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Journal of Human Evolution

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Craniofacial morphology of *Homo floresiensis*: Description, taxonomic affinities, and evolutionary implication

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ARTICLE INFO

Article history: Received 5 October 2010 Accepted 21 August 2011

Keywords: LB1/1 Homo erectus Homo habilis Cranium Face

ABSTRACT

This paper describes in detail the external morphology of LB1/1, the nearly complete and only known cranium of *Homo floresiensis*. Comparisons were made with a large sample of early groups of the genus *Homo* to assess primitive, derived, and unique craniofacial traits of LB1 and discuss its evolution. Principal cranial shape differences between *H. floresiensis* and *Homo sapiens* are also explored metrically.

The LB1 specimen exhibits a marked reductive trend in its facial skeleton, which is comparable to the H. sapiens condition and is probably associated with reduced masticatory stresses. However, LB1 is craniometrically different from H. sapiens showing an extremely small overall cranial size, and the combination of a primitive low and anteriorly narrow vault shape, a relatively prognathic face, a rounded oval foramen that is greatly separated anteriorly from the carotid canal/jugular foramen, and a unique, tall orbital shape. Whereas the neurocranium of LB1 is as small as that of some Homo habilis specimens, it exhibits laterally expanded parietals, a weak suprameatal crest, a moderately flexed occipital, a marked facial reduction, and many other derived features that characterize post-habilis Homo. Other craniofacial characteristics of LB1 include, for example, a relatively narrow frontal squama with flattened right and left sides, a marked frontal keel, posteriorly divergent temporal lines, a posteriorly flexed anteromedial corner of the mandibular fossa, a bulbous lateral end of the supraorbital torus, and a forward protruding maxillary body with a distinct infraorbital sulcus. LB1 is most similar to early Javanese Homo erectus from Sangiran and Trinil in these and other aspects. We conclude that the craniofacial morphology of LB1 is consistent with the hypothesis that H. floresiensis evolved from early Javanese H. erectus with dramatic island dwarfism. However, further field discoveries of early hominin skeletal remains from Flores and detailed analyses of the finds are needed to understand the evolutionary history of this endemic hominin species.

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Introduction

Homo floresiensis is a small-bodied, hominin species that lived on the Indonesian island of Flores in the late Pleistocene. Skeletal remains of this species are currently only known from Liang Bua, a limestone cave, where they are dated to between 74 and 17 kyr. At least 14 individuals are represented by these remains, which include LB1, an almost complete skeleton and the species holotype, popularly known as 'Hobbit' (Brown et al., 2004; Morwood and Jungers, 2009; Morwood et al., 2009; Roberts et al., 2009;

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Westaway et al., 2009). The unusual combination of extremely small brain size, short stature, and other unique physical traits of *H. floresiensis* have led some to argue that the skeletal remains represent a population of pathological modern humans. However, such proponents have been unable to indicate a specific syndrome that fully explains these traits, and there is now growing support for the hypothesis that *H. floresiensis* was a late-surviving species of pre-modern *Homo* (reviewed in Aiello, 2010).

The origins of this novel species still remain highly controversial despite lively debate and further studies following the initial reports (Brown et al., 2004; Morwood et al., 2004, 2005). In fact, nominated candidates for ancestral species of *H. floresiensis* include Javanese *Homo erectus* and pre-*erectus* grade hominins such as

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Homo habilis or even Australopithecus (e.g., Brown et al., 2004; Argue et al., 2009; Brown and Maeda, 2009; Lyras et al., 2009; Morwood and Jungers, 2009). All these possibilities have major implications for our understanding of the evolution of genus Homo. If H. floresiensis evolved from a habiline-like ancestor on Flores, then H. erectus sensu lato (H. erectus s. l.) was not the first hominin species to disperse into Eurasia, as assumed in the current Out of Africa 1 hypothesis (Morwood and Jungers, 2009). It would also imply that H. erectus and another more primitive form of Homo coexisted in Southeast Asia for a substantial period. Alternatively, if H. floresiensis originated from Asian H. erectus, then insular dwarfing to an unparalleled degree has been a significant factor in early hominin evolution on Flores (Brown et al., 2004).

Skeletal evidence of the first hominins to colonize Flores would provide direct and conclusive evidence for the evolutionary history of *H. floresiensis*, but further study of the Liang Bua hominin remains is also essential. In this paper, we provide a detailed

description of the external cranial morphology of LB1, and assess its morphological affinities.

Background and the scope of this study

The LB1 skeleton is that of an adult individual whose sex is presumed to be female on the basis of pelvic morphology (Brown et al., 2004; Jungers et al., 2009b). The cranium is almost complete (Reference number LB1/1; Figs. 1 and 2) and is the only example of a *H. floresiensis* cranium yet recovered (Morwood and Jungers, 2009). In this section, we review the published studies on its morphological affinities.

In the original reports of *H. floresiensis*, Brown et al. (2004) and Morwood et al. (2005) described "a mosaic of primitive, unique and derived features not recorded for any other hominin" in the cranium and other skeletal parts of LB1. For instance, they found that the endocranial capacity is small and comparable to



Figure 1. Facial, posterior, right lateral, left lateral, superior, and basal views of LB1/1 oriented based on the Frankfurt Horizontal. Scale = 5 cm.

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