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The Liang Bua faunal remains: a 95 k.yr. sequence from Flores, East Indonesia

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ABSTRACT

Excavations at Liang Bua, a limestone cave on the island of Flores, East Indonesia, have yielded a well-dated archaeological and faunal sequence spanning the last 95 k.yr., major climatic fluctuations, and two human species – *H. floresiensis* from 95 to 17 k.yr.[1], and modern humans from 11 k.yr. to the present. The faunal assemblage comprises well-preserved mammal, bird, reptile and mollusc remains, including examples of island gigantism in small mammals and the dwarfing of large taxa. Together with evidence from Early-Middle Pleistocene sites in the Soa Basin, it confirms the long-term isolation, impoverishment, and phylogenetic continuity of the Flores faunal community. The accumulation of *Stegodon* and Komodo dragon remains at the site in the Pleistocene is attributed to *Homo floresiensis*, while predatory birds, including an extinct species of owl, were largely responsible for the accumulation of the small vertebrates. The disappearance from the sequence of the two large-bodied, endemic mammals, *Stegodon florensis insularis* and *Homo floresiensis*, was associated with a volcanic eruption at 17 ka and precedes the earliest evidence for modern humans, who initiated use of mollusc and shell working, and began to introduce a range of exotic animals to the island. Faunal introductions during the Holocene included the Sulawesi warty pig (*Sus celebensis*) at about 7 ka, followed by the Eurasian pig (*Sus scrofa*), Long-tailed macaque, Javanese porcupine, and Masked palm civet at about 4 ka, and cattle, deer, and horse - possibly by the Portuguese within historic times. The Holocene sequence at the site also documents local faunal extinctions - a result of accelerating human population growth, habitat loss, and over-exploitation.

Introduction

Archaeological excavations at Liang Bua, a limestone cave on the island of Flores in East Indonesia, yielded tens of thousands of well-preserved vertebrate and mollusc remains. These range in age from 95 ka to the present and were differentially associated with two hominin species - *Homo floresiensis* in the Pleistocene and *Homo sapiens* in the Holocene.

Liang Bua has yielded one of the largest Late Pleistocene and Holocene faunal assemblages yet excavated in Southeast Asia. To date, the focus of the research has been on taxonomic identification of the different vertebrate and invertebrate remains represented, with some groups studied in greater detail than others (e.g., *Stegodon*). Studies of this assemblage are still in progress, but here we present some preliminary results and discuss their implications in the context of Early and Middle Pleistocene faunal assemblages from the Soa Basin of central Flores, Southeast Asian biogeography, and general evolutionary trends on islands.

The composition of the Liang Bua faunal assemblage, and changes in species composition and abundance over time, was determined by a range of factors, including contemporaneous species representation in surrounding palaeo-environments, the various means by which faunal remains were brought into the cave, differential preservation, and the methods used for archaeological recovery and identification. We have, therefore, also undertaken studies of site formation processes in the cave (e.g., of sediments

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[1] Recent excavations at Liang Bua indicate that the disappearance of *Homo floresiensis* and *Stegodon* from the sequence coincided with a volcanic eruption ~17 ka ago - not ~12 ka as previously interpreted.

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and faunal remains), palaeoenvironmental evidence outside the cave, and of the activities conducted by the hominin residents. These studies are essential if temporal changes in the faunal assemblage are to be used to indicate differences in subsistence and resource procurement between *H. floresiensis* and *H. sapiens*. This is an important consideration, since such differences cannot be distinguished on the basis of the stone artifact sequence (cf., Moore and Brumm, 2007).

Sampling methods and materials

This study focuses on material recovered from only three of the squares excavated by a joint Indonesian-Australian team at Liang Bua between 2001 and 2004, and by Raden Pandji Soejono between 1978 and 1988, i.e., Sectors IV, VII, and XI (Fig. 1). Stratigraphic profiles of these sectors are given in Morwood et al. (2009).

The excavation proceeded by 10 cm spits and/or natural stratigraphic units. Large bones found *in situ* were plotted in three-dimensions to permit accurate spatial and temporal distributions throughout the deep stratigraphic sequences. All the deposits were first dry-sieved, then wet-sieved through 2 mm mesh for maximum recovery of small vertebrate and other bioarchaeological remains.

Included in this report are *Stegodon* and other large- to intermediate-sized mammals, Komodo dragon (*Varanus komodoensis*), *Varanus hooijeri*, and bird remains from Sectors IV, VII, and XI. Molluscs from Sectors IV and VII are also included, as well as small mammals from Sectors IV and XI. The identification of small vertebrates was made principally on diagnostic cranio-dental elements. Where possible, this was taken to species level, but some faunal classes such as those of snake, fish, and amphibians, have currently only been identified to Order/Genus level.

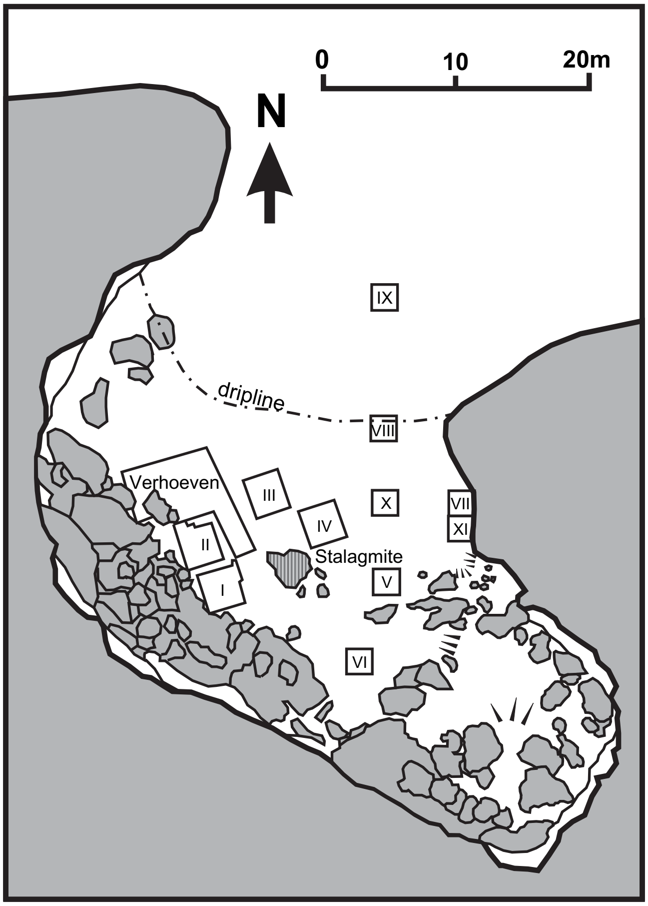

Figure 1. Horizontal plan of the excavations carried out in Liang Bua between 1964–2004, with the excavated sectors mentioned in the text indicated with roman numerals. Gray areas indicate limestone; vertical dashed limestone marks a stalagmitic structure in the center of the cave.

A taphonomic analysis and study of body part representation was also used to identify the key modes of deposition and accumulation of the large numbers of rodent remains recovered from Sector XI (Piper and Awe Due, 2006).

Taxonomic identification

The vertical and stratigraphic distributions of taxa represented in Sectors IV, VII, and XI, show major and consistent differences between the Pleistocene and Holocene levels (Fig. 2A–B; Appendixes Tables 1–3). For instance, levels below a distinctive layer of black tuffaceous silts, deposited ~17 ka in all three sectors, contain the remains of *Stegodon florensis insularis* and *Homo floresiensis*. However, these two endemic species are absent from deposits overlying the white tuffaceous silts where the first skeletal and behavioral evidence for modern humans occurs from ~11 ka ago (Morwood et al., 2005), including the use of shell as tools ~11 ka, the systematic gathering of shellfish from ~7 ka, and the first appearance of a number of introduced mammals. Here we briefly describe the taxa of particular interest that could be identified based on diagnostic remains, and provide some contextual information.

Stegodon

There are at least 47 individual *Stegodon* represented in all excavated sectors of Liang Bua. The majority of the remains are dental elements (68% of NISP) from juvenile individuals (94% of MNI), including neonates (23% of MNI) (van den Bergh et al., 2008). From 95 ka until their youngest occurrence around 17 ka, they are attributed to a distinct chrono-subspecies, *Stegodon florensis insularis*, with dental variability comparable to recent elephant populations. No size change occurs in the *Stegodon* population throughout the ~80 k.yr. Pleistocene sequence at Liang Bua, but the sub-species is distinguishable from its Early/Middle Pleistocene ancestor, *S. f. florensis,* by an average 30% linear size reduction of dental elements and slightly more advanced molar plate formula (van den Bergh et al., 2008). *Stegodon florensis* arrived in the Soa Basin of central Flores ~880 ka, following the extinction of the more primitive, dwarfed species *S. sondaari* at ~900 ka, and was present in large-bodied form until at least 680 ka (Morwood et al., 1998; van den Bergh, 1999).

Varanids

Komodo dragon (*Varanus komodoensis*) is present on Flores by ~900 ka (Sondaar et al., 1994; Morwood et al., 1998). Skeletal evidence for the species occurs throughout the Late Pleistocene sequence at Liang Bua, but only a single mandible fragment was found in the Holocene deposits indicating a reduction in abundance and distribution. However, scattered populations of Komodo dragon still occur along the north and west coasts of Flores, as well as on the nearby islands of Komodo and Rinca.

The Pleistocene Komodo vertebrae from Liang Bua are similar in morphology to those of recent adults, although most examples are slightly larger than the largest specimens examined at the Nationaal Natuurhistorisch Museum Naturalis in Leiden. The transverse diameter of the articular cup of the thoracic vertebrae varies between 26.4–37.0 mm in Liang Bua specimens versus 18.6–30.5 mm in comparative vertebrae examined. The largest recent skeleton used for comparison had a snout to tail length (STL) of

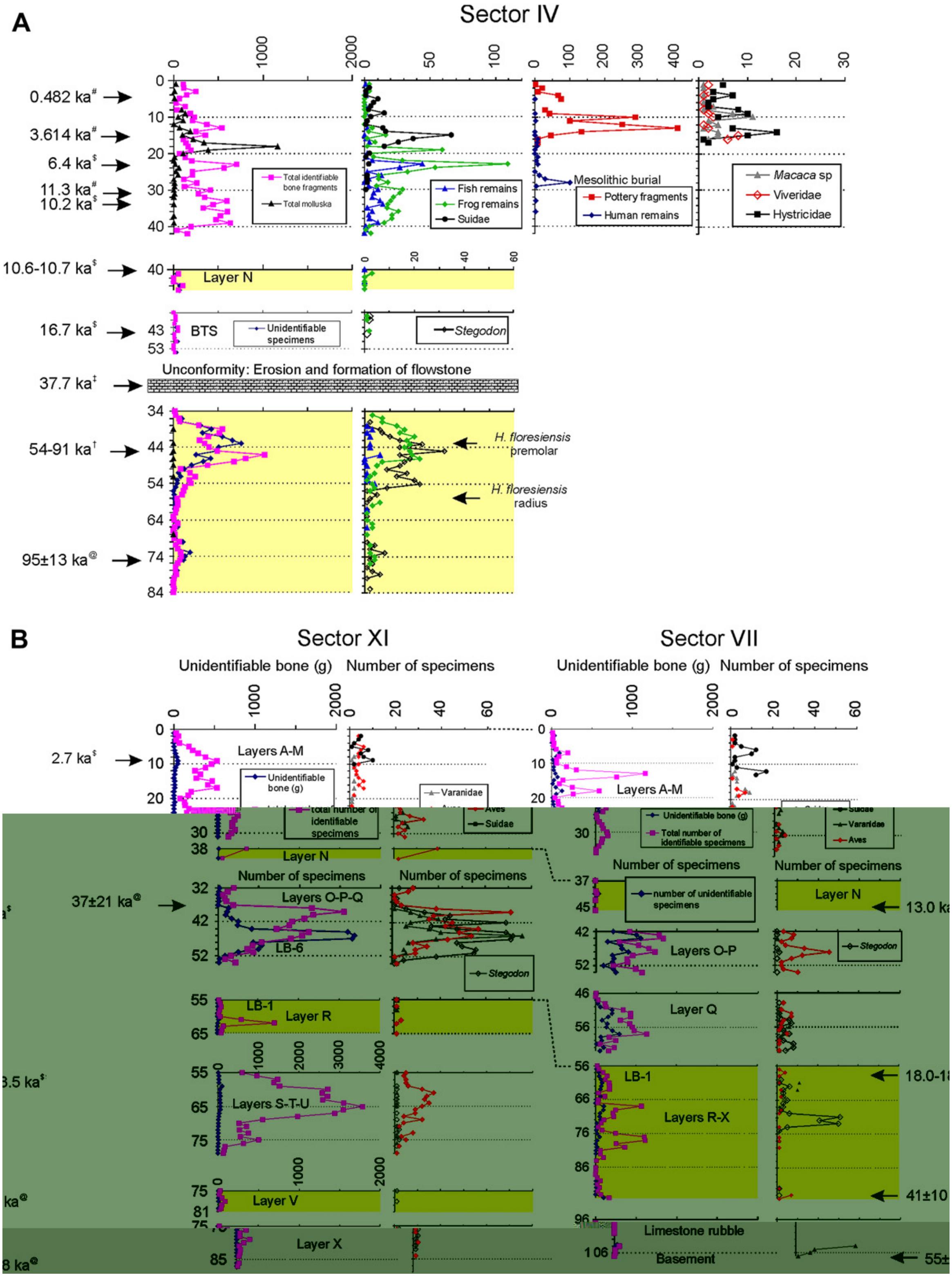

Figure 2. A. Total number of identified fossil specimens, unidentifiable bone fragments, and number of individual fossil specimens (NISP) of various taxa per excavated spit, arranged per stratigraphic unit, for Sector IV. Note that for the Holocene sequence no amounts of unidentifiable bone fragments could be given because these were not consistently recorded during the excavations before 2001. Rib fragments have generally been treated as unidentifiable bone fragments in the counts. Small recognizable skull fragment concentrations of *Stegodon* were numerous in several layers and could sometimes be fitted. To prevent overrepresentation in the graphs, 1–10 small pieces were counted as 1, 11–20 pieces as 2, etc. Frog, fish, and bat remains have not been studied in detail yet. A small part of the frog remains may actually constitute insectivore bones, the latter of which only mandibles were included in the counts presented in Appendix A. Pottery fragments of spits 6 and 7 are lacking. "Layer N" represents a white tuff marker bed also shown in Fig. 2B and the profile of Sector IV presented in Morwood et al., 2009. "BTS" represents black tuffaceous sand (also indicated in the profile of Sector IV presented in Morwood et al., 2009). Dates to the left are from various sources (Morwood et al., 2004, 2005; Westaway, 2006) and are shown to the left: #= ^{14}C ages on bulk charcoal samples as given by Soejono (1980, 1985), calibrated by Chris Turney; $= median calibrated ^{14}C ages on charcoal 650° and 850° temperature fractions conducted by Chris Turney; ‡= Uranium series dating of flowstone, conducted by J.- x. Zhao; †= coupled ESR/Uranium series dating of juvenile *Stegodon* molar conducted by Jack Rinck; @= Red TL dating of quartz grains conducted by Kira Westaway. B. Total number of identified fossil specimens, unidentifiable bone fragments, and number of individual fossil specimens (NISP) of various taxa per excavated spit, arranged per stratigraphic unit, for Sectors VII and XI. For further explanations see Fig. 2A. Note that for the entire Sector XI and for Spits 1–25 of Sector VII the amount of unidentifiable bone fragments is given in grams, whereas for the remaining part of Sector VII the total amount of unidentifiable specimens are plotted like in Fig. 2B. In Sector VII no total unidentifiable specimens were recorded completely either in grams or as individual specimens, for spit 25–36. Layer letter codes refer to the stratigraphic units as published by Morwood et al. (2004, 2005).

256.5 cm, while the largest ever recorded specimen measured ~3 m (Auffenberg, 1981). Using the regression of average articular cup transverse diameter of thoracic vertebrae against STL of recent skeletons, it follows that an individual 3 m in length would have an average cup diameter of 47 mm. Therefore, the largest fossil in the Liang Bua assemblage can be comfortably allocated to *V. komodoensis*.

A smaller varanid taxon found at Liang Bua is the extinct *Varanus hooijeri*, as first described from two other cave sites on Flores, Liang Michael and Liang Toge (Brongersma, 1958). This peculiar varanid had blunt, barrel-shaped teeth similar to those of the extant Nile Monitor, *V. niloticus*, and Gray's monitor, *V. olivaceus*, which is an endemic of the island of Luzon in the Philippines. Unlike most other monitor lizards, these living species are principally frugivores, but also feed on land snails (Auffenberg, 1988). *V. hooijeri* is present throughout the archaeological sequence, but is most abundant in the Holocene where skeletal elements show occasional signs of being burnt, probably as a result of human processing. The remains of a third varanid presently occurring on Flores, *Varanus salvator*, (Auffenberg, 1980) have not been found among the studied material to date. This species (average STL = 115.8 cm) is widely distributed throughout Southeast Asia.

Small mammals

Four endemic species of giant rat have been recorded on Flores (Hooijer, 1957; Musser, 1981). The largest, *Papagomys armandvillei*, grows to a length of 45 cm with a tail of 70 cm, and is the only extant species of that genus that definitely survives on the island (Nowak, 1991). Another species evident in the Pleistocene and Holocene deposits, *P. theodorverhoeveni,* was reported also to be extant, as Suyanto and Watts (2002) referred a recent specimen in the Museum Zoologicum Bogoriense in Cibinong, Java, Indonesia, to the fossil species. However, Zijlstra et al. (2008) showed that this assumption was based on a misidentification of a *P. armandvillei* specimen. Another giant rat genus, *Spelaeomys*, endemic to Flores, is represented at Liang Bua by just a few Pleistocene and Holocene specimens. *Spelaeomys* disappeared from the sequence ~6 ka, but its final extinction probably occurred between 4–3 k.yr., as evidenced at Liang Toge (Musser, 1981). The fourth species, *Hooijeromys nusatenggara*, was described from Middle Pleistocene deposits from Mata Menge (Musser, 1981).

Middle-sized rats are well represented in the Liang Bua deposits. Musser (1981) described two genera on Flores, *Komodomys* and *Floresomys*, represented by the species *K. rintjanus* and *F. naso*, with the former species extant but now restricted to the nearby islands of Rinca and Padar. Musser et al. (1986) replaced the preoccupied name *Floresomys* by *Paulamys*, while Kitchener and Yani (1997) argued that the species *Floresomys naso* is better placed in the genus *Bunomys* – not a view shared by Musser and Carlton (2005). Given these taxonomic uncertainties and the practical difficulties in distinguishing the mandibles of these two species, we treat *Komodomys*/*Paulamys* as a single group.

Other small mammal taxa represented include a shrew rat (represented by a single edentulous mandible), the well-known human commensal Polynesian rat (*Rattus exulans*) in upper Holocene levels, and probably the very similar endemic *Rattus hainaldi* in both Pleistocene and Holocene levels. Evidence of *Rattus rattus* has only been found in the uppermost spits. Terrestrial insectivores are represented by at least two different species of *Crocidura* and/or *Suncus* (van den Hoek Ostende et al., 2006). Neither species can be linked to the shrews currently inhabiting the island of Flores, so the mandibles most likely represent extinct endemic taxa. Several species of fruit and insectivorous bats have also been identified, the most numerous of which is *Dobsonia peroni*, a fruitbat that roosts in caves and is still extant on Flores.

Introduced mammals

During the Holocene, people translocated a number of animals to the island. At ~7 ka the first evidence for the Sulawesi warty pig (*Sus celebensis*) appears in the sequence, whereas the Eurasian pig (*S. scrofa*), Javanese or Short-tailed porcupine (*Hystrix javanica*), Masked palm civet (*Paradoxurus hermaphrodites*), and Long-tailed macaque (*Macaca fascicularis*) appear ~4 ka, at the same time as the hallmarks of the Neolithic, ground adzes and pottery, first appear in the sequence. Evidence for the local presence of deer, cattle, dog, and horse is documented by isolated finds in the uppermost levels of Sectors I (upper 30 cm), III and IV (upper 20 cm), and VII (upper 40 cm), in deposits younger than ~0.5 ka.

Birds

Bird taxa that occur sporadically throughout the archaeological sequence include Anseriformes (ducks and geese); Falconiformes (hawks and eagles: *Falco* cf. *tinnunculus* and *Aquila* cf. *fasciatus*, i.e., Bonelli's Eagle); Ciconiiformes (storks and related birds); Galliformes (chickens and pheasants: *Coturnix* spp., i.e., quails); Gruiformes (coots and rails: *Turnix* spp., i.e., buttonquails); Columbiformes (pigeons and doves: *Ducula* sp., i.e., imperial pigeon, *Ptilinopus* cf. *cincta*, i.e., black-backed fruit dove, *Treron griseicauda*, i.e., grey-cheeked pigeon, *Streptopelia bitorquata*, i.e., island collared dove); Strigiformes (owls: *Otus* spp. and *Tyto* spp.), Coraciiformes (kingfishers); Apodiformes (Swifts: *Collacalia salangana*, i.e., mossy-nest swiftlet, and *Collacalia esculenta*, i.e., glossy swiftlet); Passeriformes (perching birds: incl. Meliphagidae, i.e., honey eaters); and tentatively Psittaciformes (parrots: *Vini* sp.). Except for the mossy-nest swiftlet, bird species present in the Holocene deposits at Liang Bua still occur on Flores. The Pleistocene bird species that are no longer extant on the island include *Vini* sp., a large endemic *Tyto* sp., and a giant species of *Leptoptilos*.

Molluscs

Accumulations of freshwater, marine, and terrestrial mollusc shells occur only in the Holocene deposits at Liang Bua, with freshwater species dominating. In the Pleistocene record, rare occurrences of terrestrial snail remains form part of a natural death assemblage in the deposits (see below for further discussion). Freshwater shell is certainly human subsistence refuse, and this component of the mollusc assemblage is dominated by two species of small gastropod in the Thiaridae: *Thiara granifera* and *Melanoides tuberculata*. Species in the Neritidae are also present, including *Neritina pulligera*, *Neritodryas cornea, Neritodryas dubia, Septaria porcellana*, and *Clithon squarrosus,* as well as a few examples of as-yet unidentified neritid species. Bivalves are much less common than gastropods, with the only species thus far identified within the freshwater component being the corbiculid *Batissa violacea*. Micro-chipping and wear-facets along the ventral margin of many specimens also indicate that they may have been gathered primarily for the use as tools rather than for subsistence (Szabó and Rokus Awe Due, 2006) (Fig. 3). Marine shell occurs in low frequency, and again was most likely brought to the site for use as scrapers and the making of adornments, such as beads and pendants, e.g., fragments of the deep-sea pelagic *Nautilus pompilius* with evidence of scoring and cutting.

Taphonomic agents and processes at Liang Bua

A range of natural and cultural taphonomic processes have played significant roles in the accumulation and transformation of faunal remains at Liang Bua. As might be expected, 70 k.yr. old bones are more fragile than those of terminal Pleistocene and

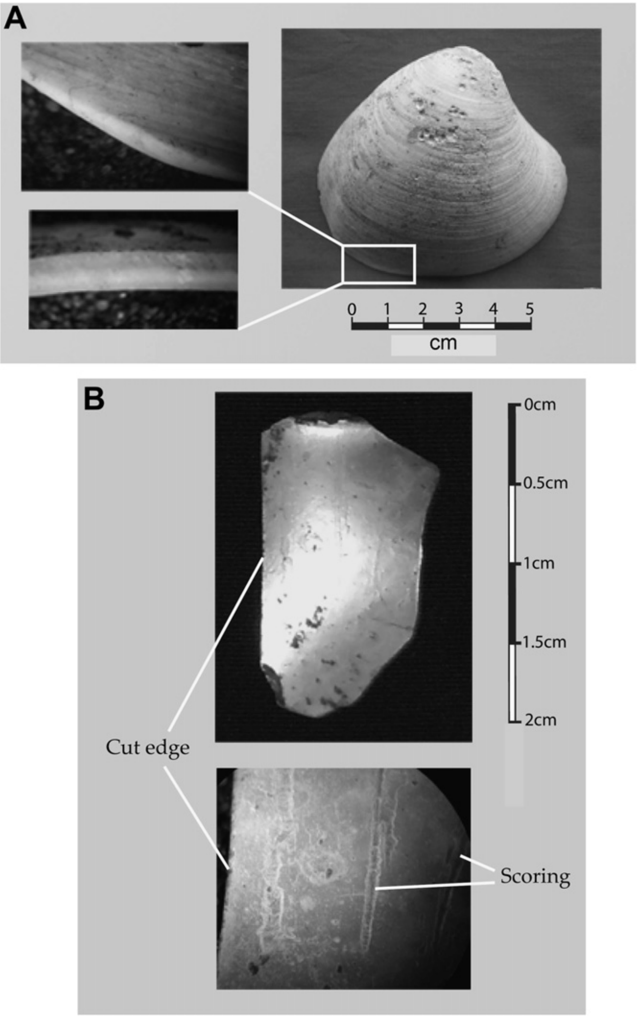

Figure 3. A: Ventral margin of a *Batissa violacea* valve showing facetted wear. Specimen from Verhoeven's original material collected from Liang Bua. B: Cut piece of *Nautilus* sp. shell with evidence of scoring. Liang Bua, Sector 11, 40–50 cm.

Holocene age, but diagnostic skeletal elements and teeth were just as easily identified in the earliest as in the most recent deposits. In general, the small vertebrate remains from all depths within the stratigraphic sequences were in excellent condition, as were Komodo dragon vertebrae - though brittle and prone to breakage. In contrast, *Stegodon* postcranial remains were generally very poorly preserved; in particular, the juvenile long bones all lack epiphyses and often show considerable superficial cracking, flaking, and dissolution. In fact, the predominance of *Stegodon* dental elements, as noted above, could be explained by selective disintegration and disappearance of bone by a combination of factors; the bones were often smashed or trampled, subjected to weathering, (partial) dissolution (especially of immature bone tissue), and rodent gnawing during prolonged exposure on the surface. While entombed, the bones would also have been leached by sporadic water flow though the sediments, and the archaeological recovery processes including excavation, dry-sieving, wet sieving, and transportation, would have caused further loss of brittle, cancellous bone and some diagnostic anatomical details.

The animal bones from Pleistocene contexts have a distinctive, even coloration that distinguishes them from the more 'mixed' assemblages recovered from the Holocene sequence (see below). Skeletal elements of both large and small vertebrates were generally a light, yellowish brown color with speckling of a dark, purplish brown concretion (possibly manganese oxide). The majority of bone fractures were transverse, irregular transverse, or irregular in shape, indicating that most breakage was post-depositional and had occurred once the bones were old and dry (see Johnson, 1985). Many small mammal, reptile, and amphibian skeletal elements demonstrate hairline cracks orientated along the long axis of shafts that have resulted, in some cases, in the slight exfoliation of cortical bone surfaces. These bone surface modifications are generally an indication of weathering prior to bone burial and often result from changes in bone moisture content through processes such as wetting and drying (Behrensmeyer, 1978).

Preliminary taphonomic analysis showed that a few bone fragments could be re-fitted, implying that this huge small vertebrate assemblage had been exposed to only minor post-depositional transport and re-organization. In short, the taphonomic assessment suggests that many bone fragments remained undisturbed on the ground surface for a reasonable length of time before being buried.

Stegodon and Komodo dragon remains were not evenly distributed throughout the Pleistocene sequence but were concentrated within two discrete areas associated with stone tools, knapping debris, charcoal, and the remains of other vertebrates, such as rat, varanid, and bird. Two *Stegodon* mandibles, crushed skull fragments, some postcranial elements, and a large number of indeterminate fragments were found with such a concentration of materials on a surface dated to ~17 ka in Sector XI (Figs. 2B, 4), while a similar concentration dated between 64–71 k.yr. (Westaway, 2006) occurred in Sector IV between 4–5 m depth (Fig. 2A). These concentrations of bones are interpreted as stratified hominin occupation layers, and include *Stegodon* bones with cut marks (Fig. 5). For instance, a costa fragment from one of the anterior ribs shows 5 parallel grooves of between 2–5 mm long on the flat cranial surface just below the articular processes. These marks are clearly distinguishable from rodent gnawing, which is commonly present as a series of ~1 mm wide, short parallel and partly overlapping grooves on the bony edges and protruding ridges of many dense bones.

The horizontal and vertical distribution of large animal remains at the site, butchery marks on some bones, and their association with concentrations of artifacts and hominin skeletal evidence, all indicate that *Homo floresiensis* was the principal agent responsible for the accumulation of such remains. Flores differed from the Asian mainland during the Pleistocene in having no other animals that could have caused such an accumulation (e.g., hyenas and porcupines). The only other large predator on the island, the Komodo dragon, though known to prey on neonatal and juvenile animals, does not accumulate bones. Rather, a number of Komodos

Figure 4. Sector XI, Spit 48, during the 2004 excavation. In this sector, the interval between 4 and 5.2 m depth is characterized by high densities of *Stegodon* bone fragments and stone artifacts. Two juvenile *Stegodon* mandibles are indicated by arrows (Photo: M. J. Morwood).

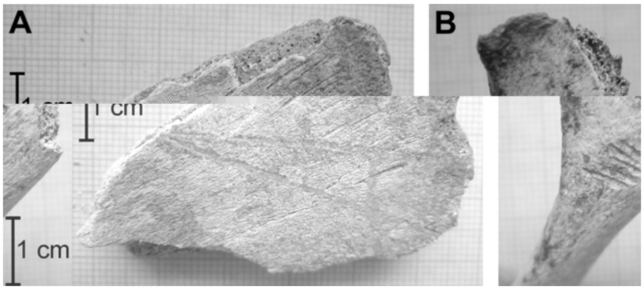

Figure 5. Cut marks on a *Stegodon* pelvis fragment (A) and rib fragment (B).

commonly converge at places where an animal has been killed or died, and they will gorge upon the remains at that location. Their digestive tracts are aggressive, capable of completely digesting bone, and at the very least will leave distinctive acid dissolution traces around the unconsumed ends of bones. No such traces were observed in the Liang Bua vertebrate assemblages.

Though the bones of small mammals, reptiles, and birds occur throughout the archaeological sequences, the greatest abundance of the intermediate- and small-sized murid taxa (~25,000 fragments) was located against the eastern wall in Sector XI at 5.9–6 m depth. The low levels of bone fragmentation and high incidences of moderate predatory digestion suggest that owls were probably the principal accumulators of this assemblage. Owls do not digest bone and hair in the same way that other predators do, but regurgitate them as pellets that accumulate on the ground below their roost sites. Bones of small prey often remain intact, or only slightly fragmented, with limited evidence for digestion concentrated in susceptible locales such as the articular ends of long bones (Andrews, 1990, 1995). This distinguishes owls from diurnal raptors and other predators that tend to dismember their prey, breaking the bones and swallowing them in pieces. The prey then passes in smaller pieces through the entire intestinal tract, resulting in a bone assemblage that is much more fragmentary and demonstrates more intensive levels of digestion.

During excavation of Sector XI, it was apparent that the sediments containing concentrations of small vertebrate remains occurred on a section of raised ground that ~18 ka formed the southern bank of a pool – in fact, the *Homo floresiensis* skeleton LB1 was recovered from the associated pool sediments (Morwood et al., 2004). The owl pellets were probably dropped from a roost site on the cave wall onto the sloping ground where, over time, they accumulated. The excellent state of preservation of the small skeletal elements and their discrete patterning suggests that the bones laid undisturbed on the ground surface for an extended period before being covered. During the period of exposure, biostratonomic agencies that might have caused fragmentation and dispersal, such as hominin activity, did not occur near the owl pellet accumulations.

Several owl species are known from Flores, including the common Barn owl (*Tyto alba*), the widely distributed common Scopsowl (*Otus scops*), and three endemic species: Wallace's Scopsowl (*Otus silvicola*), Moluccan Scopsowl (*Otus magicus*), and Flores Scopsowl [*Otus alfredi* - considered to be a red morph of *O. magicus* by Sibley and Monroe (1993)]. Only *Tyto* spp. of the known extant owl taxa of Flores regularly eats mammals, but even the barn owl would have been too small to swallow the middle-sized rats whole. Several bones from a larger owl have been recorded in the Pleistocene deposits at the site, suggesting a bigger *Tyto* sp. formerly lived on the island; it was possibly this taxon that produced the accumulation of owl pellets by the side of the pool in Liang Bua.

It is more difficult to determine the causes of accumulation of the small mammal, reptile, and amphibian remains in the terminal Pleistocene deposits. These do not demonstrate any characteristic bone surface modifications associated with predator digestion, and there is no direct indication that hominins were responsible for their accumulation. However, the bones are associated with an assemblage of large-bodied vertebrate remains including *Stegodon*, Komodo dragon, giant rat, and the remains of a large (possibly flightless) stork of the genus *Leptoptilos* (Fig. 6). Therefore, the inclusion of the associated small mammals, reptiles, and amphibians in the hominin diet cannot be completely discounted. However, the shaft of the *Leptoptilos* sp. tibiotarsus, along with many *Stegodon* bones, bear the characteristic gnawing marks of a middle-sized rodent implying that the murids might represent part of a scavenging community taking advantage of an accumulation of larger bodied mammals, birds, and reptiles brought into the cave by hominins.

As mentioned above, the Holocene faunal assemblages at Liang Bua differ considerably from those of the preceding Pleistocene. They are much more variable in coloration and state of preservation, suggesting greater re-working of bones with very different taphonomic histories. Some bone fragments, particularly the proximal and distal ends of humeri and femora of small to medium-sized murids, show the effects of predatory digestion. However, human agency is likely to have been responsible for the burnt and calcined condition of some large murid, megachiropteran, and *Varanus hooijeri* bones.

The virtual lack of molluscan remains from the early deposits at Liang Bua is in marked contrast to many other Pleistocene sites across the region, including the West Mouth and Lobang Angus at the Niah Caves in northwest Borneo from ~45 ka (Szabó, in prep.), Golo Cave in the northern Moluccas, eastern Indonesia from ~32 ka (Szabó et al., 2007), Lene Hara (O'Connor et al., 2002; O'Connor and Aplin, 2007), Macha Kuru I and Macha Kuru II in East Timor from ~35 ka (Veth et al., 2005), and Matenkupkum in New Ireland from ~33 ka (Gosden and Robertson, 1991), to name but a few. While shell does tend to decay more quickly than bone, they are both subject to many of the same taphonomic processes, such as weathering and acid dissolution. It is, therefore, unlikely that the small vertebrate remains from the Pleistocene levels of Liang Bua could survive in such remarkable condition, whereas taphonomic processes totally destroyed shell. In addition, fragments of a landsnail from Spit 45, Sector IV and from Spit 54, Sector VII, and of freshwater snail (Spit 47, Sector IV and Spit 93, Sector VII) indicate that shell could survive in the Pleistocene levels of the site, and that its general absence there is not due to post-depositional processes. Mollusc-collecting for subsistence or production of artifacts does not appear to have been a hominin activity at Liang Bua during the Pleistocene, whereas from ~11 ka modern people were exploiting mollusc species from terrestrial, freshwater and distant marine habitats, in particular after ~5 ka (Appendixes A–C, Fig. 2A–B).

Paleoenvironments and hominin behavior

The occurrence of large numbers of *Stegodon* remains in the Pleistocene levels of Liang Bua demonstrates that *Homo floresiensis* subsisted, at least in part, by hunting and/or scavenging neonatal and juvenile stegodonts Komodo dragons, endemic giant rats, and birds. The predominance of very young *Stegodon*, with the inclusion of just a few older individuals, implies that the small-bodied hominins were either unable or unwilling to tackle full-grown pygmy *Stegodon* that are estimated to have weighed 350–950 kg. As no complete adult longbones of *S. florensis insularis* have been found, this estimate is based on the similarly sized *Stegodon sompoensis* from Sulawesi, of which a complete humerus with fused epiphyses is known (van den Bergh, 1999). The composition of the Liang Bua *Stegodon* assemblage resembles that excavated from Middle Pleistocene deposits at Panxian Cave in south China, which was dominated by juvenile dental remains of the normal sized *Stegodon orientalis*, associated with stone artifacts and hominin remains. These were also interpreted as resulting from hominin activities (either hunting or scavenging) in combination with natural accumulation of young animals through accidental death (Schepartz et al., 2005).

The bone accumulations associated with *H. floresiensis* also contained the remains of Komodo dragon. Whether or not the hominins hunted live Komodos or scavenged their carcasses is a matter of speculation, but as a predator, the animal was certainly to be treated with caution. Komodo dragons are formidable, stealth predators that commonly ambush their prey on game trails or at water holes (King et al., 2002). They do not necessarily kill their prey outright – rather, the bacterium in their saliva infects the wounds caused by their razor sharp, laterally compressed and re-curved teeth (Gillespie et al., 2002). The prey eventually succumbs to sepsis and septicaemia, which may take several days, and is then easily caught and devoured. Full-grown Komodo dragons are capable of bringing down an adult male buffalo, but more commonly locate female buffalo, deer, or goat that are about to give birth and use the opportunity to take both the mother and neonate (MM, pers. obs.), or the neonate alone (Auffenberg, 1981). They would undoubtedly have fed on *Stegodon* (Diamond, 1987) and *Homo floresiensis* given the opportunity, but people can fend off Komodos with long, forked sticks, as is common practice with tourist guides on Rinca and Komodo Islands today, and the animals are themselves vulnerable to hominin predation when conditions are either too cool at night and the animals are torpid, or too hot at midday, when they are inactive to prevent overheating.

There are no notable changes in *Homo floresiensis* subsistence patterning throughout the Late Pleistocene that would indicate modifications in subsistence procurement over time. The focus appears to have been on the hunting and/or scavenging of terrestrial mammals ranging in size from *Stegodon* and Komodo dragon to rats, birds, and small reptiles. Macro and microbotanical remains, including fibres, starches, and phytoliths on associated stone artifacts also show that various plant products were being brought into the site and processed (Lentfer, pers. comm. to MM). There is currently no evidence for Late Pleistocene exploitation of marine coastal resources or the harvesting of freshwater shellfish for subsistence purposes at Liang Bua, and certainly no evidence for the production of shell tools or adornments.

The long history of the Flores fauna community changed abruptly ~17 ka when a volcanic eruption deposited a thick layer of black tuffaceous silt in Liang Bua Cave. The volcanic ash and effects to the atmosphere would presumably have had a knock-on effect, disrupting local ecological systems and influencing plant productivity. A compounding factor towards the end of the Pleistocene (17–11 k.yr.) is that the climate appears to have become gradually wetter and soils became thicker in response to increased rainfall (Westaway, 2006; Westaway et al., 2009). The loss of several bird taxa, including the large-bodied owl and stork, is mirrored on many Pacific and Southeast Asian islands at the Pleistocene/Holocene transition, with extinction rates in some cases reaching as high as 50% (Olson and Hilgartner, 1982; Steadman and Martin, 2003). The appearance of parrots for the first time just below the 12 ka white tuffaceous layer suggests that the local vegetation was changing towards more closed canopy forest.

Around ~17 ka, *Stegodon florensis insularis* and *H. floresiensis* disappeared from the Liang Bua sequence, along with some endemic bird species. However, most of the smaller mammal and reptile taxa survived into the Holocene. The resilient Komodo dragon persisted in the area until very recent times, though changes in abundance compared to the smaller *V. hooijeri* may indicate a severe reduction in population size due to the loss of *Stegodon*, an important food resource. The various intermediate-sized and giant murids also persisted until sub-recent or even recent times when *Papagomys theodorverhoeveni* disappeared, probably through habitat loss, over-hunting, and competition with introduced exotic species.

The arrival of modern humans at the site by ~11 ka is clearly evident in the hominin skeletal record, but is also signaled by the appearance of new diagnostic behaviors, including formal disposal of the dead, new ways for processing plant materials (as indicated by edge gloss on some stone artifacts), the import of resources from the coast ~40 km away (i.e., marine shell), and the use of pigments and ornaments. Initial occupation of the cave by modern humans in the Early Holocene appears to have been sparse, with relatively low densities of artifacts and faunal remains. Murids, fish, frog, fruit-eating bats, and *V. hooijeri* are consistently represented in the Early Holocene levels, and these small animals may have constituted an important part of the diet prior to the introduction of larger mammals. Burnt and calcined remains of large-bodied rats, fruit eating bats, and *V. hooijeri* show that the few resources available on Flores after the extinction of *Stegodon* were being utilized by modern humans by ~9 ka. This long-established pattern continues on the island today, with rats, other small mammals, and reptiles still making up part of the diet (RDA, pers. obs.).

The two most obvious components of modern human subsistence that separate them from earlier hominin populations on Flores, however, are the use of molluscs and the import of medium and large-bodied animals to supplement the impoverished range of such animals on the island. With respect to molluscs, there is no evidence for this in the Pleistocene deposits at Liang Bua or in the Early and Middle Pleistocene sites of the Soa Basin. Following the extinction of *Stegodon* in the terminal Pleistocene, the only large-bodied animals on Flores, apart from humans, were Komodo dragons, which were not common.

The first animal translocated to Flores was the pig at ~7 ka. In Sector IV, pig remains occur in slightly older levels, but here the bones presumably intruded into deeper levels in association with a Mesolithic burial (Fig. 2A). Recent mtDNA analysis - in addition to geometric morphometric analysis of complete lower third molars (M_3) - on recent specimens from Flores and fossil specimens from Liang Bua confirm the presence on Flores of two separate species of pig (*S. celebensis*, the Sulawesi warty pig, and *S. scrofa*). Specimens from the deepest levels at Liang Bua are clearly *S. celebensis*, whilst some later specimens are clearly *S. scrofa* that originated from the South Asian mainland and was subsequently spread through Wallacea into the Pacific region (Larson et al., 2007).

In Liang Bua, the second “Pacific” *S. scrofa* haplogroup and morphotype concurs with the appearance of Neolithic ground adzes and pottery at ~4 ka, and is associated with the introduction of several other species including the Masked palm civet (*Paradoxurus hermaphroditus*), Javan or Short-tailed porcupine (*Hystrix javanica*), and the Long-tailed macaque (*Macaca fascicularis*). This evidence clearly shows an Early Holocene human-mediated pig dispersal from Sulawesi immediately to the north, followed by a second one involving the movement of *S. scrofa* originally domesticated on mainland Southeast Asia. *Sus* remains in early-to-mid Holocene deposits at Liang Bua are rather scarce, but do become much more common during Neolithic times (Fig. 2A–B).

The Masked palm civet first appears to have been introduced to other Lesser Sunda Islands, Sulawesi, and the Philippines at the same time as the domestic pig (Simmons and Bulbeck, 2004; Larson et al., 2007). The animal inhabits forests, but is also frequently found near cultivated areas and even below building roofs, presumably to hunt rats and mice. It is therefore possible that civets were transported to the islands for pest control, as well as a food resource (Groves, 1976). Porcupine and macaque are extensively hunted on Flores today, and were probably introduced for food, but the latter is often kept as a pet across island Southeast

Asia, and feral populations might have originated from escaped exotic pets. Common domesticates on Flores today were apparently introduced much later. Diagnostic remains of cattle and deer, for instance, appear in the Liang Bua sequence only in the upper 40 cm of the sequence, presumably brought to the island by Portuguese ships less than 500 years ago. Dog similarly only occurs in the most recent levels of the site, but given their presence in Australia ~4 ka and Timor ~3 ka (Veth et al., 2005), it is likely they were introduced to Flores earlier than the available evidence indicates.

The evolutionary history of vertebrate communities on Flores

Isolated oceanic islands generally have highly endemic, impoverished, and unbalanced faunal communities, in which animals adept at crossing sea barriers are over-represented; these include proboscideans (e.g., *Elephas*, *Stegodon*), artiodactyls, murid rodents, and tortoises (e.g., Sondaar, 1977; Roth, 1990; Agenbroth, 2001; de Vos et al., 2007; Palombo, 2008 and references therein). Of particular relevance for Flores, the distribution of proboscideans on islands worldwide demonstrates their unrivalled ability among large mammals to cross open water gaps (Sondaar, 1977; Johnson, 1978). They crossed Wallace's Line reaching the oceanic island of Sulawesi and colonized islands, such as Timor and Sumba, which were beyond the dispersal capabilities of other relatively good island colonizers, such as hippos, pigs, deer, and bovids.

Although each island is unique, with its own unique faunal history, islands share a number of biogeographic characteristics. For instance, they can preserve lineages that elsewhere have long disappeared, including lemurs in Madagascar, monotremes in Australia, and *Anoa* in Sulawesi (e.g., Groves, 1976; Mittermeier et al., 2006). On the other hand, island faunas that evolved in a predator-free environment are very susceptible to extinction when humans and their commensals arrive (Morwood and van Oosterzee, 2007).

There are also consistent trends in the ways animals evolve on islands; given long enough, large mammals often downsize, while small mammals adaptively radiate to fill empty ecological niches and some increase significantly in size - a refinement of the Island Rule (Foster, 1964; c.f. Meiri et al., 2008). As a result, dwarfed proboscideans, giant tortoises, and giant rodents occurred on many islands, including Luzon (Philippines), Sulawesi, Java, and Timor in Southeast Asia (Hooijer, 1954, 1957, 1971; van den Bergh, 1999).

A wide range of factors could explain dwarfing of such large herbivores on islands. The absence of large mammalian predators, a response to limited island resources, the demographic advantages of having accelerated reproduction rates, more effective thermoregulation, or a combination of factors have been used to explain this "island rule" for insular dwarfism (e.g., Foster, 1964; Sondaar, 1977; Case, 1978; Lomolino, 1985; Roth, 1990; Raia et al., 2003; Palombo, 2008). Raia and Meiri (2006) demonstrated that the extent of dwarfism in large ungulates depends primarily on the existence of inter-specific competitors and to a lesser extent on the presence of predators. They argue that dwarfism in large herbivores is an outcome of the fitness increase resulting from the acceleration of reproduction in low-mortality environments.

In the context of such biogeographic and evolutionary trends on islands worldwide, the impoverished, unbalanced, and endemic character of the Flores fauna, before humans began introducing exotic animals in the Holocene, is clear evidence that the island was always difficult to access and never connected by (transient) land bridges to continental Southeast Asia or Greater Australia (*contra* Jacob et al., 2006; Köhler et al., 2007).

The oldest terrestrial fossil site currently known on Flores is Tangi Talo in the Soa Basin of central Flores, which dates to ~900 ka and contains Komodo dragon, a giant tortoise (*Geochelone* sp.), and *Stegodon sondaari*, the smallest *Stegodon* species known (van den Bergh, 1999; van den Bergh et al., 2008). Komodo dragon and giant tortoise are probably relict populations from much earlier times. DNA sequencing suggests a close relationship between *V. komodoensis* and *V. varius* from Australia and *V. salvadorii* distributed throughout Papua New Guinea (Fuller et al., 1998). The DNA evidence is supported by the palaeontological record, which suggests that the restricted distribution of *Varanus komodoensis* on the Flores group of islands represents a relict population of large-bodied varanids that was once much more widespread throughout the region. Large-bodied varanids are known from the Pliocene fossil deposits of the Siwalik Hills in northern India, from the Lower Pleistocene of Java, and the Pliocene of Australia (Hocknull et al., in prep.). Setiyabudi (2006) also notes that *Geochelone* populations known from the fossil records on many islands in Southeast Asia have strong morphological similarities with the Pliocene giant tortoise from the Siwalik Hills, *Colossochelys atlas*. He concludes that they all originated from the same mainland giant tortoise lineage, that they arrived on the islands large-bodied, rather than developing immense size in isolation, and that distinct morphological characteristics of giant tortoises on different islands in the region indicate each should be considered a distinct species.

Around 900 ka, a faunal turnover occurred in the Soa Basin with the extinction of *Stegodon sondaari* and giant tortoise, and the appearance in the stratigraphic sequence of the medium- to large-sized *Stegodon florensis* [body weight estimated between 850–2100 kg (van den Bergh, 1999)], and a giant rat *Hooijeromys nusatenggara*. The change may have been caused by a massive volcanic eruption; the Tangi Talo fossils are embedded in a thick tuff layer that blanketed the entire Soa Basin, while the age structure of the *Stegodon* assemblage indicates non-selective death by a catastrophic event (van den Bergh, 1999; van den Bergh et al., 2001). However, the faunal turnover is also associated with the first evidence in the Soa Basin sequence for stone artifacts - proxy evidence for the arrival of hominins (Morwood et al., 1997; van den Bergh, 1999;Brumm et al., 2006).

Stegodon florensis is closely related to a poorly known *Stegodon* species identified on Sulawesi immediately to the north (van den Bergh, 1999). In fact, Sulawesi is probably the source area for the few terrestrial animals that managed to reach Flores during the Quaternary, based on its proximity and on the prevailing southward directed ocean currents of the Indonesian Throughflow (Kuhnt et al., 2004). In contrast, strong surface currents in the deep straits between Bali and Lombok and between Sumbawa and Komodo (Hautala et al., 2001) constituted an effective barrier against overseas eastward dispersal along the volcanic Island Arc.

So far, Flores provides the only evidence anywhere for sea-crossings by hominins in the Early Pleistocene. Most likely, this was a matter of chance resulting from a tsunami-like event, perhaps washing a group of hominins offshore while clinging to up-rooted trees or flotsam. The Indian Ocean tsunami that struck the coast of Aceh on December 26, 2004, showed how humans can survive for several days on natural rafts, while being carried hundreds of kilometres with the surface currents. Dispersal at the onset of the Middle Pleistocene was further enhanced by low sea-levels, which around the Early to Middle Pleistocene transition lasted for extended periods of time, significantly decreasing the distances between islands (van den Bergh et al., 1996). The predominant north-to-south flow of ocean currents in the region also suggest that Sulawesi is the most likely source area for early hominins reaching Flores - as with the case of *Stegodon florensis*.

Similar faunal replacements also occurred in Sulawesi, where the earliest known terrestrial fossil assemblage, dated to ~2.5 Ma and comprising pygmy *Stegodon*, pygmy elephant (*Stegoloxodon celebensis,* a primitive four-tusked elephant, see Markov and Saegusa, 2008), pig (*Celebochoerus heekereni*), and giant tortoise, was later replaced by one comprising large-bodied *Stegodon* and large-bodied *Elephas* (van den Bergh, 1999). Further north, a variation on the theme may have occurred in the Philippines: in the Cagayan Valley on Luzon, fossil finds include pygmy *Stegodon*, small bodied *Elephas*, large-bodied *Elephas*, a small rhino (*Rhinoceros philippinensis*), a pig probably related to *Celebochoerus* from Sulawesi, a cervid, a bovid related to the Tamarau, and giant tortoise. No geochronological sequence for the isolated fossil finds exists (de Vos and Bautista, 2001), but stone artifacts have been recovered close to large-bodied *Elephas*. Future research will establish whether Early Pleistocene faunal turnovers in Sulawesi and the Philippines were also associated with the initial arrival of hominins.

Significantly, *Stegodon florensis* appears to have downsized on Flores between 680 ka, the age of the most recent vertebrate fossils in the Soa Basin, and 95 ka, the age of the earliest faunal remains at Liang Bua. The latter includes evidence for the dwarfed *Stegodon florensis insularis*, a subspecies 30% smaller than its Soa Basin ancestor (van den Bergh et al., 2008; c.f. inaccurate claims by Rolland and Crockford, 2005, and Meiri et al., 2008). This dwarfing of *Stegodon* occurred despite the presence of hominins on the island, but not to the same extent as *S. sondaari,* which evolved before hominins arrived.

Currently, few data exist on the faunal history of Flores between 680 ka and 95 ka. However, stone artifacts in the basal conglomerate deposit at Liang Bua show hominins were still present on the island ~193 ka (Westaway et al., 2007). The fact that *Stegodon florensis insularis* appears to be a direct descendant of S. *florensis florensis*, and that *Varanus komodoensis* spans the entire range covered by fossil finds on Flores, point towards phylogenetic continuity. The taxonomy of murid rodents has similar implications, but also shows the potential for adaptive radiation when island-size is relatively large in relation to animal-size. *Papagomys*, *Paulamys*, and *Komodomys* are more related to one another than to any other murids (Musser and Carlton, 2005), and appear to be the result of *in situ* evolution that led to a divergence into four or five endemic species to occupy vacant ecological niches. The Middle Pleistocene giant rat *Hooijeromys nusatenggara* seems to have been part of this divergence, presumably on the lineage leading to the genus *Papagomys*.

Though the modern avifauna of Flores includes a number of endemic taxa, such as the Flores Scopsowl (*Otus alfredi*), it is still markedly different from the Late Pleistocene bird assemblage from Liang Bua. Two possible endemic taxa are of note: the large-bodied barn owl (*Tyto*) is similar to the giant endemics recognized on a number of islands including the Bahamas (Olson and Hilgartner, 1982), Cuba (Arredondo, 1976), and Papua New Guinea (Steadman et al., 1999), and a large species of *Leptotilos*. (Fig. 6).

The Flores faunal island community thus seems to have maintained an inherent, undisturbed stability and phylogenetic continuity throughout the Pleistocene. There are no new successful mammalian colonizers evident in the fossil record between the Soa Basin faunal turnover around 900 ka, associated with evidence for a major volcanic eruption and the initial arrival of hominins, and a second faunal turnover at Liang Bua around 17 ka, associated with a major volcanic eruption followed by the arrival of modern humans (Morwood et al., 2004).

If the same evolutionary conditions applied to other animals on the island, then *Homo floresiensis* is likely to be a direct, endemic descendant of the Soa Basin hominin population. This is supported by the strong similarities between stone tool assemblages from the Middle Pleistocene site of Mata Menge and Liang Bua (Moore and Brumm, 2007). However, the phylogenetic history of the species remains uncertain. For instance, the small stature of *Homo*

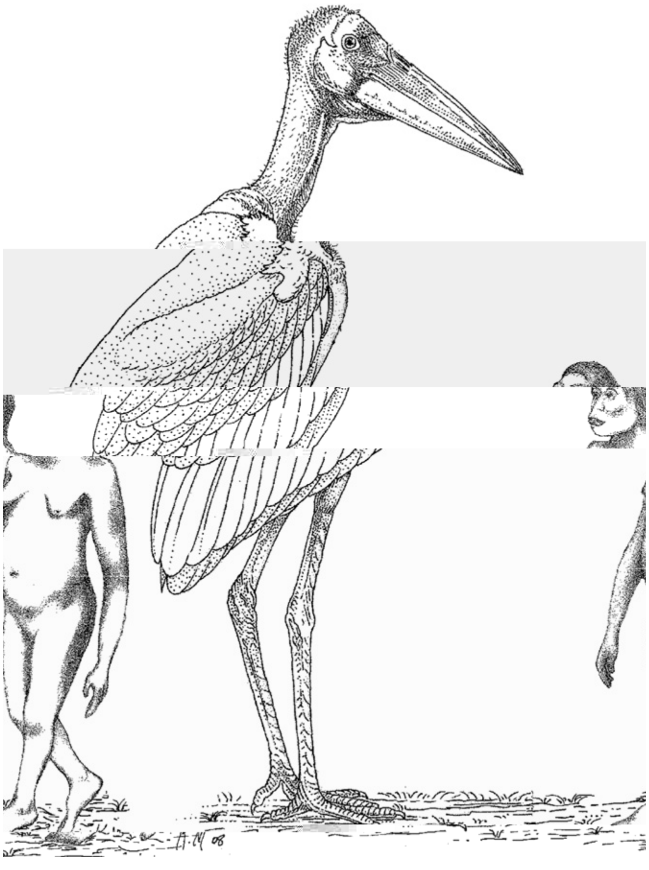

Figure 6. Reconstruction of the endemic giant bird Leptotilos sp., drawn to the same scale as *Homo floresiensis*. Drawing by Kathy Morwood, after an original drawing by Inge van Noortwijk.

floresiensis may reflect insular dwarfing of a large bodied ancestor, such as *Homo erectus* (Brown et al., 2004; Niven, 2007; van Heteren and de Vos, 2007), or the fact that the original hominin colonizers of the island were representatives of an early small-bodied lineage that survived on Flores long after source populations on the Asian mainland were replaced (Morwood et al., 2005; Argue et al., 2006).

Conclusions

The 95 k.yr. archaeological sequence at Liang Bua presents a unique opportunity to study temporal changes in the composition and structure of an isolated island vertebrate community, identify the biostratonomic and post-depositional processes that have influenced the preservation of the vertebrate and invertebrate remains from the site, and assess the impacts and subsistence and resource procurement behaviors of two different hominin taxa, *Homo floresiensis* and *H. sapiens*.

H. floresiensis was part of an endemic insular fauna with *Stegodon florensis insularis*, a variety of small- to large-bodied rodents, endemic birds, insectivores, and reptiles. The composition of the bone accumulations associated with artifacts, and other evidence for the presence of *H. floresiensis* at Liang Bua, indicates that this small-bodied hominin was hunting and/or scavenging a variety of these terrestrial resources.

Around 17 ka, the stability of the vertebrate community around Liang Bua was disrupted when a thick layer of volcanic tuff was deposited. *Homo floresiensis* and *Stegodon* both disappeared from the sequence, whereas Komodo dragon and many of the smaller endemic mammal and reptile faunas persisted into the Holocene; some are still present on Flores and the surrounding islands today.

Re-occupation of Liang Bua by modern humans around 11 ka produced very different zooarchaeological signatures to those of the preceding Pleistocene. In the earliest phases of this occupation, small mammals, reptiles, and amphibians seem to have been a principal source of protein. But shellfishing, a common feature of modern human subsistence in Southeast Asia, Australia, and Melanesia during the Late Pleistocene (Bowler et al., 2003; Barker et al., 2007), was also evident for the first time, as was the importation of marine shell for the production of artifacts and adornments.

By 7 ka, human populations were clearly moving between islands in the region and had translocated *Sus* to Flores. From 4 ka onwards, the pace of change quickened with the Neolithic, further translocations of wild and domestic taxa, and an accelerating increase in environmental impacts. Local extinction of species, such as Komodo dragon, *Varanus hooijeri*, the mossy-nest swiftlet, and some of the giant rats, occurred throughout the Holocene, as a result of human population growth, habitat loss, competition with introduced species, and over-exploitation; nests of the mossy-nest swiftlet, for instance, are commercially valuable. Today, there are few habitats on Flores that have not been extensively modified, and wildlife biodiversity on this unique island is in rapid decline.

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.jhevol.2008.08.015.

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