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The origins and persistence of *Homo floresiensis* on Flores: biogeographical and ecological perspectives

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ABSTRACT

The finding of archaeological evidence predating 1 Ma and a small hominin species (*Homo floresiensis*) on Flores, Indonesia, has stimulated much research on its origins and ancestry. Here we take a different approach and examine two key questions – 1) how did the ancestors of *H. floresiensis* reach Flores and 2) what are the possibilities for estimating the likelihood of hominin persistence for over 1 million years on a small island? With regard to the first question, on the basis of the biogeography we conclude that the mammalian, avian, and reptilian fauna on Flores arrived from a number of sources including Java, Sulawesi and Sahul. Many of the terrestrial taxa were able to float or swim (e.g. stegodons, giant tortoises and the Komodo dragon), while the rodents and hominins probably accidentally rafted from Sulawesi, following the prevailing currents. The precise route by which hominins arrived on Flores cannot at present be determined, although a route from South Asia through Indochina, Sulawesi and hence Flores is tentatively supported on the basis of zoogeography. With regards to the second question, we find the archaeological record equivocal. A basic energetics model shows that a greater number of small-bodied hominins could persist on Flores than larger-bodied hominins (whether *H. floresiensis* is a dwarfed species or a descendent of an early small-bodied ancestor is immaterial here), which may in part explain their apparent long-term success. Yet the frequent tsunamis and volcanic eruptions in the region would certainly have affected all the taxa on the island, and at least one turnover event is recorded, when *Stegodon sondaari* became extinct. The question of the likelihood of persistence may be unanswerable until we know much more about the biology of *H. floresiensis*.

1. Introduction

The island of Flores, Indonesia, has been the source of at least three of the least expected and most significant discoveries in palaeoanthropology in the last 50 years. The first and best known discovery was that of *Homo floresiensis*, ("the hobbit,") found in a late Pleistocene context at the cave of Liang Bua (Fig. 1; Brown et al., 2004; Morwood et al., 2004) and associated with a simple core and flake assemblage that extended back to ca 95 ka (Moore et al., 2009; Roberts et al., 2009). Despite concerns that the small brain size of *H. floresiensis* of only ca 400 cc^3 (or roughly the same as a chimpanzee's) precluded it from being the maker of these tools, the absence of any evidence of *Homo sapiens* on the island until the Holocene makes it the only likely candidate. The second and third major discoveries on Flores were that hominins had been present long before the late Pleistocene: at Mata Menge and Boa Lesa, stone artefacts were found associated with the remains of the large-bodied stegodon *Stegodon florensis florensis*, dated by fission track to 0.88 ± 0.07 Ma (Morwood et al., 1998), and at Wolo Sege, artefacts associated with pygmy *Stegodon sondaari* were dated by $^{40}Ar/^{39}Ar$ to a minimum age of 1.02 ± 0.02 Ma (Brumm et al., 2010). Flores is thus a unique example of an island that was never joined to a continental shelf during low sea levels but was nevertheless colonised by hominins before the late Pleistocene.

Discussion over the Liang Bua finds has largely focussed on the question of who were the ancestors of *H. floresiensis*? Or, put another way, how does *H. floresiensis* fit into the overall picture of human evolution? Three views quickly emerged over its possible ancestry: i) that it was a pathological or pygmy population of *H. sapiens* (Jacob et al., 2006; Richards, 2006; Hershkovitz et al., 2007; Perry and Domini, 2009); ii) that it was a dwarfed

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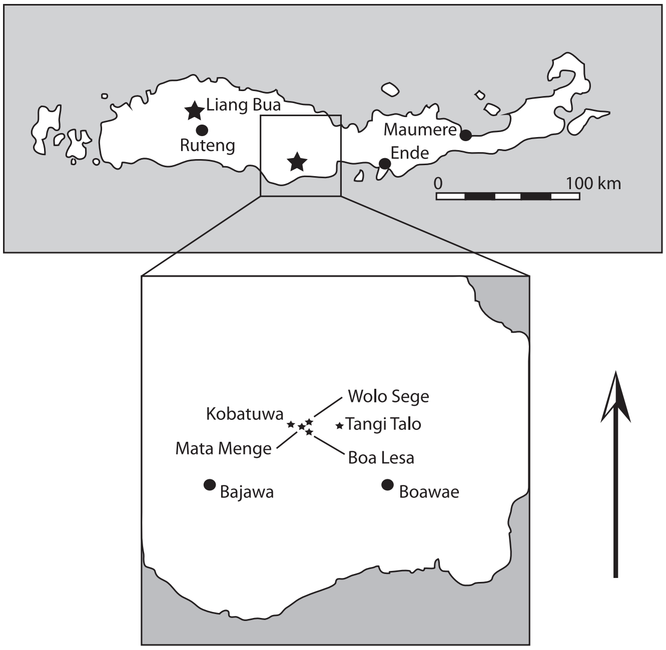

Fig. 1. Map of Flores, Indonesia, showing archaeological and palaeontological localities mentioned in the text (stars) and key towns (circles) for orientation. Adapted after Brumm et al. (2010).

population descended from the type of *Homo erectus s.s.* populations seen on neighbouring Java (Kaifu and Fujita, 2012); and iii) most contentious of all is the suggestion that it belonged to a primitive lineage that extended back to early forms of *Homo* or even *Australopithecus* that dispersed from Africa in the earliest part of the Pleistocene (Argue et al., 2006; Tocheri et al., 2007; Brown and Maeda, 2009; Falk et al., 2009; Jungers et al., 2009; Larsson et al., 2009; Morwood and Jungers, 2009; Aiello, 2010). Although most researchers now agree that the Liang Bua hominins were not pathological or pygmy *H. sapiens*, opinion is still divided between those favouring a local population of *H. erectus* or a distant and earlier lineage as its ancestors. Until we know the type (and size) of hominin that made the artefacts at Mata Menge and Wolo Sege, any discussion about the phylogenetic history of *H. floresiensis* is likely to remain inconclusive.

Here we take a biogeographical and ecological approach to the archaeology and consider two specific questions: 1) where was the likely source population for *H. floresiensis*; and 2) what are the prospects and difficulties of estimating the likelihood of its persistence on Flores for over ~1 Ma?

2. Source populations

2.1. Arrival on Flores

The question of how *H. floresiensis* – or its predecessors – arrived on Flores is an important one because Flores would always have been an island that was at least 19 km from other islands on the Sunda Shelf, even when sea levels were over 100 m lower than today (Morwood et al., 1998; Morwood and Jungers, 2009). As land connections with neighbouring islands such as Bali, Lombok and Java can be excluded, it had to arrive by sea. Only two options seem plausible. One assumes that the first hominin to reach Flores was *H. erectus*, and that it was already capable by 840 ka (the age of Mata Menge) of using watercraft for repeated sea journeys (Morwood et al., 1998; O'Sullivan et al., 2001; Bednarik, 1999; Morwood, 2001) (The same line of reasoning presumably applies to the inhabitants of Wolo Sege a million years ago.) The idea that *H. erectus* might have used watercraft was enthusiastically pursued by Bednarik (2003), who demonstrated that a sea-going boat or raft could be made by using the same type of early Palaeolithic tools found on many Middle Pleistocene sites. Indeed, one of the rafts that he built with a simple lithic technology sailed 1000 km from Timor to Australia (Nale Tasih, 1, with a crew of five). Another sailed 90 km from Bali to Lombok (Nale Tasih 4, with a crew of 12), although the Lombok Strait crossing appears to have been especially harrowing, with the crew experiencing exhaustion, and one lapsing into a coma. Bednarik (2003) has unequivocally made the point that *H. sapiens* can build and sail rafts to a known destination and with the type of tools available to *H. erectus*, but this does not necessarily imply that *H. erectus* had the cognitive and co-operative skills (or the impulse) to build a raft and sail into the unknown. At present, Flores is the sole oceanic island with evidence of hominin colonisation prior to *H. sapiens* (Table 1), suggesting that *H. erectus* was unlikely to have been making watercraft a million years ago, and still less likely to have willingly undertaken sea voyages.

The second possibility is that hominins arrived accidentally on natural rafts of vegetation that had been swept out to sea following a cyclone or tsunami (Smith, 2001; van den Bergh et al., 2008). This suggestion is not implausible: Smith (2001) cites one instance in the 19th century when a natural raft was mistaken for a three-masted ship; after the 2004 tsunami, a pregnant woman who could not swim was rescued after 5 days from a floating sago tree; and a man was saved 160 km from the coast after 8 days at sea (van den Bergh et al., 2008). These are of course the fortunate survivors of the thousands more who were never seen again. After the Krakatoa-induced tsunami of 1883, a report to The Royal Society of London described "hundreds" of bodies on pumice rafts off the African coast, having drifted across the Indian Ocean (Winchester, 2003). Some of the pumice rafts following this eruption were large enough to support large trees – including ones that washed up over 6,500 km from Krakatoa (Thornton, 1996).

It is possible to use simple modelling approaches as an additional way to examine these questions. Ruxton and Wilkinson (2012) showed that an island such as Flores could have been colonised successfully (meaning that its population survived at least 500 years and/or reached a size of 500 individuals) as a result of accidental colonisation (by, for example, small groups of humans swept out to sea on natural rafts of vegetation following a tsunami, as suggested by Smith (2001)). Crucially they also showed that the chances of a success for an accidental colonisation event were about 50% that of a planned colonisation event by a similar sized group with a balanced sex ratio and high proportion of females of breeding age. Unsurprisingly, success was much greater if the initial unplanned colonisation event was followed by other colonisation events, even if there was only a 2% chance of a new arrival (involving between 1 and 4 individuals) in any single year. (However, as suggested below, population depletion through natural disasters (such as tsunamis) has to be considered as well as likely rates of immigration). Based on both anecdotal accounts of natural rafting events and these models it seems likely that rafting on natural vegetation was the most likely means by which hominins arrived on Flores.

2.2. Companions

What of the faunas associated with *H. floresiensis*? The vertebrate fauna of Flores was undoubtedly impoverished, with only a dwarf stegodon (*Stegodon sondaari*), the Komodo dragon (*Varanus komodoensis*) and a giant tortoise (variously referred to *Colossochelys* sp. (e.g. Brumm et al., 2010) or *Geochelone* sp. (e.g. Meijer et al., 2010)) known from Tangi Talo (dating to ~0.9 Ma) (Brumm