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The fellowship of the hobbit: the fauna surrounding *Homo floresiensis*

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ABSTRACT

The Late Pleistocene Flores fauna shows a pattern observed on many other islands. It is neither aberrant nor exclusive, but the result of non-random selective forces acting upon an impoverished and disharmonic insular fauna. By comparing the Flores vertebrate fauna with other fossil insular biotas, it is apparent that the evolution of *Homo floresiensis* is part of a general pattern affecting all the inhabitants of Pleistocene Flores. Vertebrate evolution on Flores appears to have been characterized by phylogenetic continuity, low species richness and a disharmonic fauna. All three aspects stem from the isolated position of the island and have resulted in the distinct morphological characteristics of the Flores fauna. Evidence reviewed herein shows that features exhibited by *H. floresiensis*, such as small stature, a small brain, relatively long arms, robust lower limbs and long feet, are not unique, but are shared by other insular taxa. Therefore, the evolution of *H. floresiensis* can be explained by existing models of insular evolution and followed evolutionary pathways similar to those of the other terrestrial vertebrates inhabiting Pleistocene Flores.

Keywords

Dwarfing, Flores, gigantism, *Homo floresiensis*, Indonesia, insular evolution, unbalanced island faunas.

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INTRODUCTION

The peculiar nature of island faunas was famously illustrated with the finding of *Homo floresiensis* Brown *et al.*, 2004 (Morwood *et al.*, 2004, 2005). This new species of hominin was discovered in Late Pleistocene sediments in Liang Bua cave on the island of Flores in the eastern Indonesian archipelago (Fig. 1a,b). Standing about 1 m tall and with an estimated brain size of 417 cc, *Homo floresiensis*, affectionately referred to as the Hobbit, constitutes the smallest species of hominin ever found. As a contemporary of our own species, *Homo floresiensis* challenges widely held beliefs in human evolution, and its description as a separate species and its skeletal characters have given rise to intense discussion. Several authors have argued that *H. floresiensis* is not a separate species and that the hominin remains from Liang Bua represent merely a population of modern humans potentially suffering from a diverse array of pathologies, including microcephaly, cretinism and Laron syndrome (Henneberg & Thorne, 2004; Jacob *et al.*, 2006; Martin *et al.*, 2006; Richards, 2006; Hershkovitz *et al.*, 2007; Obendorf *et al.*, 2008).

Remarkably absent in the debate on *H. floresiensis* is the associated fauna. For if *H. floresiensis* evolved on Flores, the

local conditions that led to its adaptations would have influenced the other vertebrate inhabitants of the island as well. The remains of *H. floresiensis* are associated with numerous remains of the pygmy proboscidean *Stegodon florensis insularis* van den Bergh *et al.*, 2008; and the giant rats *Papagomys armandvillei* (Jentink, 1892), *Papagomys theodorverhoeveni* Musser, 1981 and *Spelaeomys florensis* Hooijer, 1957; as well as with various other murids, a number of bat species, the Komodo dragon, *Varanus komodoensis* Ouwens, 1912, and its relative *Varanus hooijeri* Brongersma, 1958, and a large number of birds, the most notable of which is a giant marabou, *Leptoptilos* sp. nov. (Fig. 2a–d) (van den Bergh *et al.*, 2009). Pleistocene Flores hosted a highly endemic insular fauna, unlike anything on the mainland. Only when *H. floresiensis* is considered within this insular setting can its evolution and the processes behind it be fully understood.

LIANG BUA

Excavations on Flores were initiated in the 1950s by the Dutch priest Theodoor Verhoeven, a missionary on the island and an

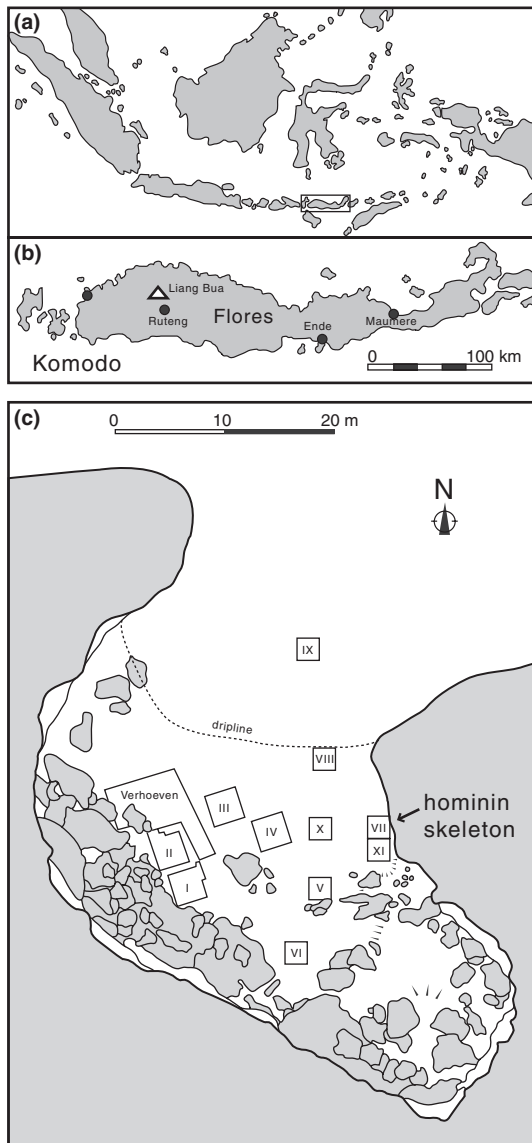


Figure 1 Map of Southeast Asia, showing (a) the location of Flores within Indonesia, (b) the location of Liang Bua Cave in western Flores, and (c) a map of the excavated sectors within Liang Bua. Panels (a) and (b) are adapted from van den Hoek Ostende *et al.* (2007). Panel (c) is adapted from Morwood *et al.* (2005).

archaeologist in his spare time. At Mata Menge and Boa Leza, two localities in the Soa Basin in central Flores, Verhoeven found the remains of *Stegodon* and a large murid in association with stone artefacts (Maringer & Verhoeven, 1970). This led him to postulate that *Homo erectus* had crossed Wallace's Line and reached the Lesser Sunda Islands early in the Pleistocene. In the summer of 1965, Verhoeven started excavating in Liang Bua, a limestone cave north of Ruteng in western Flores (Verhoeven, 1972). Liang Bua (Fig. 1c) was formed in Miocene limestone as an underground cavern by karst dissolution (Morwood *et al.*, 2004) and had been filled by various deposits derived from the weathering of limestone or washed in by

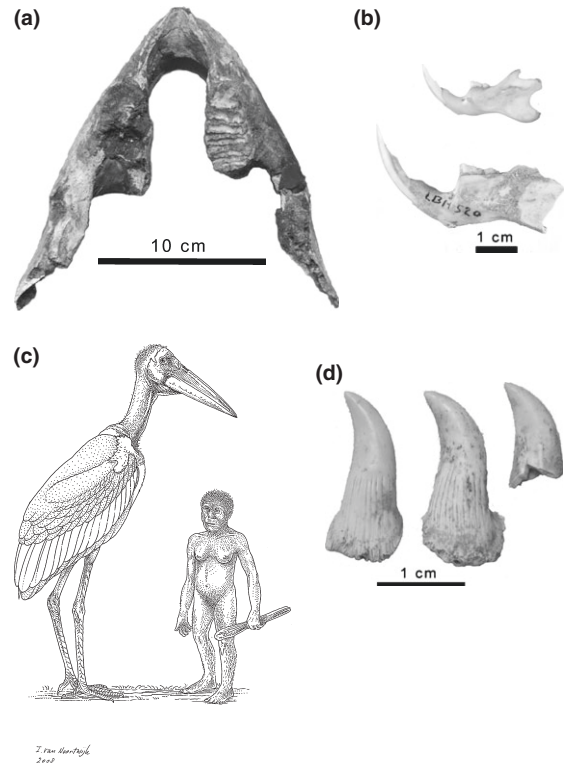


Figure 2 The fellowship of the hobbit. (a) A mandible of *Stegodon florensis insularis* from Liang Bua; (b) mandibles of *Papagomys armandvillei* from Liang Bua (below) and of extant *Rattus rattus*; (c) an artist's impression of the giant marabou *Leptoptilos* sp. nov. (estimated at 1.8 m) compared to *Homo floresiensis* (estimated at 1.0 m), drawing by I. van Noortwijk; (d) teeth from the Komodo dragon, *Varanus komodoensis*.

rivers. A test trench, 1.5 m in width and 7.0 m in length, with a depth of 2.5 m, near the western wall of the cave (Fig. 1c), yielded flakes and a human skeleton. A similar-sized additional trench was dug transversely to the test trench. The finding of several more human skeletons induced the excavators to increase the size of the second trench. According to Verhoeven, the human skeletons were similar to the 'proto-Negrito's' (modern humans) he had found in other caves on Flores. The deliberate burial of the bodies with grave goods (bronze axes, stone adzes, pottery) is consistent with Neolithic and Palaeo-Metallic-age burials of *Homo sapiens* (Morwood *et al.*, 2009). In his report, Verhoeven (1972, p. 5) merely noted that 'This cave is extra-important. One finds traces of the Neolithic as well as the Palaeolithic.' Unfortunately, exactly what traces from the Palaeolithic Verhoeven found remains unclear, as his notes are inconclusive and the human skeletons have been lost.

Excavations at Liang Bua were continued by Raden Soejono (Soejono, 1980, 1985), who excavated in 1978, 1981, 1982, 1985, 1987 and 1989. Soejono excavated 10 squares and uncovered a cultural sequence that yielded evidence for Palaeolithic through Neolithic and Metal Age occupations. However, the excavations did not extend to the Pleistocene sequence (Morwood & van Oosterzee, 2007). Soejono believed

that the deepest layers were culturally sterile. Michael Morwood, convinced that the deeper layers might fill the gap in Flores archaeology between the Early/Middle Pleistocene of the Soa Basin of Central Flores and the present, resumed the excavations in 2001. Under his supervision, an Indonesian–Australian team excavated the Pleistocene sediments and reached the bedrock of the cave.

As of 2007, 11 sectors of 1 × 1 m have been excavated (Fig. 1c), with Sectors VII and XI having been excavated to the bedrock at a depth of 11 m. The upper layers of Liang Bua, from the surface to c. 3.5 m in depth, are of Holocene age. Conspicuous layers of volcanic ash separate the Holocene layers from the underlying Pleistocene. For a detailed stratigraphy of Liang Bua, refer to Westaway *et al.* (2009) and Roberts *et al.* (2009).

Both the Holocene and Pleistocene sediments have yielded numerous remains of vertebrates. Analysis of the vertebrate remains from the Liang Bua sequence (van den Bergh *et al.*, 2009) shows that the Holocene fauna is distinctly different from that of the Late Pleistocene. The Late Pleistocene sediments yielded evidence of an endemic insular fauna, with the dwarfed hominin *Homo floresiensis*, the pygmy proboscidean *Stegodon florensis insularis*, the giant rats *Papagomys armandvillei*, *Papagomys theodorverhoeveni* and *Spelaeomys florensis*, medium- and smaller-sized rats, pteropodid and microchiropteran bats, the Komodo dragon *V. komodoensis*, another, smaller varanid, *V. hooijeri*, and birds (van den Bergh *et al.*, 2009; Meijer & Due, 2010). The oldest vertebrate remains from Liang Bua are dated at 95 ± 13 ka (thermoluminescence dating, Morwood *et al.*, 2004), and reinterpretations of the stratigraphy and radiometric dating indicate that the extinction of both the hominin and *Stegodon* coincided with a volcanic eruption at 19.0–17.9 cal. kyr BP (¹⁴C dating, van den Bergh *et al.*, 2009; Roberts *et al.*, 2009). The rodent fauna seems to be unaffected by this event. The Holocene beds (and also the terminal Pleistocene ones) have locally filled-in erosional channels that cut down into

Pleistocene layers. The Holocene sequence records the subsequent arrival of *H. sapiens* at the cave at c. 10 cal. kyr BP (¹⁴C dating, Roberts *et al.*, 2009). Later on, several exotic species are introduced to the island, including the masked palm civet (*Paradoxurus hermaphroditus*), the Sulawesi warty pig (*Sus celebensis*), the porcupine (*Hystrix javanicus*), and cattle, deer (*Cervus timorensis* and *Cervus* sp.) and horses (van den Bergh *et al.*, 2009).

THE FLORES VERTEBRATE FAUNAS

The oldest faunal evidence from Flores comes from the site of Tangi Talo, from the Ola Bula Formation in the Soa Basin. Palaeomagnetic measurements (Sondaar *et al.*, 1994), later combined with zircon fission track dating, firmly established a date of 900 ± 7 ka (Morwood *et al.*, 1998) for the fossiliferous layers. Tangi Talo yielded a vertebrate fauna with the smallest species of pygmy *Stegodon* known, *Stegodon sondaari*, with an estimated body weight of 300 kg (van den Bergh, 1999), a giant tortoise *Geochelone* sp., and the Komodo dragon, *V. komodoensis* (Fig. 3). No fossil rodents were recovered from this locality, but the quite extreme dispersal capabilities of this group (with some species even making it to the Galapagos archipelago; Dowler *et al.*, 2000) make it unlikely that this absence is real. Rather, the absence of fossil rodents at the open site of Tangi Talo may have been caused by taphonomical factors, as raptors and owls roosting in caves such as Liang Bua play an important role in the accumulation of rodent remains.

Even when taking the presence of an – as yet undiscovered – rodent fauna into account, the strong impoverishment of the oldest fauna from Flores defies our imagination, particularly when compared with recent insular ecosystems. However, similarly poor faunas are known from the fossil record. The Early Pleistocene Satir fauna from Java consists of a mastodon (*Sinomastodon bumiajuensis*), a hippopotamus (*Hexaprotodon simplex*), cervids and also the giant tortoise *Geochelone* sp. A proboscidean and hippopotamus (*Mammuthus creticus* and

Figure 3 Biostratigraphy and faunal turnovers on Flores during the Pleistocene (adapted from de Vos *et al.*, 2007). In column 'Age', H denotes Holocene; LP, Late Pleistocene; MP, Middle Pleistocene; EP, Early Pleistocene.

Species			Stratigraphy																		
			<i>Stegodon sondaari</i>	<i>Stegodon florensis</i>	<i>Stegodon f. insularis</i>	<i>Hooijeromys nusatenggara</i>	<i>Papagomys</i>	<i>Paulamys</i>	<i>Komodomys</i>	<i>Spelaeomys</i>	<i>Homo erectus</i>	<i>Homo floresiensis</i>	<i>Homo sapiens</i>	<i>Macaca</i>	<i>Hystrix javanica</i>	<i>Sus</i>	<i>Bovidae</i>	<i>Cervidae</i>	<i>Varanus komodoensis</i>	<i>Varanus hooijeri</i>	<i>Geochelone</i>
Age	Formation	Locality																			
H	Cave	Liang Bua																			
LP	Cave	Liang Bua																			
MP																					
		Ola Bula	Mata Menge Ola Bula Boa Leza Dhozo Dhalu																		
EP		Tangi Talo																			

Hippopotamus creutzburgi) are also the only large mammals known from the oldest insular fauna (Middle Pleistocene) on Crete. Here, rodents have been found, and are represented by the giant murid genus *Kritimys*. Based on these and other examples in the fossil record, the low number of vertebrates in the Flores fauna is considered real and indicative of the high degree of isolation.

The site of Mata Menge, also in the Ola Bula Formation, but stratigraphically higher up in the sequence, yielded a vertebrate fauna that is slightly younger in age, dated at 800 ± 7 ka (zircon fission track dating, Morwood *et al.*, 1998; van den Bergh *et al.*, 2009). The fauna from Mata Menge is also characterized by an extremely low number of taxa, but is distinctly different from that of Tangi Talo. This implies that a faunal turnover took place around the Early to the Middle Pleistocene transition, in which one insular fauna was replaced by another. *Stegodon sondaari* was replaced by the larger *S. florensis* at Mata Menge (Fig. 3). Furthermore, the giant tortoise became extinct, and the Mata Menge site documents the earliest record of the giant rat *Hooijeromys nusatenggara* (Morwood *et al.*, 1998; de Vos *et al.*, 2007). A number of other localities in the upper Ola Bula Formation, including Boa Leza, Ola Bula and Dhozo Dhalu, and spanning the period between 880 and 750 ka, have yielded faunas similar to that of Mata Menge. In addition to the faunal remains, Mata Menge contains *in situ* artefacts, which constitute the first proxy evidence for the presence of hominins on Flores (Maringer & Verhoeven, 1970; Sondaar *et al.*, 1994; Morwood *et al.*, 1998; Brumm *et al.*, 2006).

Between the fossil-bearing localities within the Ola Bula formation (c. 900–800 ka) and the Late Pleistocene site of Liang Bua (c. 95–0 ka) is a gap of c. 700 kyr. In addition, there is an important difference between the Liang Bua fauna, which was found in cave deposits, and the faunas from older localities with quite different environments of deposits and taphonomy. This is immediately clear from the huge amounts of micro-mammal and bird remains found in the cave (Zijlstra *et al.*, 2008; Meijer & Due, 2010). These factors need to be taken into account when comparing the Late Pleistocene assemblage with those from the Ola Bula Formation.

The Middle Pleistocene assemblage consisted of four species: *S. florensis florensis*, *H. nusatenggara*, *V. komodoensis* and hominins, as evidenced from artefacts. Of these, only the Komodo dragon has been found unaltered in Liang Bua. On the basis of dental characteristics, chronology and geography, van den Bergh *et al.* (2008) considered *Stegodon florensis insularis* from Liang Bua to be a direct descendant of the Middle Pleistocene *S. florensis* from Mata Menge. *Hooijeromys* is a genus of giant rat that is closely related to *Papagomys*, and may well be ancestral to this genus. Hominins continued to be present and, in Liang Bua, their presence is indicated by the direct evidence of the fossils of *H. floresiensis*. Thus the taxa shared by the early and late assemblages suggest phylogenetic continuity. Theoretically, the younger subspecies of the *Stegodon* could have been an immigrant from another island in the nearby archipelago. However, Timor has its own species of *Stegodon*, *Stegodon timorensis*. Furthermore, a high

degree of endemism in proboscideans on islands is a phenomenon that is well recorded in the Mediterranean (Palombo, 2007).

In addition to the presumed descendants of the Middle Pleistocene fauna, Liang Bua shows a number of lineages that were not found in the earlier deposits. Apart from the murids, this includes *Varanus hooijeri*, a monitor lizard of moderate size. The presence of numerous murids is best explained on taphonomical grounds. We noted earlier that the localities in the Ola Bula formation did not favour the preservation of pellets, whereas cave deposits as found in Liang Bua provided ample possibilities for fossilization. The presence of *V. hooijeri*, which has quite fragile bones, is also best explained by differential preservation. Nevertheless, the murid assemblage at large also seems to indicate phylogenetic continuity. According to Musser (1981), *Hooijeromys*, *Papagomys*, *Paulamys* (initially referred to as *Floresomys* by Musser) and *Komodomys* from Flores are more closely related to one another than to any other murid, which suggests that they are derived from a common ancestor on the island. *Spelaeomys* is the odd one out and appears not to be related to any of the other Flores murids (Musser, 1981). Instead, it seems part of an ancestral stock, linked to the native murids of Papua New Guinea. Whether it is the only surviving lineage of the oldest fauna or represents an immigration event later on in the Pleistocene cannot be ascertained at present.

All in all, the faunal composition of the Middle Pleistocene site of Mata Menge and of the Late Pleistocene of Liang Bua show strong similarities where the large mammals are concerned. Both sites contain *Stegodon* and Komodo dragons, as well as evidence for the presence of hominins. Differences in small mammals are explained by differential preservation, although the giant rat from Mata Menge, *Hooijeromys*, is most likely to be ancestral to the giants rats of the genus *Papagomys* found in Liang Bua.

The faunal succession (Fig. 3) suggests that Flores was recolonized by the *S. florensis* fauna following the extinction of the *S. sondaari* fauna from Tangi Talo c. 900 ka. The Liang Bua fauna can be comfortably derived from the Mata Menge fauna. This is taken as an indication that no new migration events have taken place since the Early/Middle Pleistocene faunal turnover. Consequently, all taxa present at Liang Bua must have been already present on the island in the Early Pleistocene or evolved on the island from Middle Pleistocene ancestors. Although *V. hooijeri* and *Spelaeomys* could theoretically be new immigrants, a more plausible explanation seems to be that they have not yet been found in the older deposits, which do not seem to favour the preservation of small vertebrates or fragile bones.

The faunal successions from the Middle to Late Pleistocene thus show a strong phylogenetic continuity that results from the isolated position of the island. Flores was never connected to the Sunda Shelf, and, in order to reach the island, species had to cross one of the most prominent zoogeographical barriers recognized, that is, Wallace's Line (van Oosterzee, 1997; Lomolino *et al.*, 2005).

KEY FACTORS IN THE FLORES FAUNA

In addition to phylogenetic continuity, the Flores vertebrate fauna exhibits other characteristics that stem from the isolated position of the island. The faunal sequence shows that the number of species present was low at all times. From Tangi Talo, only four species (one proboscidean, a tortoise, a crocodile and the Komodo dragon) are known. The absence of small mammals in this fauna is considered artificial. After the extinction–recolonization around the Early to Middle Pleistocene transition, the fauna was renewed, but the number of taxa remained low. Unlike the Early Pleistocene Tangi Talo sediments, Middle Pleistocene sediments yielded giant rat fossils that were assigned to the genus *Hooijeromys*. The Late Pleistocene cave deposits of Liang Bua have yielded at least 17 vertebrate species, particularly of taxa that are good dispersers such as varanids, rats, bats and birds. This higher number primarily reflects conditions of preservation, as small vertebrates are known in far larger numbers in Liang Bua than in any other locality on the island. However, the large mammal fauna can confidently be linked to the Middle Pleistocene ancestors.

The degree of isolation is a key factor in determining insular species richness, as the number of species generally decreases with increasing distance from the mainland, that is, with increasing isolation (MacArthur & Wilson, 1967; Lomolino *et al.*, 2005). Over time, the number of species on Flores was consistently low, as the various fossil localities give evidence for the presence of three large-bodied vertebrates only. This strongly suggests that the immigration of new species was very limited and a rare event. Even in times of low sea-levels, when the distance to nearby islands was decreased, the strong currents of the Indonesian Throughflow in Lombok Strait between Bali and Lombok, and in Sape Strait between Sumbawa and Komodo/Flores, appear to have posed too great a barrier for many non-flying mainland species to cross. In fact, the very rich record from Liang Bua gives no indication for any new arrivals of terrestrial vertebrates during the Middle and Late Pleistocene, with the possible exception of *Spelaeomys* and *V. hooijeri*.

All animals in the Flores fauna represent groups capable of crossing sea barriers. Proboscideans, rodents, humans, bats, birds, tortoises and lizards are all known to be able to cross substantial distances over water by either swimming (proboscideans, lizards), floating (tortoises) or rafting (rodents, lizards, hominins). Displacement by catastrophic events has also been suggested as an explanation for the arrival of vertebrates on islands, such as hurricanes for the dispersal of lizards (Censky *et al.*, 1998) or tsunamis in the case of hominin dispersal in Southeast Asia (van den Bergh *et al.*, 2009). The latter is not unlikely, considering the record of tsunami sediments in this tectonically active region (Monecke *et al.*, 2008). Absent from the fauna are mammalian carnivores and perissodactyls, which is a very common phenomenon in insular faunas (de Vos *et al.*, 2007). Even after the Middle Pleistocene extinction–immigration event, no previ-

ously unrecorded terrestrial animal taxa arrived on the island, with the possible exception of some rodents and *V. hooijeri*. The selection towards water-crossing abilities results in an ‘unbalanced’ fauna: not all animal clades from the mainland are represented in the insular fauna. In this way, insular faunas differ predictably from mainland ones, and the imbalance in insular faunas increases with greater isolation. This pattern in faunal composition is not limited to Wallacea (Sulawesi, Flores, Timor, Sumba, Philippines), but has been observed in insular faunas all over the world (de Vos *et al.*, 2007). Tortoises, proboscideans and rodents, but also artiodactyls such as deer and hippopotami, are commonly encountered as elements in many of these palaeofaunas. Both low species richness and the disharmonic nature of the fauna, in addition to the phylogenetic continuity, have affected and shaped the evolution of the vertebrate fauna of Flores. Combined, they set the stage for the evolutionary processes typical for islands, allowing the fauna to fill an array of niches not available on the continent. Particularly, the absence of mammalian carnivores and reduced interspecific competition may have removed some of the evolutionary restrictions found on the mainland.

INSULAR ADAPTATIONS IN THE FLORES FAUNA

The biogeographical isolation of islands sets the stage for a cascade of changes in ecology, reproduction, morphology and dispersal in the species that colonized them. These changes are often collectively referred to as the insular syndrome (Blondel, 2000; Lomolino *et al.*, 2005) and involve adaptive responses to a new setting with selective forces very different from those on the mainland. The nature of the vertebrate fossil record leaves us with only the morphological changes in the skeletal apparatus. Nevertheless, the skeletal remains of the Flores vertebrate fauna – as indeed of many other fossil island faunas – bear distinct traits of the adaptations that evolved in dealing with the insular environment.

Changes in body size

A change in body size is one of the most prominent and fundamental responses to an island environment. Body size affects a variety of traits, such as energy requirements, dispersal potential and ecological interactions. A general trend in body size of extant insular mammals was first noted by Foster (1964) and became known as the ‘island rule’ (Van Valen, 1973), which a number of authors (Sondaar, 1977; Heaney, 1978; Lomolino, 1985, 2005 and references therein) further elaborated upon. Although there remains unexplained variation, suggesting that the ‘rule’ is not applicable in all cases (for instance, Meiri *et al.*, 2008), a tendency for large ungulates to become smaller (dwarfism) and for small mammals to become larger (gigantism) within an insular setting (Lomolino, 2005; de Vos *et al.*, 2007 and references therein) has been widely noted.

Body size evolution in insular mammals does not result from one selective force in particular, but rather from a combination of factors varying in importance between species, and depending on spatial and temporal scales of analysis. According to Lomolino (2005), immigrant selection and ecological release from larger competitors and predators, which are factors promoting gigantism, are most important in the smaller species. In large-bodied vertebrates, resource limitation and the release from the need to outgrow predators promote dwarfism. Raia & Meiri (2006) suggested that the extent of dwarfism in large herbivores depends on competition rather than on the presence of predators, which would imply that resource limitation is more important than the absence of carnivores. Palombo (2007) relates the size of insular elephants in the Mediterranean to the presence or absence of artiodactyl competitors.

In a more diverse fauna within a continental setting, a small body size, as in insectivores and rodents, is advantageous in that predators can be avoided by hiding. Moreover, a small body size may enable a species to specialize in a diet and be more energy-efficient than other and larger competing species (Lomolino, 2005). In an insular setting, mammalian predators may be absent and competition less intense, thereby lessening the advantages of being small: they no longer outweigh the advantages of being larger, thus promoting gigantism. An additional advantage of gigantism may be to outgrow the predators that *are* present on the island, for example the raptors. Insular gigantism in small mammals is best known in murine rodents. Fossil remains of giant rats have been found on a number of islands in Southeast Asia, including Timor, Flores, Sulawesi and the Philippines, but also on various Mediterranean (de Vos *et al.*, 2007), Canary (Crusafont-Pairo & Petter, 1964) and Caribbean (Biknevicius *et al.*, 1993) islands. Many Pleistocene rodents found on Mediterranean islands are all larger than their continental ancestors, such as *Hypnomys* (Balearics), *Leithia* and *Maltamys* (Sicily and Malta), *Kritimys* and *Mus bateae/Mus minotaurus* (Middle and Late Pleistocene of Crete, respectively). This does not imply that all rodents in insular environments evolve larger body size. For instance, certain oryzomine rodents from the Caribbean display gigantism whereas other endemic genera from Bonaire, for example, show no increase in size (Zijlstra *et al.*, in press). *Mus cyprioticus*, from Cyprus, which was identified as a Pleistocene survivor based on DNA analysis (Cucchi *et al.*, 2006), is not particularly large. On the Late Miocene palaeo-islands of Gargano (Italy), giant forms such as *Stertomys*, *Hattomys* and *Mikrotia* lived alongside smaller representatives of their respective families (Freudenthal, 1976). A remarkable example of insular gigantism comes from the giant hedgehogs from the genus *Deinogalerix*, also from the Miocene of Gargano, of which *Deinogalerix koenigswaldi* constitutes the largest insectivore known, with a skull length of c. 200 mm (Butler, 1980). But here, too, a small-sized gymnure was present beside its giant relative (van den Hoek Ostende, 2001). This combination of gigantism in some rodents but not in others is also reflected in the Flores murids.

The two species of *Papagomys* and *Spelaeomys* are giant forms, whereas *Komodomys* and *Paulamys* are middle-sized rats.

For mammals on the mainland, large size functions as a defence mechanism against predators, enhances domination over competitors and is advantageous for long-distance migrations. In the absence of predators, there is no longer a need for these traits. The limited resources on an island favour a more efficient use of energy, and long-distance migrations become unnecessary or, rather, impossible. The best-known examples of dwarfism in large mammals are in insular proboscideans, which can show dramatic decreases in size in comparison to mainland species. Dwarf proboscideans are known from islands all over the globe. In the Mediterranean, dwarf proboscideans from the genus *Elephas* have been found on Crete, Malta, Rhodos, Tilos and Cyprus (Palombo, 2003, 2007). The most extreme case of dwarfism within proboscideans is found on Sicily: the Late Pleistocene *Elephas falconeri* has a shoulder height of only 0.9 m, one quarter that of its mainland ancestor *Elephas antiquus* (Palombo, 2003). In North America, dwarf mammoths have been found on the Californian Channel Islands (Agenbroad *et al.*, 1999). In Asia, dwarf species of the genus *Stegodon* have been found in Japan, the Philippines, Sumba, Timor and Sulawesi. Dwarfism in hippopotami is also well known from Crete, Sicily and Malta, with the smallest species being *Phanourios minor* from Cyprus. Within insular deer, examples of dwarfism are found in the Pleistocene on the Philippines (de Vos & Bautista, 2003) and on the Ryukyu Islands of Japan (de Vos, 2006), with the smallest species of deer found in the genus *Candiacervus* from Crete, which measured only 0.4 m in height (de Vos, 2000). Notably, the evolution of insular deer on Crete did not entail a linear decrease in size, but rather an adaptive radiation in which several size classes are found (de Vos, 1984, 2000). On the palaeo-islands of Gargano and Scontrone, a cervoid, *Hoplitomyx*, is found with typical island adaptations. As on Crete, the genus displays a large variation in size (Van der Geer, 2008).

On Flores, both dwarfism and gigantism are evident in the fossil faunas. The Flores rodent fauna contains seven species of rat within the genera *Paulamys*, *Papagomys*, *Hooijeromys*, *Komodomys* and *Spelaeomys*. Four species, *Papagomys armandvillei*, *P. theodorverhoeveni*, *H. nusatenggara* and *S. florensis*, are endemic giants (Hooijer, 1957; Musser, 1981). Three species of these giant rats are found at Liang Bua. The largest, *Papagomys armandvillei*, is the only extant species of that genus (Nowak, 1991; Zijlstra *et al.*, 2008). The oldest fossil murid from Flores is *H. nusatenggara*, known only from the Middle Pleistocene localities Ola Bula and Mata Menge. The similarities between *Hooijeromys* and *Papagomys*, already observed by Musser (1981), suggest that the former species may have been ancestral to *Papagomys*. According to Musser & Carleton (2005), *Paulamys*, *Papagomys* and *Komodomys* are more closely related to each other than to other species of murids from Southeast Asia, and appear to have resulted from *in situ* evolution leading to an adaptive radiation to occupy vacant ecological niches. *Spelaeomys* is the odd one out and may represent an old immigrant (Musser, 1981).

Dwarfism is evident in the Flores *Stegodon* remains from both the Early and Middle to Late Pleistocene. *Stegodon sondaari* from the Early Pleistocene locality at Tangi Talo is the smallest known species of this genus (van den Bergh, 1999). Based on regression of adult femur length this dwarf had an estimated body weight of 300 kg. *Stegodon sondaari* became extinct at the Early/Middle Pleistocene faunal turnover and was replaced by the larger *S. florensis* (estimated body weight 850 kg; van den Bergh *et al.*, 2008). Unfortunately, no full-grown long bones are known from *S. florensis insularis*, but size comparison of homologous molars and milk molars indicates a linear size reduction of 30% compared to its direct ancestor. This size reduction may have been induced by lack of competition from other large herbivores on Flores (van den Bergh *et al.*, 2008). Palombo (2007) related reduced dwarfing in proboscideans to the presence of interspecific competitors such as cervids on Mediterranean islands. Notably, artiodactyl competitors are missing in both the *sondaari* and *florensis* faunas. The larger size of *S. florensis* cannot be explained by herbivore competition, but may be related to the presence of predatory animals on the island (van den Bergh *et al.*, 2008).

Shifts in body proportions

The changes in body size that occur in an insular setting are often accompanied by adaptations in the limbs affecting locomotion. In the absence of mammalian carnivores, but with rocky substrates, stability is favoured over speed. Many insular herbivores therefore adopted 'low gear' locomotion (Leinders & Sondaar, 1974; Bover *et al.*, 2005), and are characterized by limbs that show a tendency towards reduced relative length and the fusion of elements, resulting in shorter and more robust limbs. Such adaptations are most prominent in the distal limb elements and increase stability, thereby reducing the energy costs. A shortening and fusion of the distal limb, as well as a loss of the shock-absorbing spring mechanism in the feet, was observed in *Myotragus*, the mouse-goat from the Balearic islands (Köhler & Moyà-Solà, 2001; Bover *et al.*, 2005), as well as in certain species of the Philippines and Cretan deer radiations (Van der Geer, 2005). In the cervoid *Hoplitomeryx* from Gargano, the navicuboid has fused completely with the metatarsus, and the metapodals display shortening (Leinders, 1984; Van der Geer, 2008). In both the Sicilian pygmy elephant, *Elephas falconeri*, and the Cypriot pygmy hippo, *Phanouris minor*, the ulna/radius and tibia/fibula have become fused to enhance the stiffness of the limbs. A similar energy-reducing adaptation has been observed in *S. florensis insularis*. van den Bergh *et al.* (2008) described a fused ulna/radius of a juvenile, a finding in agreement with characteristics of other insular proboscideans (van den Bergh, 1999).

Changes in sense organs and dentitions

In addition to changes in body size and the locomotor system, common features in insular species are changes in the sense organs and teeth. In addition to the size reduction, the teeth of

S. florensis insularis are characterized by hypsodonty with respect to mainland *Stegodon* (van den Bergh *et al.*, 2008). A high degree of hypsodonty is also found in other endemic island stegodonts, such as *S. sondaari* and *S. sompoensis* from Sulawesi, and results from parallel evolution interpreted as an adaptation to the consumption of more abrasive food containing grit, such as grasses (van den Bergh, 1999). The evolution of *Myotragus* on the Balearic Islands resulted in increased hypsodonty and ever-growing incisors in the lower jaw (Köhler & Moyà-Solà, 2004). Dental adaptations can also be found in small mammals. The Gargano murid *Mikrotia*, in addition to becoming hypsodont, dramatically increased the number of ridges on the first lower and last upper molar (Freudenthal, 1976). Alterations of the dentition, including incisors that grew throughout the individual's life in *Myotragus* and increased hypsodonty, provide animals with increased feeding efficiency, which is essential for survival in environments with limited energy resources.

Alongside alterations in dentition, insular species may exhibit changes in brain size and sense organs. Mainland herbivores have their eyes located on either side of the skull to have a view of almost 180° for each eye. Under conditions of predator release, insular species show a tendency to have the eyes oriented more anteriorly instead of laterally, thus providing stereoscopic vision. *Myotragus* shows a distinct forward-orientation of the eyes, unlike mainland goats (Köhler & Moyà-Solà, 2004). The altered orientation of the eyes in *Myotragus* was accompanied by a decrease in brain size of up to 50% relative to extant bovids with similar body size (Köhler & Moyà-Solà, 2004). Another case of reduced brain size was found in recently extinct dwarf hippos from Madagascar (Weston & Lister, 2009), which show that the reduction of brain size in insular species can be greater than predicted from the scaling of brain size to body size in mainland species. Because nervous tissue is one of the most energetically expensive types of tissue, a decrease in brain size reduces the animal's energy budget (Kaas, 2000; Isler & van Schaik, 2006).

HOMO FLORESIENSIS

Considering the morphological adaptations of many insular mammals, such as changes in body size, shifts in body proportions, and alterations in dentition and sense organs, and similar morphological patterns in members of the Flores faunas, it is evident that the Flores vertebrates were subject to intense evolution resulting from the extreme 'insular' character of the island. It is hard to imagine that hominins on the island were somehow not affected by the same evolutionary forces.

Homo floresiensis provides us with a rare case of insular endemism in hominins, of which only a few examples are known. Spoor & Sondaar (1986) reported the finding of hominin fossils from the Late Palaeolithic of Sardinia. The unusual morphology of these fossils, including the robustness of the zygomatic process and the large size of the alveoli, was interpreted as evidence for endemism. In addition, the Neolithic remains from the Palau islands (Berger *et al.*, 2008)

and the Late Palaeolithic remains from Okinawa Island in Japan (Suzuki & Hanihara, 1982) exhibit morphological features different from those of mainland populations, including small stature. *Homo floresiensis* has an extremely small stature, estimated at 1.06 m (Brown *et al.*, 2004), which is unprecedented in *Homo* and closer to size estimates of *Australopithecus afarensis* and *A. africanus* (McHenry, 1991). Based on cranial and post-cranial morphology, it is hypothesized that *H. floresiensis* evolved after long-term isolation through insular dwarfing from a large-bodied ancestor (Brown *et al.*, 2004; Morwood *et al.*, 2004, 2005; van Heteren & de Vos, 2007; Lyras *et al.*, 2008). *Homo erectus* is the prime candidate for the role of ancestor of *H. floresiensis*, as it was the only hominin present in Southeast Asia in the Pleistocene. Having reached Java by the Early Pleistocene (Swisher *et al.*, 1994; van den Bergh *et al.*, 1996), *H. erectus* was almost certainly present on Flores by the Middle Pleistocene (Sondaar *et al.*, 1994; Morwood *et al.*, 1998), as evidenced by the artefacts from the site of Mata Menge. Bromham & Cardillo (2007) showed that insular primates conform to the island rule and undergo shifts towards smaller body size in an insular environment. We therefore suggest that after its arrival on Flores, *H. erectus* followed the evolutionary path towards dwarfism and decreased in body size as a response to the absence of mammalian carnivores and the limited energy resources, as might any large-bodied mammal in an insular setting. Moreover, the observed size decrease in *H. floresiensis* when compared to *H. erectus* (c. 52% of *H. erectus*) falls within the range of other insular primates (Bromham & Cardillo, 2007). Therefore, the evolution of *H. floresiensis* can be explained by insular dwarfing of *H. erectus*. Such a scenario is in parallel with its regional contemporary *S. florensis* and conforms to the evolutionary responses of other large-bodied insular mammals, including primates (Lomolino, 2005; Bromham & Cardillo, 2007; de Vos *et al.*, 2007).

A major argument raised to contest the idea that insular dwarfing is responsible for the evolution of *H. floresiensis* is that its small brain size could not be accommodated within predictions from mammalian brain-body scaling models (Martin *et al.*, 2006). The estimated brain size of 417 cc (Falk *et al.*, 2005) is smaller than predicted on the basis of its body size and falls well outside the range for the genus *Homo* (Falk *et al.*, 2005, 2009) as accepted hitherto. However, evidence to the contrary is starting to accumulate. Of particular relevance here is the fossil bovid *Myotragus* from the Mediterranean island of Majorca. Compared with mainland bovids, *Myotragus* underwent significant reductions in brain size and associated sense organs (Köhler & Moyà-Solà, 2004). These changes are interpreted as adaptive outcomes delivering more efficient energy use under the prevalent environmental conditions of the insular ecosystem of Majorca, characterized by the absence of predation and limitation of energy resources (Köhler & Moyà-Solà, 2004). A study by Weston & Lister (2009) on the brain size of recently extinct Malagasy dwarf hippos shows that the process of insular dwarfing can, in principle, result in brain sizes smaller than predicted from scaling models. Therefore,

the small brain size of *H. floresiensis* can be explained by the process of insular dwarfing as an adaptation to an insular environment with limited energy resources (see also Niven, 2007). The hypothesis that a decrease in brain size in primates can occur under natural conditions as a consequence of resource limitations is supported by Taylor & van Schaik (2007), who observed differences in brain size in populations of orang-utans occurring in different habitats that were shown to differ in resource quality.

Homo floresiensis has unique body proportions, with long arms and relatively short legs, robust limb bones and exceptionally long feet (Brown *et al.*, 2004; Morwood *et al.*, 2005; Jungers *et al.*, 2009a,b). These features have been explained as evidence for a close relationship with *Australopithecus* (Jungers *et al.*, 2009a,b). Shifts in limb proportions similar to those in *H. floresiensis* have been observed in other insular mammals as well and indicate a different mode of locomotion. A shortening of the lower leg in combination with robust feet was also found in the Late Pleistocene Minatogawa people of Okinawa Island in Japan (Baba & Endo, 1982). In addition, extinct dwarf hippopotami from Crete and Cyprus (Spaan *et al.*, 1994), the dwarf deer *Candiacervus* from Crete, the endemic cervoid of Gargano, *Hoplitomeryx* (Van der Geer, 2005), and the mouse-goat of the Balearic Islands, *Myotragus* (Köhler & Moyà-Solà, 2001), all show a shortening and increased robustness of the distal limb bones, and sometimes even fusion of limb elements. Such changes in the locomotor system increase the stability of the animal during locomotion and are interpreted as adaptations to 'low gear' locomotion, favourable in an energy-restricted and predator-free ecosystem. The exceptionally long feet of *H. floresiensis*, which prevented high speed or endurance running (Jungers *et al.*, 2009a), and short, robust limbs would have contributed to an increased stability of *H. floresiensis* during locomotion and conform to evolutionary pathways observed in other insular mammals.

Homo floresiensis displays an unusual mixture of primitive and derived features (Brown *et al.*, 2004; Falk *et al.*, 2005, 2007; Morwood *et al.*, 2005; Tocheri *et al.*, 2007; Lyras *et al.*, 2008; Argue *et al.*, 2009; Jungers *et al.*, 2009a,b). The small endocranial volume, short stature, morphology of the carpals and robustness of the limbs are shared with australopithecines, whereas the reduced prognathism, mandibular and dental morphology, metatarsal morphology and shape of the brain are considered more derived. The shoulder configuration was found to be transitional between early hominins and modern humans (Lordkipanidze *et al.*, 2007; Larson *et al.*, 2009). It is this mosaic of characters that puzzles most scientists. However, in many insular mammals, derived features are lost and a return to the primitive condition is observed. An explanation for this mix is pedomorphosis. Skull features, tusk structure and the proportions between the cranium, axial skeleton and limbs of *Elephas falconeri*, the smallest insular proboscidean from the Mediterranean, are explained by precocious stunting of ontogenetic growth (Palombo, 2003). van Heteren & de Vos (2007) explained the mix of derived and primitive features of *H. floresiensis* in a similar fashion.

A recent cladistic analysis of 60 cranial and post-cranial characters of *H. floresiensis* by Argue *et al.* (2009) indicated that *H. floresiensis* is an early member of the genus *Homo* that evolved in the Late Pliocene or Early Pleistocene. On the basis of their results, Argue *et al.* (2009) refuted the insular dwarfing hypothesis. However, the loss of derived features in insular evolution introduces a number of homoplasies, which in a cladistic analysis can easily be misconstrued for synplesiomorphies. This would lead to a more primitive position of the island form, exactly as was found by Argue *et al.* (2009). Given the small difference in tree length between the most parsimonious solution and the one in which *H. floresiensis* is derived from *H. erectus*, we find the cladistic analysis unconvincing. A careful evaluation of the characters, to see whether any homoplasies can indeed be attributed to typical insular developments, is needed to resolve this.

CONCLUSIONS

The Flores vertebrate fauna displays a high degree of endemism, a low species richness and phylogenetic continuity from the Middle to the Late Pleistocene. This has clearly affected the vertebrate fauna of the island, which shows examples of both dwarfism and gigantism, and the presence of adaptive radiation to fill available niches. All in all, Flores fits all the textbook characteristics of an insular vertebrate fauna, and the evolution of all its Pleistocene inhabitants should be considered in this framework. Thus, the distinct morphological characteristics displayed by *H. floresiensis* are not pathological, aberrant or exclusive. Instead, they can be explained as part of the insular syndrome, as the characteristics of *H. floresiensis* are adaptations to an insular environment and have evolved under long-term isolation. Many of the characteristics, such as short stature, robust lower limbs, large feet and a small brain are shared by a number of other insular mammal taxa from Flores and other islands. They are the result of similar evolutionary forces acting upon insular taxa resulting from the isolated disharmonic nature of island biotas. Rather than being an aberrant hominin, *H. floresiensis* represents a typical island species, with features that, considering other insular vertebrates, are in fact nothing out of the ordinary. The combination of the high endemism, low species richness and phylogenetic continuity on Flores directed the evolution of the vertebrate fauna and ultimately culminated in the evolution of a species of dwarf hominin.

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BIOSKETCH

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