and *Paranthropus*. Based on these comparisons, we conclude that it is unlikely that LB1 is a microcephalic human, and it cannot be attributed to any known species. Its attribution to a new species, *Homo floresiensis*, is supported.
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Keywords: H. floresiensis; Liang Bua 1; LB1; H. habilis; Australopithecus; H. erectus; H. sapiens; H. ergaster; Microcephalic; Multivariate statistics; Phylogenetic analysis; Insular island dwarfism

Introduction

In October 2004 a remarkable partial adult skeleton from excavations in Liang Bua cave on the island of Flores, Indonesia, was described (Brown et al., 2004). Liang Bua 1 (LB1), dated to 18 ka by Accelerator Mass Spectrometry (AMS) radiocarbon dating and bracketed by luminescence ages of 34 ± 4 ka and 14 ± 2 ka (Morwood et al., 2004), is described as a small-bodied hominin with an endocranial volume (380–

410 cm^3) and stature (1 m) similar to, or smaller than, *Australopithecus afarensis*. LB1 has, however, substantially reduced facial height and prognathism compared to *A. afarensis*, and it lacks the masticatory adaptations of that species. Brown and colleagues (2004) attribute LB1 to a new species, *H. floresiensis*, based upon a unique mosaic of primitive and derived features compared with other hominins. As such, *H. floresiensis* could be the end product of a long period of isolation of *H. erectus* or early *Homo*, a process known as insular dwarfism, or it could be the descendant of an unknown small-bodied and small-brained hominin which had earlier arrived on Flores from the Sunda Shelf (Morwood et al., 2004). In 2005, Morwood, Brown, and colleagues described new *Homo* material from the Liang Bua site: another mandible, tibia, and radius,

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as well as the right humerus and ulna of LB1. The radius was found 40 cm above a calibrated radiocarbon age of 13.1 ka, and its inferred age is 12 ka. They conclude that this population of hominins should be included in the genus *Homo* but cannot be attributed to either *H. erectus* or *H. sapiens*; therefore, its genealogy remains uncertain.

Discussions since its announcement have raised the issue of whether LB1 is truly a member of early *Homo*, or a case of human dwarfism or microcephaly. Henneberg and Thorne (2004) compared 15 measurements of the skull of LB1 with those of a 2000-year-old microcephalic skull from Crete described by Poulianos (1975). They concluded that both skulls are characterized by very small braincases, but their faces are within three standard deviations of the normal human range. They cited small braincases and normal-sized faces as characteristics of secondary microcephaly, and therefore suggested that LB1 is a microcephalic modern human. Further, they estimated the stature of LB1 to be 151−162 cm, similar to that of a skeleton dated to ~3500 years ago excavated from the Liang Toge cave on Flores (Jacob, 1967), and suggested that LB1 is therefore not dwarfed.

In view of the claims that LB1 is a microcephalic, we present a description of the various forms of this condition before undertaking morphometric and morphological comparisons to individuals with microcephaly. We also compare LB1 to pygmoid *H. sapiens* to test the hypothesis that LB1 conforms to this morphology. Finally, we undertake cranial and postcranial morphometric and morphological comparisons of LB1 with extant and fossil *Homo* to test the hypothesis that LB1 is a previously unknown hominin.

Microcephaly

Microcephaly is a heterogeneous disorder characterized by a marked reduction of brain growth with or without other abnormalities. The heterogeneity of the condition poses problems for clinical evaluation as well as for biological and genetic analysis (Mochida and Walsh, 2001). Microcephaly is defined by an occipitofrontal (head) circumference that is two standard deviations (SD) below the mean for the person's age and sex (Mochida and Walsh, 2001; Dobyns, 2002; Verloes, 2004; Gilbert et al., 2005); severe cases are three SD below the mean (Richards, 1985; Gilbert et al., 2005). Microcephaly is reported to occur in ~2% of newborns and is a feature of more than 400 syndromes (Gilbert et al., 2005), found in disorders that interfere with the normal growth of the brain (Mochida and Walsh, 2001). Clinically, it is divided into 'high functioning' microcephaly (Gilbert et al., 2005) (also known as primary or true microcephaly, microcephaly vera, or hereditary microcephaly [Richards, 1985]) and 'low functioning' microcephaly (Verloes, 2004) (also known as secondary microcephaly or microcephaly with simplified gyral pattern [MSG]). Microcephaly vera is present at birth and is characterized by a narrow and sloping forehead and pointed vertex, with no intrauterine or postnatal growth retardation or associated abnormalities. Life span may be normal and mental retardation is of varying severity (Mochida and

Walsh, 2001). 'Low functioning' microcephaly develops postnatally and is characterized by a reduced number and shallow appearance of gyri (convolutions on the surface of the cerebral hemisphere), very shallow sulci, and a normal to thin cortex. Most affected individuals have frontal lobes smaller than the remainder of the brain, have profound mental retardation, and die at an early age (Dobyns, 2002). These two types of microcephaly may be a continuous phenotype (Mochida and Walsh, 2001; Verloes, 2004).

The incidence of hereditary microcephaly is 1/30,000 in Japan, 1/250,000 in Holland, 1/2,000,000 in Scotland (Woods et al., 2005: 719), and predicted to be between 1/25,000 and 1/50,000 in Sweden (Böök et al., 1953: 643). It is seen more commonly in regions with high consanguinity rates, such as Turkey, Pakistan, and Arab countries of the Middle East (Mochida and Walsh, 2001: 155). In Pakistan, the incidence is 1/10,000 (Woods et al., 2005: 719), although Verloes (2004) reports the frequency of 'congenital microcephaly' as 3/100 to 4/100.

In the following review of microcephalic syndromes, we focus on those that include short stature as a symptom because LB1 is estimated to have been only 106 cm tall.

Microcephalic primordial dwarfism

Primordial dwarfism includes various specific types of severe proportionate dwarfism. Microcephalic dwarfism is a type of primordial dwarfism in which the head and brain of the individual are notably small. To our knowledge, the following syndromes have been described within the category of microcephalic primordial dwarfism:

- Seckel syndrome [synonyms: Bird-headed dwarfism, Nanocephalic dwarfism, Seckel type dwarfism, Microcephalic primordial dwarfism I (Faivre and Cormier-Daire, 2003)] (http://www.orpha.net/data/patho/GB/uk-seckel.pdf)
- Majewski's microcephalic osteodysplastic primordial dwarfism type I (MOPD I) [synonyms: Osteodysplastic primordial dwarfism, Taybi-Linder syndrome, Brachymelic primordial dwarfism, Cephaloskeletal dysplasia, Low-birth-weight dwarfism with skeletal dysplasia] (http://www.ncbi.nlm.nih.gov/entrez/dispomim.cgi?id=210710)
- Majewski's microcephalic osteodysplastic primordial dwarfism type II (MOPD II) [synonym: Osteodysplastic primordial dwarfism Type II]
- Majewski's microcephalic osteodysplastic primordial dwarfism type III (MOPD III) [synonyms: Osteodysplastic primordial dwarfism Type III, Microcephalic osteodysplastic primordial dwarfism, Caroline Crachami type, MOPD, Sicilian fairy type] (http://www.ncbi.nlm.nih.gov/entrez/dispomim.cgi?id=210730)

Seckel syndrome is defined on the basis of two clinical cases from Chicago and thirteen cases of nanocephalic dwarfism reported in the literature over a 200-year period (Seckel, 1960). The syndrome is a rare autosomal recessive disorder

characterized by growth delays prior to birth, resulting in low birth weight. Growth delays continue after birth, resulting in short, but proportionate, stature. Other physical features associated with Seckel syndrome include an abnormally small head (microcephaly), unusual facial features including a beak-like protrusion of the nose, abnormally large eyes, a narrow face, an unusually small jaw (micrognathia), and absence of some teeth (http://my.webmd.com/webmd_today/home/default). Joint defects including clubfoot and trident hands may be present, as well as some physical disfunctions such as malformation of the genitourinary tract and mental retardation (http://www.whonamedit.com/synd.cfm/869.html). In addition, some infants may exhibit permanent fixation of the fifth fingers in a bent position, dysplasia (malformation) of the hips, and radial dislocation (http://my.webmd.com/webmd_today/home/default).

Majewski and colleagues (1982) distinguish three types of osteodysplastic primordial dwarfism from Seckel syndrome: MOPD I, MOPD II, and MOPD III. They observe that in these forms, severe microcephaly is present at birth, but postnatal growth deficiency is less severe than in Seckel syndrome. It is now agreed that MOPD Type I is the same as Seckel syndrome (http://www.ncbi.nlm.nih.gov/entrez/dispomim.cgi?id=210710). There is also now a consensus that the MOPD Type I and III (Majewski and Goecke, 1982; Majewski et al., 1982) and Taybi-Linder syndrome are variants of the same entity, reflecting different ages of the same condition (Hall et al., 2004: 56). It follows, then, that MOPD III may also be considered a variant of Seckel syndrome.

MOPD II, however, is a distinct disorder in which individuals at birth have abnormal body proportions and short limbs (Hall et al., 2004); Seckel dwarfs, on the other hand, have normal body proportions. While it is not clear to which microcephalic syndrome LB1 is compared by Henneberg and Thorne (2004), we compare LB1 with the cranial aspects of microcephaly as it is manifested in MOPD II. Our decision is based on the fact that LB1 has relatively short legs, thereby conforming to the short limb symptom of MOPD II. Cranially, MOPD II does not differ from Seckel syndrome but is more rigorously described.

Archaeological evidence

Several cases of microcephaly have been documented in the archaeological record. Smith and Wood Jones (1910, cited in Brothwell, 1981) noted a microcephalic female excavated from a burial dated to the New Kingdom (18–20th Dynasty) of Egypt. Frazer (1879, cited in Richards, 1985) reported the discovery of a microcephalic cranium from excavations of a tenth century burial at Donnybrook, Ireland. Neither of these individuals has been fully described.

Wells (1942) described a skull with a cranial capacity of 485 cm³ from an ancient burial ground in Peru. The face was large in proportion to the vault and the orbits were large and deep. Hrdlička (1943) considered it a female aged 16–17 years. The alveolar arch was broader and larger than in normal individuals, resulting in a greater alveolar prognathism than

normal. No other skeletal remains were discovered, but Hrdlička suggested that it might have had a short stature based upon the dimensions of the foramen magnum.

The cranium of a microcephalic was excavated from a Minoan Period grave on eastern Crete dated to ~2000 years ago (Poulianos, 1975). The skull (Fig. 1) is of a person about twenty years old. It was buried in a very small chest-shaped coffin, which suggests a short stature for the individual. The width of the skull is narrow in comparison with the length, the frontal bone retreats, and there is alveolar prognathism and a well-developed mental prominence. The cranial capacity is 350 cm³, and Poulianos (1975) concluded that the skull is that of a microcephalic. It is to this skull that Henneberg and Thorne (2004) compared LB1.

Campillo (1977) described a specimen from a Bronze Age burial in a cave on the island of Mallorca, Spain, tentatively considered to be the skull of a four-year-old child. It had a cranial capacity of 907 cm³, and the skeleton was of small stature. Campillo (1977) concluded that it was a case of microcephaly.

Two skulls from the anthropological collections of the Department of Anatomy in Brno, Czech Republic, were reported by Dokládal and Horácková (1994). One is a female of about 30 years and has a cranial capacity of 355 cm³; the other is a male of approximately 60 years with a cranial capacity of 405 cm³. In both skulls the facial skeleton is reduced by 10–15% when compared to the norm, but the neurocranium is smaller by 30–40%.

One of three crania from a cave burial in Japan dated to the Yayoi Period (300 BC–AD 300) belongs to an adult male microcephalic (Fig. 2; Suzuki, 1975). The cranial capacity is 730 cm³, half the size of modern Japanese male skulls from the same district and lower than the smallest capacities reported for the Andaman and Krumbai populations (950 cm³ and 970 cm³, respectively).

Richards (1985) described and analyzed the skeleton of a three-year-old child recovered from salvage excavations at San Jose, California, dated to 1100–1700 years before present.
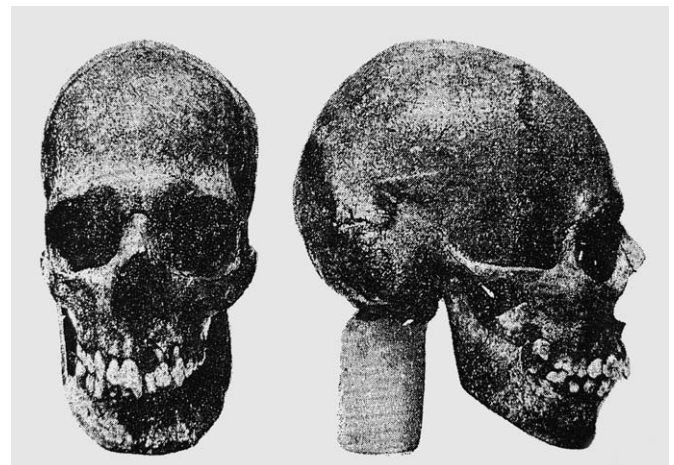

Fig. 1. Frontal and right lateral views of the Minoan microcephalic. Reproduced with kind permission from Nickos A. Poulianos.
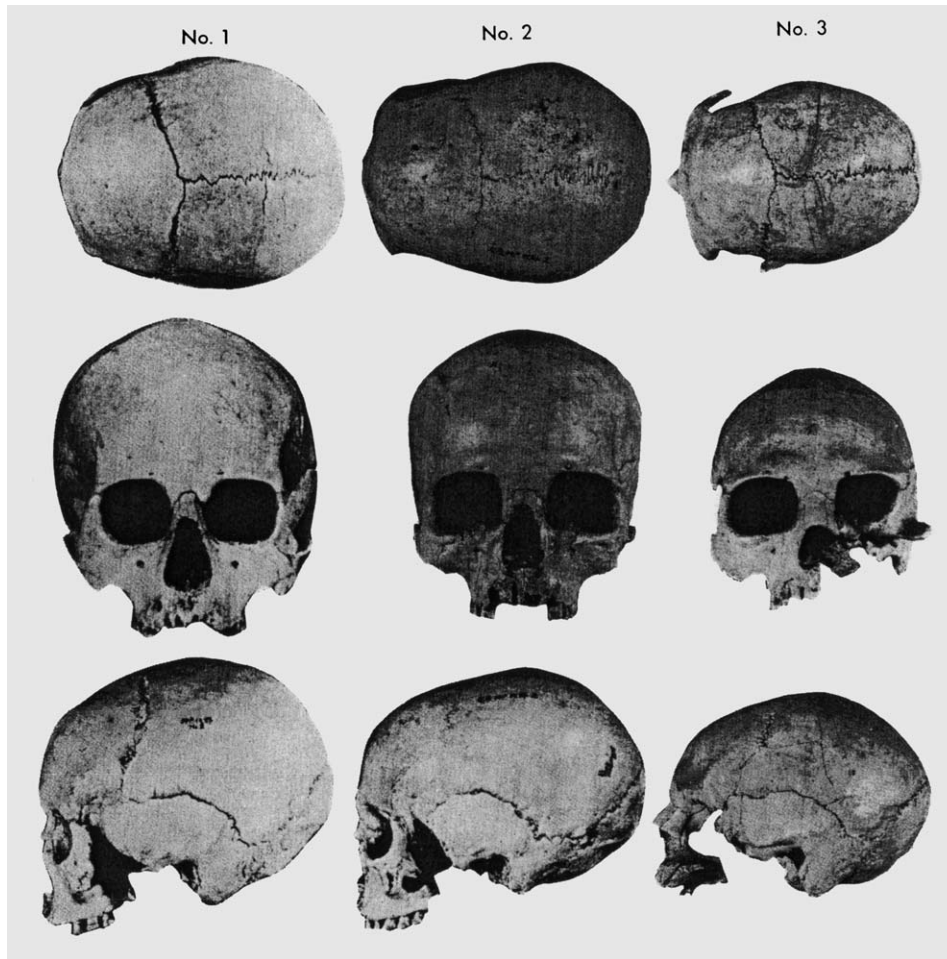
Fig. 2. Comparative superior, frontal, and left lateral views of three crania from the early Yayoi Period, Japan, excavated from Sano Cave Site, Chiba Prefecture, Japan in 1925. No. 1 is an adult male, No. 2 is an adult female, and No. 3 is microcephalic. Reproduced with kind permission from Dr. Matsubara, Department of Geology, National Science Museum, Tokyo.

The cranial vault size (630 cm^3) is similar to that of a normal six-month-old child, and the facial skeleton is equivalent to that of a nine-month-old. Gross structural abnormalities are found in the frontal, parietal, and temporal lobes, while the occipital appears normal. The child has extremely small frontal lobes and significant reduction of the cerebral cortex. The surface detail of the endocast shows a sulcus and gyri pattern similar to a nine-month-old infant. There are no abnormalities in the long bones, although there may be some growth retardation.

Materials and methods

Sample

We undertake morphometric and morphological analyses of the cranium and postcranium to examine the possible affinities of LB1 to a sample of *Homo*, *Australopithecus*, and *Paranthropus* individuals. Our analyses rely upon published descriptions of LB1 by Brown and colleagues (2004) and Morwood and colleagues (2004, 2005). We have not examined the original LB1, which is under embargo at the present time (P. Brown, pers. comm., 2005).

Our fossil sample is restricted to those specimens for which comparative data to LB1 is available (Table 1). Several published data for LB1 include measurements from basion (basion-bregma, basion-nasion, basion-prosthion), but basion is missing for many of the *H. erectus* fossils from Sangiran and Zhoukoudian, nor is it available for Trinil, Sambungmacan 3, *H. rudolfensis* KNM-ER 1470, *H. habilis* 1805, or Dmanisi 2882. We do not, therefore, include these specimens in the cranial metric analyses. We also omit the subadult specimens KNM-WT 15000 and Dmanisi D2700. Nevertheless, we consider the remaining fossils included in our analyses a reasonable range of fossil *Homo*. It should be noted here that we view *H. erectus* as an exclusively Asian species (specifically Javanese) and refer to the African fossils from Koobi Fora as *H. ergaster*.

Of the research on microcephaly from the archaeological record discussed above, only two publications (Poulianos, 1975; Suzuki, 1975) include relevant cranial metric data. Unfortunately, there are no microcephalic human skulls available to us for the purposes of this study, so our comparative sample is limited to two specimens. Other comparative samples included in our analyses, where possible, are combined male

Table 1
Cranial and postcranial data sources and information

	Specimen/Sample	Location	Age	Species	Measurement Reference
Cranial Analyses					
Analysis 1[a]	Minoan microcephalic	Greece	c. 3000 years old	*H. sapiens*	Poulianos, 1975.
	Liang Toge	Flores	3550 ± 525 BP	*H. sapiens*	Jacob, 1967.
	LB1	Flores	95−74 ka to 12 ka	*H. floresiensis*	Brown et al., 2004.
	Sangiran 17	Java	>1.0 Ma	*H. erectus*	Groves, n.d.
	KNM-ER 3733	East Africa	1.78 Ma	*H. ergaster*	Rightmire, 1990.
	OH 24	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	KNM-ER 1813	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	Sts 5	South Africa	2.8−2.3 Ma	*A. africanus*	Wood, 1991.
	584 pooled males and females from 29 populations	Worldwide	modern	*H. sapiens*	Howells, 1996.
	Pan paniscus and *Pan troglodytes*; pooled males and females	Africa	modern	*Pan paniscus* and *Pan troglodytes*	Groves, n.d.
Analysis 2[b]	Sano microcephalic	Japan	c. 2000 years old	*H. sapiens*	Suzuki, 1975.
	LB1	Flores	95−74 ka to 12 ka	*H. floresiensis*	Brown et al., 2004.
	Sangiran 17	Java	>1 Ma	*H. erectus*	Groves, n.d.
	Solo 5 (Ngandong 6)	Java	27 ± 3 to 46 ± 4 kya	*H. erectus*	Groves, n.d.
	KNM-ER 3733	East Africa	1.78 Ma	*H. ergaster*	Rightmire, 1990.
	KNM-ER 3883	East Africa	1.55−1.6 Ma	*H. ergaster*	Rightmire, 1990.
	OH 24	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	KNM-ER 1813	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	OH 5	East Africa	2.3 to between 1.2−0.7 Ma	*P. boisei*	Wood, 1991.
Analysis 3[c]	LB1	Flores	95−74 ka to 12 ka	*H. floresiensis*	Brown et al., 2004.
	Solo 6, 9, 10, and 11 (Ngandong 7, 10, 11, and 12)	Java	27 ± 3 to 46 ± 4 kya	*H. erectus*	Groves, n.d.
	Sangiran 17	Java	>1 Ma	*H. erectus*	Groves, n.d.
	Dmanisi 2280	Republic of Georgia	<1.8 Ma	*H. erectus*, *H. georgicus*, or *H. ergaster*	Gabounia et al., 2000; Vekua et al., 2002.
	KNM-ER 3733	East Africa	1.78 Ma	*H. ergaster*	Rightmire, 1990.
	KNM-ER 3883	East Africa	1.55−1.6 Ma	*H. ergaster*	Rightmire, 1990.
	KNM-ER 1813	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	OH 24	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	KNM-ER 406	East Africa	1.65−1.87 Ma	*P. boisei*	Wood, 1991
	Sts 5	South Africa	2.8−2.3 Ma	*A. africanus*	Wood, 1991.
Analysis 4[d]	LB1	Flores	95−74 ka to 12 ka	*H. floresiensis*	Brown et al., 2004.
	Sangiran 17	Indonesia	>1 Ma	*H. erectus*	Groves, n.d.
	KNM-ER 3733	East Africa	1.78 Ma	*H. ergaster*	Rightmire, 1990.
	KNM-ER 1813	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	OH 24	East Africa	1.7−1.88 Ma	*H. habilis*	Wood, 1991.
	Sts 5	South Africa	2.3−2.8 Ma	*A. africanus*	Wood, 1991.
Postcranial analysis[e]	LB1	East Africa	95−74 ka to 12 ka	*H. floresiensis*	Brown et al., 2004.
	KNM-WT 15000	East Africa	1.55 Ma	*H. ergaster*	Ruff and Walker, 1993b.
	OH 62	East Africa	1.8 Ma	*H. habilis*	lower estimate: Hartwig-Scherer and Martin, 1991; higher estimate: Haeusler and McHenry, 2004.
	BOU-VP-12/1	East Africa	∼2.5 Ma	*A. garhi*	Asfaw et al., 1999.
	A.L. 288-1	East Africa	3.2 Ma	*A. afarensis*	Asfaw et al., 1999.
	Chimpanzee (17 ♀, 12 ♂)	East Africa	modern	*Pan troglodytes*	Groves, n.d.
	Gorilla (6 ♀, 44 ♂)	East Africa	modern	*Gorilla gorilla*	Groves, n.d.
	Chinese (8 ♀, 21 ♂),	Hong Kong	modern	*H. sapiens*	Donlon, 1990.
	Hawaiians (33 ♀, 22 ♂),	Mokapu	modern	*H. sapiens*	Donlon, 1990.
	African Americans (39 ♀, 36 ♂)	Terry Collection	modern	*H. sapiens*	Donlon, 1990.

Table 1 (*continued*)

Specimen/Sample	Location	Age	Species	Measurement Reference
European Americans (35 ♀, 38 ♂),	Terry Collection	modern	*H. sapiens*	Donlon, 1990.
Aboriginal Australians (62 ♀, 66 ♂)	South eastern Australia	modern	*H. sapiens*	Donlon, 1990.

[a] Measurements analyzed are maximum cranial length (GOL), maximum cranial breadth (XCB), basion-bregma height (BBH), basion-prosthion length (BPL), orbital height (OBH), orbital breadth (OBB), maximum frontal breadth.

[b] Measurements analyzed are GOL, XCB, BBH, biauricular breadth (AUB), OBH, OBB, maximum frontal breadth.

[c] Measurements analyzed are GOL, XCB, BBH, AUB, biasterionic breadth (ASB).

[d] Measurements analyzed are GOL, XCB, basion-nasion length (BNL), BBH, AUB, nasion-prosthion length (NPL), BPL, nasal breadth (NLB), maximum frontal breadth.

[e] Radius and femur measurements.

and female samples of *Pan troglodytes*, *Pan paniscus*, and *Homo sapiens* (including African pygmies and Andaman Islanders).

Cranial metric analyses

The goal of the cranial metric analyses is to assess similarities and differences in crania after the effect of size is removed. We sought a technique that would separate, as far as possible, the effects of size and shape in the analyses. Therefore, we use a log-transformed geometric mean (after Darroch and Mosimann, 1985), which Jungers and colleagues (1995) found satisfied the requirements of recognizing Operational Taxonomic Units.

We undertake four cranial morphometric analyses using Canonical Variates Analysis (CVA). CVA assumes that there are multiple groups that can be unambiguously defined in space. Thus, CVA is useful for highlighting group differences and assisting in classifying objects whose group membership is unknown; it can be used both as a descriptive and as a classification tool (Jobson, 1991: 242; Krzanowski and Marriott, 1995). Our research involves a number of known groups (species) and one individual of unknown group membership (LB1). Therefore, we use CVA because it preserves the distances that exist between the early hominin groups and *H. sapiens*, it allows us to observe what can and cannot be separated in terms of groupings, and, more importantly, it allows us to examine the relationship of LB1 to these groups. The target cases (LB1, the Minoan microcephalic, the Sano 3 microcephalic, and the 'pygmoid' from Liang Toge) are left ungrouped.

Analyses 1 and 2: LB1 and microcephalic individuals. The first two cranial analyses focus on microcephalic individuals. Using the observations made by Brown and colleagues (2004), LB1 is examined for traits of microcephaly. In Analysis 1, we compare LB1 to the Minoan microcephalic male (Poulianos, 1975) and to the 'pygmoid' from Liang Toge, Flores, dated to 3550 ± 525 BP (Jacob, 1967) (Table 1). Although not mentioned by Henneberg and Thorne (2004), we also compare LB1 in Analysis 2 to the Sano 3 microcephalic from the early Yayoi period in Japan (Fig. 2; Table 1) (Suzuki, 1975). These individuals cannot be compared in one analysis due to a lack of comparative data. Morphological comparisons

use published material, including photographs. Illustrative material for the Liang Toge individual is available in Jacob (1967).

Analyses 3 and 4: LB1 and early Homo. In response to the suggestion that *H. floresiensis* is an end product of insular island dwarfism (Brown et al., 2004), or the descendant of a previously unknown small-bodied and small-brained hominin that may have arrived on Flores from the Sunda Shelf (Morwood et al., 2004), two further analyses are undertaken. Analysis 3 includes a relatively large range of fossil *Homo* (Table 1) by limiting the analysis to five vault variables. Analysis 4 increases the number of variables to nine. Although fewer comparative specimens can be included in this latter analysis, we are still able to examine basal-facial aspects of the cranium in one or more specimens from the species *A. africanus*, *H. habilis*, *H. ergaster*, and *H. erectus*.

Postcranial metric analyses

Limb proportions in hominins are important both for reconstructing locomotor behavior and clarifying phylogenetic relationships (Jungers, 1982). The relationship between the upper and lower limbs provides the most useful information on the affinities of a specimen (Haeusler and McHenry, 2004). In 2005, Morwood and colleagues compared the ratio of the femur to humerus and ulna of LB1 with those in hominins and *Pan paniscus*. They estimated a humerofemoral index for LB1 of 84.5, which is outside the range of variation for *H. sapiens* and is the same as that of A.L. 288-1 (*A. afarensis*).

The present study explores another relationship between upper and lower limbs: the femoral length and estimated length of the radius. This analysis uses a different data set, enabling an independent assessment of the relationship between the upper and lower limbs. No radius has been found for LB1, but Morwood and colleagues (2005) estimated the radius length to be 190 mm based upon the ulna length. In this study, we compare the ratio of the estimated radius to femur length of LB1, with that of *H. habilis*, *H ergaster*, *A. afarensis*, *A. garhi*, *Pan troglodytes*, and *Gorilla gorilla*. The postcranium of *H. ergaster* is of particular importance in this analysis as a potential analogue for *H. erectus* in the absence of comparable postcrania from that species; it is presumed that the postcranium of

H. ergaster would probably be similar to that of *H. erectus*, although this remains to be tested (Ruff and Walker, 1993a).

Sources for the postcranial comparative measurements are provided in Table 1. Three estimates are used for OH 62: a lower estimate by Hartwig-Scherer and Martin (1991) and two estimates based upon Haeusler and McHenry (2004). A number of geographically widespread populations of *H. sapiens* are used in order to show the range of variation within a single species over a large latitudinal gradient. In all cases, the maximum length of the radius and femur was used, with the exception of *H. sapiens* where the physiological length of the femur was used (the use of physiological length, rather than maximum length, is of minor significance when dealing with indices characterizing different species; Aiello and Dean, 1990). In order to examine 'dwarfed' *H. sapiens*, data from two types of pygmies are examined: African pygmies (in the absence of available data from Andaman pygmies used in the cranial metric analyses) and the 'pygmoid' skeleton from Liang Toge (LT) from Flores (Jacob, 1967). For African pygmies, femur lengths are given as means for males and females (*n* = 40, sexes combined) (Ruff, 1994). Instead of radius length, the means for male and female forearm length is given (23 females, 26 males) (Shea and Bailey, 1996).

Results

Cranial metric analyses

Table 2 and Figures 3—6 present the results for the four cranial metric analyses.

*Analysis 1: LB1, the Minoan microcephalic, and Liang Toge (*Fig. 3*).* Most of the variance is explained in the first Canonical Variate (97.1%). LB1 is separate from *H. sapiens* on CV1 and differs from the Minoan microcephalic. LB1 has a relatively greater basion-prosthion length in relation to its cranial height; that is, it is relatively more prognathic than the Minoan. The Minoan clusters with *H. sapiens*, although it is at the periphery of the distribution of this species. A small amount of variance is explained on CV2 (only 1.7%), which may suggest that LB1 has a relatively longer cranium in relation to its height than the Minoan.

The LT 'pygmoid' and the Andaman Islanders cluster with other *H. sapiens*, and LB1 is well separated from them. Although LB1 appears to be separate from Sangiran 17, the separation is caused by only a small proportion of the variance (1.7%), and LB1 is similar to this specimen in its degree of prognathism relative to cranial height (CV1). LB1 lies relatively close to *H. ergaster* (KNM-ER 3733) on both axes; it is slightly less prognathic than the latter but similar in its cranial length/height relationship. LB1 is separate from both specimens of *H. habilis* and is well separate from Sts 5 (*A. africanus*). While it is close to OH 24 on CV2, this represents only a small amount of the total variance as stated above.

*Analysis 2: LB1 and the microcephalic Sano specimen (*Fig. 4*).* The microcephalic Sano specimen is on the periphery of the distribution of *H. sapiens* and differs from LB1 in

Table 2
Data matrix for cranial analyses 1—4

		CV1	CV2
Analysis 1			
Eigenvalue		10.29	0.18
% Var.		97.1	1.7
Variable	Max. cranial length	0.445	0.721
	Max. cranial breadth	0.177	−0.434
	Basion-bregma	0.535	−0.548
	Basion-prosthion	−0.569	0.238
	Max. frontal breadth	−0.003	−0.073
	Orbital height	−0.156	−0.038
	Orbital breadth	−0.101	0.198
Analysis 2			
Eigenvalue		0.57	0.10
% Var.		72.7	12.4
Variable	Max. cranial length	−0.186	0.685
	Max. cranial breadth	0.317	−0.392
	Basion-bregma	0.725	0.555
	Biauricular breadth	−0.531	0.093
	Max. frontal breadth	−0.015	−0.047
	Orbital height	−0.145	−0.486
	Orbital breadth	−0.153	−0.282
Analysis 3			
Eigenvalue		1.04	0.11
% Var.		85.9	8.9
Variable	Max. cranial length	−0.161	−0.164
	Max. cranial breadth	0.254	0.910
	Basion-bregma	0.661	−0.540
	Biauricular breadth	−0.602	0.243
	Biasterionic breadth	−0.222	−0.249
Analysis 4			
Eigenvalue		0.61	0.19
% Var.		64.0	20.2
Variable	Max. cranial length	−0.040	0.516
	Max. cranial breadth	0.414	−0.270
	Basion-bregma	0.633	0.201
	Basion-nasion	−0.165	0.051
	Basion-prosthion	−0.352	−0.426
	Biauricular breadth	−0.271	0.157
	Max. frontal breadth	0.124	−0.113
	Biasterionic breadth	−0.263	0.179
	Orbital breadth	−0.019	−0.023

having a relatively higher cranium in relation to its biauricular breadth. That is, LB1 retains the more primitive condition.

LB1 is again close to KNM-ER 3733 (*H. ergaster*) and relatively close to KNM-ER 3883 (*H. ergaster*) and OH 24 (*H. habilis*). They have comparable ratios of cranial length/height relative to cranial widths and orbital heights. LB1 is separate from *H. erectus* specimens Sangiran 17 and Solo 5, and from *H. habilis* KNM-ER 1813, *A. africanus* Sts 5, and *P. boisei* KNM-ER 406. To varying degrees, these specimens have relatively longer vaults in relation to vault width and orbital height (CV2).

Analysis 3: LB1 and early Homo *(*Fig. 5*).* LB1 clusters with archaic *Homo* and is well separated from *H. sapiens*. LB1 and the archaic *Homo* differ from *H. sapiens* in having greater biauricular and biasterionic breadths in relation to vault height. LB1 is close to KNM-ER 3733 (*H. ergaster*). LB1 is separate
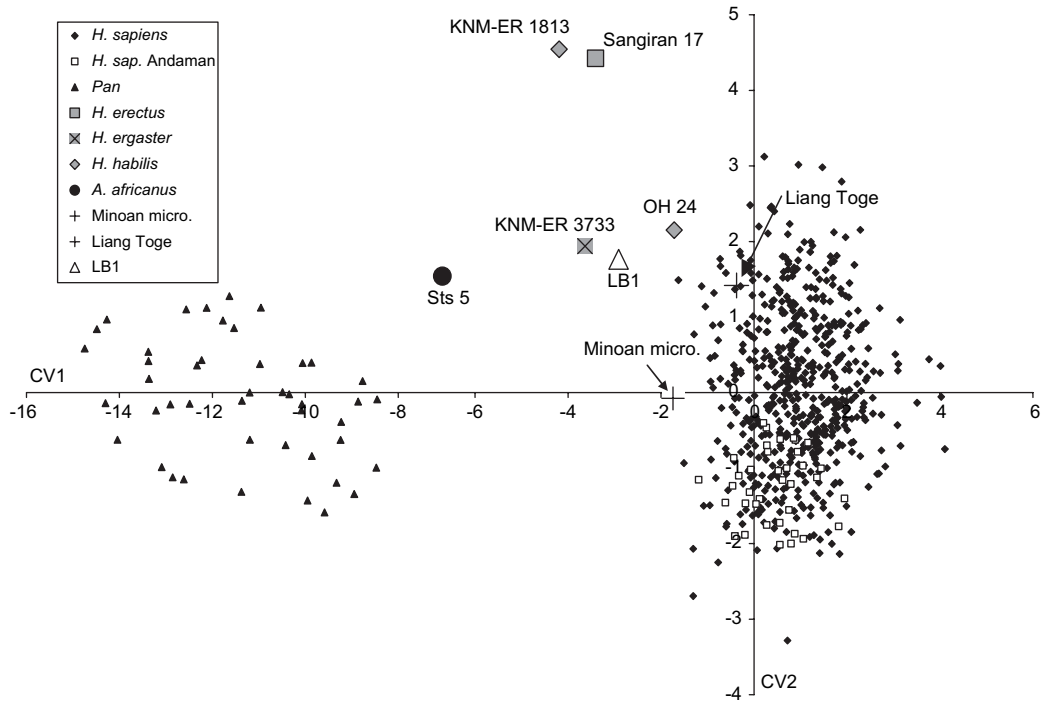
Fig. 3. Analysis 1: LB1 compared to the Minoan microcephalic, the Liang Toge 'pygmoid', Andamans pygmies, and archaic *Homo*. *Pan* are included for comparative purposes. Canonical Variate (CV) 1 represents 97.1% of the variance; CV 2 represents 1.7% of the variance. See Table 2 for statistical results.

from Dmanisi D2280, which is relatively broader at the biauricular and upper cranial planes in relation to its cranial height, and separate from the Solo specimens and Sangiran 17, although it is similar to Solo 5 in its cranial height/biauricular breadth relationship.

Analysis 4: LB1 and early Homo *expanded variable set (*Fig. 6*).* This analysis increases the number of variables to nine and includes two basal-facial dimensions. This reduces the number of specimens that can be included, but nevertheless retains specimens from the relevant species.
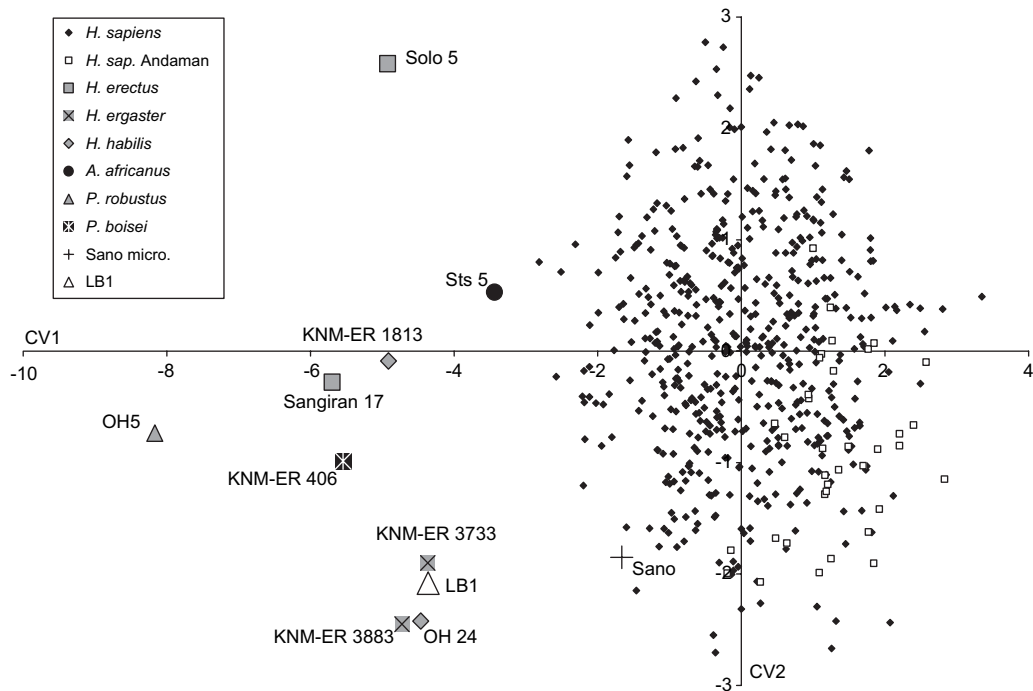
Fig. 4. Analysis 2: LB1 compared to the Sano 3 microcephalic, Andamans pygmies, archaic *Homo, A. africanus, P. robustus,* and *P. boisei.* CV 1 represents 72.7% of the variance; CV 2 represents 12.4% of the variance. See Table 2 for statistical results.
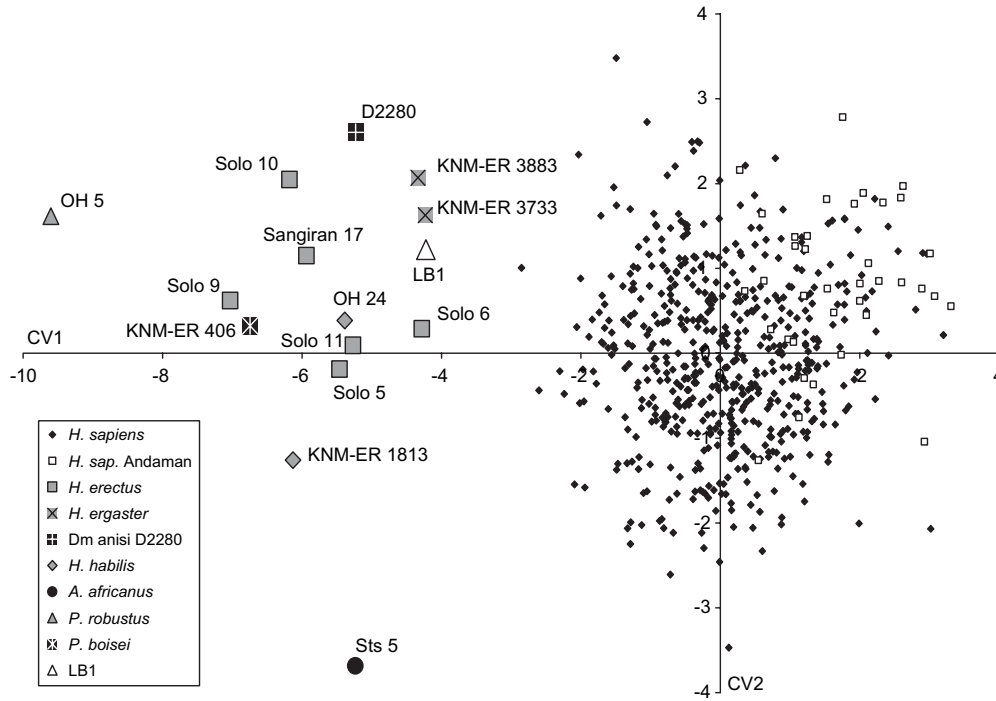
Fig. 5. Analysis 3: LB1 compared to a range of early *Homo*, including Dmanisi D2280, *A. africanus*, *P. robustus*, and *P. boisei*. CV 1 represents 85.9% of the variance; CV 2 represents 8.9% of the variance. See Table 2 for statistical results.

LB1 is separate from all other specimens in this analysis. It is well separated from OH 24 (*A. africanus*), KNM-ER 1813 (*H. habilis*), Sangiran 17 (*H. erectus*), and *H. sapiens*. Its nearest neighbour is *H. ergaster* KNM-ER 3733, but it is nevertheless distant from this specimen.

Cranial comparisons

There are a number of non-metric conditions for MOPD II that cannot be addressed in morphometric analyses. These include: cranial capacity less than 1000 cm^3, recession of the
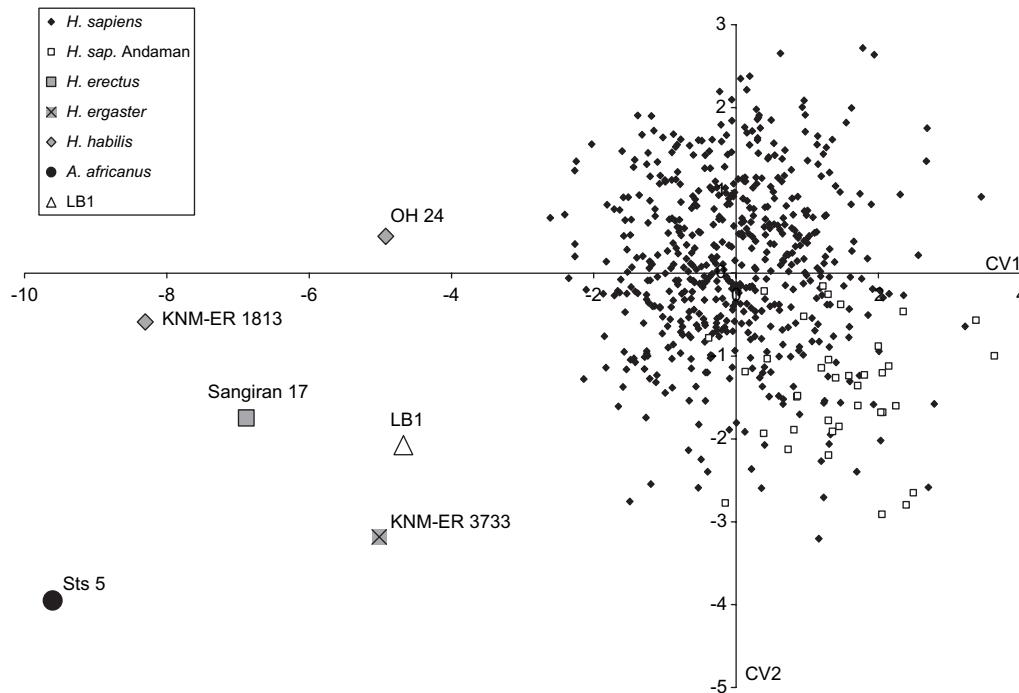

Fig. 6. Analysis 4: LB1 compared to a range of early *Homo*, *A. africanus*, *P. robustus,* and *P. boisei*. CV 1 represents 64.0% of the variance; CV 2 represents 20.2% of the variance. See Table 2 for statistical results.

frontal and parietal bones, flattening of the occipital bones, receding mental protuberance, elevated nasal root that is broad and continuous with the eyebrow and the supraorbital ridges, hypoplastic supraorbital ridges, and small primary and secondary teeth which may have mottled or hypoplastic enamel (Hall et al., 2004). Here, we compare LB1 to the 'pygmoid' from Liang Toge (LT) and to the Minoan and Sano 3 microcephalics. Information pertaining to LB1 is from Brown and colleagues (2004).

Cranial capacity. The cranial capacity of LB1 (380–410 cm^3) is small compared to both microcephalics (530 and 730 cm^3) and especially 'pygmoids' such as the individual from Liang Toge (1204 cm^3).

Recession of the frontal and parietal bones. The frontal bones of LB1 rise steeply, at approximately 55° to the Frankfurt Plane, from the supraorbital sulcus for some distance before flattening along the cranial vault (see Fig. 1 in Brown et al., 2004), similar to that observed in early and later fossil hominins. The frontal bone of the Minoan forms a smooth curve that slopes initially 60° from glabella to bregma (Fig. 1). The frontal of Sano 3 slopes at 70° (Fig. 2) and then forms a stronger curve than that of the Minoan. Sano 3 more closely resembles the normal *H. sapiens* condition, while LT (see Plate 28 in Jacob, 1967) is of course very typically human-like.

The LB1 parietal bones gradually slope inward toward bregma, forming a low, rounded arch in frontal view (see Fig. 2 in Brown et al., 2004). A similar shape is found on the Sano 3 cranium, but it is slightly more rounded in the region of the temporal lines (Fig. 2). The parietal bones of the Minoan are strongly recessed, forming a low peak at bregma (Fig. 1). The parietal part of the vault of LT is vertical but flat and continues gradually into the rounded occipital contour (see Plate 28 in Jacob, 1967). LB1 does not reflect the condition in the Minoan, Sano, or LT cranium; rather, it resembles early fossil hominins. Overall, in frontal view, the temporal bones of LB1 slope slightly medially as do those of Sano 3 (Fig. 2), while those of the Minoan bulge laterally (Fig. 1). The Minoan vault is notably higher than that of LB1 and Sano 3. Both the Minoan and Sano 3 exhibit parietal bossing which is not present on LB1. In posterior view, the shape of LB1's cranium is pentagonal, with the maximum width at the lower part of the cranium, again resembling the primitive hominin condition. The maximum widths of the Minoan and Sano 3 crania are at a higher point: at or near the temporal lines. In superior view, the microcephalic skulls (Figs. 1 and 2) are elliptical in comparison to LB1, which is more rounded.

Flattening of the occipital bones. LB1, the Minoan, and Sano 3 exhibit flattening of the occipital bone, with the rear of the Minoan cranium appearing foreshortened and that of Sano 3 more extended (compare Figs. 1 and 2). The Minoan has a very gracile occipital torus (Fig. 1), while none is evident on the weak relief of the LT occipital (Jacob, 1967). The LB1 occipital contrasts with those of the Minoan, Sano 3, and LT in having a strongly flexed occipital curvature, with the length of the nuchal area dominating over the occipital segment. It has a developed occipital torus that forms a low and extended

mound (Brown et al., 2004), which reflects the primitive form of *Homo*. As such, LB1 does not reflect the microcephalic condition as observed in the specimens described, nor does it exhibit the 'pygmoid' condition.

Receding symphysis. The Minoan's symphysis recedes, but below this there is a very marked, pointed mental protuberance (Fig. 1). It appears to have the upside down 'T' characteristic of *H. sapiens* as described by Schwartz and Tattersall (2000). There is no lower jaw available for Sano 3. None of the clinical descriptions, as far as we know, state that microcephalic individuals lack a chin; all microcephalic individuals illustrated in, for example, Seckel (1960), Majewski and Goecke (1998), Jeffery and Berkovitz (2002), Hall and colleagues (2004), and Halder and colleagues (1998), have a typical *H. sapiens* mental protuberance that may or may not recede. LT's well-developed mental protuberance sits under a prognathic alveolar protrusion (see Plate 28 in Jacob, 1967). LB1, however, has no mental protrusion. Rather, the mandible is rounded and bulbous within the transverse section, falling away from the alveolar margin (Brown et al., 2004), reflecting an early *Homo* condition.

Nasal form. Both the Minoan and Sano 3 individuals have prominent nasal bones, depressed at the root, that slope gradually towards glabella (Figs. 1 and 2), whereas LB1 has a widely angled, not strongly recessed nasal root and a flat nasal skeleton. The entire midfrontal region in LB1 is flattened (see Fig. 1 in Brown et al., 2004), whereas in the microcephalics it is prominent. The nasal region of LB1, however, was damaged at discovery (Brown et al., 2004). While examination of the original may clarify this comparison, it is clear that postmortem damage does not account for the nasal root morphology in its entirety.

Supraorbital ridges. The Minoan individual shows very little development of the supraorbital ridges (Fig. 1). Sano 3 appears to have gracile ridges that flare somewhat at the trigone (Fig. 2), and LT has extremely gracile ridges, where visible (Jacob, 1967: Fig. 28). In contrast, LB1 has well-developed, prominent, and rounded supraorbital tori (not gracile ridges) that are thickest medially (although note that only the right side is undamaged and shows this feature clearly) and laterally as they sweep around to join the zygomatic. They are separated from the frontal squama by a supraorbital sulcus (Brown et al., 2004). Again, LB1 does not reflect the pathological condition as observed in the microcephalic specimens nor does it reflect the condition of LT, but is reminiscent of early fossil *Homo*.

Other cranial characters. There are other differences between LB1, the microcephalic individuals, and LT. The zygomatic arches of LB1 are more robust than those of the Minoan, Sano 3, and LT, and they flare laterally. The LB1 cranium is much narrower than the face, so that the zygomatic arches are seen when the skull is viewed from above, whereas the faces of the Minoan (as judged from the frontal view) and LT are no wider than the cranium. From above, the zygomata of Sano 3 are nearly the width of the posterior frontal. From below, LB1 shows a deep postorbital constriction (see Fig. 2 in Brown et al., 2004) which LT and the microcephalic cases

do not exhibit. LB1 has strongly developed nasal pillars compared to the more gracile pillars of the two microcephalic individuals. The orbits are more rounded than those of the Minoan and Sano 1, which exhibit the squarer, human-like shape. There is no evidence on the basicranium of a vaginal crest on LB1, but one is evident on the Minoan (Poulianos, 1975). The external auditory meatus of LB1 is small and circular, resembling australopithecines in particular, and the tympanic plate entirely lacks the inferior expansion universal in *H. sapiens*. Information about the orbits and nasal pillars of LT is not available.

Postcranial metric analyses

Results are reported as a radiofemoral index (radius length × 100/femur length) (Fig. 7) and as a bivariate plot of the length of the radius and femur (Fig. 8).

The radiofemoral index for LB1 is 67.9; that is, LB1 has a shorter radius than femur, but it is not as relatively short as the radius of *H. ergaster*, and falls outside the range of *H. sapiens* (Fig. 7). For this index, LB1 lies closest to BOU-VP-12/1, and is more distant from A.L. 288-1, OH 62a (data from Hartwig-Scherer and Martin, 1991), OH 62b and OH 62c (data from Haeusler and McHenry, 2004), and the LT 'pygmoid'. The latter is slightly outside the range of *H. sapiens*, while the African pygmies are at the high end of the range of this group.

The bivariate plot (Fig. 8) shows two distinct clusters: the African apes with their relatively long radii, and *H. sapiens* with their relatively short radii. The radius and femur of the African apes are almost of equal length, whereas in *H. sapiens* the radius is slightly more than half the length of the femur. LB1 is intermediate between the African apes and *H. sapiens*, with the radius being approximately three-quarters the length of the femur. While its femur length is comparable to A.L.

288-1 and OH 62 (when the lower estimates for radius length by Hartwig-Scherer and Martin, 1991 are used), LB1 has a shorter radius than these specimens and is not comparable to KNM-WT 15000 (*H. ergaster*), which clusters with *H. sapiens*. African pygmies and the LT 'pygmoid' exhibit some of the longest forearms and radii relative to femur length.

Thus, assuming that the estimate for the radius length by Morwood and colleagues (2005) is correct, LB1 is more similar in limb proportions to *A. garhi* than to A.L. 288-1 (*A. afarensis*), OH 62 (*H. habilis*), KNM-WT 15000 (*H. ergaster*), or *H. sapiens*. The postcranial limb bones of LB1 are, however, extremely short. It is possible, then, that these trends may suggest a scaling relationship between limb proportions: it may be that the separation of LB1 and the other small hominins (and the pygmies) is a reflection of LB1's small size. Finally, the limb proportions follow a similar pattern to those reported for the humerofemoral relationship of LB1 with extant apes, hominins, and *H. sapiens* (Morwood et al., 2005).

Postcranial morphological comparisons

In MOPD II, the bones are described as thin, with disproportionate shortening of the forearm, a small femoral head, short femoral neck, high and narrow pelvis with small iliac wings, flattened acetabulum, and bowed long bones (Sigaudy et al., 1998; Hall et al., 2004). Neither the tibia nor the femur of LB1 are in any way 'thin', even though muscle attachment sites on the femur are not well defined (Brown et al., 2004). There is no sign of metaphyseal flaring or triangular epiphyses in LB1, whereas in MOPD II individuals, widening of the metaphyses of the long bones is common (14/16) as are triangular epiphyses (12/15) (Majewski and Goecke, 1998). While disproportionate shortness of the forearms relative to the legs is commonly found in MOPD II individuals (Majewski and Goecke, 1998; Fukuzawa et al., 2002; Hall et al., 2004), the
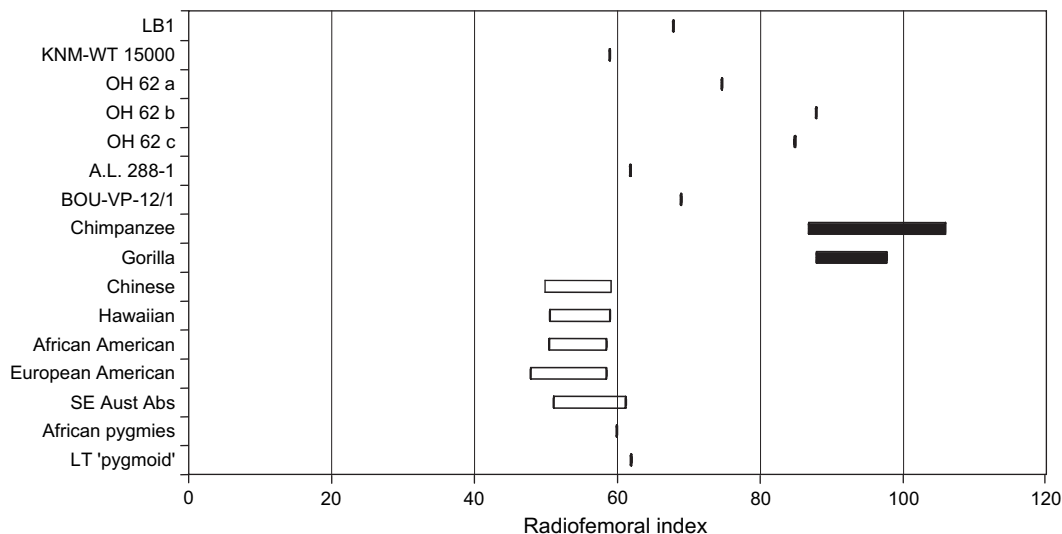

Fig. 7. Radiofemoral index (radius length × 100/femur length) in *Homo sapiens*, extant African apes, and fossil hominins. See Table 1 for a full description of the samples. Three values are shown for OH 62. OH 62a uses the femur and radius length estimate by Hartwig-Scherer and Martin (1991), OH 62b uses the lower end of the range for femur length and an estimate of the radius based on ulna length by Haeusler and McHenry (2004), while OH 62c uses the upper end of the range for femur length and an estimate of the radius based on the ulna length by Haeusler and McHenry (2004).
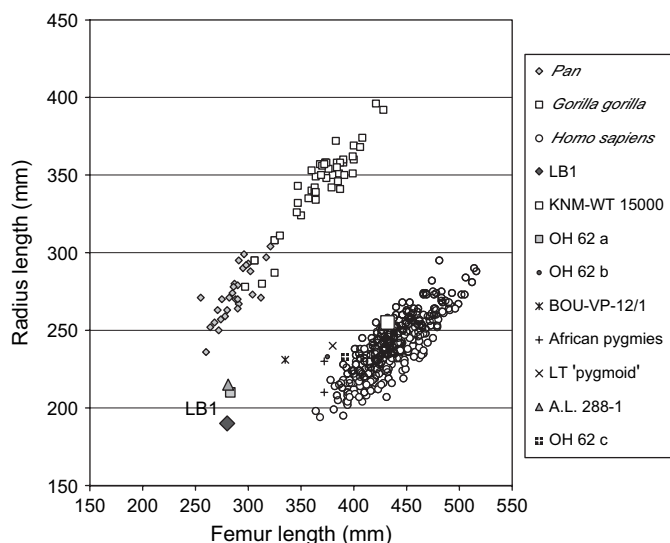
Fig. 8. Bivariate plot of radius length and femur length in *Homo sapiens*, extant African apes, and fossil hominins. See Table 1 for a full description of the samples. Three points are shown for OH 62. OH 62a uses the femur and radius length estimate by Hartwig-Scherer and Martin (1991), OH 62b uses the lower end of the range for femur length and an estimate of the radius based on ulna length by Haeusler and McHenry (2004), while OH 62c uses the upper end of the range for femur length and an estimate of the radius based on ulna length by Haeusler and McHenry (2004).

preceding analysis shows that disproportionate *lengthening* of the forearm is found in LB1. The femoral head of LB1 is not small relative to the shaft, the neck is long, the ilium is broad with flaring iliac wings, and the acetabulum is not flattened. The only feature of the long bones which LB1 has in common with MOPD II individuals is a bowed tibia.

Discussion

A cranial morphometric and morphological comparison of LB1 with microcephalic individuals suggests that LB1 is unlikely to be a microcephalic *H. sapiens*, at least not of the MOPD II type. In the craniometric analyses, the Minoan and Sano 3 microcephalics are within the range of *H. sapiens*, although the Minoan is on the edge of the range of this species. LB1 is outside the range of *H. sapiens* and separated from the two microcephalics. For the microcephalics to cluster with LB1 in the analyses, they would have to possess a greater degree of prognathism, a lower vault, and wider biauricular breadths, which one might consider an unlikely set of characteristics for *H. sapiens*. We note, however, that we were only able to include two microcephalic individuals in the metric analyses for want of published data. Microcephaly is an extremely heterogeneous condition and, while our results are suggestive, it may be that they would differ should a larger sample of microcephalics be studied.

When the cranial morphology of MOPD II individuals is compared to that of LB1, however, the only condition they have in common is a small cranial capacity. In no other way does LB1's cranial morphology correspond to that of MOPD II. Further, except for a bowing of the tibia, LB1 does not

display any of the postcranial morphologies commonly found in these individuals. Likewise, LB1 separates from the LT 'pygmoid' in the cranial metric analyses and does not display its modern human morphological features. LB1 is separate from the Andaman sample in the cranial analyses and does not reflect the postcranial proportions of any African pygmy populations. It would appear unlikely, then, that LB1 is either a microcephalic or pygmoid *H. sapiens*.

From the published descriptions of LB1 (Brown et al., 2004; Morwood et al., 2005), we propose that LB1 exhibits many cranial characters suggestive of an early *Homo* morphology: maximum cranial width at the lower part of the cranium, strongly flexed occipital curvature with the nuchal area dominating over the occipital segment, an occipital torus, rounded external auditory meatus, absence of mental protuberance, lingual buttressing of the symphysis, well-developed supraorbital tori with a supraorbital sulcus, laterally flaring zygomatic arches, deep postorbital constriction, strongly developed nasal crests, and absence of a vaginal crest. When considering cranial shape in the metric analyses, LB1 is separated from Sangiran 17 (*H. erectus*) in all but one analysis and is always separate from the Solo specimens. It is also separate from KNM-WT 15000 and OH 24 (*H. habilis*) in three of the analyses, from Dmanisi D2280 in the one analysis in which this specimen could be included, and from the specimens of *A. africanus*, *P. robustus*, and *P. boisei*. LB1 tends to cluster somewhat with KNM-ER 3733, except in Analysis 4 where the two are fairly well separated. The cranio-facial shape of LB1 differs from the two *H. habilis* specimens OH 24 and KNM-ER 1813, *H. erectus* Sangiran 17, *H. ergaster* KNM-ER 3773, and *A. afarensis* Sts 5 (Analysis 4). This suggests that the LB1 cranium is distinct from these species, although we recognize that sample size is small. Further, LB1 has a tiny cranium, and, despite our use of geometric mean to adjust for size, it is possible that the result is partially affected by scaling issues. On balance, we suggest that the LB1 cranial shape is distinct from these fossils.

The postcranial investigation suggests that *H. floresiensis* has a long radius relative to its femur. If *H. floresiensis* is a dwarfed form of *H. erectus*, then the forearms may not have reduced at the same rate as that of the lower limbs. This shows some parallelism with *H. sapiens*, in that African pygmies and the Liang Toge 'pygmoid' have long forearms relative to femur lengths. However, the difference between pygmy populations and other *H. sapiens* populations is very small compared to that between *H. floresiensis* and *H. ergaster*.

LB1 clusters with *A. garhi* rather than with *H. ergaster* in the postcranial analyses. If Morwood and colleagues' (2005) estimate for the LB1 radius is correct, and our analyses are not affected by any scaling issues, then we propose that the radius/femur proportions of LB1 show greater similarity to *A. garhi* than to *H. ergaster*.

Brown and colleagues (2004) suggest that the morphology of LB1 is the result of a long period of evolution on an island where small body size had some selective advantage. Insular dwarfism is unknown for *Homo* to date, so we must turn to models based on other mammals that have adapted to island

environments for an indication of what might happen if *Homo* were subjected to the same phenomenon. Insular dwarfism of mammals may occur when a founder population reaches an island and becomes reproductively separated from the original population. The founder population is likely to be small and therefore only contain a fraction of the genetic variation of the parent species (Foster, 1964; Sondaar, 1976; Dayan and Simberloff, 1998). Adaptive changes due to isolation may then operate on the available gene pool. These changes can vary depending on the mammal and the environment in which it is located. A common morphological change in large mammals on islands is a decrease in size. (Conversely, some small mammals increase in size). A range of explanations for this island rule have been proposed (for a discussion, see Foster, 1964; Sondaar, 1976; Dayan and Simberloff, 1998). But a change in size does not necessarily produce equal reductions in scale of all features (Sondaar, 1976).

The ancestral population of an insular dwarf population can usually be identified by looking at morphological similarities. For example, the ancestors of the Mediterranean island hippopotamus (Sondaar, 1976), *Stegodon* on Flores (Hooijer, 1975), and *Myotragus* on the Balearics (Alcover, 1976), are identifiable based on morphological similarities. It might be expected, then, that if LB1 had been subjected to insular dwarfism, it would bear some resemblance to its ancestral population and that this population could be identified.

In this scenario, the small cranial capacity of LB1 is the result of selective pressures, but what could result in such a small brain size? Köhler and Moyà-Solà (2004) found that the brain mass of the bovid *Myotragus*, isolated from its parent population and predators on the Balearic islands, underwent significant reduction. Reduction of predation risk on the island may explain the *Myotragus* decrease. In a high risk environment, alertness is a life-and-death matter. Relaxation of this risk reduces selection for alertness and brain mass may decrease accordingly. The reduction in cranial capacity of LB1, then, may have evolved if the environment on Flores was predator-free during the time LB1's population was evolving. However, the known presence of the Komodo dragon (*Varanus komodoensis*), crocodiles, and sharks, and the probable presence of pythons on Flores at this time, might argue against a 'predator-free' hypothesis for LB1's reduced cranial size.

Despite its relatively small cranial capacity, Falk and colleagues (2005) found that a virtual endocast of LB1 possessed an expanded prefrontal cortex and temporal lobes relative to fossil hominins (Brodmann's area 10) (Falk et al., 2005). Area 10 is involved in higher cognitive processing, such as the ability to retrieve memory from an individual's past experiences and the capacity to plan responses to changing conditions. The configuration of the prefrontal cortex and wide temporal lobes are derived conditions relative to *H. erectus* and other early hominins, and Falk and colleagues (2005) conclude that LB1's brain could not have been a miniaturized version of *H. erectus* (or *H. sapiens*). The implication is that LB1 possessed developed cognitive abilities and was able to plan, respond to conditions, use memories, and transfer information between group members (after Allman et al., 2002). Weber

et al. (2005), however, in a study of 19 microcephalic modern humans, found great variability in overall brain shape, with some specimens showing small frontal and temporal lobes and some displaying extremely wide temporal lobes. They discern no typically diagnostic brain shape and convolution pattern. Further, they found that Brodmann's area is relatively enlarged in seven of their specimens, and cite a male individual with a cranial volume of 485 cm^3 and prominent Brodmann's area 10 who was able to walk but had severe speech limitations. Thus, the correlations between endocranial morphology and behavior remain somewhat unclear.

The stature of LB1 might be akin to that of earlier *Homo*. LB1 is estimated to be 106 cm tall based upon Jungers' predictive equation developed from human pygmies (Brown et al., 2004), although this is likely an overestimation because of the low cranium of LB1. The stature of *H. habilis* based on OH 62 and the Jungers' equations is 103.6 cm, shorter than the predicted stature for LB1 (above), or between 105 cm and 126 cm using other formulae (e.g., Trotter and Gleser, 1952; Oliver, 1976; Feldesman and Lundy, 1988). More recent, longer, estimates of femur length for OH 62 would suggest larger sizes for *H. habilis* (Haeusler and McHenry, 2004). It is unclear, then, if our predicted stature of LB1 is within the (as yet unknown) range of *H. habilis*, although it would at best be at the low end of this range. It is, however, similar to the estimated 105 cm stature of female *A. afarensis* (McHenry, 1992) and somewhat shorter than the 115 cm estimate for female *A. africanus*. The radial-femoral relationship of LB1 appears almost identical to *A. garhi*; its radius is smaller than, but of similar proportions to *A. garhi*.

While the issue of stature and the cause of the small cranial capacity of LB1 will require further exploration, LB1 nevertheless has a mosaic of morphological features not seen in *Homo* to date. For this reason, Brown and colleagues (2004) attributed it to a new species, *H. floresiensis*. Our analyses support this attribution. While LB1 is close to *H. ergaster* in two cranial analyses, and *H. ergaster* is LB1's nearest neighbor in the third analysis, these similarities relate to vault shape only. LB1 is separate from all species in Analysis 4, where a wide range of cranial variables are included. LB1 has a smaller cranial capacity than any *Homo* known to date, yet may display complex endocranial morphology which supports higher cognitive capabilities.

This combination of australopithecine and very early *Homo* morphology, and the tendency for LB1 to separate from *H. erectus* in the cranial analyses, argue against *H. floresiensis* having evolved from an endemic *H. erectus*. There are several other possible explanations:

1. *H. floresiensis* represents a previously unknown early hominin that shares cranial similarities with KNM-ER 3733 and limb proportions with *A. garhi*. In this case, it likely evolved in Africa and diffused to Southeast Asia before the disappearance of *A. garhi* (or an unknown, similarly-proportioned species) in Africa.
2. The morphology of *H. floresiensis* may have evolved from a founder population of archaic *Homo* that possessed, or

developed, a more advanced endocranial anatomy in relation to its postcranial characteristics, either on Flores or in some intermediate region, if Falk and colleagues' assessment of its cranial capabilities proves correct.

3. *H. floresiensis* represents a previously unknown hominin that was in the process of evolving from *Australopithecus* to *Homo* when it diffused from Africa. In this case, diffusion would have occurred before the appearance of the fully derived *Homo* morphology, that is, prior to about 2 Ma. The relatively complex brain and suggested conceptual abilities would argue that *H. floresiensis* had the ability to diffuse from Africa and survive, on Flores at least, until 12,000 years ago.

Each of these possible explanations implies a relatively early diffusion from Africa. Regardless of the timing of this event, it is puzzling how this species arrived on Flores, an island that Metcalfe (2002) and Hall (2001) depict as having been separated from other land masses since at least the Early Pliocene. They note, however, that it is not possible to be very precise about past water depths in the region of Wallacia, and that there are disagreements about the magnitude of eustatic changes. Local, small-scale tectonic movements in this geologically unstable region may have provided temporary land links that facilitated colonization by hominins. Watercraft would facilitate access to Flores (Morwood et al., 1998), but our state of knowledge about the cognitive abilities of *H. floresiensis* is not developed enough to enable speculation about this species' ability to use watercraft.

Conclusion

Cranial and postcranial analyses of LB1 suggest that this skeleton is unlikely to be a microcephalic *H. sapiens*; the only similarity it shows to this morphology is a small endocranial volume. Broader studies comparing a large sample of microcephalic human material to LB1 will undoubtedly contribute to this debate. LB1 does not approximate pygmy or 'pygmoid' morphologies. On the contrary, it shows many characters found in early *Homo*. Our analyses show that LB1 probably did not evolve from *H. erectus*, from which it differs in cranial shape, degree of prognathism, and limb proportions. The cranial morphology of LB1 is different from all archaic *Homo* specimens in this study, although there are indications that it may be most similar to *H. ergaster* KNM-ER 3733. Postcranially, it exhibits primitive limb proportions like *A. garhi*, having a long radius relative to its femur, assuming the estimated length for the radius is correct. LB1 is short in stature; it has a small cranial capacity that nevertheless is suggested to be neurologically complex. This combination of cranial and postcranial traits is unique, and we support the attribution by Brown and colleagues (2004) of LB1 to a new species: *H. floresiensis*. We have suggested a number of possible hypotheses for the evolution of *H. floresiensis*, and expect that future testing and, perhaps, the discovery of more skeletal material will greatly contribute to our understanding of this remarkable discovery.

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