Temporal shifts in the distribution of murine rodent body size classes at Liang Bua (Flores, Indonesia) reveal new insights into the paleoecology of *Homo floresiensis* and associated fauna

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A R T I C L E I N F O

A B S T R A C T

Liang Bua, the type locality of *Homo floresiensis*, is a limestone cave located in the western part of the Indonesian island of Flores. The relatively continuous stratigraphic sequence of the site spans the past ~190 kyr and contains ~275,000 taxonomically identifiable vertebrate skeletal elements, ~80% of which belong to murine rodent taxa (i.e., rats). Six described genera are present at Liang Bua (*Papagomys*, *Spelaeomys*, *Hooijeromys*, *Komodomys*, *Paulamys*, and *Rattus*), one of which, *Hooijeromys,* is newly recorded in the site deposits, being previously known only from Early to Middle Pleistocene sites in central Flores. Measurements of the proximal femur ($n = 10{,}212$) and distal humerus ($n = 1186$) indicate five murine body size classes ranging from small (mouse-sized) to giant (common rabbit-sized) are present. The proportions of these five classes across successive stratigraphic units reveal two major changes in murine body size distribution due to significant shifts in the abundances of more open habitat-adapted medium-sized murines versus more closed habitat-adapted smaller-sized ones. One of these changes suggests a modest increase in available open habitats occurred ~3 ka, likely the result of anthropogenic changes to the landscape related to farming by modern human populations. The other and more significant change occurred ~60 ka suggesting a rapid shift from more open habitats to more closed conditions at this time. The abrupt reduction of medium-sized murines, along with the disappearance of *H. floresiensis*, *Stegodon florensis insularis* (an extinct proboscidean), *Varanus komodoensis* (Komodo dragon), *Leptoptilos robustus* (giant marabou stork), and *Trigonoceps* sp. (vulture) at Liang Bua ~60–50 ka, is likely the consequence of these animals preferring and tracking more open habitats to elsewhere on the island. If correct, then the precise timing and nature of the extinction of *H. floresiensis* and its contemporaries must await new discoveries at Liang Bua or other as yet unexcavated sites on Flores.

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1. Introduction

Flores, an oceanic island within the Indonesian archipelago (Fig. 1), lies east of the Wallace Line (Wallace, 1869). For most of the 20th century it was widely accepted that *Homo sapiens* (modern humans) was the only hominin species to have reached this island—probably sometime within the past ~50 kyr—despite

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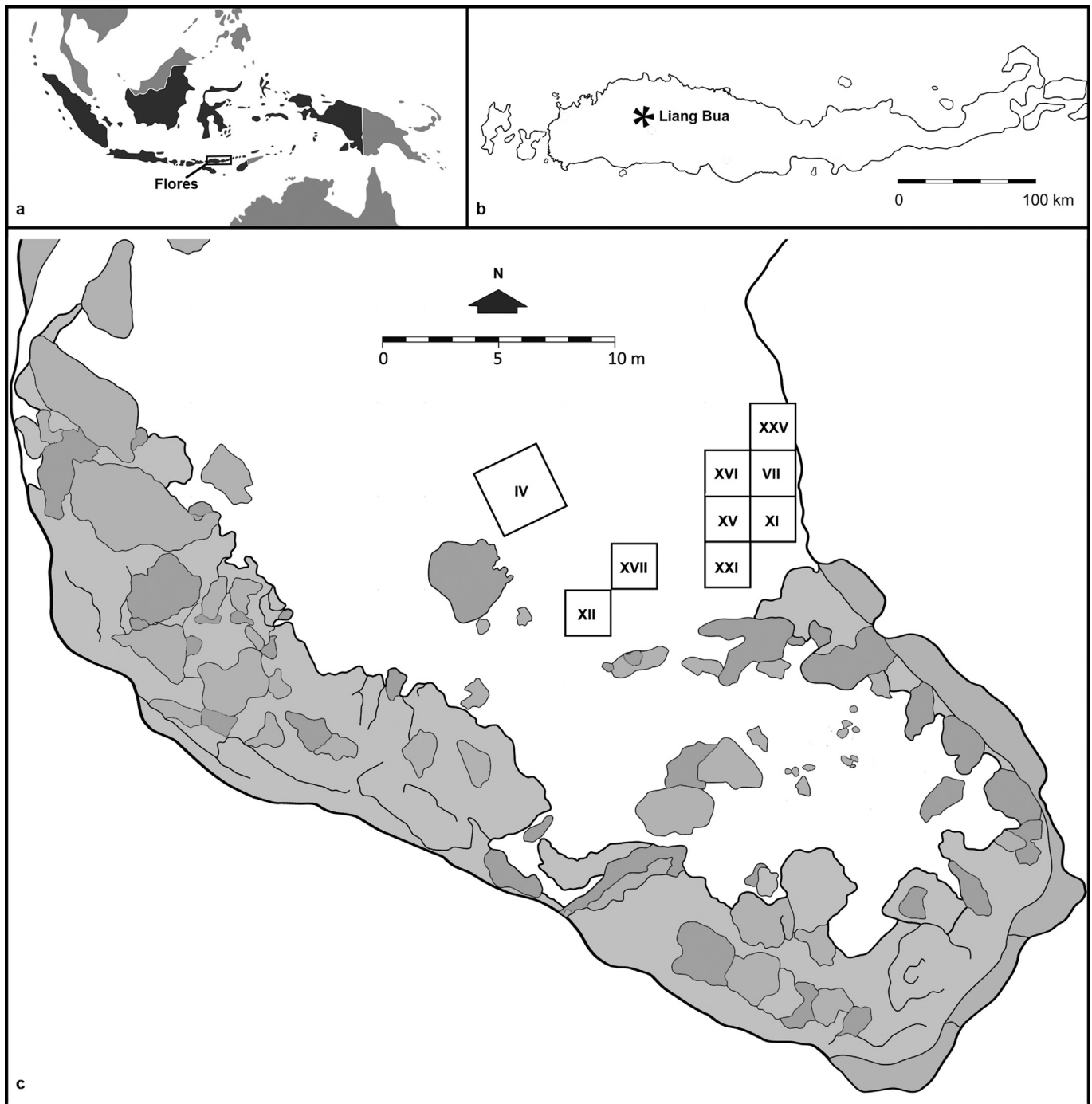
Figure 1. Location and excavation plan of Liang Bua: a) Location of Flores along the Indonesian Archipelago; b) location of Liang Bua in western Flores; c) excavation plan of sectors discussed in this study.

evidence suggesting that stone artifacts from central Flores were about 710 ka (Maringer and Verhoeven, 1970a,b,c; von Koenigswald and Ghosh, 1973). However, continued archaeological research on the island has demonstrated that premodern hominins dispersed to Flores by at least 1 Ma (Brumm et al., 2010). Putative descendants of this Early Pleistocene hominin dispersal event are represented by Middle Pleistocene stone artifacts and *Homo floresiensis*-like dentognathic fossils at Mata Menge (Morwood et al., 1998; Brumm et al., 2016; van den Bergh et al., 2016) and Late Pleistocene skeletal and cultural remains of *H. floresiensis* at Liang Bua (Brown et al., 2004; Morwood et al., 2004, 2005; Sutikna et al., 2016a).

At Liang Bua, *H. floresiensis* is typically found in association with four other animals that have body masses greater than ~3 kg (van den Bergh et al., 2008, 2009; Hocknull et al., 2009; Meijer and Awe Due, 2010; Meijer et al., 2013, 2015): stegodon (*Stegodon florensis insularis*, a proboscidean), Komodo dragon (*Varanus komodoensis*), giant marabou stork (*Leptoptilos robustus*), and vulture (*Trigonoceps* sp.). All of these taxa are last observed in situ in the stratigraphic sequence ~60—50 ka (Sutikna, 2016; Sutikna et al., 2016a,b, 2018). Most faunal analyses from Liang Bua have focused primarily on *H. floresiensis* and these other large-bodied taxa; but some studies have also centered on smaller animals, such as shrews

(van den Hoek Ostende et al., 2006b), bats (Ouwendijk et al., 2014), and birds (Meijer et al., 2013, 2017), as well as murine rodents (i.e., rats; van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2012, 2015; Veatch, 2014), which are consistently represented throughout the ~190 kyr sequence (Sutikna, 2016; Sutikna et al., 2018).

Apart from introduced mice (*Mus* spp.), there are twelve species of murine rodents known from Flores (Table 1; Fig. 2; Hooijer, 1957; Musser, 1981; Musser et al., 1986; Kitchener et al., 1991a,b). Eight of these species are extant on Flores or on its immediate satellite islands, including *Papagomys armandvillei, Komodomys rintjanus, Paulamys naso, Rattus rattus, Rattus argentiventer, Rattus norvegicus, Rattus exulans,* and *Rattus hainaldi* (Musser, 1981; Kitchener et al., 1991b). All of the species of *Rattus* on Flores are widely distributed throughout Southeast Asia and most were likely introduced by modern humans sometime during the past few thousand years (Musser, 1981; van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2015). However, *R. hainaldi* is a small native species endemic to Flores (Kitchener et al., 1991a) and recent genetic evidence suggests that *Rattus exulans* may also have been a Flores endemic prior to ultimately dispersing widely beyond the island (Thomson et al., 2014), a suggestion previously proposed based on external morphology (Schwarz and Schwarz, 1967). Thus, both *R. hainaldi* and *R. exulans* are possible descendants of one or more early non-human-mediated dispersals of small-bodied *Rattus* to Flores.

The Flores murine fossil record extends from the Early/Middle Pleistocene to recent times, with material recovered from several sites within the So'a Basin as well as at Liang Toge and Liang Bua (Hooijer, 1957, 1967; Musser, 1981; Musser et al., 1986; van den Bergh et al., 2009; Brumm et al., 2010, 2016; Locatelli, 2011; Locatelli et al., 2012, 2015). This record preserves evidence of past populations of a diverse array of extant murines and of other taxa that are either extinct or at least presumed to be (e.g., *Papagomys theodorverhoeveni, Spelaeomys florensis,* and *Hooijeromys nusatenggara*). In total, there is considerable variation in dental size and morphology among the extant and extinct murine taxa on Flores (Fig. 2; Musser, 1981; Musser et al., 1986), indicating a fairly

continuous range of murine body sizes, from ~50 g (mouse-sized) to ~2000 g (common rabbit-sized; Table 1; Fig. 2).

Small mammals are typically sensitive to shifts in local ecology and thus small mammal assemblages often provide useful information for paleoecological reconstructions, including those that relate to the human fossil and archaeological record (Andrews, 1990; Avery, 1999, 2001, 2003, 2007; Flannery, 1999; Avenant, 2000; Reed, 2003; Matthews et al., 2005; van Dam et al., 2006; Hernández Fernández et al., 2007; Le Fur et al., 2009; Andrews and O'Brien, 2010; Blois et al., 2010; Demirel et al., 2011; Armstrong, 2015; Bennàsar et al., 2015; Nel and Henshilwood, 2016; Gomez Cano et al., 2017; Blanco et al., 2018; Madern et al., 2018). Although no discernible temporal trends have ever been observed in murine molar size for any given taxon on Flores (Musser, 1981; Locatelli, 2011; Locatelli et al., 2012, 2015), there is variation in the types of known preferred habitats for extant taxa (Table 1). For instance, the preferred habitats of *K. rintjanus* (~100—200 g) are primarily open grasslands intermittent with patches of short forests, but they may also be found in short palm and deciduous forests (Musser and Boeadi, 1980; Musser, 1981; Clayton, 2016a). Not surprisingly, this taxon displays morphological adaptations well suited for living in dry or seasonally dry shrubland environments such as sandy-colored upperparts, well-furred feet, and relatively large bullae (Musser and Boeadi, 1980; Musser, 1981), and is referred to as "a gerbil-like savanna species" (Musser et al., 1986:9). In contrast, *R. hainaldi* (a ~40—100 g) prefers more closed, montane forested habitats (Kitchener et al., 1991a; Suyanto, 1998; Clayton, 2016b) and *P. armandvillei* (~1200—2500 g) also prefers more closed or semiclosed forested habitats (Table 1; Musser, 1981; Suyanto, 1998; Gerrie and Kennerley, 2017). Thus, the relative abundances of these taxa in any given temporal period should reasonably reflect the degree to which the habitats in the area surrounding Liang Bua were more open or more closed.

At Liang Bua, approximately 275,000 recovered skeletal elements have been identified to family rank and ~220,000 of these belong to murines (Sutikna, 2016; Sutikna et al., 2018). Postcranial elements clearly dominate the murine assemblage throughout the

Table 1
The extant and extinct rats found on Flores.

Taxon	Body mass range (g)	Flores endemic[a]	Extant	Known or presumed diet[b]	Known or presumed behaviors[b]	Known or presumed habitat preferences[b]	Original descriptions
Papagomys armandvillei	1200—2500[c]	Yes	Yes	Leaves, fruits, and insects	Terrestrial, burrowing	Closed, semiclosed	Jentink (1892), Sody (1941)
Papagomys theodorverhoeveni	600—1600[d]	Yes	Uncertain	Fruits and insects	Terrestrial	Closed, semiclosed	Hooijer (1957b), Musser (1981)
Spelaeomys florensis	600—1600[d]	Yes	Uncertain	Leaves, flowers, buds	Arboreal	Closed	Hooijer (1957b)
Hooijeromys nusatenggara	300—600[d]	Yes	Uncertain	Unknown	Terrestrial	Open, semiopen	Musser (1981)
Paulamys naso	100—200[e]	Yes	Yes	Fungi, insects, snails, earthworms	Terrestrial, burrowing	Closed, semiclosed	Musser (1981), Musser et al. (1986)
Komodomys rintjanus	100—200[f]	Yes	Yes	Unknown	Terrestrial	Open, semiopen	Sody (1941), Musser and Boeadi (1980)
Rattus norvegicus	150—300[g]	No	Yes	Omnivore	Terrestrial	Commensal	
Rattus rattus/tanezumi	100—230[g]	No	Yes	Omnivore	Terrestrial	Commensal	
Rattus argentiventer	100—220[d]	No	Yes	Omnivore	Terrestrial	Commensal	Robinson and Kloss (1916)
Rattus hainaldi	40—100[h]	Yes	Yes	Unknown	Terrestrial, nesting	Closed, semiclosed	Kitchener et al. (1991a,b)
Rattus exulans	40—100[h]	No[i]	Yes	Omnivore	Terrestrial	Commensal	Peale (1848)

[a] Known only from Flores and/or satellite islands of Komodo, Rinca, and Padar.
[b] Based on information in Musser (1981), Musser and Boeadi (1980), Kitchener et al. (1991a,b), and Suyanto (1998).
[c] Based on data in Musser (1981) and three extant specimens with known body masses (1495—2285 g) in the collections of the Zoological Museum in Bogor, Indonesia.
[d] Based on molar sizes and other information in Musser (1981).
[e] Based on molar sizes and other information in Musser (1981) and Musser et al. (1986) and one extant specimen with a known body mass of 120 g (Kitchener et al., 1991a,b).
[f] Based on molar sizes and other information in Musser and Boeadi (1980) and Musser (1981).
[g] Based on recorded body weights of specimens in the collections of the National Museum of Natural History (USNM) in Washington, D.C.
[h] Based on body weights and other information of *Rattus exulans* in Tamarin and Malecha (1972), but applies to small *Rattus* sp. generally.
[i] Although currently widespread, this taxon may have originally been endemic to Flores (Thomson et al., 2014).
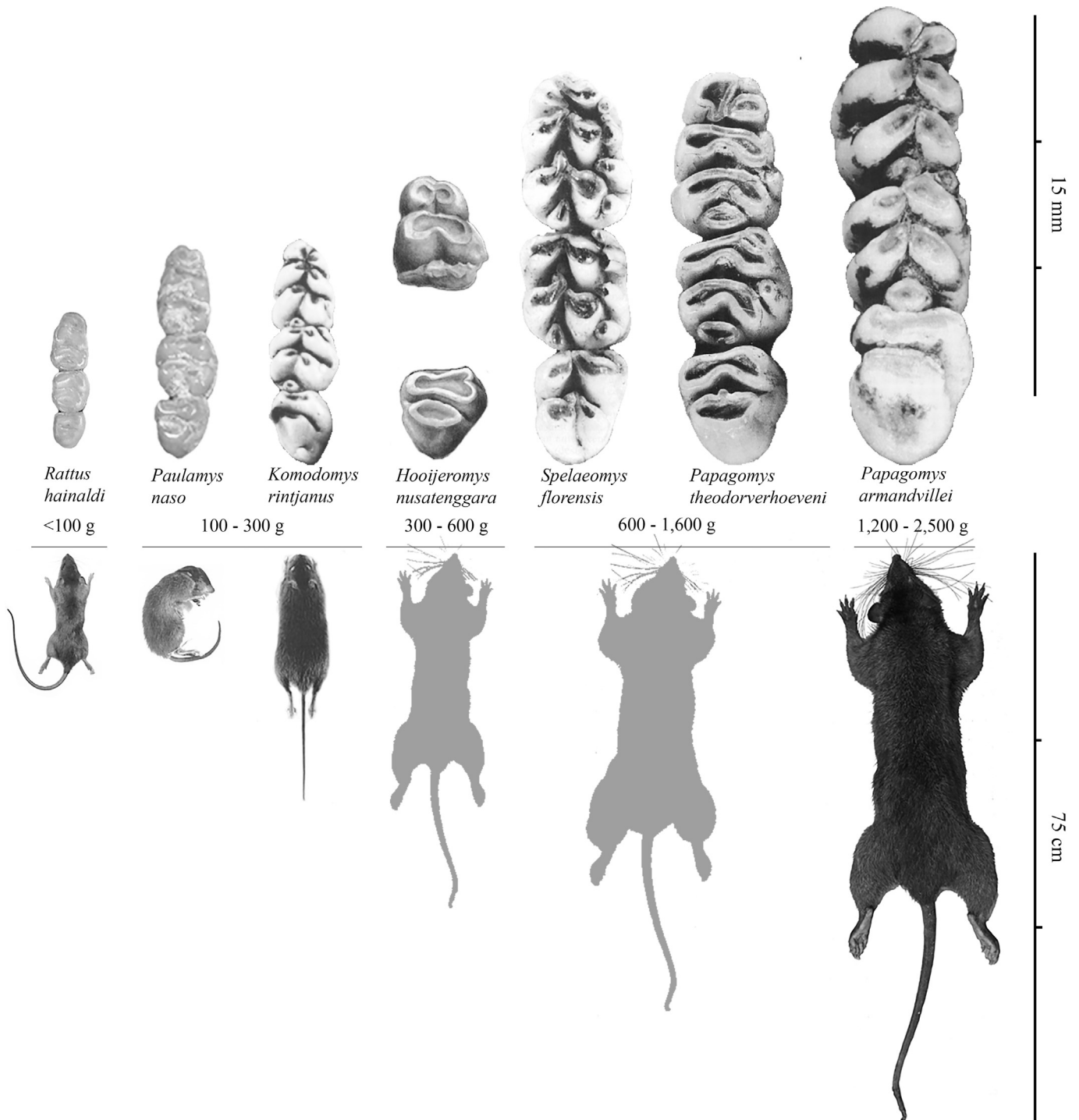
Figure 2. Right mandibular molar rows (above) and corresponding images of rats (below) endemic to Flores that illustrate the five body size categories defined and used in this study. From left to right, *Rattus hainaldi* (a photograph of *Rattus exulans* is shown), *Paulamys naso*, *Komodomys rintjanus*, *Hooijeromys nusatenggara*, *Spelaeomys florensis*, *Papagomys theodorverhoeveni*, and *Papagomys armandvillei*. Images modified from Musser (1981) and Kitchener et al. (1991a,b). Sizes of the rat images for *Hooijeromys nusatenggara*, *Spelaeomys florensis*, and *Papagomys theodorverhoeveni* are estimated based on their respective molar sizes.

entire ~190 kyr-sequence at Liang Bua as crania, jaws, or teeth comprise less than 10% of this total. As Flores is an oceanic island with a depauperate fauna, the list of agents potentially responsible for the accumulation of this murine assemblage is relatively small but includes birds (common barn owls, eagles, and vultures), reptiles (Komodo dragons and other varanids, snakes), and hominins (*H. floresiensis* and modern humans; Morwood et al., 2004, 2005;

Hocknull et al., 2009; Meijer et al., 2013; Sutikna et al., 2018). Komodo dragons, vultures, and snakes have high levels of digestive acids that typically dissolve bone (Auffenberg, 1981; Housten and Copsey, 1994) minimizing the likelihood that these taxa contributed to the accumulation of small mammal remains at this site. The Flores fossil record also notably lacks any nonhuman mammalian carnivores, although civets and domestic dogs were introduced to

the island by modern humans after ~3 ka (van den Bergh et al., 2009; Sutikna et al., 2018). Thus, for a majority of the stratigraphic sequence (~190–3 ka), the most likely predators responsible for the murine assemblage were either avian or hominin.

Previous studies of small mammal assemblages accumulated by avian predators indicate a bias to preserve the proximal femur and distal humerus (Andrews, 1990), and these are indeed the most frequent murine elements recovered at Liang Bua. Although systematic taphonomic analyses are underway to assess the specific processes involved in the accumulation of murine remains at Liang Bua, ~75% of 1576 humeri from smaller murines (body mass < 300 g) show low levels of digestion suggesting that a majority of this assemblage undoubtedly derives from owl and other raptor pellets (Veatch, 2014). The larger murines (body mass > 300 g), however, are beyond the typical size range of owl prey (~25–160 g; Table 1; Morris, 1979; Gubanyi et al., 1992). Thus, these larger murine taxa at Liang Bua were likely accumulated by a combination of non-avian predators (i.e., hominins) and natural deaths (Meijer et al., 2013; Veatch, 2014).

In this study, size variation in the murine assemblage is explored using measurements of the proximal femur and distal humerus as proxies for body mass. Species identification is not possible based solely on postcranial element size, given the likely overlapping ranges in body mass among some of these taxa, as well as overall similarities in their postcranial skeletons (Musser, 1981). Instead, the goal is to accurately identify different size classes of murine—which provide a useful combination of taxonomic and ecological information—and quantify their abundances at Liang Bua. These abundances are then examined relative to the most recent stratigraphic and chronological interpretations of the site (Sutikna et al., 2016a, 2018; Morley et al., 2017) as a means to identify shifts or stases in the distributions of murine body-size classes throughout the past ~190 kyr sequence that may have paleoecological and/or anthropogenic implications.

Previous paleoclimate and paleoenvironment reconstructions of Flores based on analyses of speleothems from Java and Flores inferred six main climatic/environmental periods spanning 49–5 ka (Westaway et al., 2009a). Between 49 and 17 ka, regional conditions shifted from being wet and organically rich (49–39 ka) to dry and organically poor (36–17 ka) with rainfall levels decreasing during the intervening 3 kyr period (Westaway et al., 2009a). These data suggest closed woodlands and montane forests may have been more prevalent in the area surrounding Liang Bua between 49 and 39 ka—and especially between 44 and 41 ka, during which time the sampled stalagmites grew particularly quickly—before shifting to more open habitats between 36 and 17 ka (Westaway et al., 2009a).

If these regional interpretations accurately reflect the local conditions surrounding Liang Bua, then we should expect to see changes in the distributions of murine body sizes at the site during these two respective temporal intervals, with taxa that prefer more forested habitats (e.g., *Papagomys* spp., *R. hainaldi*) being more prevalent during the earlier period and those that prefer more open habitats (e.g., *Komodomys*) being more prevalent during the later period. After the last glacial maximum, which occurred between 26.5 and 19.0 ka (Clark et al., 2009), conditions rapidly become increasingly wetter (17–15 ka), followed by the return of the monsoon (15–11 ka), ultimately returning to a stable period (11–5 ka) that was wet and organically rich (Westaway et al., 2009a). With these greater amounts of rainfall, open habitats would have given way to more closed woodland and montane forested ones (Westaway et al., 2009a), and we should once again expect to see a shift from more open habitat-adapted murines to more closed habitat-adapted ones.

An additional and longer paleoclimate record based on speleothems from Liang Luar, another cave ~800 m southeast of Liang Bua,

spans the past ~92 kyr and suggests a substantial reduction of vegetation cover and switch to C_4 grasses occurred in this area between ~69 and 62 ka (Scroxton et al., 2013, 2015; Scroxton, 2014). If this local interpretation is accurate, then during this interval we should expect to observe greater abundances of open habitat-adapted murines in comparison to those that prefer closed habitats. In contrast, this paleoclimate record suggests that during the temporal intervals before and after ~69–62 ka there was likely a mix of closed and open habitats available surrounding Liang Bua, but with the former much more common than the latter (Scroxton et al., 2013, 2015; Scroxton, 2014). Thus, we should expect to observe greater abundances of closed habitat-adapted murines during both of these periods.

2. Materials and methods

2.1. Stratigraphic units

The Liang Bua stratigraphy is currently divided into eight main stratigraphic units (Units 1–8), based on the eight tephras identified within the Liang Bua depositional sequence. The oldest and youngest units are further divided into five subunits (Sutikna, 2016; Sutikna et al., 2018, Tables 2 and 3; Fig. 4). Unit 1 consists of the oldest deposits at Liang Bua and is divided into two subunits (1A = ~190–120 ka; 1B = ~120–60 ka), whereas Unit 8 consists of Holocene sediments and is divided into three subunits (8A = 12–5 ka; 8B = 5–3 ka; 8C = < 3 ka).

The murine skeletal material examined here was the result of excavations of multiple 2 × 2 m areas (referred to as Sectors) at Liang Bua (Fig. 1). The excavations proceeded in 10 cm intervals (referred to as spits) while following all observable sedimentary layers (Sutikna et al., 2018). Almost all of the murine remains were recovered during wet-sieving of sediments from each excavated interval (i.e., recorded by spit and sedimentary layer) using 2 mm mesh.

2.2. Faunal analysis

We surveyed murine dentognathic remains from Liang Bua to confirm the presence of taxa identified by previous studies and to explore whether additional taxa are also present within the assemblage. Taxonomic identifications were based on diagnostic features, including molar size and morphology (Sody, 1941; Hooijer, 1957; Musser and Boeadi, 1980; Musser, 1981; Musser et al., 1986; Kitchener et al., 1991a,b). Molar sizes, in combination with known body masses for extant taxa, suggest a relatively wide range of murine body sizes are present in the Liang Bua assemblage (Table 1; Fig. 2).

Femoral head diameters (FHD) and articular breadths of the distal humerus (DAB) were measured using digital hand calipers from a comparative sample of 31 specimens with known body masses (representing 19 extant murine species) and 35 specimens without specimen-specific body mass data (representing an additional 15 murine taxa; Fig. 3; Supplementary Online Material [SOM] Fig. S1). All of these taxa are native to the Indo-Australian region and derive from the collections of the American Museum of Natural History and the Smithsonian Institution's National Museum of Natural History. This sample includes murine rodents that range in body mass from tiny shrew mice such as *Microhydromys richardsoni* from New Guinea (~11 g) to giant murines like *Phloeomys cumingi* from the Philippines (~1820 g). Both measurements show a reasonably consistent relationship with body mass based on these comparative data (SOM Fig. S1). Approximately non-overlapping ranges of FHD and DAB values were then used to define measurement ranges for five reasonably distinct body size categories

Table 2
Summary of measured femoral head diameters by stratigraphic unit[a], approximate age range, and body size category.

Unit	Age range (ka)	Unit description	NISP[b]					
			Small	Medium	Large	Huge	Giant	Total
8C	3—0	Neolithic to Present	258	283	23	13	4	581
8B	5—3	Neolithic transition	128	25	14	15	8	190
8A	12—5	Above T8 to Neolithic transition	302	43	18	29	11	403
7	13—12	T7 to T8	7	0	0	1	0	8
6	18—13	Above T6 to beneath T7	235	101	20	21	5	382
5	46—18	Above T5-capping flowstone to T6	147	35	14	17	3	216
4	47—46	Above T3 to flowstone above T5	17	3	0	1	1	22
3	50—47	T3	0	0	0	0	0	0
2	60—50	Between T2 and T3	118	14	3	7	5	147
1B	120—60	*H. floresiensis*-bearing sediments	2131	4431	139	22	15	6738
1A	190—120	Underlying gravel-rich layer	307	1176	39	2	1	1525
		Total NISP	3650	6111	270	128	53	10,212

[a] Stratigraphic units and approximate age ranges as defined and described by Sutikna (2016) and Sutikna et al. (2018).
[b] NISP = number of identified specimens.

(in increasing order): small (<~100 g), medium (~100—300 g), large (~300—600 g), huge (~600—1100 g), and giant (>~1100 g; Fig. 3; SOM Fig. S1). For instance, FHD values less than 2.5 mm most likely represent small-sized taxa (e.g., *R. exulans*-size, < ~100 g) whereas FHD values between 2.5 and 3.75 mm most likely represent medium-sized taxa (e.g., *R. rattus*-size, ~100—300 g).

Using digital hand calipers, FHD and DAB were measured from a sample of 10,212 murine femora and 1186 humeri (minimum number of individuals = 5197 and 622, respectively) recovered from excavations at Liang Bua. The femoral sample represents a majority of identifiable proximal bone ends retaining femoral heads deriving from multiple Sectors (IV, VII, XI, XII, XV, XVI, XVII, XXI, and XXV) whereas the humeral sample represents all identifiable distal bone ends retaining articular surfaces deriving solely from Sector XXI (Fig. 1). Each bone was then assigned to a body size category based on its measurement and the abundances of all size classes across all stratigraphic units were tabulated (Tables 2 and 3).

Statistical analyses were conducted using RStudio version 1.0.143 (RStudio Team, 2016) and PAST version 3.15 (Hammer et al., 2001). Chord distance (CD) analyses were used to measure similarity in the distribution of murine body sizes at Liang Bua through time. Stratigraphic units with similar abundances of each body size category will have CD values equal or close to 0, while those with completely dissimilar abundances will have CD values ~1.4, i.e., $\sqrt{2}$ (Ludwig and Reynolds, 1988). Unweighted pair group method with arithmetic mean (UPGMA) cluster analyses of all pairwise CD values were used to compare all stratigraphic units based on their respective compositions of murine body size categories (Legendre and Legendre, 1998). Evenness through the stratigraphic sequence was measured using the unbiased Simpson index (1 − D′), which here represents the probability that two randomly sampled specimens will belong to different body size categories, in order to further explore temporal

changes in murine body size distribution. Although this index is sometimes sensitive to changes in richness, it does not vary systematically as a function of sample size (Faith and Du, 2017). An unbiased Simpson index value near to 0 indicates that a given stratigraphic unit is dominated by a single murine body size category, whereas values ~0.8 (1−1/5, where 5 is the number of body size categories) indicate all body size categories are equally abundant.

Finally, the relationships between stratigraphic units based on their respective taxonomic abundances were examined using correspondence analysis, which is a multivariate statistical technique that provides an overall measure of variation across all units at once. Differences between all adjacent stratigraphic units in the abundance of a specific size class were evaluated for statistical significance using adjusted residuals derived from contingency table analysis (e.g., Grayson and Delpech, 2003; Lyman, 2008) in order to facilitate the interpretation of the multivariate results. The adjusted residuals are equal to standard normal deviates, in which absolute values greater than 1.96 are significant at α = 0.05.

3. Results

Our survey of murine dentognathic remains (n = 817) focused on three stratigraphic units (1B, 2, and 8C) and confirmed the presence of all taxa previously identified at Liang Bua (Musser, 1981; Musser et al., 1986; van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2012, 2015; Thomson et al., 2014). We also identified murine teeth and jaws that clearly belong to three other taxa, all of which fall into the large-bodied size class (~300—600 g) based on molar and jaw size relative to the comparative and Liang Bua samples (Fig. 2). Similar body size ranges were also obtained for the femoral and humeral samples, suggesting that the absolute

Table 3
Summary of measured femoral head diameters (FHD) and distal humeral articular breadths (DAB) by stratigraphic unit[a], approximate age range, and body size category from Sector XXI.

| Unit	Age range (ka)	Unit description	NISP[b] (FHD | DAB)					
			Small	Medium	Large	Huge	Giant	Total
8C	3—0	Neolithic to Present	5 | 11	5 | 10	1 | 2	2 | 5	2 | 1	15 | 29
8B—5	46—3	above T5-capping flowstone to Neolithic transition	36 | 28	8 | 6	3 | 4	3 | 4	3 | 0	53 | 42
4	47—46	Above T3 to flowstone above T5	1 | 7	2 | 5	0 | 1	0 | 2	0 | 0	3 | 15
2	60—50	Between T2 and T3	59 | 110	10 | 22	2 | 10	5 | 6	1 | 1	77 | 149
1B	120—60	*H. floresiensis*-bearing sediments	309 | 227	495 | 675	21 | 38	3 | 9	1 | 2	829 | 951
		Total NISP	410 | 383	520 | 718	27 | 55	13 | 26	7 | 4	977 | 1186

[a] Stratigraphic units and approximate age ranges as defined and described by Sutikna (2016) and Sutikna et al. (2018).
[b] NISP = number of identified specimens.

a. Humerus
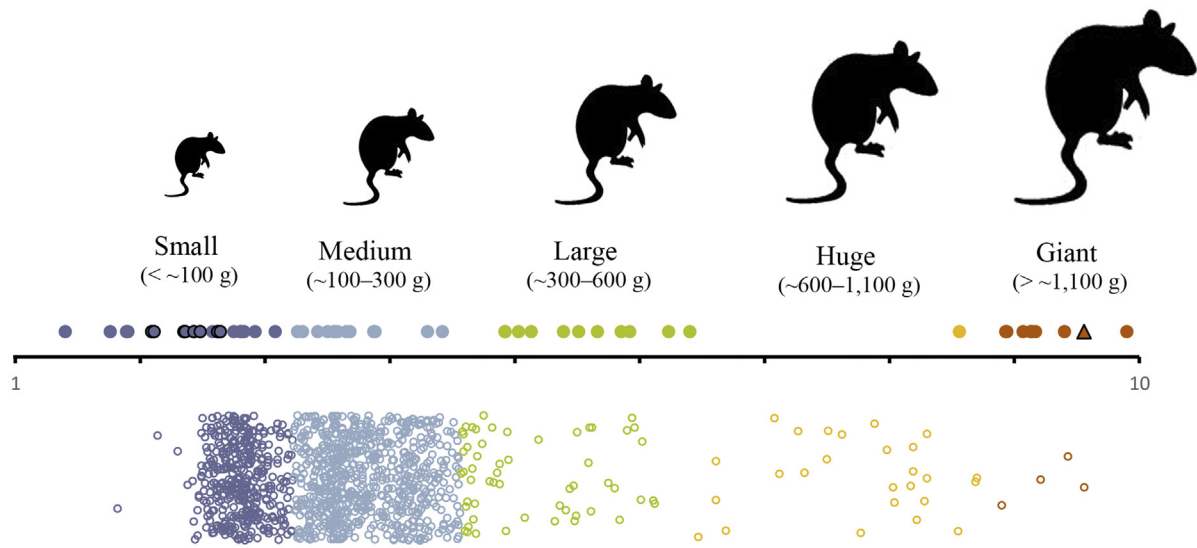
b. Femur
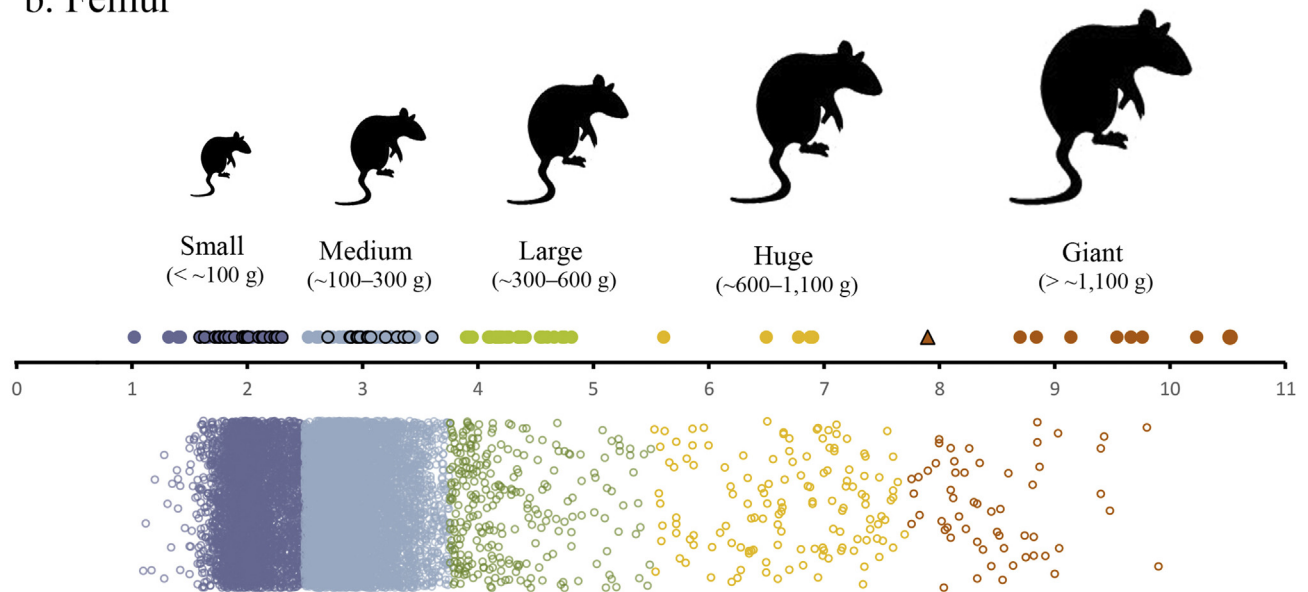
Figure 3. Body size categories based on the humeral distal articular breadth (DAB; a) and femoral head diameter (FHD; b) of extant murine species. Liang Bua FHD and DAB values are jittered below the respective x axis and compared with those of extant taxa with known body masses. The comparative sample consists of murine rodents of small (<~100 g; dark blue; such as *Rattus exulans*), medium (~100—300 g; light blue; such as *Rattus rattus*), large (~300—600 g; green; such as *Parahydromys asper*), huge (~600—1100 g; yellow; such as *Hyomys goliath*), and giant (>~1100 g; red; such as *Papagomys armandvillei*, represented as a triangle). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

sizes of the femoral head and distal humerus reasonably track the expected differences in body mass among these Flores taxa (Figs. 2 and 3; SOM Fig. S1; Musser, 1981). Of the Flores taxa that are also included in the comparative sample, *R. exulans* (~40—100 g) and *R. rattus* (~100—230 g) show discrete body size ranges that correspond with the small and medium-sized clusters from the Liang Bua murines (Fig. 3). Larger taxa—comparable in size to species such as *Parahydromys asper* (~400 g), the waterside rat from New Guinea, *Hyomys goliath* (~1000 g), the eastern white-eared rat from New Guinea, and *P. cumingi* (~1800 g), the southern giant slender-tailed cloud rat from the Philippines—are also well-represented at Liang Bua but occur at lower relative abundances. Nonetheless, the

postcranial measurements demonstrate that a reasonable continuum of large, huge, and giant-sized murines are present in the Liang Bua assemblage (Fig. 3).

The number of identified femoral and humeral specimens (NISP) are summarized in Tables 2 and 3 by body size category and stratigraphic unit. Only a small number of specimens were recovered from Units 3 and 7, which primarily consist of tephras T3, and T7 and T8, respectively. As these bones most likely represent elements reworked into these units during the deposition of these respective tephra, they and any other bones that could not confidently be assigned to one of the defined stratigraphic units were excluded from further analyses.
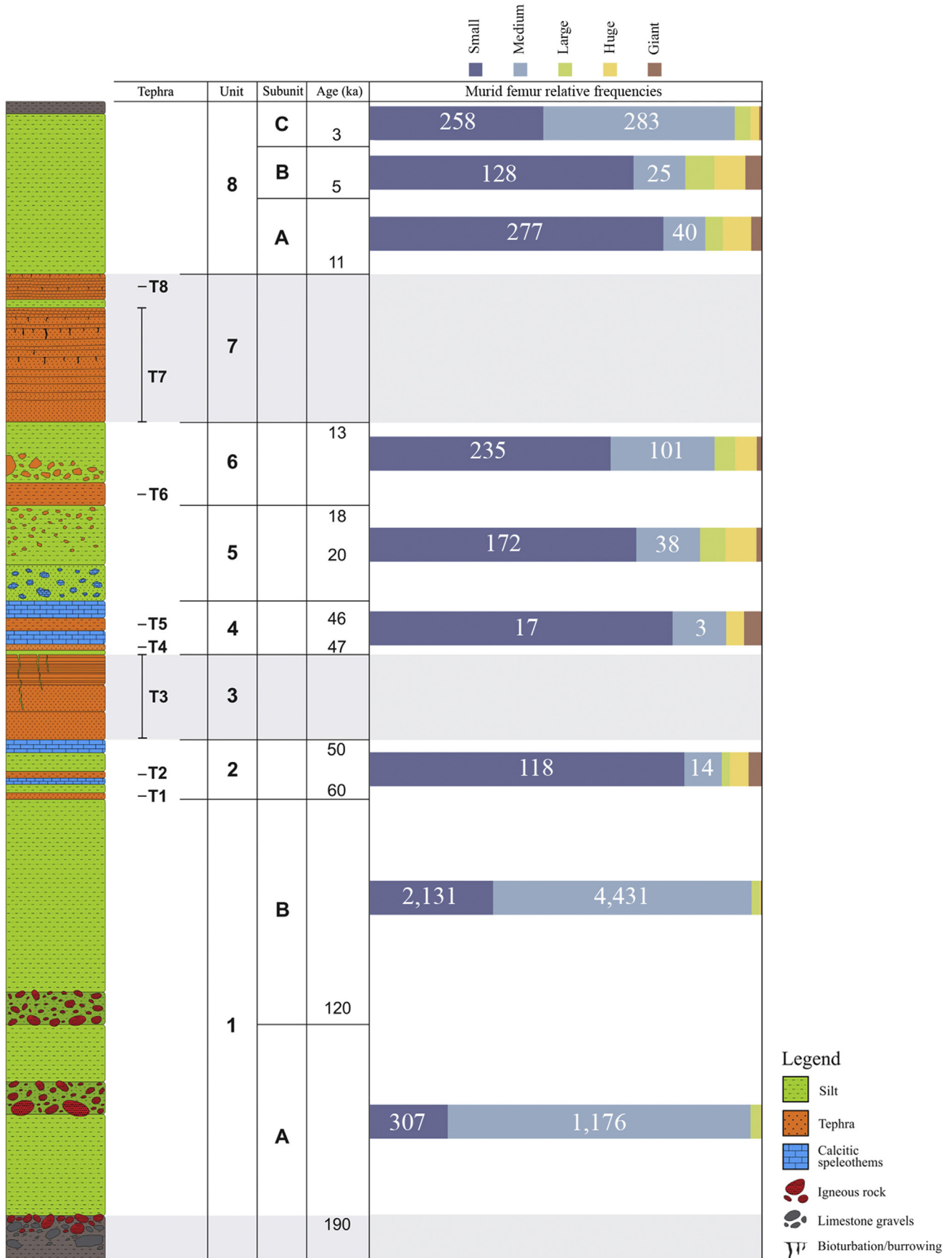
Figure 4. Relative frequencies of murine body size classes (based on 10,212 femoral head diameters) within each stratigraphic unit. Absolute numbers of small and medium murines are included in each bar.

Murine femora and humeri show similar patterns of size-class distribution throughout all stratigraphic units sampled in Sector XXI (Table 3; SOM Fig. S2; SOM Table S1), indicating that these fore- and hind limb elements are preserved in relatively similar proportions to each other in the Liang Bua assemblage. Medium-sized murines are most abundant within Units 1B (note Unit 1A has not been excavated in this Sector) and 8C, but they are noticeably less abundant in the intervening units. This temporal pattern in murine size-class distribution closely resembles the murine femoral data obtained from the eight other Sectors sampled suggesting that the smaller sample sizes of single Sectors are still sufficient to capture the overall murine postcrania accumulation patterns (Fig. 4). However, given the large femora sample that includes all eleven stratigraphic units, we focus our attention on reporting and discussing the results using this more comprehensive dataset.

The CD values for the assemblages across successive pairs of assigned depositional units are shown in Figure 4. Of all successive pairs, the greatest changes occur from Units 1B to 2 (CD = 0.96), which represents before and after the deposition of tephras T1 and T2 (~60 ka), and from Units 8B to 8C (CD = 0.63), which represents before and after the introduction of pottery at Liang Bua (~3 ka). Medium-sized murines dominate Units 1A and 1B (77.1% and 65.7% of NISP, respectively)—these are almost exclusively *Komodomys* based on the results of our dental survey (Table 4)—with relatively fewer large to giant-sized murines compared to more recent units. In Unit 2, which is above T2 but beneath T3 (~60—50 ka), small-sized murines (e.g., *R. hainaldi*) dominate (80.3% of NISP) with significantly fewer medium-sized murines compared to Units 1A and 1B (see also Table 4). Units 4—8B, all of which occur stratigraphically above tephra T3 (~50—47 ka) and together extend from the Late Pleistocene until ~3 ka, show small, gradual changes in the murine composition (CD = 0.08—0.26). Finally, in Unit 8C, murines of medium size are once again frequent but not to the same degree as they were in Units 1A and 1B (see also Table 4).

Cluster analysis of all pairwise chord distances between units results in two main clusters, with Units 1A, 1B and 8C forming one cluster and all other units forming the other (Fig. 5). Within the first cluster, Units 1A and 1B are more similar to each other than either is to Unit 8C. Within the second cluster, Unit 6 is most unlike all of the remaining units, which form two additional clusters. The first of these includes Units 2, 4, and 8A, while the second includes Units 5 and 8B. In the former cluster, Units 2 and 8A are more similar to one another than either is to Unit 4.

Analysis of evenness in murine body size categories throughout the stratigraphic sequence, using the unbiased Simpson index, also indicates some major differences between the assemblages (Fig. 6). The most marked shifts in evenness occur between Units 1A and 1B (increase), 1B and 2, and 6 and 8A (decreases). An overall trend

toward increasing evenness (i.e., all murine body size categories are more similarly abundant) is observed from the base to the top of the sequence but is not statistically significant (Spearman's rho [rs] = 0.17, $p < 0.67$).

Axes 1 and 2 of the correspondence analysis explain 96.0% and 2.6% of the variance in the abundances of murine body size categories, respectively (Fig. 7). Units 1A and 1B show the most negative scores along axis 1; these deposits are dominated by medium-sized murines (77.1% and 65.7% of NISP, respectively) followed by small-sized murines (20.1% and 31.6% of NISP, respectively) and low numbers of the other body size categories (≤2.6% of NISP; Table 2). Units 2 through 8B show the most positive scores along axis 1; these deposits are dominated by small-sized murines (61.5—87.5% of NISP) followed by medium-sized murines (9.5—26.4% of NISP) in all except Unit 7, where 1 of 8 femora (12.5%) is from a large-sized murine. Finally, Unit 8C falls in the middle of axis 1 due to its more equal numbers of medium and small-sized murines (48.7% and 44.4% of NISP, respectively). Overall, the observed changes are mostly driven by shifts in the abundances of medium-sized murines relative to all other sizes, and relative to small-sized murines especially, as indicated by the statistically significant adjusted residuals derived from contingency table analysis of murine body size class abundances across all adjacent stratigraphic units (Table 5).

4. Discussion

### 4.1. Murine body size classes and taxonomy at Liang Bua

Previous studies of murine dentognathic remains from Liang Bua, along with the results of our dental survey, suggest murines of small (*R. hainaldi* and *R. exulans*), medium (*Komodomys* cf. *rintjanus*, *P. naso*, and *R. rattus*), huge (*P. theodorverhoeveni* and *S. florensis*), and giant body size (*P. armandvillei*) are present (Musser, 1981; Musser et al., 1986; van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2012, 2015; Thomson et al., 2014). There have also been reports of what is probably a third species of *Papagomys* (Musser et al., 1986; de Vos et al., 2007) as well as a 'shrew rat' (see also Musser et al., 1986; van den Bergh et al., 2009; van den Hoek Ostende et al., 2011). We also observed molars and jaws of these as yet undescribed species, although they are rare in the assemblage overall, and both likely belong to our large-bodied size class. Based on molar size, the third species of *Papagomys* would have been slightly smaller in body size than *P. theodorverhoeveni* (Fig. 8). Although the molars of the shrew rat at Liang Bua are markedly reduced in size, as is typical for shrew rats (a label applied to various specialized but non-monophyletic animalivorous murines from Sulawesi, the Philippines, and New Guinea; e.g., Helgen and Helgen, 2009), the mandible is relatively large and suggests a body mass comparable to that of *Anisomys imitator*, the uneven-toothed rat of New Guinea (400—600 g).

We also found dentognathic remains of *Hooijeromys*, another large-bodied taxon known only from fossils recovered in central Flores at Early/Middle Pleistocene sites within the So'a Basin (Musser, 1981; Brumm et al., 2016). In the Liang Bua murine assemblage, teeth and jaws similar in size and morphology to that described by Musser (1981) for the holotype of *H. nusatenggara* are present (Fig. 8; Table 4). We tentatively refer these specimens to *Hooijeromys* cf. *nusatenggara* until more detailed taxonomic comparisons can be made with the holotype and referred material, which consists of a maxillary fragment with three molars and two mandibular molars, respectively (Musser, 1981).

In total, the postcranial and dentognathic remains at Liang Bua and our extant comparative sample indicate that a relatively wide but continuous range of murine body sizes were present at the site throughout the past ~190 kyr. Approximately 95% of the femora and humeri analyzed are from small (<~100 g) and medium-sized

Table 4
Number of identified specimens (NISP) of murine mandibular and maxillary dentaries from Sectors XXI and XII.

Taxon	Size	1B	2	8C	Total
Rattus hainaldi and *R. exulans*	Small	17	21	12	50
Komodomys cf. *rintjanus*	Medium	680	12	14	706
Paulamys naso	Medium	1	0	0	1
Rattus rattus	Medium	0	0	15	15
shrew rat	Large	0	0	2	2
Hooijeromys cf. *nusatenggara*	Large	4	0	2	6
Papagomys sp.	Large	0	2	1	3
Spelaeomys florensis	Huge	1	0	0	1
Papagomys theodorverhoeveni	Huge	7	9	2	18
Papagomys armandvillei	Giant	11	0	4	15
		721	44	52	817
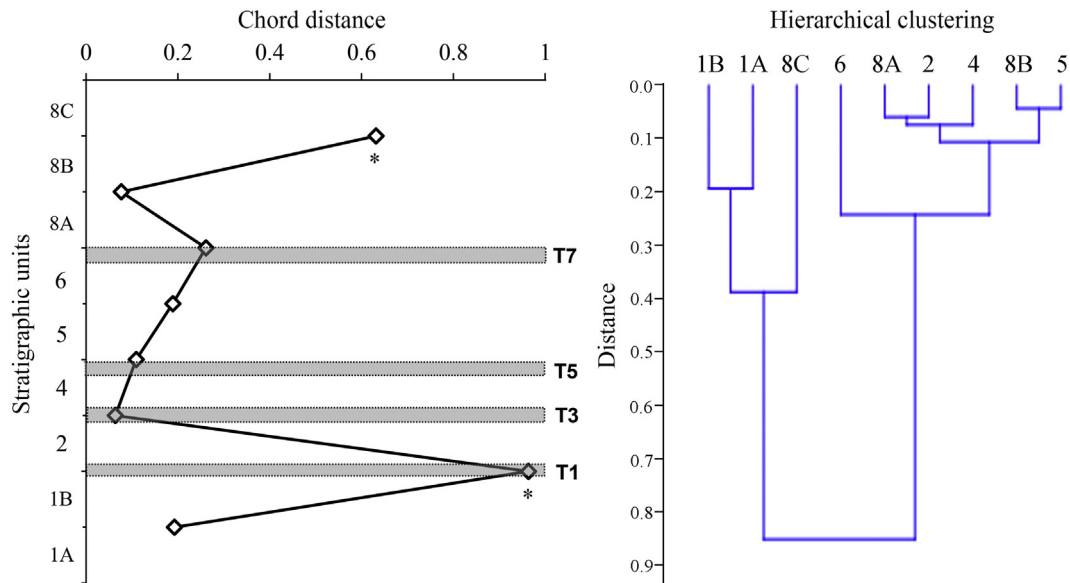
Figure 5. Chord distance (CD; left) and cluster (right) analyses of murine body size composition across stratigraphic units based on femoral head diameter data from nine sectors. Asterisks indicate significant CD values (diamonds) transitioning from Units 1B to 2 and from Units 8B to 8C. Note Units 1A, 1B, and 8C cluster together.

(~100−300 g) murines, while only ~5% are from larger ones (>~300 g; Tables 2 and 3).

4.2. Taphonomy

Small mammal cave assemblages are often the result of owl pellets accumulating over time (Dodson and Wexlar, 1979; Morris, 1979; Andrews, 1990; Gubanyi et al., 1992). At Liang Bua, barn owls (*Tyto* sp.) are well represented throughout the entire stratigraphic sequence and are the most abundant roosting raptor identified from the Late Pleistocene units (Meijer et al., 2013, 2015). Based on the low levels of digestion observed on the non-passerine avian assemblage (Meijer et al., 2013) and a sample ($n = 1576$) of murine humeri (Veatch, 2014), the abundant small and medium-sized murines at Liang Bua were mostly accumulated by barn owls (*Tyto* sp.).

Barn owls are small mammal specialists roosting and hunting in predominantly more open landscapes (e.g., shrubland, savanna, grassland) and often use caves as nesting sites (Andrews, 1990; Bruce et al., 2014). Unlike some raptors that hunt and roost in

Figure 6. Unbiased Simpson evenness index of murine body size abundances through time. Upper and lower margins represent 95% confidence intervals.

separate habitats and prey upon specific type of small rodents (Fernández-Jalvo et al., 2016), barn owls are less selective and will spend both activities in similar habitats consuming non-specific prey types (i.e., whichever species is available)—making their pellet accumulations more representative of local ecologies than predatorial bias (Glue, 1967; Andrews, 1990). Compared to most other raptors, barn owls also tend to leave minimal bone damage in the form of low digestion, postcranial breakage, and bone loss (Dodson and Wexlar, 1979; Andrews, 1990). While most behavioral and environmental data collected from barn owls derive from European and North American localities, many Late Pleistocene Southeast Asian archaeological sites report frequent barn owl activity with low degrees of bone damage (Hawkins et al., 2017a,b, 2018). However, vultures (*Trigonoceps* sp.), eagles (*Aquila* sp.), Brahminy kites (*Haliastur* cf. *indus*), and goshawks (*Accipiter* sp.) are also represented at Liang Bua (Meijer et al., 2013, 2015) and may also have contributed to the murine assemblage.

Conversely, the accumulation of larger-sized murines (~300−2500 g) at Liang Bua is likely due to hominins and/or natural deaths. While some depictions have suggested that *H. floresiensis* was hunting these larger-sized murines (Fig. 9), there is not yet any taphonomic evidence that supports such an interpretation. A systematic taphonomic study of the Liang Bua murine assemblage is underway to determine whether there is reasonable evidence (e.g., burning, cut marks, and tooth marks) to ascertain the degree to which hominins were responsible for parts of the total murine assemblage. While such taphonomic data are required to evaluate all of the likely sources of the murine accumulation at Liang Bua, owls (*Tyto* sp.) are almost certainly the major accumulator of the small and medium-sized murines (~95% of the total murine assemblage) found within the cave deposits, and thereby, these remains should reasonably reflect changes in local ecology through time.

4.3. Abundances of murine body size classes through time

All stratigraphic units at Liang Bua contain postcranial evidence of murines from each of the five body sizes classes used in this study (Tables 2 and 3), except Units 3 and 7, which consist mostly of volcanic tephra deposits. Element frequencies within each unit vary
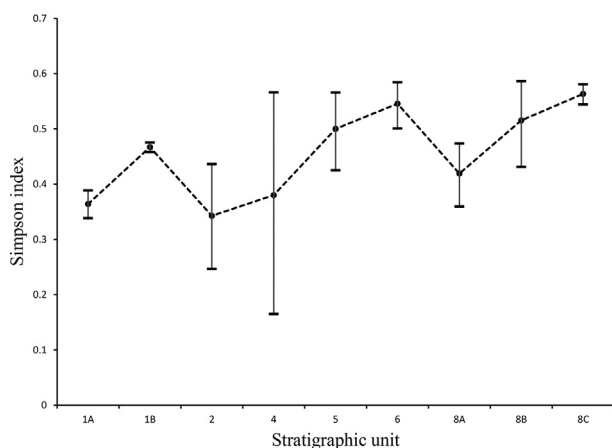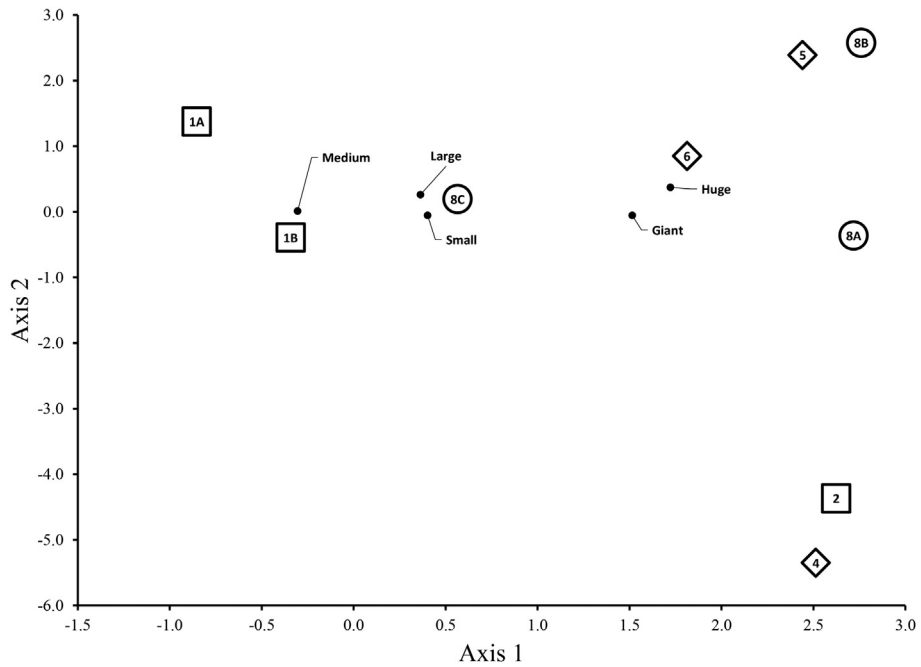
Figure 7. Correspondence analysis of murine body size abundances within stratigraphic units. Axes 1 and 2 represent 95.7% and 2.7% of the variance, respectively. Unit symbols: >50 ka, squares; 50 to 12 ka, diamonds; 12 ka to present, circles.

Table 5

Adjusted residuals (ARs) derived from contingency table analysis of rat body size class abundances in adjacent stratigraphic units. ARs to be read as standard normal deviates (values > |1.96| are statistically significant at α = 0.05 and are shown in bold). Positive values indicate an increase in abundance relative to the preceding stratigraphic unit whereas negative values indicate a decrease in abundance.

Size class	Stratigraphic unit							
	1A to 1B	1B to 2	2 to 4	4 to 5	5 to 6	6–8A	8A to 8B	8B to 8C
Small	**8.89**	**12.44**	−0.33	−0.89	−1.60	**4.04**	−1.93	**−5.50**
Medium	**−8.57**	**−14.10**	0.60	0.31	**2.87**	**−5.71**	0.89	**8.69**
Large	−1.20	−0.02	−0.68	1.23	−0.63	−0.50	1.46	−1.91
Huge	1.28	**8.21**	−0.04	0.56	−1.14	0.97	0.30	**−3.62**
Giant	1.26	**7.08**	0.27	−1.10	−0.08	1.41	0.96	**−3.40**
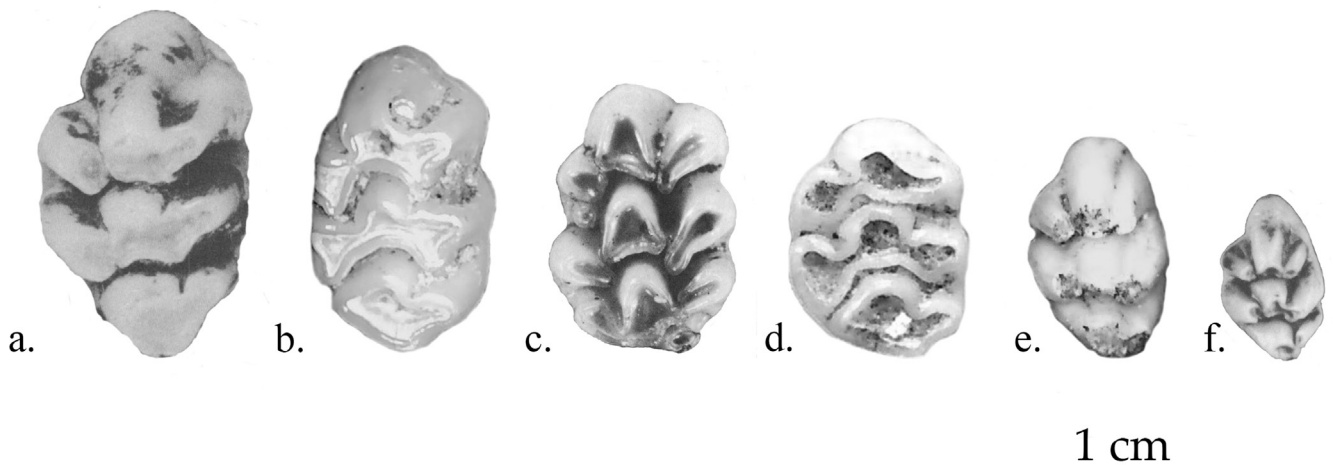
Figure 8. Left maxillary first molars of murines from Liang Bua. a) *Papagomys armandvillei*; b) *Papagomys theodorverhoeveni* (image flipped); c) *Spelaeomys florensis*; d) probable third species of *Papagomys* (image flipped); e) *Hooijeromys* cf. *nusatenggara;* and f) *Komodomys rintjanus*. Images of *Papagomys armandvillei* (RMNH, 18301; holotype), *Spelaeomys florensis* (LT 205), and *Komodomys rintjanus* (MZB 9016) are modified from Musser (1981), whereas the other images are from specimens recovered during excavations at Liang Bua.

Figure 9. a) One of the authors (M.W.T.) and Bonefasius Sagut measure a modern giant rat (*Papagomys armandvillei*) at Liang Bua. b) A reconstruction of *Homo floresiensis* carrying a giant rat over the left shoulder by paleoartist Peter Schouten (image is modified from its original form).

but reasonably match the frequencies of total bones recovered from each unit (e.g., Sutikna et al., 2018), which are likely due to a combination of the amount of time represented within each unit and variation in the rates of sedimentation and bone deposition. Interestingly, the relative abundances of these size classes across successive stratigraphic units reveal two major changes in murine body size distribution among the Liang Bua taxa that likely indicate concomitant ecological events as well as longer periods of general stability in between.

Units 1A to 2: ~190—50 ka Earlier studies linked the intensive use of the cave by *H. floresiensis* to wet, forested conditions (e.g., Westaway et al., 2009b), but it is important to note that this interpretation was based on the fact that most of the skeletal remains of *H. floresiensis* were originally but erroneously thought to be ~18—13 ka old (Brown et al., 2004; Morwood et al., 2004, 2005; Roberts et al., 2009). As *H. floresiensis* and the large-bodied taxa associated with it have yet to be discovered in situ at Liang Bua after ~50 ka (Sutikna et al., 2018), the paleoclimate and paleoenvironment reconstructions of Flores during the past 50,000 years (Westaway et al., 2009a,b) more aptly detail the environmental context surrounding the probable Late Pleistocene arrivals of modern humans to the island (Morley et al., 2017; Sutikna et al., 2018).

Small and medium-sized murines dominate Units 1A and 1B (~190—60 ka), but in Unit 2 (~60—50 ka) the numbers of medium-sized murines noticeably drop resulting in relatively larger abundances of smaller and larger-sized murines (Tables 2—4). This distributional change in murine body size classes from Units 1B to 2 resulted in the largest chord distance we observed in our analyses (CD = 0.96; Fig. 5). Based on a combination of dentognathic and postcranial evidence, the significant decrease in medium-sized murines from Units 1 to 2 is almost certainly due to reduced numbers of *Komodomys* relative to increased numbers of *R. hainaldi* (Table 4). Stratigraphically, these units are separated from each other by two volcanic tephras (T1 and T2) that were deposited ~60 ka (Sutikna et al., 2016a). These two tephras also directly overlie the

sediments from which all skeletal remains thus far attributed to *H. floresiensis* have been recovered (Sutikna et al., 2016a). Thus, the observed shifts in *Komodomys* and *R. hainaldi* abundances may have important implications for understanding why skeletal evidence of this hominin species has yet to be found above T1.

Examination of only the three largest murine size categories (large, huge, and giant) results in a similar pattern as that observed for the entire sample (Table 6). Units 1A, 1B, and 8C are distinguishable from the other units based on their greater abundances of large-sized murines, which we suspect mostly represent *Hooijeromys* cf. *nusatenggara*, because dental remains of this taxon were identified in these units more often than the other two large-sized murines were (i.e., the shrew rat and *Papagomys* sp.; Table 4).

The observed decline in *Komodomys* and probably *Hooijeromys* as well in Unit 2 (Table 4), however, is consistent with the paleoclimate record for this region of Flores that spans the past ~92 ka based on speleothems from Liang Luar, which is located ~800 m southeast of Liang Bua (Scroxton et al., 2013, 2015; Scroxton, 2014). This paleoclimate record suggests a substantial reduction of vegetation cover and a switch to C_4 grasses occurred in this area between ~69 and 62 ka (Scroxton et al., 2013, 2015; Scroxton, 2014). Stable isotope analyses of remains from sites ~880—650 ka in the So'a Basin (central Flores) of *Hooijeromys* and the proboscidean *Stegodon florensis* (the putative ancestor of the stegodon represented at Liang Bua; van den Bergh et al., 2008, 2009) show that these animals were grazers, primarily consuming C_4 grasses and preferring open habitats (Brumm et al., 2016). Assuming *Stegodon florensis insularis* at Liang Bua was also a grazer, the reduced number of stegodon remains recovered from Unit 2 compared to Unit 1B (Sutikna, 2016; Sutikna et al., 2018) most likely suggests a major shift in available C_4 grasses in the habitats surrounding Liang Bua after ~60 ka. We suspect that the large numbers of medium-sized murines (primarily *Komodomys*) and *Stegodon* as well as the relative higher proportions of large-sized murines (mainly *Hooijeromys*) in Unit 1B, which spans ~120—60 ka, were mostly accumulated during the ~69—62 ka open period and also during

Table 6
Adjusted residuals (ARs) derived from contingency table analysis of rat body size class (large, huge, and giant only) abundances in adjacent stratigraphic units. ARs to be read as standard normal deviates (values > |1.96|) are statistically significant at $\alpha = 0.05$ and are shown in bold). Positive values indicate an increase in abundance relative to the preceding stratigraphic unit whereas negative values indicate a decrease in abundance.

Size class	Stratigraphic unit							
	1A to 1B	1B to 2	2 to 4	4 to 5	5 to 6	6–8A	8A to 8B	8B to 8C
Large	**−2.09**	**−5.02**	−0.70	1.16	0.21	−1.31	0.68	1.73
Huge	1.44	**3.54**	0.09	0.00	−0.38	0.44	−0.90	−0.73
Giant	1.37	**3.01**	0.46	−1.80	0.30	1.14	0.32	−1.40

possible preceding C_4-dominated intervals prior to 92 ka (and thus not recorded in the Liang Luar speleothem record) in Units 1A and 1B. Unfortunately, difficulties in precisely dating these sediments preclude refining these units into shorter temporal intervals at present.

If our interpretation of these data is correct, then it helps explain why there is such a density of these C_4-adapted animals, as well as predators and/or scavengers of *Stegodon* (i.e., Komodo dragon, giant marabou stork, vulture, and *H. floresiensis*) in Unit 1 compared to all other subsequent units (Sutikna et al., 2018). In other words, as more open habitats shifted away from the areas surrounding Liang Bua by ~60 ka, so did *H. floresiensis* and these associated taxa, and thus the likelihood of their remains ending up in the cave's sediments diminished.

Units 4 to 8B: ~47–3 ka Almost no change in murine body size distribution was observed from Units 2 to 4 (CD = 0.06). This suggests that the major volcanic eruption that resulted in the deposition of tephra T3 (Unit 3) at Liang Bua, although likely initially devastating to the surrounding ecosystem, ultimately had little effect on the local murine populations and the habitats available to them. This is an interesting result relative to patterns observed for the entire faunal and stone artifact assemblages, wherein the transition from Units 2 to 4 marks the disappearance of *Stegodon*, Komodo dragon, giant marabou stork, and vulture from Liang Bua, as well as a marked shift to chert as a preferred raw material for hominin stone tool manufacture (Sutikna, 2016; Sutikna et al., 2018). If this megafaunal disappearance and the shift in raw material preference does, in fact, indicate the earliest presence of modern humans at Liang Bua and on Flores (Sutikna, 2016; Sutikna et al., 2018), then it appears their initial impact on the local murine fauna was minimal.

The observed changes in murine body size distribution from Units 4 to 5 and 5 to 6 remain modest (CD = 0.12 and 0.19, respectively) but reveal small increases in medium and large-sized murines (again, most likely *Komodomys* and *Hooijeromys*, respectively), probably reflecting a return of some open habitats in the greater area surrounding Liang Bua, particularly during Unit 6 (~18–13 ka). However, larger areas of closed habitat surrounding Liang Bua during this interval are suggested by the huge-sized murines, which are found in their greatest abundances in Units 5 through 8B (5.5–7.9% of NISP; 46–3 ka). Huge-sized murines are represented at Liang Bua by *P. theodorverhoeveni* and *S. florensis*, both of which are considered extinct, forest-adapted taxa (Musser, 1981). These results only partially correspond with the paleoclimate reconstruction of Westaway et al. (2009a), which predicted more open habitats during the 36–17 ka period. The observed discrepancy is most likely due to the broader, regional nature of these paleoclimate data and reconstruction relative to the local signal from the Liang Bua murines. Indeed, the Liang Bua murine signal more closely matches the speleothem record of stable carbon isotopes from nearby Liang Luar, which provides a local vegetation signal rather than a regional climate signal (Scroxton, 2014).

A relatively greater change is observed from Units 6–8A (CD = 0.26) and this, once again, is driven by a decrease in the medium-sized murines (Figs. 4 and 5). Unit 8A samples the early

Holocene from ~12 to 5 ka and the change in murine body size distribution is consistent with predictions of greater amounts of rainfall during this period following the return of the monsoon 15–11 ka (Westaway et al., 2009a; Scroxton, 2014). In other words, the change in murine body size distribution appears to have been driven by ecological shifts wherein open habitats were replaced by more closed woodland and montane forested ones (Westaway et al., 2009a; Scroxton, 2014). Almost no change in murine body size distribution occurs between Units 8A to 8B. Indeed, the observed CD value (0.08) is the second smallest in the entire sample and suggests that the surrounding paleoecology during this ~2 kyr interval remained largely similar to that of Unit 8A.

Units 8B to 8C: ~3 ka to the present The transition between Units 8B and 8C reveals another major shift (CD = 0.63), as medium-sized murines show their largest increase observed across the entire sequence and large-sized murines are more frequent than both huge and giant-sized ones. A pattern where medium-and large-sized murines are more abundant than small- and both huge and giant-sized ones, respectively, is only observed in Units 1A, 1B, and 8C (Table 2).

Previous research suggests that modern humans were transitioning to a more sedentary lifestyle in the area surrounding Liang Bua between ~5 and 3 ka (Unit 8B), wherein pottery appears for the first time (~3 ka) and the proportions of introduced large mammals (e.g., pigs) noticeably increase, which is a pattern that continues into Unit 8C (Morwood et al., 2009; Sutikna, 2016; Sutikna et al., 2018). Moreover, several intentional modern human burials accompanied with pottery, pig tusks, and stone adzes as grave goods appear in Unit 8C as well (Morwood et al., 2009; Sutikna, 2016; Sutikna et al., 2018). In combination, these data suggest that there was a shift to sedentism from the mid-Holocene onward that is probably associated with the adoption and subsequent intensification of agricultural practices (Morwood et al., 2009; Sutikna, 2016; Sutikna et al., 2018). This interpretation is further supported by the results of the current study as Unit 8C marks the first time in ~57 millennia that medium-sized murines increase beyond 30% of NISP (from 13.2% in Unit 8B to 48.7% in Unit 8C) and come nearest to their previous dominant abundances in Units 1A and 1B (77.1% and 65.7%, respectively).

The return of medium-sized murines is likely due in part to an increase in *Komodomys* (Table 4) but also to the appearance of introduced *Rattus* such as *R. rattus*, as evidenced by dentognathic remains (Table 4; Locatelli et al., 2015). The speleothem record from Liang Luar does not suggest that any substantial reduction of vegetation cover and/or switch to C_4 grasses occurred in this area at any time during the past ~15 kyr, but a slight trend toward more enriched ^{13}C isotope values is observed during the past ~5 kyr (Scroxton et al., 2013, 2015; Scroxton, 2014). This suggests that modern human populations may have been clearing forests in the area to provide suitable spaces for living and/or farming as well as, in turn, unintentionally providing new opportunities for the more open habitat-adapted medium-sized murines to flourish. However, these modern human subsistence behaviors did not cause native C_4 grasses to return to the area in any major way. Farming activities

during this period likely involved a combination of domesticated C_3 and C_4 plants such as rice and foxtail millet, respectively (Bellwood, 2005), and this could possibly explain why the local speleothem record does not shift more dramatically during this period to more enriched ^{13}C isotope values. In other words, the human-mediated shift in Unit 8C to a greater availability of more open habitats surrounding Liang Bua is distinct from the climate-mediated shift in Unit 1B that almost completely reduced the availability of more closed habitats.

5. Conclusions

The results of this study on murine body size variation through time demonstrates that the Liang Bua murine assemblage encodes significant details about the paleoecology of the area immediately surrounding the cave. Most importantly, the major relative reduction in medium-sized murines and concomitant rise in small-sized murines observed immediately after ~60 ka reasonably corresponds with the disappearance of *H. floresiensis*, the proboscidean *Stegodon florensis insularis*, and other associated large-bodied taxa (i.e., body mass > ~3 kg) from Liang Bua ~60–50 ka. These shifts are also consistent with the local ^{13}C speleothem record indicating a sudden decrease in available C_4 vegetation and a return to more closed, forested conditions after ~62 ka (Scroxton et al., 2013, 2015; Scroxton, 2014). Thus, the disappearance of *H. floresiensis* and these other large-bodied taxa at Liang Bua may simply be the consequence of them tracking their preferred, more open habitats to elsewhere on the island, as is likely the case with the medium-sized murine *Komodomys*. If this explanation is correct, then the precise timing of the extinction of *H. floresiensis*, *Stegodon*, giant marabou stork, and vulture must await new discoveries at Liang Bua or other as yet unexcavated sites on Flores.

Supplementary Online Material

Supplementary online material to this article can be found online at https://doi.org/10.1016/j.jhevol.2019.02.002.

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