A Morphological Analysis of the Humerus and Calcaneus of Endemic Rats from Liang Bua, Flores, Indonesia

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Dedication

I would like to dedicate this thesis to my loving and supportive family. To my parents (Ray and Dawn Veatch) who have always encouraged me to pursue my ambitions. To my sisters (Virginia and Sarah Veatch) who have been very patient and supportive during these last few years, especially to my little sister who has listened to countless explanations and discussions on rats. I would also like to include my grandmother (Gigi), aunts (Beth Aikens and Pam Veatch) uncle (Mike Veatch) and cousins (Elijah Aikens and Jason Veatch). Thank you all for your constant love and support.

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Abstract of Thesis

A Morphological Analysis of the Humerus and Calcaneus of Endemic Rats from Liang Bua, Flores, Indonesia

Liang Bua, an archaeological cave site on the Indonesian island of Flores, is best known as the type locality of the enigmatic hominin species, *Homo floresiensis*. Excavations at Liang Bua have recovered a very large number of vertebrate remains, including more than 230,000 bone fragments identified as murine rodents (order Rodentia, family Muridae, subfamily Murinae; i.e., rats). Previous research on the rats of Liang Bua indicates that at least five genera are represented (*Papagomys*, *Spelaeomys*, *Komodomys*, *Paulamys*, and *Rattus*), including species of small, medium, huge, and giant body size. The materials used in this study derive primarily from excavations at Liang Bua of Sector XXI, a 2 x 2 m area excavated in 2010. A suite of 22 measurements were used to analyze humeri (n = 1474) and calcanei (n = 372) from this assemblage in order to address questions about Liang Bua rat size, taxonomy, functional morphology, and taphonomy.

Murine dental remains from Sector XXI show that rats of giant (*Papagomys armandvillei*), huge (*Papagomys theodorverhoeveni* and *Spelaeomys florensis*), large (*Hooijeromys* cf. *nusatenggara*), medium (*Komodomys* spp. and *Paulamys naso*) and small (*Rattus hainaldi* and *Rattus exulans*) body size are present. All of these taxa, except *S. florensis* and *P. naso*, were also plausibly identified through a series of multivariate analyses of the postcranial elements studied here. Functional analyses of the preserved humeri and calcanei suggest multiple terrestrial rats inhabiting densely forested habitats (*P. armandvillei, P. theodorverhoeveni*, *Hooijeromys*) as well as open grassland

environments (*Komodomys* spp.). Taphonomic analyses of the humeri suggests that owls (*Tyto* sp.) were the primary accumulating agent of a majority of the murine assemblage based on characteristic digestive etching and breakage patterns observed on the bones. In total, these analyses of two postcranial elements indicate that considerable variation in size and morphology is present among the Liang Bua rats. This variation reflects a diverse array of murine taxa that differ dramatically from one another not only in body size, but also in shape and ecological adaptations.

Table of Contents

Dedication iii

Acknowledgements iv

Abstract of Thesis v

List of Figures viii

List of Tables xi

Chapter 1: Introduction 1

The known taxonomy of the Flores rats (extant and fossil) 2

Papagomys armandvillei

Papagomys theodorverhoeveni

Spelaeomys florensis

Hooijeromys nusatenggara

Komodomys rintjanus

Paulamys naso

Commensal *Rattus* spp.

Purpose of Study 14

Chapter 2: Materials and Methods 17

Chapter 3: Results 21

Size variation and attribution to size class and taxon 21

Humerus

Calcaneus

Summary

Functional morphology 27

Humerus

Calcaneus

Taphonomy 31

Chapter 4: Discussion 32

List of Figures

Figure 1. Map showing the location of Liang Bua, Flores and other islands of the Indonesian archipelago 46

Figure 2. *Papagomys armandvillei*: A modern specimen from Flores (A-B, E; photographs courtesy of the Liang Bua Team); Images of the maxillary (C) and mandibular (D) molar rows (modified from Musser, 1981) 48

Figure 3. *Papagomys theodorverhoeveni*: Images of the mandibular molar row (A) and maxillary 1st and 2nd molars (B) (Images modified from Musser, 1981 and Locatelli, 2011 respectively) 49

Figure 4. *Spelaeomys florensis:* Images of the maxillary tooth row (A) and mandibular tooth row (B) (images modified from Musser, 1981) 50

Figure 5. *Hooijeromys nusatenggara:* Images of the maxillary tooth rows (A) and an illustration of the 1st and 3rd mandibular molars (B) All images modified from Musser, 1981. Scale = 2 mm 51

Figure 6. *Paulamys naso:* Photograph of a modern specimen of *P. naso* (WAM M32000) (A) an illustration of maxillary tooth row (B) and an illustration of a mandibular tooth row (C) All images modified from Kitchener et al. (1991) in which no scale was provided 52

Figure 7. *Komodomys rintjanus:* A photograph of specimen MZB 9020 from Rinca Island (A) maxillary tooth row (B) and mandibular tooth row (C). All images modified from Musser, 1981 53

Figure 8. Commensal *Rattus* spp. on Flores: Mandibular tooth row of *R. rattus/tanezumi* (A) Maxillary tooth row of *R. argentiventer* (B) Cranial central views of *R. exulans* (left) and *R. norvegicus* (right) (C) Mandibular tooth row of *R. hainaldi* (D). Images A, B, C modified from Musser, 1981 and image D modified from Kitchener et al., 1991b 54

Figure 9. Images showing mandibular tooth rows of the murids from Flores: *P. armandvillei* (A) *P. theodorverhoeveni* (B) *Spelaeomys* (C) *Hooijeromys* (D) *P. naso* (E) *K. rintjanus* (F) *R. hainaldi* (G). All images modified from Musser, 1981 55

Figure 10. Map of previous excavations at Liang Bua. Sectors excavated between 2010 and 2012 outlined in red with Sector XXI (2010) highlighted in bold red 57

Figure 11. Murine mandibular alveolar lengths from Sector XXI (data provided by Kate McGrath): Taxonomic identifications and size ranges 59

Figure 12. Murine mandibular molar breadths from Sector XXI (data provided by Kate McGrath): Taxonomic identifications and size ranges; other murine data provided by Guy Musser (from MCZ, MZB, UF, Liang Toge and Liang Bua) and Matt Tocheri (from Liang Bua and the Soa Basin); published data from Hooijer (1957b) are also included 60

Figure 13. Humerus PCA with group size distinction. Small (X), Medium (O), Large (reverse triangle), Huge (square) and Giant (triangle). Known *P. armandvillei* (left) and *R. exulans* (right) specimens are indicated by closed, black circles 61

Figure 14. 3D scatterplot of the humerus with identified group size 62

Figure 15. PCA of the humerus with identified group size. Taxonomy is represented by colors based on Figure 14. Known *P. armandvillei* (red; left) and *R. exulans* (orange; right) specimens are represented by closed circles 63

Figure 16. 3D scatterplot of the humerus with identified group size. Taxonomy is represented by colors *P. armandvillei* (red), *P. theodorverhoeveni* (orange), *Spelaeomys* (purple), *Hooijeromys* (green), unknown (yellow), large *K. rintjanus* (grey), small *K. rintjanus* and *P. naso* (dark blue), and small *Rattus* spp. (light blue). Known *P. armandvillei* (red; right) and *R. exulans* (orange; left) specimens are represented by closed circles 64

Figure 17. Calcaneus PCA with group size distinctions. Small (X), Medium (O), Large (reverse triangle), Huge (square) and Giant (triangle). Known *P. armandvillei* (left) and *R. exulans* (right) specimens are indicated by closed, black circles 65

Figure 18. 3D scatterplot of the calcaneus with identified group size 66

Figure 19. Calcaneus PCA with identified group size. Size class and taxonomy is represented by colors based on figure 18. Known *P. armandvillei* (red; left) and *R. exulans* (orange; right) specimens are represented by closed circles 67

Figure 20. 3D scatterplot of the calcaneus with group size. Taxonomy is represented by colors: *P. armandvillei* (red), *P. theodorverhoeveni* (orange), *Spelaeomys* (purple), *Hooijeromys* (green), unknown (yellow), *K. rintjanus* and *P. naso* (dark blue), and small *Rattus* spp. (light blue). Known *P. armandvillei* (red; right) and *R. exulans* (orange; left) specimens are represented by closed circles 68

Figure 21. Size comparisons between dentition (circles), calcaneus (squares) and humerus (triangles). Taxonomy is represented by colors: *P. armandvillei* (red), *P. theodorverhoeveni* (orange), *Spelaeomys* (purple), *Hooijeromys* (green), unknown (yellow), *K. rintjanus* and *P. naso* (grey) and small *Rattus* spp. (light blue) 70

Figure 22. Hypothesized humeri from Sector XXI at Liang Bua: (A) Giant (*P. armandvillei*) (B) Huge (*P. theodorverhoeveni)* (C) Huge (*Spelaeomys*) (D) Large (*Hooijeromys*) (E) Large ("Unknown") 71

Figure 23. Hypothesized calcanei from Sector XXI at Liang Bua: (A) Giant (*P. armandvillei*) (B) Huge (*P. theodorverhoeveni*) (C) Huge (*Spelaeomys*) (D) Large (*Hooijeromys*) (E) Large ("Unknown") 72

Figure 24. Humerus: Relative size distribution of fossil and extant taxa of various age ranges 74

Figure 25. 3D scatterplot of the humeri at various developmental stages comparing *Phloeomys cumingi* (black diamonds), *Uromys caudimaculatus* (black circles) and *Hydromys chrysogaster* (black reverse triangle) with *P. armandvillei* (red triangles), *Hooijeromys* (green reverse triangles) and unknown (yellow reverse triangles) from Liang Bua 75

Figure 26. *P. cumingi* humeri at various stages of development 77

Figure 27. Rat species abundance recorded by depth. Light grey bars indicate number of identified specimens (NISP). Black bars indicate number of species recorded at a certain depth. 'H' and 'P' correspond to Holocene and Pleistocene deposits 78

Figure 28. Examples of digestion on the humeral distal articular surface (A) Low (B) Moderate 79

Figure 29. Examples of weathering damage to bone surface (A) BWS 1. Scale = 3 mm (B) BWS 4. Scale = 3 mm 80

Figure 30. Examples of bone modification from rodent teeth (A) Scale = 4 mm (B) Scale = 2 mm 81

Figure 31. Examples of bone modification from an unknown predator (A) scale = 2 mm (B) Scale = 1 mm (C) Arrows indicate bone cracking. Scale = 0.5 mm 82

Figure 32. Example of additional bone modification showing oblique marks on the distal, posterior portion of the diaphysis (A) scale = 2 mm (B) scale = 1 mm 84

Figure 33. Jitter plot of fossil humeri illustrating hypothesized size groups of *Tyto* spp. prey body size ranges. Dashed line separates Holocene from Pleistocene deposits 85

Figure 34. Relative comparisons of number of identified specimens (NISP) and number of identified species between avifauna from Sector XI (modified from Meijer et al., 2010) and murine postcrania from Sector XXI 86

List of Tables

Table 1. Body size estimates of the rats from Flores 47

Table 2. Definitions of rodent locomotor behavior (modified from Samuels & Valkenburgh 2008) 56

Table 3. Measurements and descriptions of variables for the humerus and calcaneus 58

Table 4. Humerus: Averages and standard deviations for each attributed murine species 69

Table 5. Calcaneus: Averages and standard deviations for each attributed murine species 69

Table 6. Calcaneal SHR index (shelf to heel ratio) of murines from Liang Bua compared to known semi-aquatic (*Hydromys*), terrestrial (*Leopoldamys*) and arboreal rats (*Crateromys*) 73

Table 7. Percent increase in various dimensions of the humerus from juveniles (no epiphyseal fusion) to adult (full epiphyseal fusion) 76

Table 8. Humerus taphonomic summary: Breakage, digestion, and weathering stages organized by spit and Holocene and Pleistocene 83

Table 9. Number of identified specimens and percentage of abundance (in parentheses) of dentition, humeri and calcanei between Holocene and Pleistocene deposits in Sector XXI 87

Introduction

The limestone cave site of Liang Bua on the island of Flores in the eastern Indonesian archipelago (Figure 1) attracted attention worldwide following the surprise discovery in 2003 of skeletal remains belonging to a previously unknown hominin species (Brown et al., 2004; Morwood et al., 2004). With a small stature (~106 cm) and body mass (~30-35 kg) (Jungers et al., 2009), as well as small brain (~400 cc; Falk et al., 2005; Kaifu et al., 2011) and primitive wrist (Tocheri et al., 2007; Orr et al., 2013), shoulder (Larson et al., 2007), and body proportions (Morwood et al., 2009; Jungers et al., 2009), these remains are now recognized as *Homo floresiensis*, a species distinct from *Homo sapiens*. *Homo floresiensis* is associated with a number of other interesting large animals (i.e., body mass > 9 kg), including pygmy stegodon (*Stegodon florensis insularis*; van den Bergh et al., 2008, 2009), Komodo dragon (*Varanus komodoensis*; Hocknull et al., 2009), giant marabou stork (*Leptoptilos robustus*; Meijer and Due, 2010; Meijer et al., 2013), and vulture (*Trigonoceps* sp.; Meijer et al., 2013). Although research on the Liang Bua fauna to date has focused primarily on *H. floresiensis* and these other large-bodied taxa, a range of murine rodent taxa (rats) truly dominates the assemblage (van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2012). For example, out of approximately 300,000 recovered skeletal elements identified to taxonomic family, more than 230,000 belong to rats (Matt Tocheri, in litt.).

The known taxonomy of the Flores rats (extant and fossil)

Twelve species of murine rodents larger than mice of the genus *Mus* have been documented from Flores (Musser 1981; Musser et al., 1986; Hooijer, 1957; Kitchener et al., 1991a) and eight of these are known to still be extant (Musser, 1981; Kitchener et al.,

1991a; Kitchener et al., 1991b). Extant species on Flores include *Papagomys armandvillei* (endemic), *Paulamys naso* (endemic), *Rattus exulans, Rattus hainaldi* (endemic), *Rattus rattus/tanezumi*, *Rattus argentiventer*, and *Rattus norvegicus*; and *Komodomys rintjanus* (endemic) is known as an extant species on the immediately adjacent islands of Rinca and Padar (Musser, 1981; Kitchener, 1991b). All of these species of *Rattus*, with the exception of *R. hainaldi*, which is endemic to Flores, are widely distributed in Southeast Asia and thought to have been introduced to Flores by modern humans during the mid to late Holocene (Musser et al., 1981; Locatelli, 2011; Locatelli et al., 2012). However, recent genetic evidence suggests that *R. exulans* may also originate from Flores (Thomson et al., 2014).

The fossil and subfossil record of Flores includes evidence both of murine taxa that are known as modern animals (*Papagomys armandvillei, Paulamys naso, Komodomys rintjanus, R. exulans, and R. hainaldi*), and of other taxa not known as modern animals, and thus presumed extinct (*Papagomys theodorverhoeveni, Spelaeomys florensis, Hooijeromys nusatenggara*). The murine fossil record on Flores extends from the early Pleistocene to recent times, with material recovered from several sites within the Soa Basin (Musser, 1981; Hoojier, 1957b), Liang Bua (Musser, 1981; Musser et al., 1980; van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2012) and Liang Toge (Hooijer, 1957a). These taxa vary greatly in terms of dental size and morphology (Musser, 1981; Musser et al., 1986), with body size estimates ranging between 1,200 g (common rabbit-sized) and 72 g (mouse-sized). For the purposes of this study, these taxa were grouped into the following five size classes based on dental size (in decreasing order): giant, huge, large, medium, and small (Table 1). Known characteristics and

approximate temporal ranges for each of these species are summarized below, from largest to smallest body size.

Papagomys armandvillei (Figure 2)

Papagomys armandvillei is extant and known only from Flores. It is a very large rat with relatively short ears and tail and a chunky body (Musser, 1981). The coat is primarily a dark brown or tan color with darker pigment on the midline of the head and body (Musser, 1981). The ventral coating is a paler gray color with a "slight tan suffusion" (Musser, 1981: 75). These coloration differences contrast mostly under the chin, hands, and feet, as well as under the middle of the body (Musser, 1981). Overall, *P. armandvillei* has been characterized as a terrestrial rat, well adapted for a burrowing and land-dwelling habitat while consuming leaves, fruits, and possibly insects (Musser, 1981). Body size is estimated at roughly 1,200 g based on cranial and dental dimensions (Amori et al., 2012). The remains of *P. armandvillei* have been presented as evidence of the hunting and scavenging strategies of *H. floresiensis* in the Late Pleistocene, and of modern humans in the early and later Holocene (Morwood et al., 2009; Locatelli et al., 2012).

Papagomys armandvillei was originally described in the genus *Mus* by Jentink (1892) (at a time when a wide array of murine rodents were classified in *Mus*) and subsequently transferred to the genus *Mallomys*, a large endemic rat of New Guinea, by Thomas in 1898 (Thomas, 1898; Musser, 1981; Hooijer, 1957b) based especially on its gigantic size. Sody (1941) erected the genus *Papagomys* for *armandvillei* because of differences in dental morphology compared to *Mallomys* (Musser, 1981). Subfossil fragments of this species were first collected along with two additional giant rat taxa by

Fr. Theodore Verhoeven in 1952 from Holocene cave deposits at Liang Toge, located in western central Flores (Hooijer, 1957b, Musser, 1981). The teeth recovered from Liang Toge have identical dental features and are generally larger than those of extant *P. armandvillei* specimens, suggesting the fossil sample represented a larger version of the extant rat. Hooijer formalized this distinction by naming the Liang Toge fragments *P. a. besar* (Hooijer, 1957b; Musser, 1981). The lower first and third molars tend to have similar width dimensions, while the second molar tends to be relatively wider, all with simple "chevron-shaped" laminae (Musser, 1981: 82). A full description of craniodental morphology was provided by Musser (1981) (see also Hooijer, 1957b).

Papagomys theodorverhoeveni (Figure 3)

A second species of *Papagomys* was described by Hooijer (1957b) from cave deposits at Liang Toge, which were carbon dated to 3,550 years before present (Jacob, 1967). Hooijer (1957b) initially described eighteen mandibular fragments as a new taxon, *P. verhoeveni* (Musser, 1981). Further analyses by Musser (1981) showed that the mandibular and maxillary fragments Hooijer designated as the holotype for *P. verhoeveni* were actually fragments of *P. armandvillei*. The remaining seventeen fragments, however, did represent a second species of *Papagomys* (Musser, 1981). This species was named *Papagomys theodorverhoeveni* by Musser, recognizing Hooijer's original intent of naming the species after Fr. Theodor Verhoeven, an early explorer of Flores' fossil and archaeological records (Musser, 1981). The holotype (Specimen 12) is a fragment of right mandible with a preserved molar row (M_{1-3}) (Musser, 1981). Differences between this species and *P. armandvillei* include aspects of molar size and occlusal surface

morphology (Figure 2 and 3). The lower molar cusps are more complex, set farther apart, and are more erect than the more forward slanting lower molar cusps of *P. armandvillei* (Hooijer, 1957b; Musser, 1981). The M_3 of *P. theodorverhoeveni* is also relatively narrower than M_{1-2} compared to the tooth row of *P. armandvillei* (Hooijer, 1957b; Musser, 1981). Due to its slightly smaller dentition, it is hypothesized that *P. theodorverhoeveni* (~ 700-1,000 g) is also slightly smaller than *P. armandvillei* in body size (Musser, 1981). Musser (1981) also suggests this species most likely occupied a different ecological niche based on the complexity of the occlusal surface of the mandibular molars.

A recent study of murine dental material from Liang Bua attributed a number of maxillary fragments to *P. theodorverhoeveni* (Locatelli, 2011; Locatelli et al., 2012). These maxillary molars differ from those of *P. armandvillei* mostly in size but also morphology (Locatelli, 2011). The upper molar rows in *P. theodorverhoeveni* are thinner with more triangular cusp patterns than the wider tooth rows and rounder cusps of *P. armandvillei* (Locatelli, 2011).

Unfortunately, all that is currently known about *P. theodorverhoeveni* derives from the subfossil jaw fragments discussed above. Thus, an important goal of this study is to plausibly identify postcranial material that belongs to this taxon.

Spelaeomys florensis (Figure 4)

Spelaeomys florensis was also initially described from the Liang Toge deposits and was regarded as having the most abundant recovered elements (Hooijer, 1957b). The holotype (Specimen 1) consists of a right maxilla with preserved M^{1-3} and has an

extremely complex occlusal surface (Hooijer, 1957b). This surface contains high, nearly erect cusps and the molars are long relative to their widths (Musser, 1981). The width of the upper second molar relative to the first in *S. florensis* is comparable to that in *P. armandvillei* and *P. theodorverhoeveni*; however, its third molar is significantly narrower (see Fig. 10; Musser, 1981). Overall, the dental dimensions of *S. florensis* suggest a body size (~600-900 g) more similar to that of *P. theodorverhoeveni* than *P. armandvillei* (Musser, 1981).

Spelaeomys is easily distinguishable from *Papagomys* based on differences in molar morphology. In addition to the complex, overlapping cusp pattern, *S. florensis* has three additional cusps (t1bis, t7, and posterior cingulum) not observed in *Papagomys* (Musser, 1981). These differences in occlusal cusp pattern and morphology suggest a distant relationship between *Spelaeomys* and the other Floresian rats (Musser, 1981). In comparison with other murines from neighboring islands, the shape, quality and position of the cusps most resembles those from *Mallomys* from New Guinea (Musser, 1981). Although similar morphological features of the palatal bridge and zygomatic process of *Spelaeomys* possibly suggest a relationship to *Papagomys*, the cranial and dental variation in *Spelaeomys* are most similar to *Mallomys* (Musser, 1981). Therefore, *Spelaeomys* has been hypothesized to be more closely related phylogenetically to the radiation of "old endemic" rats from New Guinea and Australia (which include *Mallomys*) than to other southeast Asian murine taxa, such as *Papagomys* and the other native Floresian rats (Musser, 1981)

Spelaeomys is also thought to have occupied a different ecological niche than *Papagomys* (Musser, 1981). The hypsodont molars in *Spelaeomys* suggest differences in

diet from the simpler occlusal morphology of *Papagomys* (Musser, 1981). Specifically, *Spelaeomys* is thought to have ingested leaves, flowers and buds (Musser, 1981). Musser (1981) also hypothesized an arboreal habitus, however with no evidence of postcranial morphology, specific locomotor or habitat adaptations in *Spelaeomys* are unknown. Identifying postcranial elements representing *S. florensis* is thus an important goal of this study.

Hooijeromys nusatenggara (Figure 5)

Hooijer (1957a) described the remains of a few tooth fragments from Olabula, an eroded sandstone site on the Soa Plateau located in the Central Ngada Province, Flores. The sediments were initially described as Middle or Upper Pleistocene in age, though no radiometric dates were available (Musser, 1981). More recent work at multiple sites within the Soa Basin has obtained radiometric dates between ~1.0 and 0.8 million years ago (Morwood et al., 1999; Brumm et al., 2010). Musser (1981) provided the first description of *Hooijeromys nusatenggara*, a new genus and species named after D.A. Hooijer, based on a right maxillary fragment with M^{1-3}. There was another right maxillary fragment recovered with a complete tooth row, however the occlusal surface was badly worn. An isolated upper third molar and three lower molars were recovered from the site of Boa Leza, just a few miles west from Olabula (Ola Bula) and tentatively attributed to this taxon (Musser, 1981).

Morphologically different from *P. armandvillei* and *P. theodorverhoeveni*, *Hooijeromys* is diagnosed as having low cusps on both the upper and lower molars, smaller teeth in a relatively larger bony palate, and a simple cusp pattern. Based on tooth

row size and morphology, Musser (1981) suggests that *Hooijeromys* was similar in body size to *Uromys anak* (450-1000 g) and *Mesembriomys gouldii* (700-900 g), which are large rat species from New Guinea and Australia respectively (Flannery, 1995; Watts and Aslin, 1981). Thus, *H. nusatenggara* was likely a large-bodied rat, smaller in body size than *P. armandvillei*, *P. theodorverhoeveni*, and *Spelaeomys* (Musser, 1981). *Uromys* is considered a terrestrial rat, however there is no conclusive evidence to suggest *Hooijeromys* was arboreal or terrestrial in habitus (Musser, 1981). The overall configuration of the large bony palate, shorter tooth row, and wide, robust zygomatic plate suggests that *Hooijeromys* was very different from *P. armandvillei* and *P. theodorverhoeveni* morphologically and ecologically (Musser, 1981). Therefore, the identification of postcrania belonging to this taxon could provide important information pertaining to ecological relationships among the larger-bodied rats of Flores.

Paulamys naso (Figure 6)

A series of five unique dental fragments of a medium-sized murine were recovered by Fr. Verhoeven at Liang Toge. Based on differences in dental morphology, Musser (1981) suggests that these five fragments belong to a rat unlike any murine described on Flores and proposed a new genus and species, *Floresomys naso*. Later however, Musser realized that an earlier publication had erected the name *Floresomys* for a sciuravid genus (Fries et al., 1955), making the name unavailable for this Flores murine; Musser renamed the generic name as *Paulamys* (Musser, 1986). The holotype of *naso* consists of a small piece of mandible containing the lower molar row and a piece of incisor (Musser, 1981). Fragments identified as *Paulamys* were distinguished from all

Rattus species found on the island based on having short molar rows, thick laminae on the occlusal surfaces of the molars, a large anterior cusp on the second molar, and a body size similar to *Rattus norvegicus* (200-300 g). These specimens also have slim incisors and an elongated dentary anterior to the tooth row, suggesting a long rostrum (Musser, 1981). While these features are characteristic of "shrew rats" (e.g. *Chrotomys* or *Rhynchomys* of the Philippines), the overall morphology described for *P. naso* does not suggest a close phylogenetic relationship with these other rats (Musser, 1981). Instead, Musser (1981) suggested that *P. naso* was a terrestrial rat with a diet similar to *Bunomys*, a genus from Sulawesi sharing many similarities in size and dental morphology.

In 1989 an expedition led by the Western Australian Museum and Museum Zoologicum Bogoriense trapped a long nosed rat near Kelimutu in central south Flores that was identified as the first modern specimen of *P. naso* (weighing ~120 g) (Kitchener et al., 1991a). Morphological comparisons and phylogenetic relationships of this new specimen (WAM M32000) were analyzed to determine the systematic relationship of *Paulamys* compared to 12 other genera including *Rattus* and *Bunomys* (Kitchener et al., 1991). Phylogenetic analyses included 29 characters provided by Musser (1981) (Kitchener et al., 1991a). Initial results indicated that *Paulamys* is likely sister to *Bunomys* (Kitchener et al., 1991a), and indeed, Kitchener et al. (1991a) formally classified the species in the genus *Bunomys*, as *B. naso*. Other authorities have continued to maintain *Paulamys*, represented only by *P. naso*, as a generic lineage distinct from *Bunomys* of Sulawesi (Musser and Carleton, 2005).

Morphological descriptions suggest a relatively close relationship with *Rattus*, but with the following differences: short tail relative to body length, moderately large body

size, long rostrum, lacks dorsolateral ridges on braincase, slight beading of dorsolateral interorbital region, and an absence of cusp t_3 on the upper M^{1-3} (Kitchener et al., 1991a). The overall medium size of the animal suggests adaptive differences compared to the much larger body sizes of *Papagomys*, *Spelaeomys*, and *Hooijeromys* (Kitchener et al., 1991a). *Paulamys* differs from *Komodomys* by having a relatively flattened and longer rostrum, simple occlusal surfaces of the molars, and a relatively similar sized M_2 compared to M_1 (Kitchener et al., 1991a).

The modern *Paulamys* specimen was collected in a dense rainforest environment in a dry creek bed (Kitchener et al., 1991a). Scattered shrubs and dense ferns covered the terrain, with vines abundant throughout the area (Kitchener et al., 1991a). Stomach remains included oligochaete worms, insect larva, unidentified plant and vegetable matter, and small amounts of seeds, insects and fungal material (Kitchener et al., 1991a), indicating an omnivorous diet. The shape of the hind pads suggests a terrestrial habitus with occasional burrowing to access underground foods and dig among leaf litter (Kitchener et al., 1991a). With this wild-caught specimen of *P. naso*, many of Musser's (1981) original speculations regarding the phylogeny, habitus, and diet of this species were confirmed (Kitchener et al., 1991a).

Komodomys rintjanus (Figure 7)

Komodomys rintjanus (~140 g) was originally known exclusively from the islands of Rinca and Padar off the western coast of Flores (Musser and Boeadi, 1980). The species was originally described as a member of the genus *Rattus* (Sody, 1941) but was subsequently removed to a new, monotypic genus (*Komodomys*) after further analyses by

Musser and Boeadi (1980). The first documented Floresian example of this rat was recovered from Fr. Verhoeven's excavations at Liang Toge (Musser, 1981). These sediments produced many specimens that were attributed to *Rattus exulans, Rattus argentiventer,* and *Rattus rattus/tanezumi.* Additional analyses by Musser suggested that one of these specimens ("Specimen 5") belongs to *Komodomys* because of similar dental and mandibular features compared with the holotype specimen of *K. rintjanus* (Musser, 1981). Specimen 5 consists of a left mandibular fragment with an incisor and preserved tooth row (Musser, 1981). The lower molars are relatively large and wide compared to the absolute size of the mandible (Musser, 1981). The lower M_1 and M_3 have similar width dimensions while M_2 is substantially wider (Musser, 1981). The long rostrum and nasals are more similar to some Australian murines (e.g., *Conilurus*) than to either *R. argentiventer* or *R. rattus/tanezumi*, possibly indicating an adaptation to savanna woodlands (Musser and Boeadi, 1980).

Rattus hainaldi (Fig. 8D)

Rattus hainaldi (~ 50 g) is an extant species of murine collected on Flores in 1990 during the same biological survey that collected *Paulamys naso* from south central Flores (Kitchener et al., 1991b). Collected near the locality of Desa Longko, this rat, so far known only from Flores, is morphologically distinct from all other species of *Rattus* by the following combination of features: small body size (but slightly larger than *R. exulans*), relatively longer tail, bicolored with whitish ventral coat and a dark brown dorsal coat, and a moderately long rostrum (Kitchener et al., 1991b). The upper and lower molar occlusal surfaces are simple and similar to other *Rattus* spp. as characterized by

Musser (1981) from Flores, especially *R. exulans* (Kitchener et al., 1991b). However, genetic analyses of *R. hainaldi* indicate that it is distinct from *R. exulans, R. rattus/tanezumi* and *R. argentiventer* (Kitchener et al., 1991b). Little is yet known about this species, including its precise phylogenetic relationships among *Rattus*-like murines (Musser and Carleton, 2005).

Commensal *Rattus* spp. (Figure 8)

At least four additional species of *Rattus* have been found living on Flores (*R. norvegicus, R. argentiventer, R. rattus/tanezumi*, and *R. exulans*), although it is still debated whether any of these species are native to the island (Musser, 1981; Thomson et al., 2014). They are the only murine species on Flores that also occur west of the Wallace Line, and are typically associated with human settlements (Musser, 1981).

Rattus norvegicus (~200-300 g), the Brown or Norway rat, is a medium-sized, globally-distributed rat found in the general region mainly in port cities in mainland Asia, on larger southeast Asian islands, and in Australia (Musser, 1981). The lower molars are comparable in size to *K. rintjanus,* however the occlusal surface and cranial features distinguish this larger rat from *Komodomys* and from other species of *Rattus* (Musser, 1981).

Rattus rattus/tanezumi (~200 g), the Black or House rat, is a taxonomic complex of commensal rats distributed globally, and especially common in southeast Asia. *Rattus rattus sumbae* was a subspecies of house rat originally described from the island of Sumba just south of Flores, and sometimes applied to populations from the Lesser Sundas, including Flores (Musser, 1972); this name is currently included in the

taxonomic synonymy of *Rattus tanezumi* (Musser and Carleton, 2005). Specimens found on Flores fall between the mean molar row size range of *R. rattus/tanezumi* from Sumba (8.3 mm) and from Bali (6.9 mm). Due to taxonomic uncertainties in the region, specimens found on Flores are perhaps best referred to as *Rattus rattus/tanezumi* at present (see Musser, 1981; Musser and Carleton, 2005).

Rattus argentiventer (~100 g), the Ricefield rat, occurs throughout the mainland of Southeast Asia, the Sunda Shelf, the Lesser Sunda Islands (including Flores), Sulawesi, the Philippines, and New Guinea (Musser, 1981). Unlike the considerable morphological variation seen in the *R. rattus/tanezumi* complex, populations of *R. argentiventer* from throughout the region are morphologically quite similar to one another. This is hypothesized to be the result of recent human interaction involved in the spread of this rat species across these regions (Musser, 1981). *Rattus argentiventer* is similar to *R. rattus* in tooth and body size, but differs in pelage coloration, cranial features and habitat (Musser, 1981). Differentiating these two species from the dentition is difficult because of similar occlusal surface patterns and lower molar size (Musser, 1981).

Rattus exulans (~50 g), the Pacific rat, is one of the most widespread species of *Rattus*, extending throughout the Indo-Australian region, including to some of the most remote islands of the Pacific (Musser, 1981). In a recent paper by Thomson et al. (2014), phylogeographic analyses of *R. exulans* indicate the oldest lineage with the greatest amount of genetic diversity originates from Flores, leading to the hypothesis that Flores is the place of origin for this species (Thomson et al., 2014). Specimens of *R. exulans* from

Flores compared those from Sulawesi are similar in mandibular molar lengths, and are smaller than measurements for the *R. rattus/tanezumi* complex (Musser, 1981).

Purpose of Study

As mentioned above, Liang Bua preserves an incredibly large number of murine remains. This large accumulation of murine remains suggests a range of interesting research questions. Did all Flores murines live contemporaneously in the area surrounding Liang Bua? Did they occupy different ecological niches? Do they vary in relative abundance through the stratigraphic sequence and if so, why?

Most studies of rodent morphology, taxonomy, and paleontology primarily involve the study of skulls and teeth, especially characteristics of the molars. However, of the 230,000 murine skeletal elements identified to date at Liang Bua, only just over 20,000 include jaw fragments with complete or partial molar rows, or isolated molars. Thus, the abundant murine postcranial remains at Liang Bua offer tremendous opportunities to test hypotheses about murine diversity and evolution, and ecological and environmental change through time. In order to be able to address important questions about the rats of Flores, a substantial amount of research is clearly required toward examining the postcranial variation in size and shape within the assemblage. At present, there is hardly any information regarding the postcranial anatomy of the Flores murines (Musser, 1981). The small pieces of information that do exist, apply only to some of the taxa that are known with absolute certainty to still live on the island. For example, *P. armandvillei* is the largest of the Flores endemic rats (Musser, 1981; Hooijer, 1967) but very few modern specimens that include postcranial material are preserved in museum

collections around the world. Although precise body masses and ranges of variation are unknown for many of these rat taxa, murine rodents scale reasonably well in terms of dental and body size (Amori et al., 2012). In this respect, the murine fossil and extant record on Flores suggests a full range of body sizes from giant (*P. armandvillei*) to smaller-sized rats (*R. exulans*).

Therefore, the first goal of this study is to explore the size variation in two of the most abundant murine postcranial elements (humerus and calcaneus) in the Liang Bua assemblage and attempt to assign these elements to the various size classes and taxa present at Liang Bua. In undertaking this work, it was assumed that relative sizes of these postcranial elements will be similar to size differences characterizing dental measurements for the known taxa. For example, published studies of dental and jaw remains from Liang Bua (Musser, 1981; Musser et al., 1986; van den Bergh et al., 2009; Locatelli, 2011; Locatelli et al., 2012) suggest there should be postcranial elements from rats of small (*R. exulans* and *R. hainaldi*), medium (*K. rintjanus*), huge (*P. theodorverhoeveni* and *S. florensis*), and giant body size (*P. armandvillei*). Based on teeth and jaws, *P. theodorverhoeveni* is described as similar in morphology but overall slightly smaller in body size than adult *P. armandvillei* (Musser, 1981; Hooijer, 1967b). Thus, postcranial elements exhibiting similar morphology to *P. armandvillei* but an overall smaller size range probably represent *P. theodorverhoeveni*. Additionally, rats of large body size (i.e., larger than medium-sized rats but smaller than huge-sized ones, such as *Hooijeromys*) have not been identified in any published analyses of Liang Bua murid dental remains (Musser, 1981; Musser et al., 1986; van den Bergh et al., 2009; Locatelli,

2011; Locatelli et al., 2012). Evidence of large-sized rats might therefore expected to be absent also in the postcranial remains observed in this study.

A second goal of this study is to explore the shape variation present in the humeri and calcanei of the Liang Bua rats in relation to locomotor functional anatomy. The functional anatomy of the humerus and calcaneus can provide information regarding locomotor adaptations to different substrates (e.g., terrestrial vs arboreal; Samuels and Valkenburgh, 2008; Youlatos, 2003). Musser (1981) described the Flores murines as likely terrestrially adapted animals, with one species (*S. florensis*) as possibly arboreal. Arboreal rodents typically show higher joint mobility and grasping ability (i.e. larger articular and joint surfaces), both of which are important features for climbers. Major limb elements tend to exhibit more gracile features, with elongated and proportional limb elements compared to terrestrial rodents (Samuel and Valkenburgh, 2008). On the other hand, terrestrial rodents tend to have more robust features for stability. For instance, midshafts of the humeri and femora tend to be larger with thicker cortical bone than arboreal rodents (Samuel and Valkenburgh, 2008). Thus, shape differences in the humerus and calcaneus may distinguish *S. florensis* from the likely similarly sized *P. theordorverhoeveni*, if Musser's (1981) hypothesis (based on dental features alone) that *S. florensis* is more arboreal is correct.

Finally, a third goal of this study is to identify the accumulating agents of the Liang Bua murine assemblage. Evidence of digestion of small mammals has been analyzed by identifying gastric etching on the incisors (Andrews, 1990); however, digestive signals on postcranial remains have also been well documented, including the distal end of the humerus (Andrews, 1990). In the absence of any evidence of non-human

mammalian carnivores on Flores prior to around 4,000 years ago (van den Bergh et al., 2009), it is hypothesized that avian, reptilian, or hominin predators are most likely responsible for the large accumulation of murine remains at Liang Bua. This study attempts to clarify which of these predators is the primary accumulating agent.

Materials and Methods

The materials used in this study derive primarily from excavations at Liang Bua of Sector XXI (Figure 10), a 2 x 2 m area excavated in 2010 by a joint collaboration between the National Center of Archaeology in Indonesia (Wahyu Saptomo and Thomas Sutikna) and the Smithsonian Institution's Human Origins Program (Matt Tocheri). A total of 163 complete mandibular tooth rows from this Sector were measured previously by Kathryn McGrath (Hominid Paleobiology Program, The George Washington University) and assigned to seven taxa based on known ranges of dental size and diagnostic morphology (Musser, 1981; Musser et al., 1986). The taxa identified from these dental remains and the number of identified specimens for each taxon were as follows: *P. armandvillei* (11), *P. theodorverhoeveni* (14), *S. florensis* (1), *H.* cf. *nusatenggara* (3), *K. rintjanus* (101), *P. naso* (1), and small-bodied *Rattus* (i.e., *R. hainaldi* and *R. exulans*) (32). These dental data suggest that the Liang Bua murines represented in Sector XXI should exhibit a full range of body sizes, from giant *P. armandvillei* to small-bodied *Rattus* (Figures 11-12).

Based on these dental data, each taxon was classified into one of five body size categories (Table 1). *Papagomys armandvillei*, the largest rat known from Flores, was classified as "Giant". *Papagomys theodorverhoeveni* and *S. florensis* were classified as

“Huge.” as both are probably slightly smaller than *P. armandvillei* (Musser, 1981). *Hooijeromys* cf. *nusatenggara* was classified as “Large” as it is likely smaller in body size than *P. theodorverhoeveni* and *S. florensis* but larger than the remaining taxa (Musser, 1981). *Komodomys rintjanus* and *P. naso* were classified as “Medium” and are known to be similar in body size to medium-sized species of *Rattus* (e.g., *R. rattus/tanezumi*) (Musser, 1981). Finally, *R. hainaldi* and *R. exulans* were classified as "Small."

A total of 1846 fossil murine skeletal elements from Liang Bua and 15 comparative species (52 specimens) were used in this study to explore variation in postcranial size and shape. Of these fossil elements, 1474 were humeri (MNI = 743) and 372 were calcanei (MNI = 194). Additional comparative specimens consisted of extant muroid species, mostly murines from the Indo-Australian region, from the American Museum of Natural History (AMNH) and the Smithsonian's National Museum of Natural History (USNM). A total of twelve linear measurements were collected for the humerus and ten measurements for the calcaneus, all recorded to 0.01 mm using digital hand calipers (Table 3). These measurements were based on previous studies of small mammal postcranial anatomy that focused on the relationship between functional anatomy and locomotor behavior (Samuels and Valkenburgh, 2008; Green et al., 2012; Salton and Sargis, 2008; Argot, 2001).

A principal components analysis (PCA) was performed using a covariance matrix for each element in order to visualize overall variation in size and shape. Because the Liang Bua humeri were often fragmentary, the PCA was performed using only seven measurements taken on the distal end in order to maximize the available sample, whereas

the calcaneus PCA used all ten of the measured variables (Figures 13 and 17). Comparative specimens of *R. exulans* (Small) and *P. armandvillei* (Giant) were included in both PCAs in order to determine the likely minimum and maximum size limits within the sample. Variation within each element was further explored using 3D scatterplots of measurements that generated the clearest clustering patterns (Figures. 14, 16, 18, and 20). The observed clusters within each PCA and 3D scatterplot were then assigned to one of the five hypothesized size classes: Giant, Huge, Large, Medium, and Small (Table 1). The combined results were used to assess the likely taxonomic identification of each element based on overall bone size and shape; however, the morphological characteristics of the large, huge, and giant-sized specimens were also reexamined in detail before final taxonomic attribution (Figures 16 and 20). Finally, the results for both elements were compared with the dental data to explore the possible relationship between molar and postcranial size variation within each species and/or size class (Figure 21).

Rodents, and particularly murines, exhibit a variety of locomotor behaviors including terrestrial, semi-aquatic, arboreal, semi-fossorial, fossorial, ricochetal, and gliding behaviors (see Table 2; Samuel and Valkenburgh, 2008). While many rodent species are highly versatile in their ecology, many highly specialized taxa have evolved in different geographic and habitat contexts, exhibiting diverse skeletal morphologies that can be used to interpret locomotor behaviors (Samuels and Valkenburgh, 2008). Based on previous descriptions and hypotheses for the known Flores murines, the locomotor behaviors of these taxa are likely terrestrial, fossorial, and possibly arboreal (Table 2). For the functional morphology portion of this study, a comprehensive review of modern and fossil rodent locomotor functional anatomy (Samuels and Valkenburgh, 2008) was

used to qualitatively assess the likely locomotor adaptations of the Flores murine taxa based on the observed morphological characteristics of the humerus and calcaneus.

For the taphonomic portion of this study, the humeral distal ends were analyzed according to the digestion stages described and defined by Andrews (1990). Low digestion is characterized by a rounding and/or softening of the distal articular edges with a sandpaper-like appearance on the surface of the bone (Andrews, 1990). Medium digestion starts to show pitting on the distal articular surfaces with some removal of cortical bone on the medial and lateral condyles (Andrews, 1990). Some splitting may occur on the diaphysis, however this signal is more homogenous and subtle on the bone surface compared to flaking caused by weathering (Andrews, 1990). Lastly, high digestion causes removal of the distal articular features through extensive corrosion, affecting both cortical and trabecular bone (Andrews, 1990). Each humerus was also inspected for weathering damage based on the stages defined by Behrensmeyer (1978)

Results

Size variation and attribution to size class and taxon

Humerus

The PCA results for the humeral data show a considerable range along PC1, which explains 94% of the variance and is largely a function of overall size (Figure 13). Posterior articular breadth was one of the strongest contributors to the variation observed along PC1. Combining this variable with ML and AP mid-shaft diameters (both not included in the PCA) produced a 3D scatterplot with the clearest clustering patterns (Figure 14). The distributions of specimens observed in both the PCA and 3D scatterplot results indicate a reasonably continuous range of humeral sizes are present in the Liang Bua sample representing small *R. exulans*-sized to giant *P. armandvillei*-sized rats.

A distinct cluster of small humeri was observed in both plots (Figures 13-16), representing 265 specimens. These must represent small species of *Rattus*, presumably R. *exulans* and/or *R. hainaldi*, but no clear size or shape variation was uncovered that might allow for discrimination between these two small-bodied taxa. A medium-sized cluster is also distinguishable in both plots and represents the largest cluster of all measured humeri. These most likely represent *Komodomys* based on the fact that 99% of the mandibular molar rows of medium-sized rats from Sector XXI were assigned to this genus. Other medium-sized rats (i.e., *P. naso* and commensal species of *Rattus*) most likely represent only a very small number of the measured humeri given the extremely low frequencies of positively identified dental elements of these taxa from this Sector. However, the PCA results suggest that this cluster of medium-sized humeri can be further divided into two groups, one smaller and one larger (Figures 13 and 15). The Sector XXI dental remains attributed to *Komodomys* also suggest that a larger and smaller version of

this taxon may be present. Together, the humeral and dental data suggest that there are at least two species of *Komodomys* represented in the Liang Bua murid assemblage. The smaller humeri and molars probably represent *K. rintjanus*, while the larger ones likely represent a larger medium-sized but as-yet-unnamed species of *Komodomys* (Figures 15-16).

Other measured humeri fall outside of the small and medium-sized rat clusters described above. The largest of these humeri clearly represent *P. armandvillei*, as they cluster with the modern museum specimens included for this giant rat taxon (Figures 13-16). Two of the remaining clusters most likely represent large (*Hooijeromys*) and huge-bodied rats (*P. theodorverhoeveni* and *Spelaeomys*). A final cluster of nine humeri is even more challenging to assign to either a size class or taxon given the observed distributions. For instance, these nine humeri show similar ML and AP midshaft diameters as *Komodomys*. However, their posterior articular breadths and other dimensions are considerably larger than in *Komodomys* (and more similar to those with much larger midshafts) suggesting they may represent a larger-bodied taxon, such as *Hooijeromys* (Figures 15 and 16). Articular breadths may be less influenced by ontogenetic development than midshaft thicknesses and measurements that cross epiphyseal boundaries (e.g., maximum distal breadth).

To try to shed light on this problem, small comparative ontogenetic samples of giant (*Phloeomys*, a Philippine endemic), large (*Uromys*, native to New Guinea and Australia), and medium-sized rats (*Hydromys*, native to New Guinea and Australia) were examined. Overall, specimens with unfused epiphyses displayed shorter humeri and thinner midshafts compared to those with fused epiphyses (Figure 25). However, other

patterns were identified among these taxa. For example, in *Hydromys* and *Uromys* the posterior articular breadth increases throughout development (Table 7), whereas in *Phloeomys* it appears to reach its maximum size earlier during growth. Although these comparative ontogenetic data are limited at present, they suggest the following alternative hypotheses. First, if these nine humeri represent a taxon with a *Phloemys*-like growth trajectory, then they may be younger examples of the large-bodied group (*Hooijeromys*) where the midshaft dimensions lag behind the growth of the distal end. Alternatively, if these have a *Uromys*-like growth trajectory (recall *Uromys* is thought to be similar in size to *Hooijeromys*), then the nine humeri in question may actually represent an as yet unidentified murine taxon at Liang Bua that is similar in size to *Hydromys* (larger medium-sized) with a comparable pattern of humeral growth (Figures 24 and 25). The functional morphology of these noted differences in humeral anatomy are discussed further below following the presentation of the calcaneal results.

Calcaneus

The PCA results for the calcaneal data show a continuous size distribution along PC1 that explains 94% of the variance (Figure 17). Maximum length best explains the variation along PC1 while the difference between the lengths of the calcaneal heel and shelf best explains the variation observed on PC2. Combining these three variables together (maximum length, heel length, shelf length) produced a 3D scatterplot with the clearest clustering patterns (Figure 18). The distribution of specimens observed in both the PCA and 3D scatterplot results indicates a reasonably continuous range in calcaneal size, representing small to giant-sized rats in the Sector XXI sample.

Unlike the humeral results, only two small-sized calcanei were identified in both the PCA and 3D scatterplots (Figures 17-20). This unexpected result is most likely due to the fact that the calcanei of small *Rattus* can easily slip through the 2 x 2 mm mesh used for sieving during excavations at Liang Bua. The largest calcaneal cluster includes 239 specimens and represents medium-sized rats. In contrast to the humerus PCA, this medium-sized cluster is not as easily divided into two parts; however, the observed range of variation of this cluster is relatively large for the otherwise small size of these elements. Although this cluster may contain small numbers of *P. naso,* a majority most likely represent *Komodomys* based on the large sample of dental remains identified as this genus from Sector XXI. There is no additional distinguishable group within the medium-sized cluster that that clearly signals differentiation between *K. rintjanus* and the hypothesized larger species of *Komodomys* (Figures 19-20).

Other calcanei belonging to large, huge, and giant-sized taxa were observed well outside the range of the small and medium-sized clusters. Like the humerus PCA, the largest of these calcanei clearly represent *P. armandvillei* as they cluster with known specimens of this taxon (Figures 17-20). Identifying the remaining large (*Hooijeromys*) and huge-sized (*P. theodorverhoeveni* and *Spelaeomys*) taxa is again more challenging; however, the calcanei clustering patterns are more easily distinguishable than in the humerus PCA. For example, along PC1 three elements cluster together just beyond the range of medium-sized *Komodomys* and most likely represent a large-bodied taxon (*Hooijeromys*) (Figure 19). The larger cluster of huge-sized calcanei most likely represent *P. theodorverhoeveni* as they share similar morphological features with *P. armandvillei* but are slightly smaller in size. However, two clusters ranging in these larger size classes

are more challenging to assign taxonomically. In the 3D scatterplots, these groups have a proportionally shorter heel length relative to the length of the articular surfaces of specimens with similar maximum lengths (Figures 19-20). These groups are also distinguished in the calcaneus PCA because they have longer shelf lengths, representing two distinguishable clusters along PC2 that are separate from those hypothesized to represent *P. theodorverhoeveni* and *Hooijeromys*. The larger of these two clusters could possibly represent *Spelaeomys* while the smaller one may represent the "unknown" taxon observed in the humeral analyses.

Summary

The combined results of the humerus and calcaneus suggest a wide variety of giant (*P. armandvillei*) to smaller (*R. exulans*) sized murines are present in the sample. *Papagomys armandvillei* humeri range from 5.49 mm to 5.09 mm in midshaft thickness (AP diameter) and 21.93 mm to 20.24 mm in maximum calcaneal length. *Papagomys theodorverhoeveni* humeri range from 4.75 mm to 4.29 mm in midshaft thickness and 18.07 mm to 15.11 mm in calcaneal length. The calcaneal cluster hypothesized to belong to *S. florensis* displays calcaneal lengths ranging from 16.11 mm to 13.84 mm, overlapping considerably in size with those attributed to *P. theodorverhoeveni*. This overlap with *P. theodorverhoeveni* is consistent with the degree of size overlay in the dental measurements of *S. florensis*. Humeri attributed to *Hooijeromys* range from 4.36 to 3.53 mm in midshaft thicknesses and from 13.28 to 12.45 mm in calcaneal lengths. The group classified as "unknown" ranges in humeral midshaft thicknesses from 3.38 to 2.36 mm and calcaneal lengths from 12.29 to 10.17 mm. *Komodomys* displays the widest range of humeral midshaft diameters, from 3.65 to 1.48 mm, and calcaneal lengths, from

10.95 to 6.77 mm. Finally, small *Rattus* (i.e., *R. exulans* and *R. hainaldi*) humeri range from 2.39 to 1.25 mm in midshaft thickness and 5.86 to 5.3 mm in calcaneal length. The full ranges of these postcranial proportions for each size class and taxon of rat are shown in Tables 4-5.

One of the difficulties in attempting to assign these postcranial remains to specific taxa is having neither comparative material nor precise measures and ranges of body size available. Only some of the extant Flores murine species have recorded body masses and most of these are based on a single specimen. Moreover, body masses are unknown for the extinct species. However, a comparison of known dental dimensions against the postcranial measurements collected in this study shows a consistent distribution of dental and postcranial measurements between the five size classes (Figure 21). *Papagomys armandvillei* and small *Rattus* are clearly the largest and smallest murines respectively within the assemblage, and provide the maximum and minimum body size limits for the Flores murines (Figure 21). The relative sizes and frequency distributions of the humeri and calcanei attributed to *P. theodorverhoeveni, S. florensis, Hooijeromys,* and *Komodomys* are consistent with those of the identified dental remains from Sector XXI, suggesting that these taxonomic allocations of postcranial material may be reasonable.

Functional Morphology

Humerus

Functional analysis of the humeri suggests that *P. armandvillei*, *P. theodorverhoeveni* and *H.* cf. *nusatenggara* show adaptations for terrestrial habits while exhibiting some evidence of fossorial behavior. The shape of the humerus is wide with a thick midshaft and a large anterioposteriorly oriented elliptical humeral head. Of the 550 humeri which preserved the proximal end, 96.7% displayed an unfused head. When attached, a large bicipital groove was present suggesting powerful forelimb flexion (Salton and Sargis, 2008). The delto-pectoral crest extends laterally to roughly the midshaft and gradually blends into the distal end of the diaphysis. The lateral ridge curves posteriorly before joining the capitulum, forming a somewhat prominent lateral condyle (Salton and Sargis, 2008). Both the olecranon and coronoid fossa are deep with a continuous capitulum and trochlea (Salton and Sargis, 2008). All of these humeri have an epicondylar fossa and a substantial medial supra-epicondylar ridge extending up the diaphysis and joining (just slightly) to the delto-pectoral ridge. The medial condyle is somewhat prominent and extends both medially and superiorly with both a small anterior and posterior depression under the epicondylar foramen.

Interestingly, a group of seventeen humeri were noticeably distinct from all others examined in having a comparably larger distal end relative to a smaller midshaft (Figure 16). Both the medial and lateral ridges of these specimens are severely reduced with a visually short distal shaft length compared to the length of the distal articular surface. The capitulum and trochlea are continuous and the epidondylar foramen is present (qualitatively similar to the larger identified murines), but the medial condyle is shorter in

length, however the epiphysis was unfused. These features have been identified in aquatic rodents, which tend to have a larger distal end of the humerus compared to the relative thickness of the midshaft, to help propel the animal forward in a paddle-like motion (Samuels and Valkenburgh, 2008). As discussed above, the semi-aquatic rat *Hydromys chrysogaster* displays similar humeral measurements and morphological characteristics (Figure 25). It is possible that a larger medium-sized murine, similar in size and semi-aquatic adaptations to *H. chrysogaster*, is represented in the Sector XXI sample. However, if this is true then there is an absence of dental remains for this taxon.

Calcaneus

Little has been discussed regarding the functional morphology of the calcaneus in rodents with respect to locomotor behaviors (Stains, 1959; Shimer, 1906). Most descriptions have been in relation to the forelimb or hindlimb in general, with less focus on specific features of the calcaneus (Elissamburu and Santis, 2011; Salton and Sargis, 2008; Green et al., 2012). However, the calcaneus plays an important role in locomotion, as most of the strength in foot propulsion is dependent on the calcaneus to push the animal forward (Shimer, 1906). Calcaneus shape varies considerably among rodent taxa, however all rodent calcanei consist of a trochlear process with astragalar and cuboid articular facets (Stains, 1959). The length and curvature of the calcaneal body and tuberosity varies within murines, but all functional features of the articular surface (distal cuboid facet to the most proximal point of the posterior articular surface) are present (Stains, 1959). This study provides one of the first descriptions of murine fossil calcanei and their functional implications for locomotor behavior.

The calcanei attributed to *P. armandvillei, P. theodorverhoeveni* and *H.* cf. *nusatenggara* also indicate adaptations for terrestrial locomotion. The calcaneal body is thick in both the medio-lateral and superior-inferior breadths. The posterior tuberosity (the attachment of the Achilles tendon) creates a groove that extends from the edge of the superior surface along the surface of the epiphysis, and a small inferior notch on the ventral side of the heel. The most posterior point of the posterior articular surface is approximately half of the total length of the calcaneus. Similar morphology characterizes the terrestrial primate taxon, *Theropithecus,* as compared to arboreal primates, such as *Presbytis,* that display a short heel length relative to the shelf length (Youlatos, 2003). The lateral edge of this surface forms the most superior point of the calcaneus and terminates along the same horizontal plane as the lateral trochlear process. This process forms a long antero-posteriorly flat surface with rounded edges, and forms a 90 degree angle to the lateral edge of the cuboid facet. The medial sustentaculum tali is triangular in shape, containing a large medial talar articular facet.

A possible diagnostic feature of terrestrial, arboreal, or semi-aquatic locomotor behaviors in murines is the length of the heel relative to the articular surface, or shelf area. For example, modern humans have a relatively long heel compared to that of orangutans and chimpanzees (Kidd 1999). Shelf to heel length ratios (SHR) were calculated for the Sector XXI calcanei by dividing the length of the heel by the length of the shelf. These were then compared with the SHR of known terrestrial (*Leopoldamys*), arboreal (*Crateromys*), and semi-aquatic (*Hydromys*) murines (Table 6). The results suggest that this feature does not distinguish between the known terrestrial (SHR = 0.777) and arboreal (SHR = 0.750) taxa examined here. However, the extended length of

the heel in *Hydromys* is distinctive (SHR = 1.182), and may represent an adaptation for its semi-aquatic lifestyle. All of the Sector XXI calcanei displayed SHR most similar to those of the comparative terrestrial and arboreal taxa sampled, with the exception of the two clusters cautiously attributed to *S. florensis* and the "unknown" taxon respectively.

These two enigmatic groups of calcanei display shorter heels and longer shelf lengths (SHR = 0.498 and 0.443). Compared to the other Sector XXI calcanei, the lateral trochlear processes are less pronounced and more curved on the posterior and anterior ridges. The sustentaculum tali are also less triangular in shape and more posteriorly oriented. All articular surfaces are also larger in size relative to the calcanei attributed to *Papagomys* and *Hooijeromys*, although the calcaneal body is similarly thick in both the medial-lateral and superior-inferior breadths. The overall calcaneal shape and morphology observed in *S. florensis* and the "unknown" group are surprisingly unlike those of the known terrestrial, arboreal or semi-aquatic taxa included for comparison. However, the observed SHR of these two groups are consistent with *a priori* predictions of arboreal adaptation based on the comparative morphology of great apes and humans. Clearly, further research across a broader sample of arboreally and terrestrially-adapted murine taxa, as well as those with other distinct locomotor behaviors, is needed to resolve these questions.

Taphonomy

The humeri were heavily fragmented and typically preserved in five main parts: distal end, distal end with part of the distal diaphysis, distal end with midshaft, proximal end with midshaft, or whole. A small portion (~3%) retained a fused proximal epiphysis, suggesting the murine assemblage comprised of mostly immature rats (probably corresponding mainly to subadult and young adult age classifications). The calcaneus also preserved surprisingly well with little fragmentation.

The exterior surfaces of the humeri were well preserved despite the fragmentary nature of the bones. There was little indication of rolling (i.e. fluvial transportation) or signs of intense flaking on the bone surface. The majority of the assemblage shows minimal, if any, signs of weathering; however, elements that were too fragmentary to measure tended to have a higher degree of weathering than elements that were measurable (Figure 29). Out of the 1,461 elements inspected for weathering conditions, 9.6% were classified as Behrensmeyer Weather Stage (BWS) 0 (no signs of cracking or breaking), 80.6% were classified as BWS 1 (shows cracking parallel to fiber structure), and 9.5% were classified as BWS 2 (flaking of cortical bone due to cracking) based on Behrensmeyer (1978).

A majority of the assemblage also shows small amounts of digestive etching with a concentration of evidence occurring on the distal articular surfaces of the humerus (Figure 28). Diaphyses exhibited little to no evidence of digestion, although this was difficult to distinguish from weathering effects. Out of the 1,631 elements inspected for digestion, 16.0% showed no digestion, 77.9% showed low digestion, and 5.6% showed medium digestion (Table 8). Three fragments from the Late Pleistocene were identified

as having high or heavy degrees of digestion, causing a higher degree of fragmentation and were not measureable for taxonomic identification. These findings are consistent with avian digestive signals observed in Andrews (1990) with 83.9% of elements showing signs of digestion by birds of prey (Figure 28). These digestive signals are consistent with previous taphonomic analyses of small avian (i.e. swiftlets) assemblages at Liang Bua (Meijer et al., 2013). Breakage patterns were also recorded and are summarized in Table 8.

Discussion

This is the first study of murine postcranial remains from Flores, using the abundant and well preserved assemblage from Liang Bua (Sector XXI). The observed ranges in murine size and shape from this assemblage provides new and important information about the taxonomy, functional morphology, and taphonomy of these small mammals that have inhabited the area surrounding Liang Bua from ~95,000 years ago to the present (Roberts et al., 2009; van den Bergh et al., 2009).

The postcranial anatomy of the humerus and calcaneus suggest a diverse array of differently sized murine species lived within the surrounding habitats of Liang Bua throughout the late Pleistocene and Holocene (Table 9). The results of this study indicate a large concentration of medium and small-sized murines is present throughout the sequence with a surprising amount of size and shape variation among the three largest size classes. The large to giant-sized taxa identified from these postcranial remains and the number of identified specimens for each taxon were as follows: *P. armandvillei* (6), *P. theodorverhoeveni* (19), *S. florensis* (4), and *H.* cf. *nusatenggara* (26) (Figures 22-23).

This is the first study to report evidence of *Hooijeromys* cf. *nusatenggara* at Liang Bua. Dental remains as well as attributed postcrania were identified in the lower (Late Pleistocene) and upper (Holocene) spits of Sector XXI. While the earliest documentation of *Hooijeromys* on Flores is from the Middle Pleistocene at Mata Menge and Olabula, it is uncertain as to when *Hooijeromys* disappears from the fossil record (Morwood et al., 1998; Musser, 1981). Therefore, this is the first study to present possible evidence that *Hooijeromys* is represented in the Holocene record of Flores.

All postcranial elements within the small-sized cluster are consistent with the relative dental size range and frequency distribution for *R. hainaldi* / *R. exulans* (Figures 13-20, Tables 6-7). Similarly, the medium-sized cluster almost certainly represents mostly *Komodomys* and probably some *P. naso* as well (Figures 13-20). Multivariate analyses of the humeral data recovered one larger and one smaller group within the medium-sized assemblage, in addition to the small-sized cluster of *R. exulans* and *R. hainaldi* (Figures 13-20). The larger cluster of medium-sized rats suggests a potentially larger species of *Komodomys* is present within the assemblage while the smaller cluster most likely represents *K. rintjanus* as well as some *P. naso*. Unfortunately, comparative material of both *Komodomys* and *Paulamys* were inaccessible, making morphological distinctions between these two taxa difficult. Therefore, this study was unable to identify any shape characteristics that might reasonably distinguish *Komodomys* from *Paulamys*; however, the likely small number of *Paulamys* specimens in the sample (based on the dental remains) suggests this should be a focus of further study.

Ambiguity surrounding the humeri and calcanei functional morphology assigned to *S. florensis* and "unknown" may reflect variation in ontogeny rather than taxonomy.

Although the majority (96.7%) of the murine assemblage have unfused epiphyses, the humeri and calcanei attributed to *S. florensis* and "unknown" most likely represent younger individuals compared to those who have achieved fully adult size and shape. These differences are most pronounced in the shape of distal humerus and the length of the calcaneal heel in *S. florensis* and "unknown" in particular. When these dimensions are compared with known specimens of varied developmental stages, similar patterns of ontogeny indicate that the shape variation identified in *S. florensis* and "unknown" could be explained by immaturity and not differences in locomotor behavior or taxonomy.

If this morphology is a product of ontogenetic development, then the humeri and calcanei of *S. florensis* and the "unknown" group may not be preserved in the Sector XXI assemblage. Instead, these elements in question most likely represent younger *Papagomys* spp. and younger *Hooijeromys,* respectively. It is also relevant to consider that only a single specimen of *S. florensis* was identified in the Sector XXI murine dental assemblage. Evidence of a fairly large-sized shrew rat has been identified at Liang Bua and could potentially be represented by the "unknown" group (Guy Musser, in litt.); however, the morphological proportions of the distal end and the midshaft are still very similar to those observed in younger, terrestrial rats and no mandibular remains resembling a large-sized shrew rat were observed. Thus, the absence of postcranial elements belonging to *Spelaeomys* in Sector XXI is not particularly surprising. It is also a possibility that the postcrania of *Spelaeomys* simply does not differ significantly from that of one or more of the other large to giant-sized rats present in the assemblage. Until a more complete skeleton of *Spelaeomys* is recovered in association with its distinctive dental morphology, this important question will remain unclear.

The functional anatomy of *P. armandvillei, P. theodorverhoeveni* and *Hooijeromys* suggest these rats were primarily terrestrial in habitus. It is common for terrestrial rodents to engage in some burrowing activity (Samuels and Valkenburgh, 2008), resulting in common features like a wide and robust distal humerus and enlarged articular surfaces. Overall, the morphology of the humeri and calcanei attributed here to *P. armandvillei, P. theodorverhoeveni* and *Hooijeromys* suggest a terrestrial habitus with possibly some fossorial behavior primarily based on the shape of the distal humerus and diaphysis. These rats most likely inhabited densely forested habitats based on the hypothesized behaviors of extant *P. armandvillei*.

Although *S. florensis* is hypothesized to be an arboreal taxon (Musser, 1981), there were no humeri observed in this analysis that exhibited clear arboreal adaptations. Given that only one dental fragment was positively identified to this taxon, it may be that humeri of *S. florensis* were not present in the Sector XXI sample. If they were present in the sample, then they were indistinguishable from the humeri attributed to *P. theodorverhoeveni*.

The size and functional anatomy of the examined murine postcranial elements from Liang Bua are consistent with knowledge of the preferred habitats of extant murine taxa on Flores (Musser, 1981; Kitchener et al., 1991a, 1991b). Together, these data suggest that a wide range of suitable murine habitats have surrounded Liang Bua for the past 95,000 years. These habitats include densely vegetated rainforests and possible wetlands (*Papagomys*, *Hooijeromys*, and *Paulamys*) along with more open grasslands with isolated patches of palms and open forests (*Komodomys*).

Bone accumulation of small mammals in caves is most likely the result of predation (Andrews, 1990). Other forms of accumulation include fluvial transport and pitfalls, however the evidence obtained from the Liang Bua murine assemblage indicates that predation is the most likely cause. Evidence of digestive etchings (68.4%) on the distal ends of the humeri suggests that raptors were the primary accumulating agent of these assemblages (Fig. 33; Meijer et al., 2013). Raptor remains recovered from Liang Bua include the common barn owl (*Tyto* sp.), eagles (*Aquila* sp.), the Brahminy Kite (*Haliastur indus*), vulture (*Trigonoceps* sp.), and Marabou stork (*Leptoptilus robustus*) (Meijer et al., 2013).

The Brahminy Kite, vulture, and Marabou stork were probably not major contributors to the murine accumulation based on known feeding behaviors of extant taxa. The Brahminy Kite primarily consumes fish, although some accounts have documented it occasionally consuming smaller mammals (Hanneke Meijer, in litt.). Modern Marabou storks and vultures in Africa typically scavenge much larger prey (> 40 kg). Eagles (*Aquila* spp.) are known for preying on small mammals up to ~880 g (Gliwicz, 2008). It is possible that this raptor contributed to the Liang Bua murine assemblage, but probably only in a minor way. Instead, owls, which often nest in caves, are the most likely culprit.

The common barn owl (*Tyto* sp.) has been recorded in both the Late Pleistocene and Holocene deposits at Liang Bua (Meijer et al., 2013). Modern barn owls have an estimated prey body-mass intake of <200 g and typically select smaller and/or younger rats (Andrews, 1990). *Tyto* remains recovered from the Late Pleistocene deposits at Liang Bua suggest this taxon was approximately 15% larger than typical modern barn owls in

Flores (Hanneke Meijer, in litt.). Therefore, this species probably could have consumed prey up to ~250-300 g (Hanneke Meijer, in litt. Figure 33). Approximately 85% of the murine accumulation at Liang Bua includes small (*R. exulans* and *R. hainaldi*) and medium-sized (*Komodomys* spp. and *P. naso*) taxa, all of which fall well within the preferred prey size range of *Tyto* (Figure 27). It is possible that some of the younger large-sized (*Hooijeromys*) murines were also the result of owl kills as well. Thus, barn owls were most likely responsible for a majority of the accumulation of small and medium-sized murine remains recovered from Sector XXI.

In addition to weathering and digestive damage, animal tooth marks were also identified (18 elements) in the murine assemblage. Most observations were identified as rodent gnaw marks located on the lateral or medial side of the diaphysis; however, some were identified on the distal articular surfaces as well. One small-sized humerus from the Late Pleistocene (recovered between 305-315 cm depth) showed 5 unexpected pits and numerous depressions, with a maximum diameter of 0.39 mm (Figure 31). Additional analyses is needed prior to the identification of these marks, however some candidates include a small varanid or snake, or possibly owl or eagle talons. Although the puncture marks share similar morphology to those left by crocodiles and larger varanids (D'Amore and Blumenschine 2009; Delaney-Rivera et al., 2009; Njau et al., 2006; Landt et al., 2007), their small size make these possibilities highly unlikely. Similarly, studies of raptors transporting prey have shown that most puncture holes appear in the innominate primarily behind the acetabular fossa (Hockett, 1994). Regardless of the ultimate cause of these marks, this is clearly a rare event within the assemblage and not a significant contributing factor to the accumulation of murine remains.

One other form of bone modification was identified on a small-sized humeral fragment from the Late Pleistocene deposits (spit 46) (Figure 32). These marks consist of a series of localized, oblique striations on the distal, posterior region of the diaphysis. They are uniform in directionality but are not precisely parallel to one another. The internal groove morphology consists of a V-shaped longitudinal cross-section of equal width; however, the groove is neither deep nor sharp. Based on known descriptions of stone-tool assisted cut marks (Blumenschine and Selvaggio, 1988; Blumenschine et al., 1996; Binford 1981; Braun et al., 2008), the identified striations are most likely a product of a sharp-edged implement used for cutting and/or removing soft tissue (Briana Pobiner, in litt.; David Braun, in litt.).

Evidence for digestion was minimal on the larger *Papagomys* humeri, indicating that the predator was either a scavenger and did not ingest the limbs of the rats, or the prey was outside the body size limits for the predator and was unable to ingest the prey whole (Andrews, 1990). It has been suggested that the presence of giant rats in the Late Pleistocene deposits of Liang Bua are an indication of *H. floresiensis* foraging behavior (Morwood et al., 2009). However, small to medium-sized rats are typically eaten whole over an open fire by modern human hunter gatherers (Landt et al., 2007), and tend to leave notches, tooth pits and punctures, and crenulated edges on rat bones (Landt et al., 2007; Lloveral et al., 2009). No direct evidence of human tooth marks was found on any of the rat postcranial elements examined in this study, although one specimen displayed possible stone tool-assisted cut marks. This small-sized murine humerus (i.e., *R. exulans* or *R. hainaldi*) from the Late Pleistocene deposits contained oblique cut marks on the distal portion of the posterior diaphysis, close to the tricep brachii tendon. This

anatomical location is optimal for defleshing of larger game, however little literature is available with respect to the defleshing of small mammals for human consumption (Fernandez-Jalvo et al., 1999). The identified striations are very similar to those found on megafaunal remains as well as those from experimental archeology (i.e. multiple, localized marks creating a V-shaped indention; Braun et al., 2008). Experimental research on butchering, cooking and consumption of rabbits show cut marks located on the distal humeral epiphyseal region from disarticulation (Lloveras et al., 2009). While it is tempting to interpret these marks as possible evidence of *H. floresiensis* butchering a small-sized rat, the rare occurrence in the assemblage makes the implications unclear.

Conclusion

The results of this initial study on two postcranial elements from a single Sector from Liang Bua show that the abundant murine postcranial remains recovered preserve a wealth of information about the paleobiology and paleoecology of the Flores rats. Additional studies are clearly warranted as these abundant remains offer significant opportunities to test hypotheses about murine diversity and evolution, and ecological and environmental change through time. Further investigations of the Liang Bua murine postcranial assemblage will impart a better understanding of the biological and ecological landscape surrounding Liang Bua through the past 100,000 years, as well as provide key contextual information for interpreting the remains of hominins and other animals recovered from the site.

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Figure 1. Map showing the location of Liang Bua, Flores and other islands of the Indonesian archipelago.

Table 1. Body size estimates of the rats from Flores.

Species	Size Class	Weight (g)
Papagomys armandvillei	Giant	~1,200
Papagomys theodorverhoeveni	Huge	
Spelaeomys florensis	Huge	
Hooijeromys nusatenggara	Large	
Paulamys naso	Medium	~120
Komodomys rintjanus	Medium	~140
Rattus norvegicus	Medium	~200
Rattus rattus sumbae	Medium	~200
Rattus argentiventer	Small	~100
Rattus exulans	Small	~50
Rattus hainaldi	Small	

Figure 2. *Papagomys armandvillei*: A modern specimen from Flores (A-B, E; photographs courtesy of the Liang Bua Team); Images of the maxillary (C) and mandibular (D) molar rows (modified from Musser, 1981)

Figure 3. *Papagomys theodorverhoeveni*: Images of the mandibular molar row (A) and maxillary 1st and 2nd molars (B) (Images modified from Musser, 1981 and Locatelli, 2011 respectively)

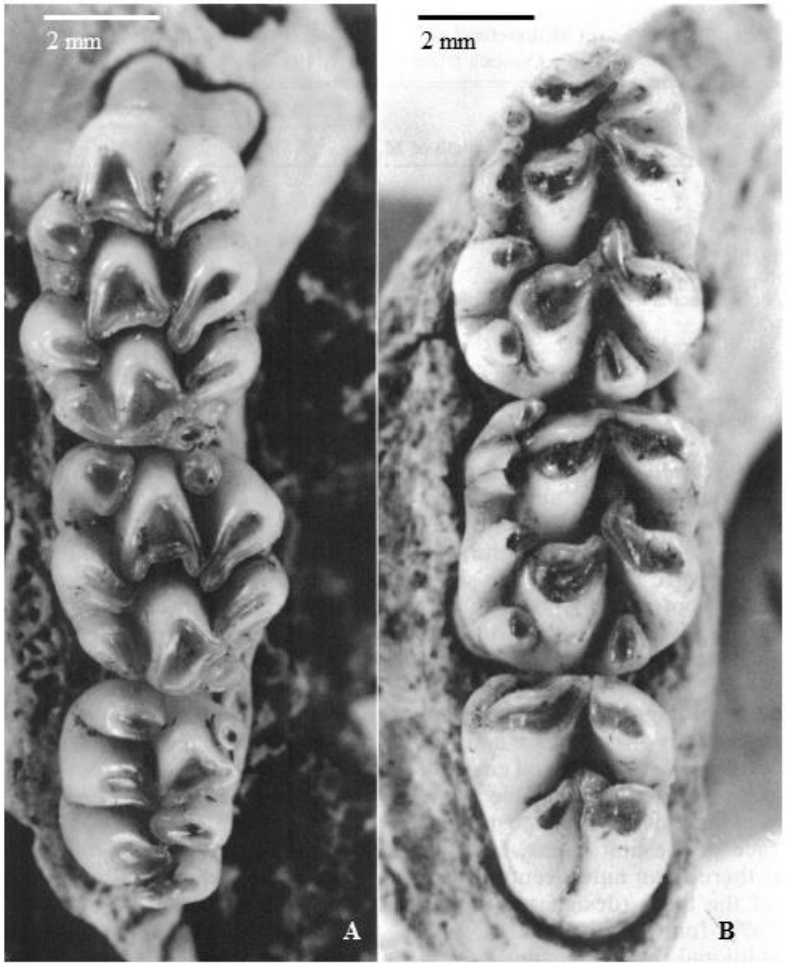

Figure 4. *Spelaeomys florensis:* Images of the maxillary tooth row (A) and mandibular tooth row (B) (images modified from Musser, 1981)

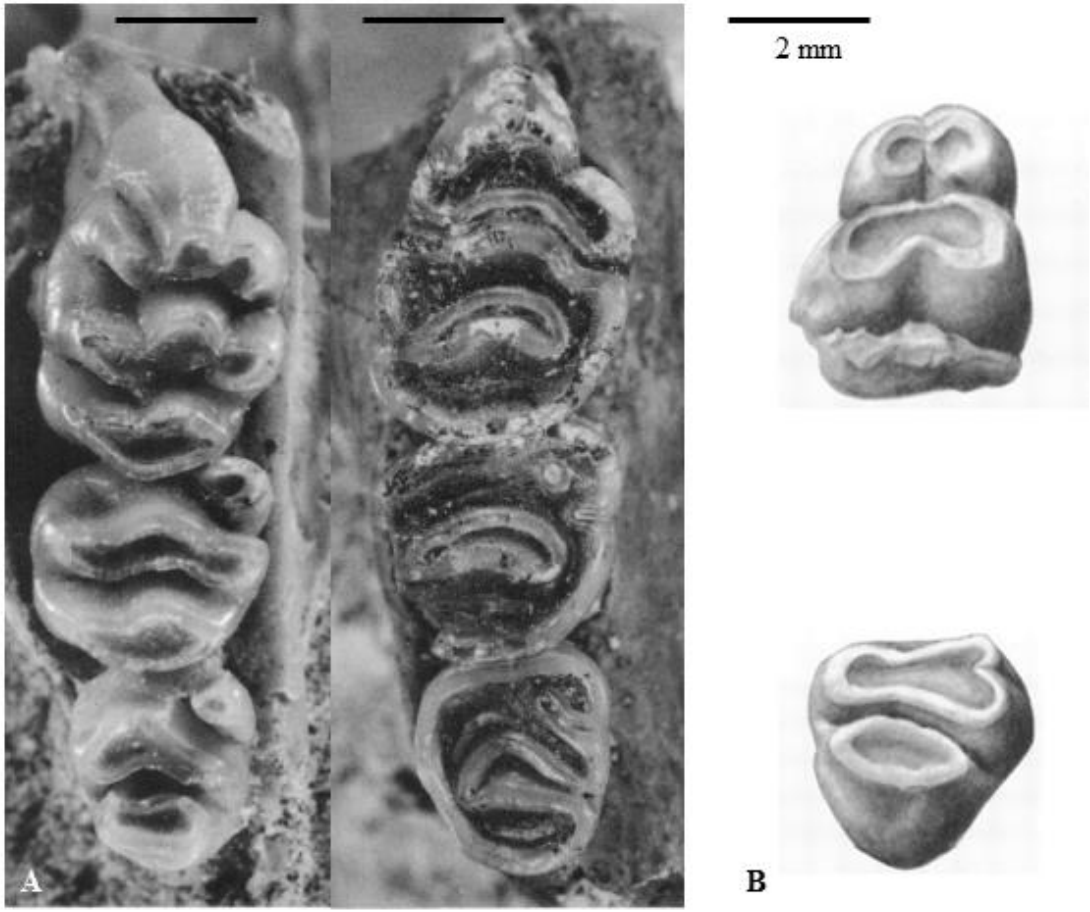

Figure 5. *Hooijeromys nusatenggara:* Images of the maxillary tooth rows (A) and an illustration of the 1st and 3rd mandibular molars (B) All images modified from Musser, 1981. Scale = 2 mm.

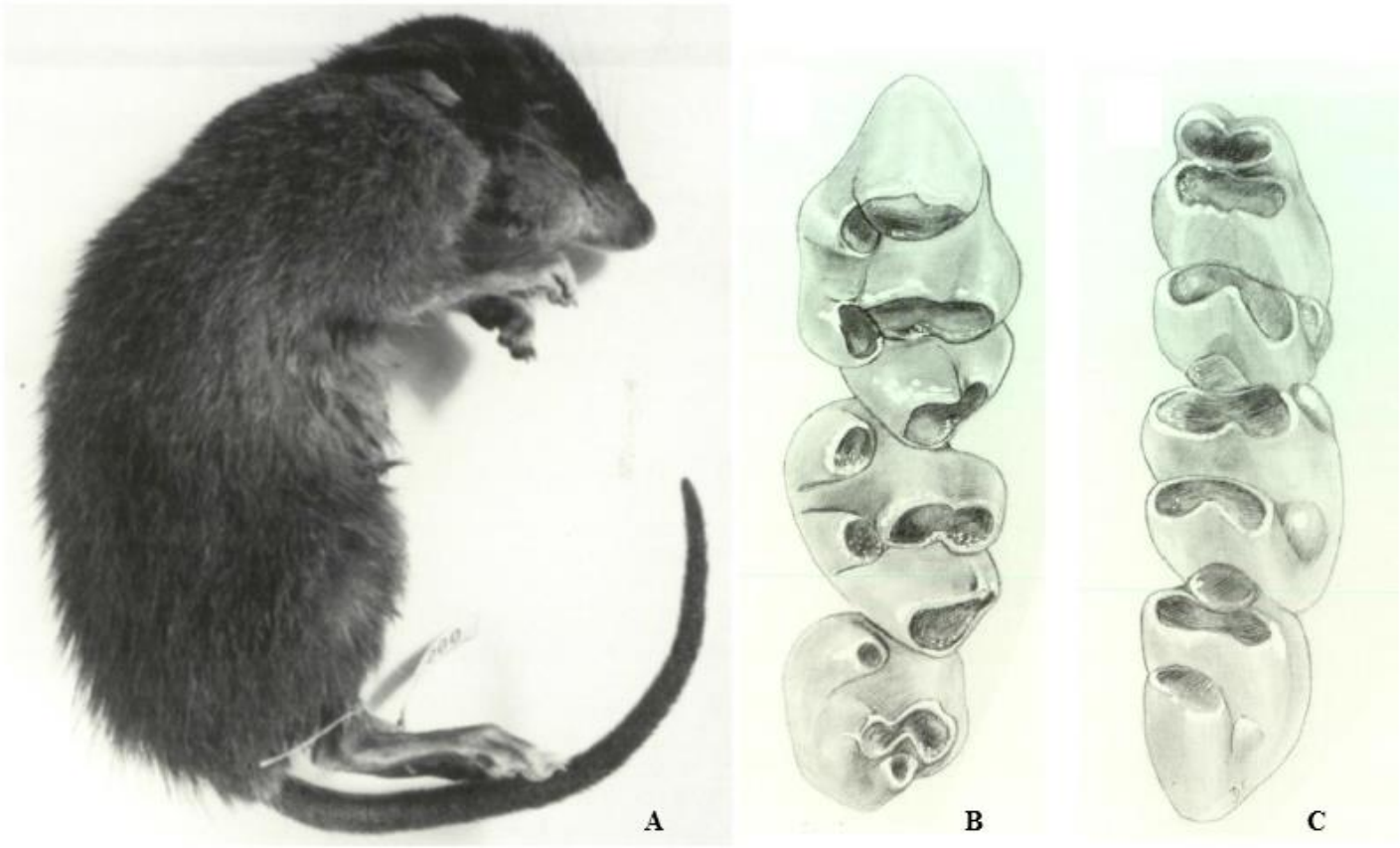

Figure 6. *Paulamys naso:* Photograph of a modern specimen of *P. naso* (WAM M32000) (A) an illustration of maxillary tooth row (B) and an illustration of a mandibular tooth row (C) All images modified from Kitchener et al. (1991) in which no scale was provided.

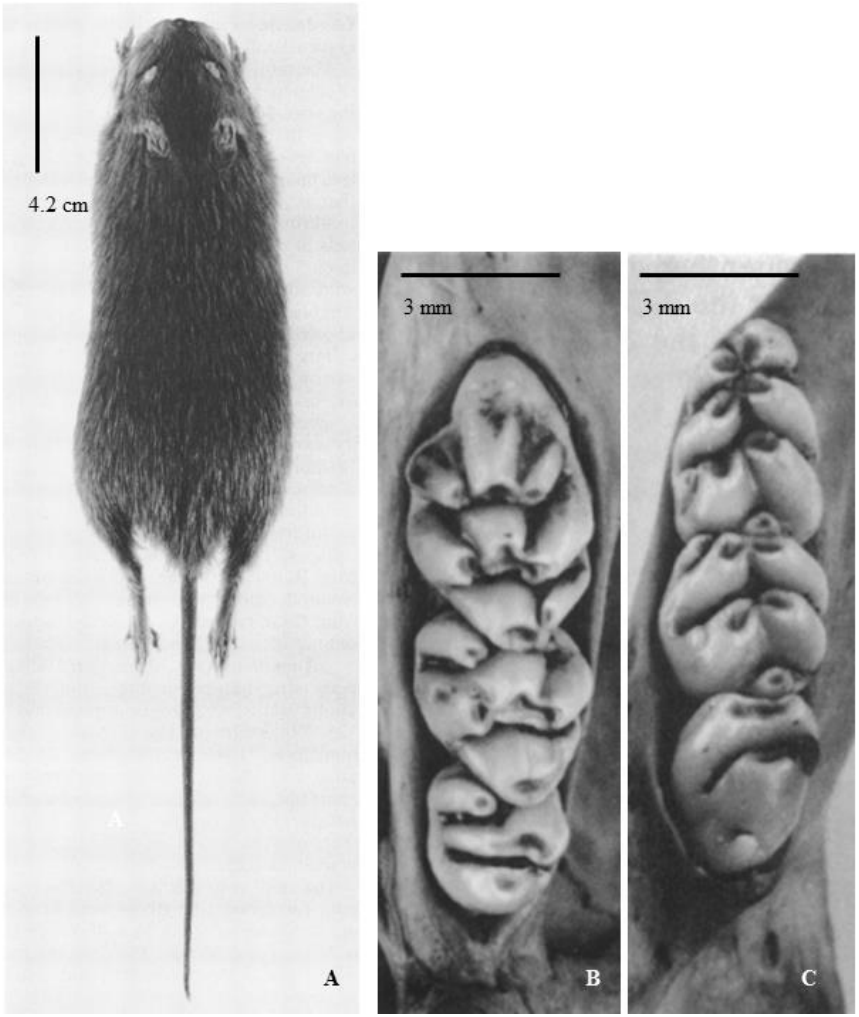

Figure 7. *Komodomys rintjanus:* A photograph of specimen MZB 9020 from Rinca Island (A) maxillary tooth row (B) and mandibular tooth row (C). All images modified from Musser, 1981.

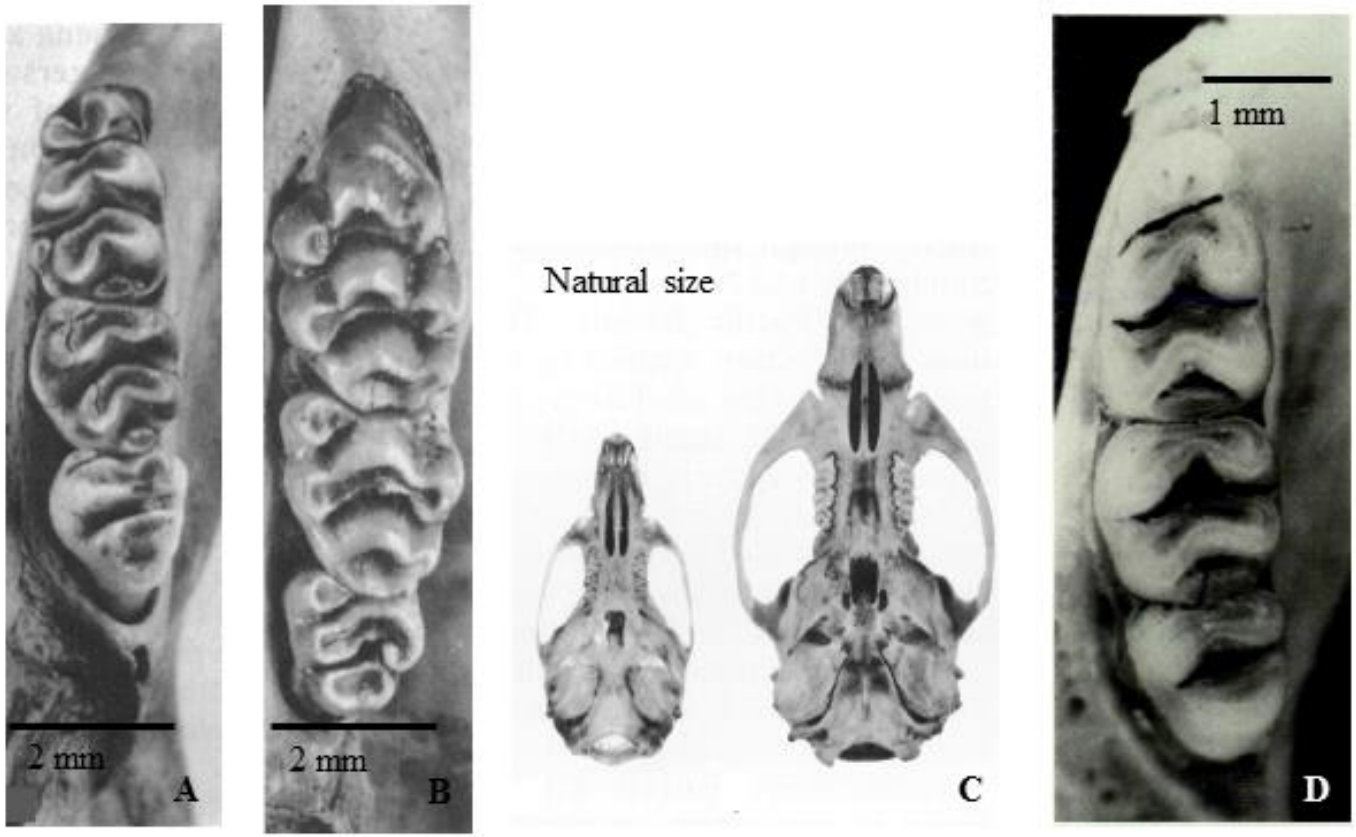

Figure 8. Commensal *Rattus* spp. on Flores: Mandibular tooth row of *R. rattus/tanezumi* (A) Maxillary tooth row of *R. argentiventer* (B) Cranial central views of *R. exulans* (left) and *R. norvegicus* (right) (C) Mandibular tooth row of *R. hainaldi* (D). Images A, B, C modified from Musser, 1981 and image D modified from Kitchener et al., 1991b.

Figure 9. Images showing mandibular tooth rows of the murids from Flores: *P. armandvillei* (A) *P. theodorverhoeveni* (B) *Spelaeomys* (C) *Hooijeromys* (D) *P. naso* (E) *K. rintjanus* (F) *R. hainaldi* (G). All images modified from Musser, 1981.

Table 2. Definitions of rodent locomotor behavior (modified from Samuels & Valkenburgh 2008).

Locomotor category	Definition
Terrestrial	Rarely swims or climbs, may dig to make a burrow (but not extensively), may show salutatory behavior (quadrupedal only), never glides (e.g. rats and mice)
Arboreal	Capable of and regularly seen climbing for escape, shelter, or foraging (including seasonal species) (e.g. tree squirrels and erethizontid porcupines)
Semi-fossorial	Regularly digs to build burrows for shelter, but does not forage underground (e.g. ground squirrels)
Fossorial	Regularly digs to build extensive burrows as shelter or for foraging underground (e.g. gophers and mole rats). Display a predominantly subterranean existence.
Semi-aquatic	Regularly swims for dispersal, escape, or foraging (e.g. beavers and muskrats)
Ricochetal	Capable of jumping behavior characterized by simultaneous use of the hind limbs, commonly bipedal (e.g. Kangaroo rats)
Gliding	Capable of gliding through the use of a patagium, commonly forage in and rarely leave trees (e.g. flying squirrels)

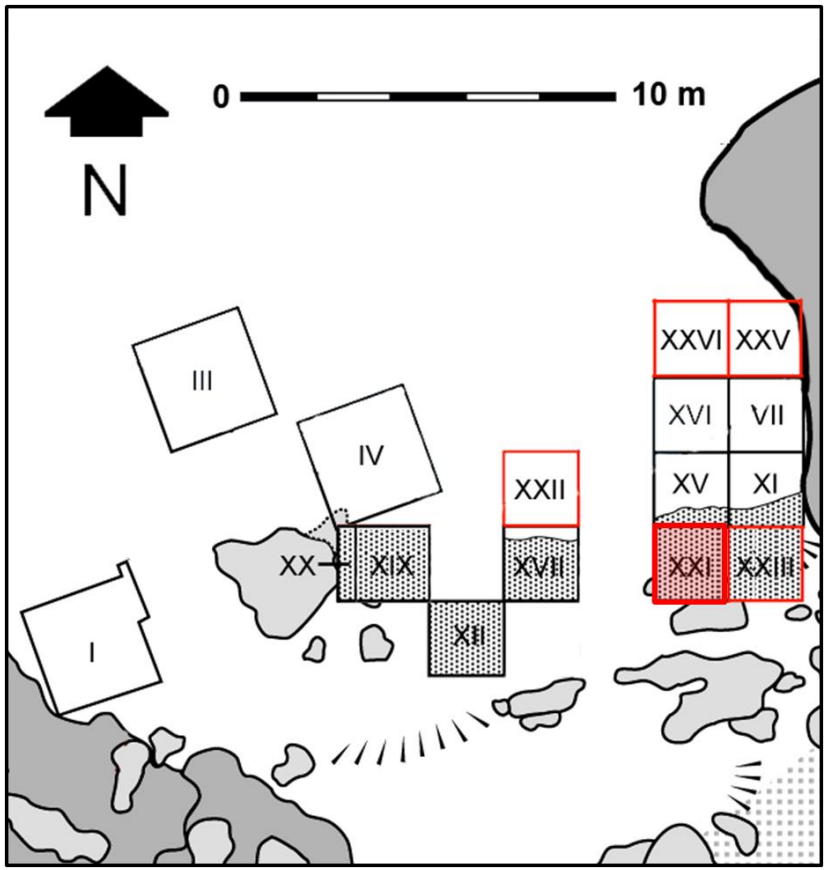

Figure 10. Map of previous excavations at Liang Bua. Sectors excavated between 2010 and 2012 outlined in red with Sector XXI (2010) highlighted in bold red

Table 3. Measurements and descriptions of variables for the humerus and calcaneus.

Measurement	Description
Humerus	
Maximum Length	Total Length from the most distal end to the most proximal end with the humeral head detached.
ML Head Diameter	Maximum breadth at the epiphyseal suture line from the medial to lateral side.
AP Head Diameter	Maximum breadth at the epiphyseal suture line from the anterior to posterior side.
ML Midshaft Diameter	Measured maximum breadth at the midpoint of shaft where the deltoid tuberosity merged with the shaft.
AP Midshaft Diameter	Measured maximum depth at the midpoint of shaft where the deltoid tuberosity merged with the shaft.
ML Distal Width	Maximum breadth from medial to lateral condyles.
AP Distal Depth	Maximum depth from the anterior to posterior distal end including the lateral ridge.
AP Trochlea Thickness	Maximum depth of the trochlea and capitulum.
Length of Medial Condyle	Maximum length of the medial condyle from the trochlea to the most medial point.
Anterior Articular Breadth	Measured the width of the trochlea and capitulum on the anterior surface.
Posterior Articular Breadth	Measured the width of the trochlea and capitulum on the posterior surface.
AP Min Articular Thickness	Measured the minimum thickness between the trochlea and capitulum.
Calcaneus	
Maximum Length	Measured from the most anterior point of the cuboid articular surface to the most posterior point of the heel.
Maximum Breadth	Maximum breadth from the most medial point on the sustentaculum talar ridge to the most lateral point on the trochlear process.
Heel Length	Measured from the most posterior point of the superior talar articular surface to the most posterior point on the heel.
Shelf Length	Measured from the most posterior point of the superior talar articular surface to the most anterior point at the cuboid articular surface.
Mid Point to Heel Length	Measured at the midpoint of the superior talar articular surface to the most posterior point on the heel.
Mid Point to Cuboid Length	Measured at the midpoint of the superior talar articular surface to the most anterior point of the cuboid articular surface.
Mid Heel Breadth	Maximum breadth of the calcaneal body.
Mid Heel Height	Maximum height of the calcaneal body.
Posterior Heel Breadth	Maximum breadth of the most posterior portion of the heel.
Posterior Heel Height	Maximum height of the most posterior portion of the heel.

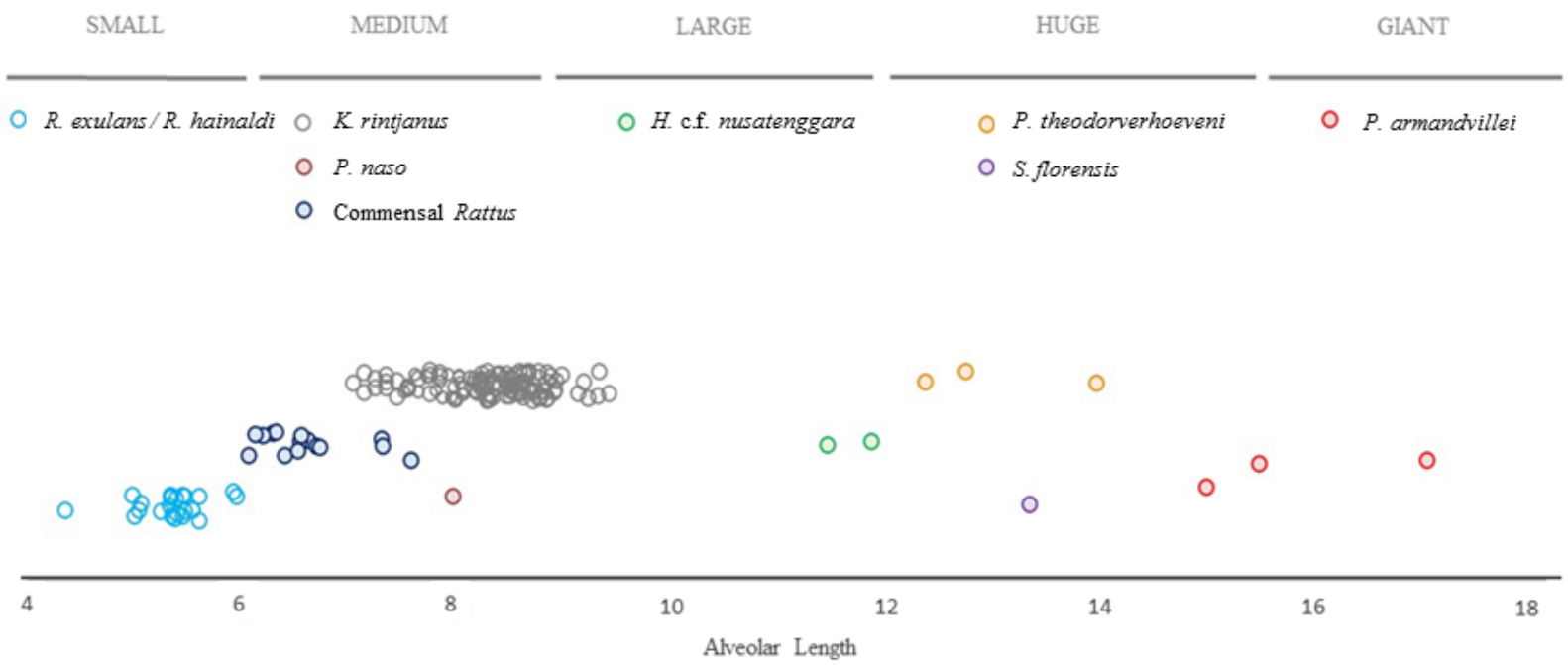

Figure 11. Murine mandibular alveolar lengths from Sector XXI (data provided by Kate McGrath): Taxonomic identifications and size ranges.

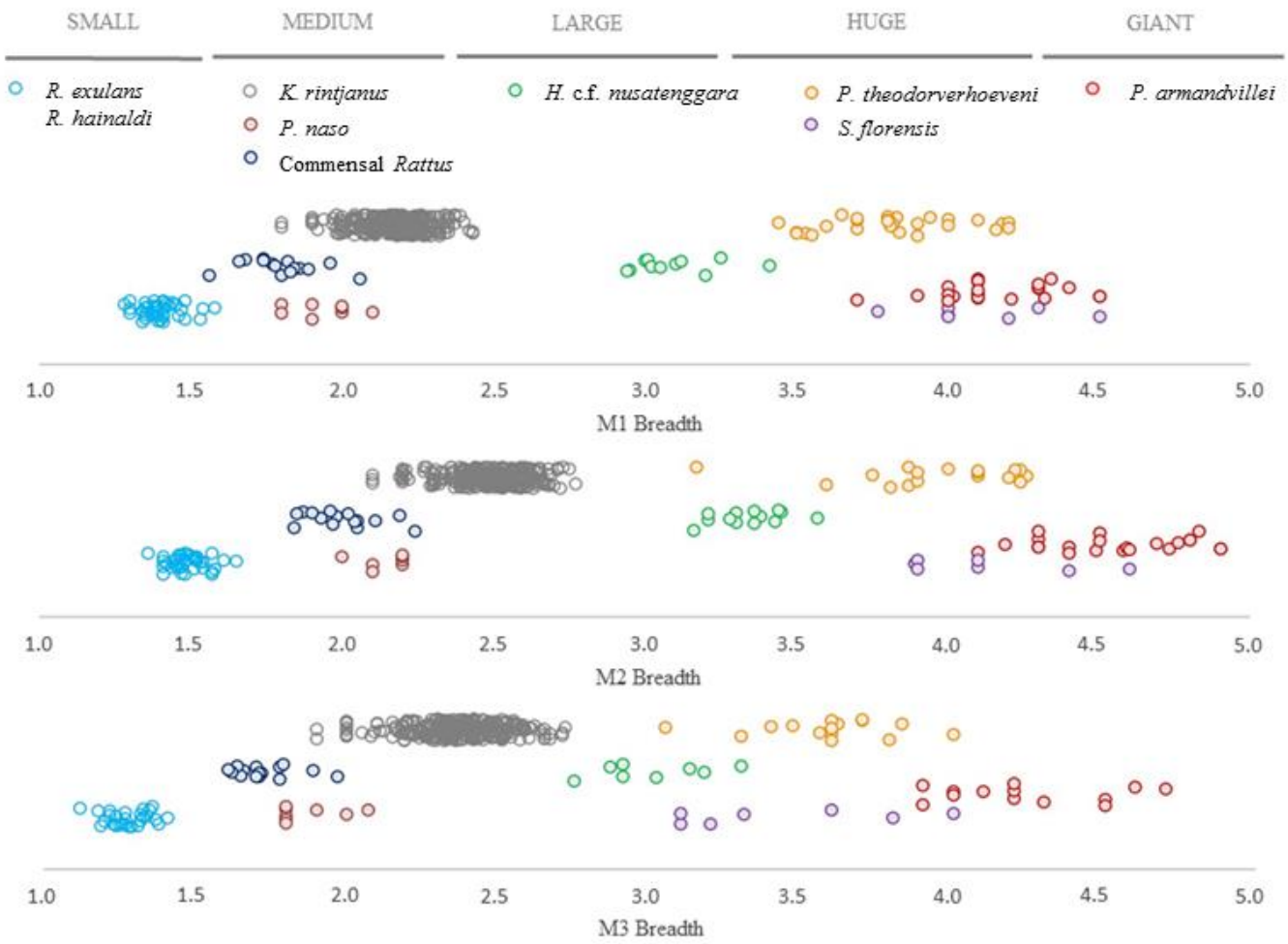

Figure 12. Murine mandibular molar breadths from Sector XXI (data provided by Kate McGrath): Taxonomic identifications and size ranges; other murine data provided by Guy Musser (from MCZ, MZB, UF, Liang Toge and Liang Bua) and Matt Tocheri (from Liang Bua and the Soa Basin); published data from Hooijer (1957b) are also included.

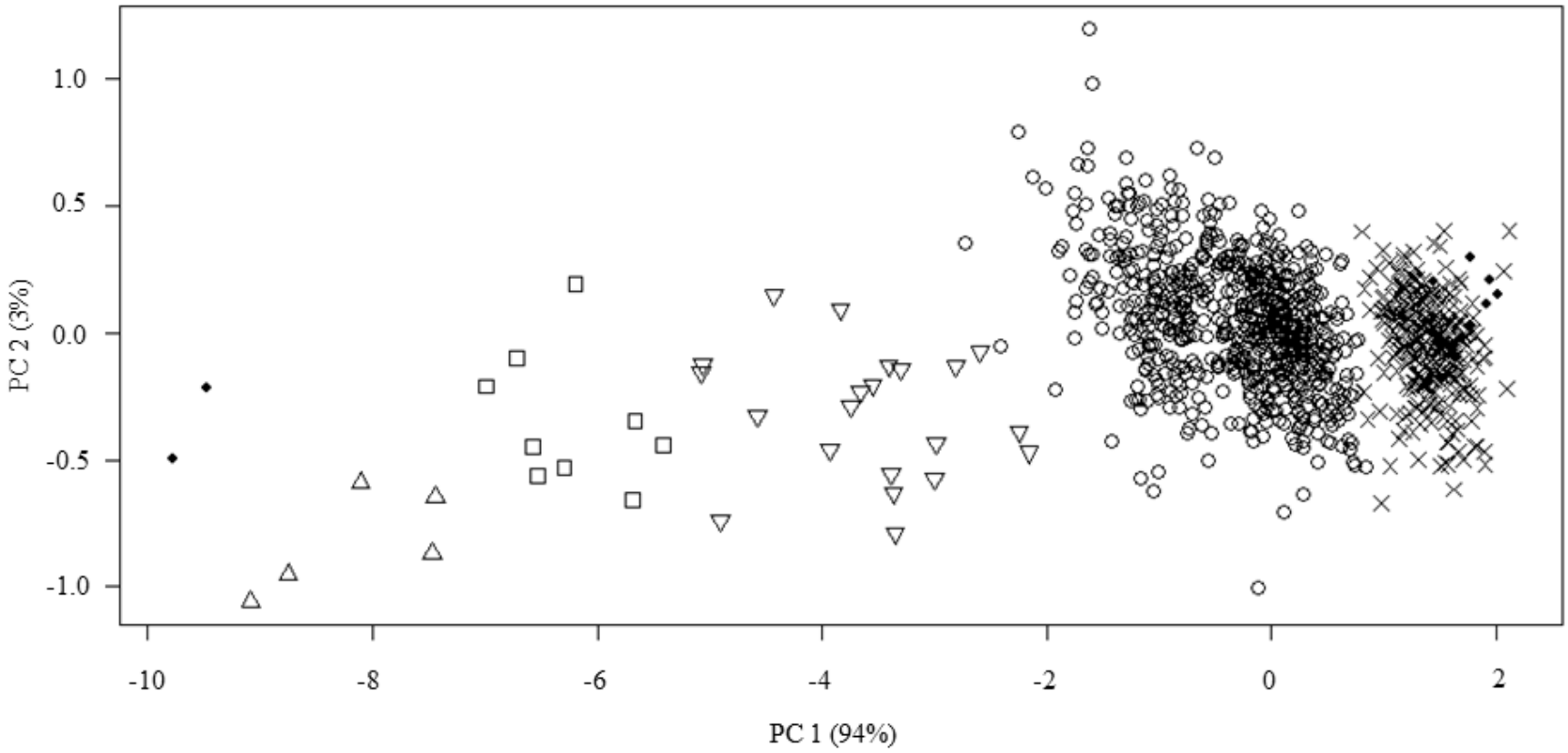

Figure 13. Humerus PCA with group size distinction. Small (X), Medium (O), Large (reverse triangle), Huge (square) and Giant (triangle). Known *P. armandvillei* (left) and *R. exulans* (right) specimens are indicated by closed, black circles.

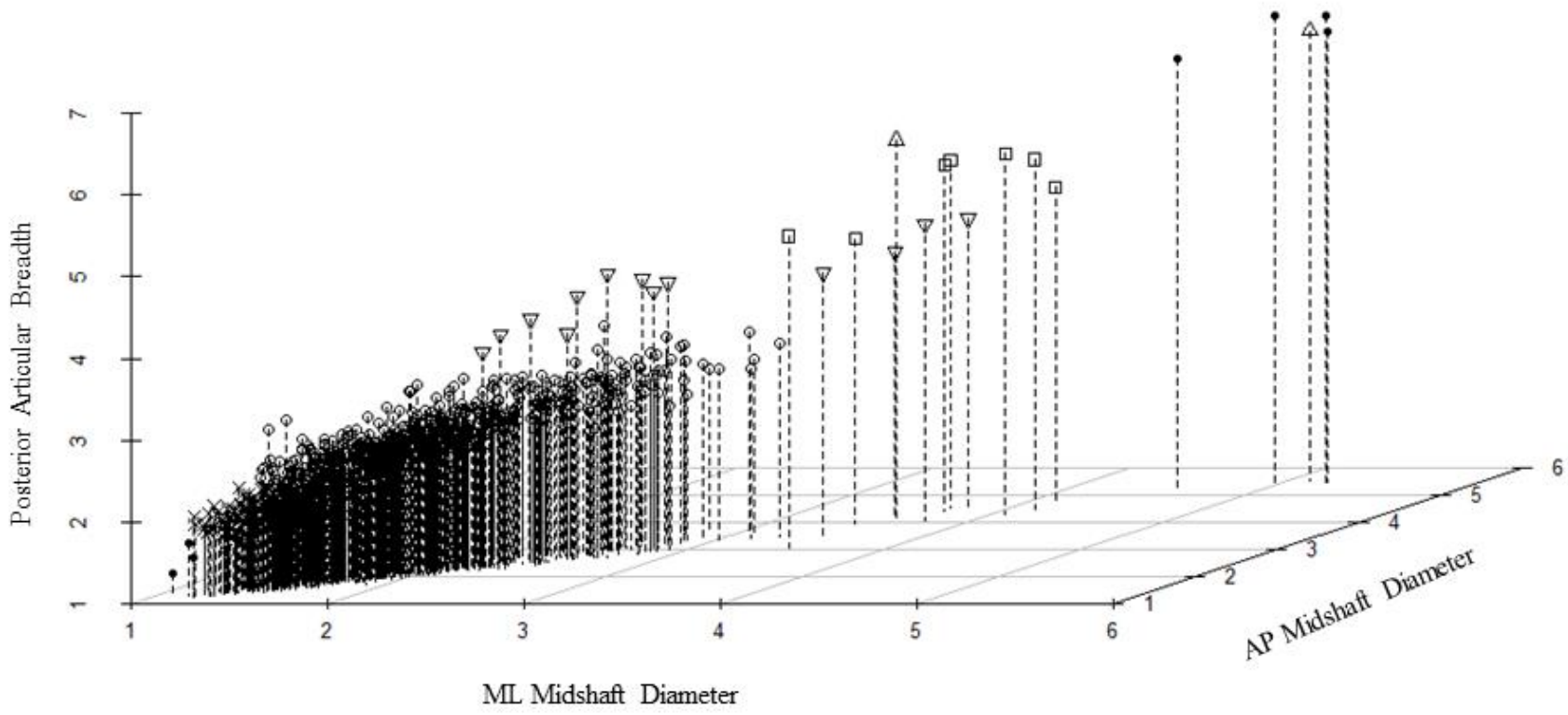

Figure 14. 3D scatterplot of the humerus with identified group size based on original PCA.

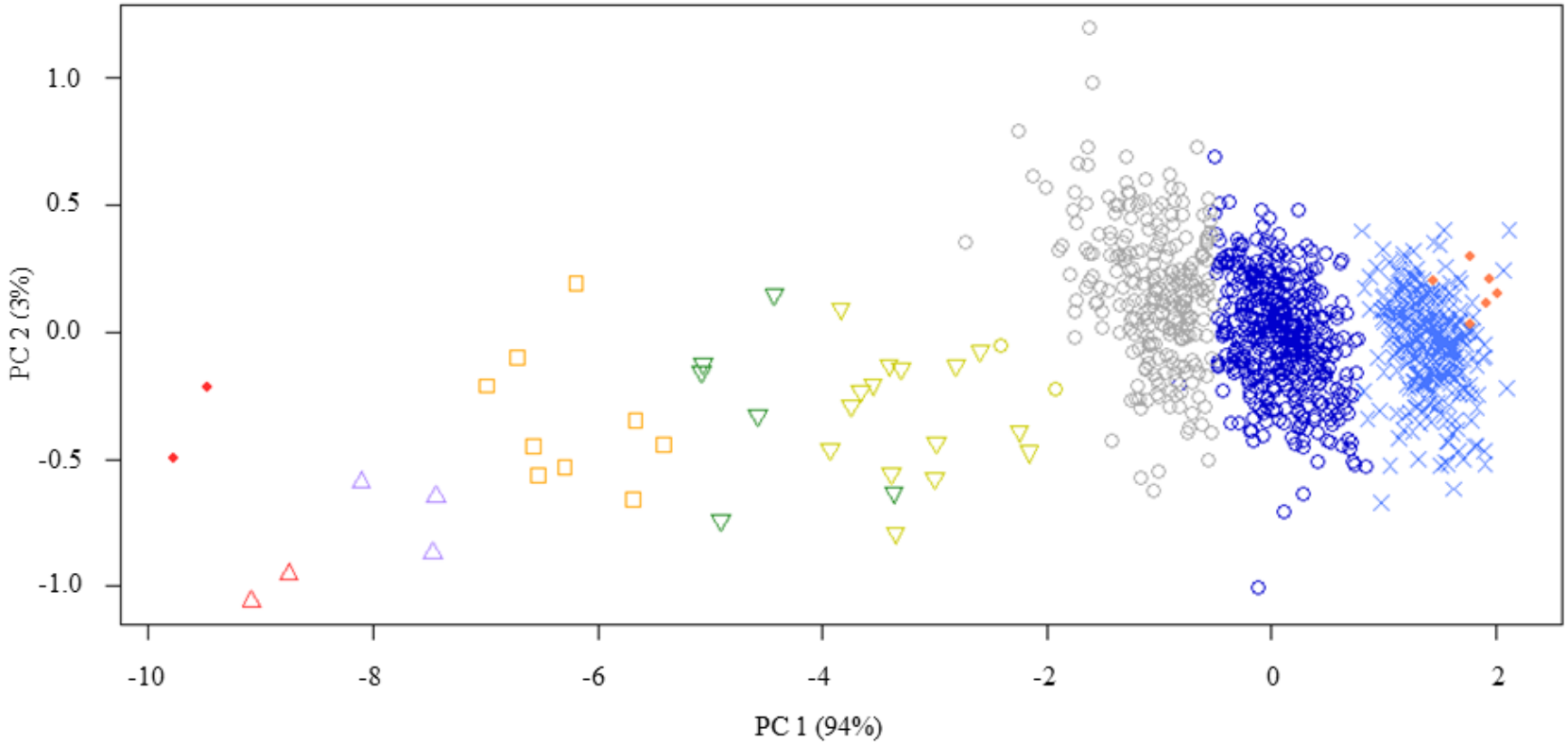

Figure 15. PCA of the humerus with identified group size. Taxonomy is represented by colors based on Figure 14. Known *P. armandvillei* (red; left) and *R. exulans* (orange; right) specimens are represented by closed circles.

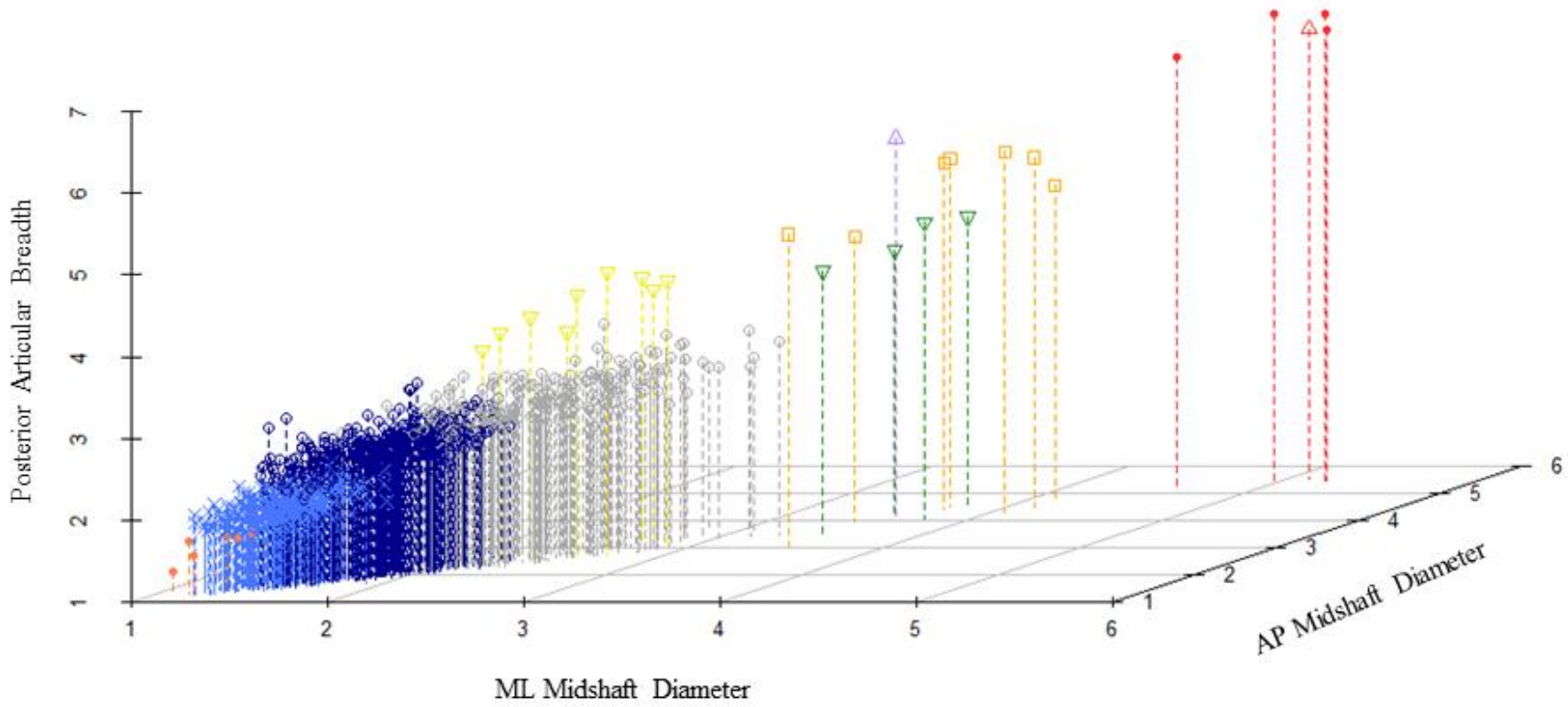

Figure 16. 3D scatterplot of the humerus with identified group size. Taxonomy is represented by colors: *P. armandvillei* (red), *P. theodorverhoeveni* (orange), *Spelaeomys* (purple), *Hooijeromys* (green), unknown (yellow), large *K. rintjanus* (grey), small *K. rintjanus* and *P. naso* (dark blue), and small *Rattus* spp. (light blue). Known *P. armandvillei* (red; right) and *R. exulans* (orange; left) specimens are represented by closed circles.

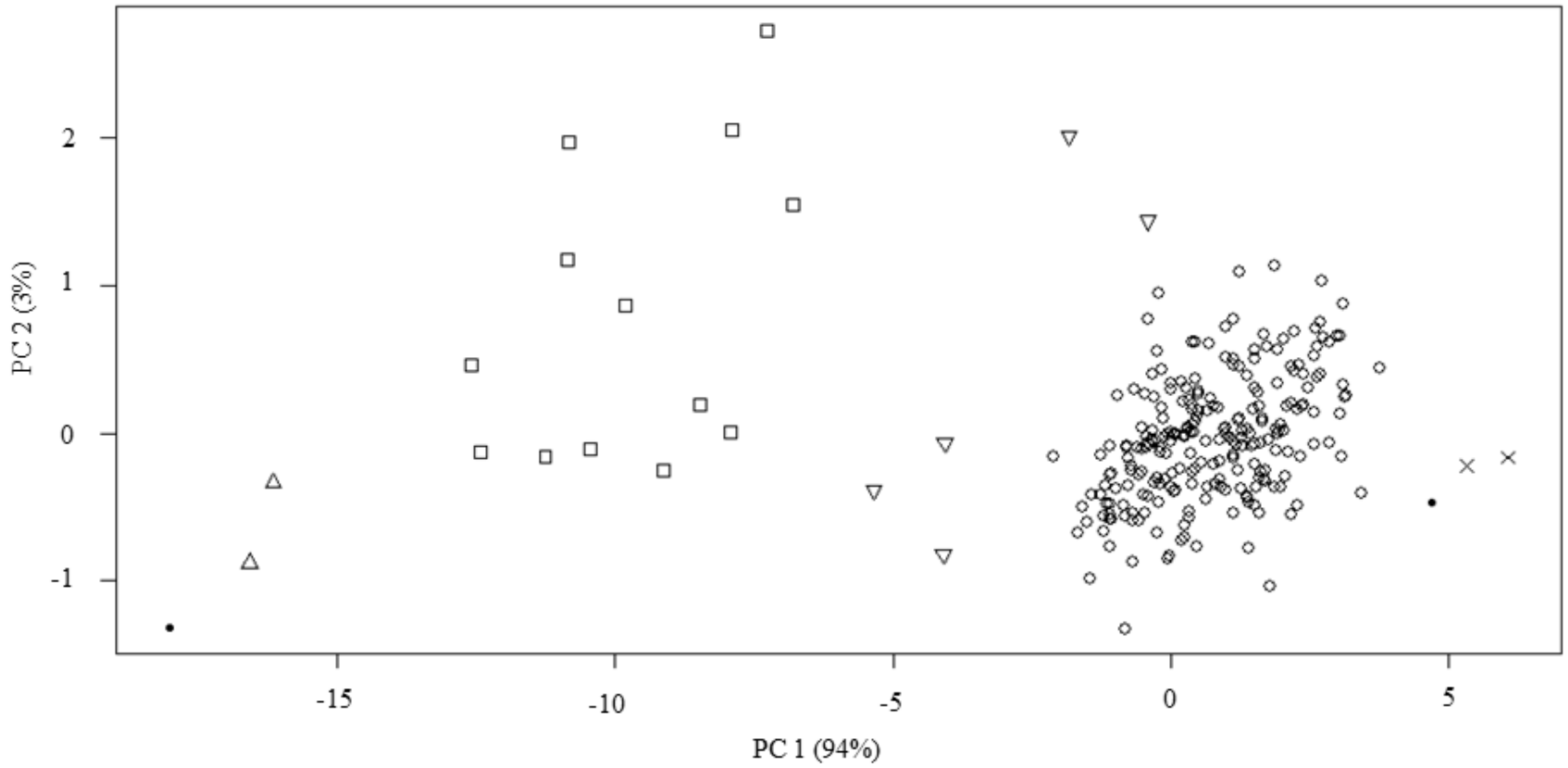

Figure 17. Calcaneus PCA with group size distinctions. Small (X), Medium (O), Large (reverse triangle), Huge (square) and Giant (triangle). Known *P. armandvillei* (left) and *R. exulans* (right) specimens are indicated by closed, black circles.

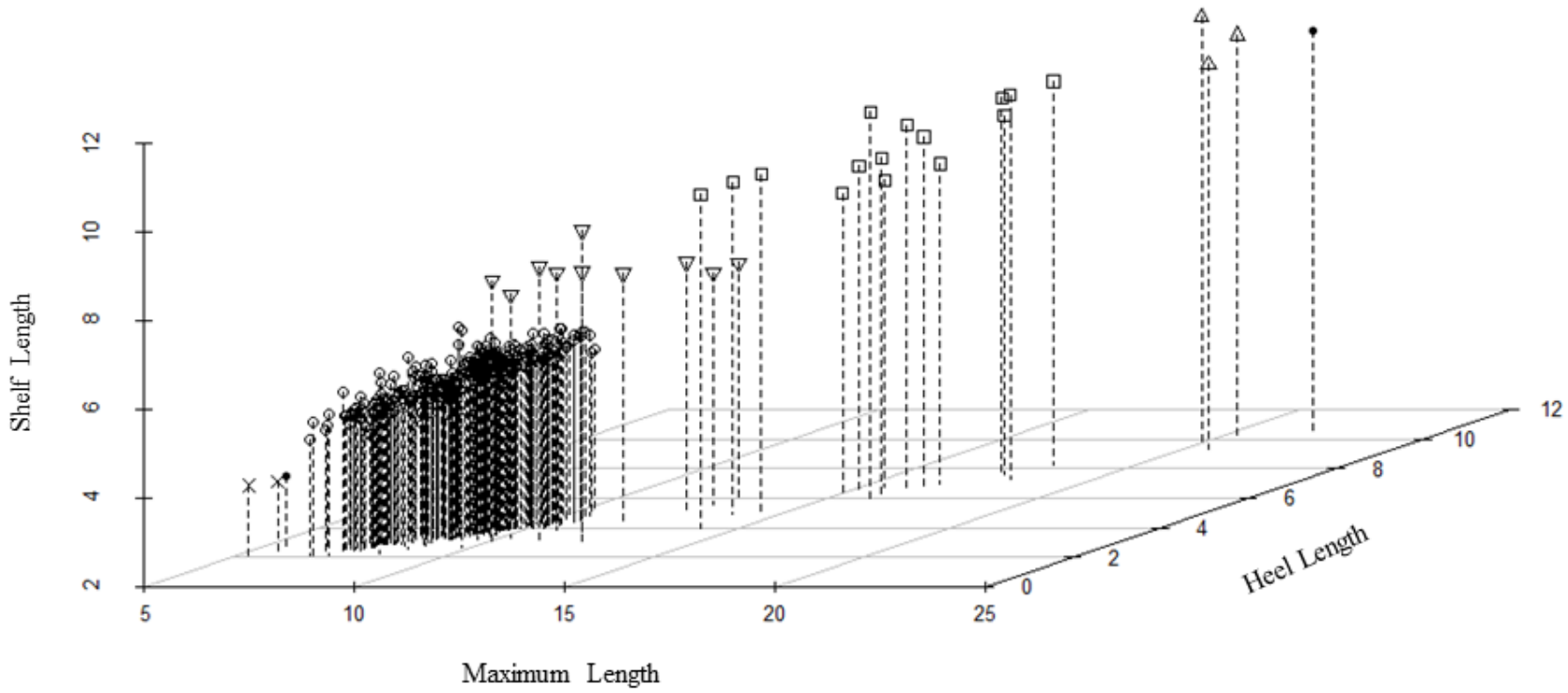

Figure 18. 3D scatterplot of the calcaneus with identified group size based on original PCA.

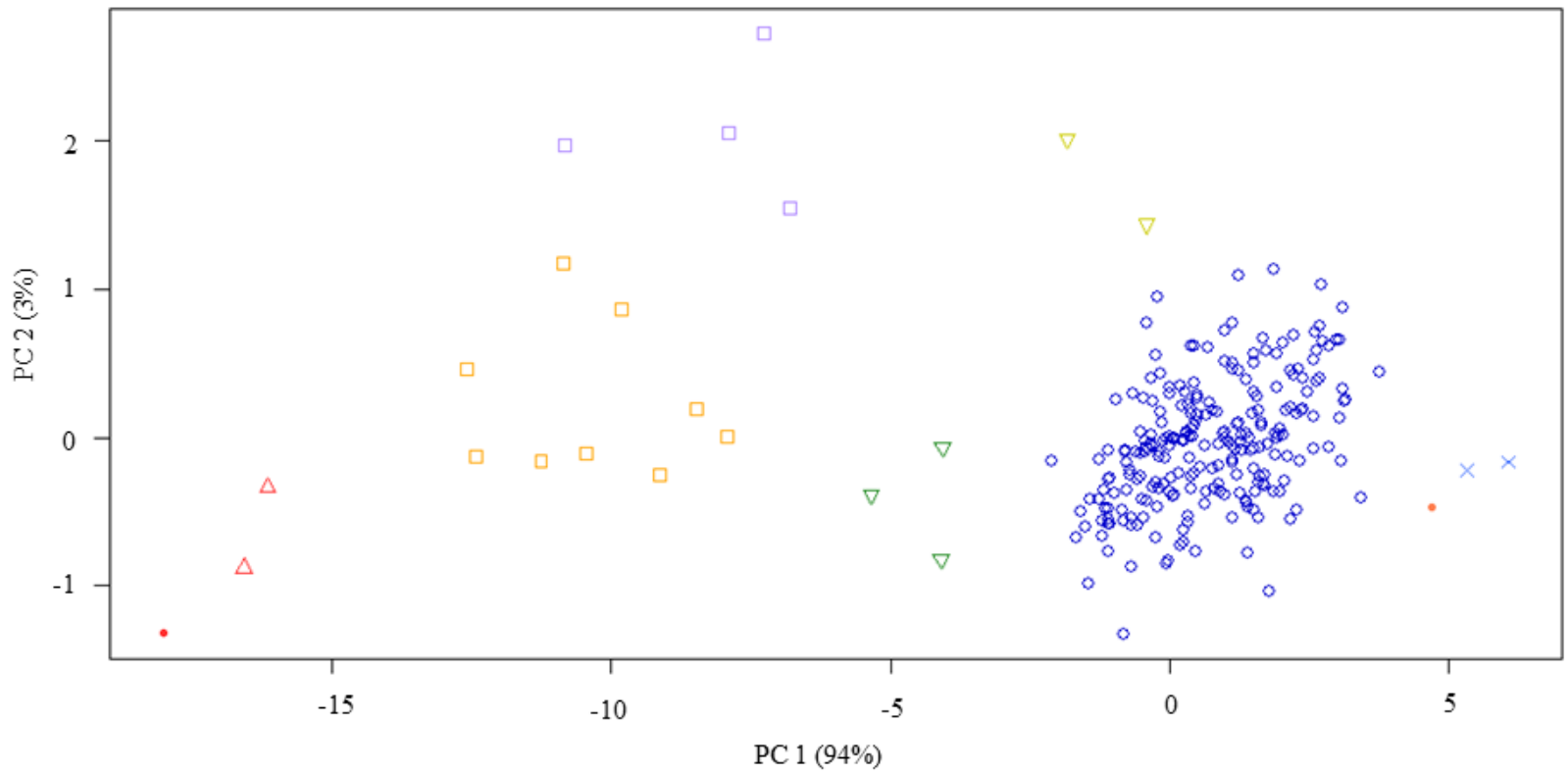

Figure 19. Calcaneus PCA with identified group size. Taxonomy is represented by colors based on Figure 18. Known *P. armandvillei* (red; left) and *R. exulans* (orange; right) specimens are represented by closed circles.

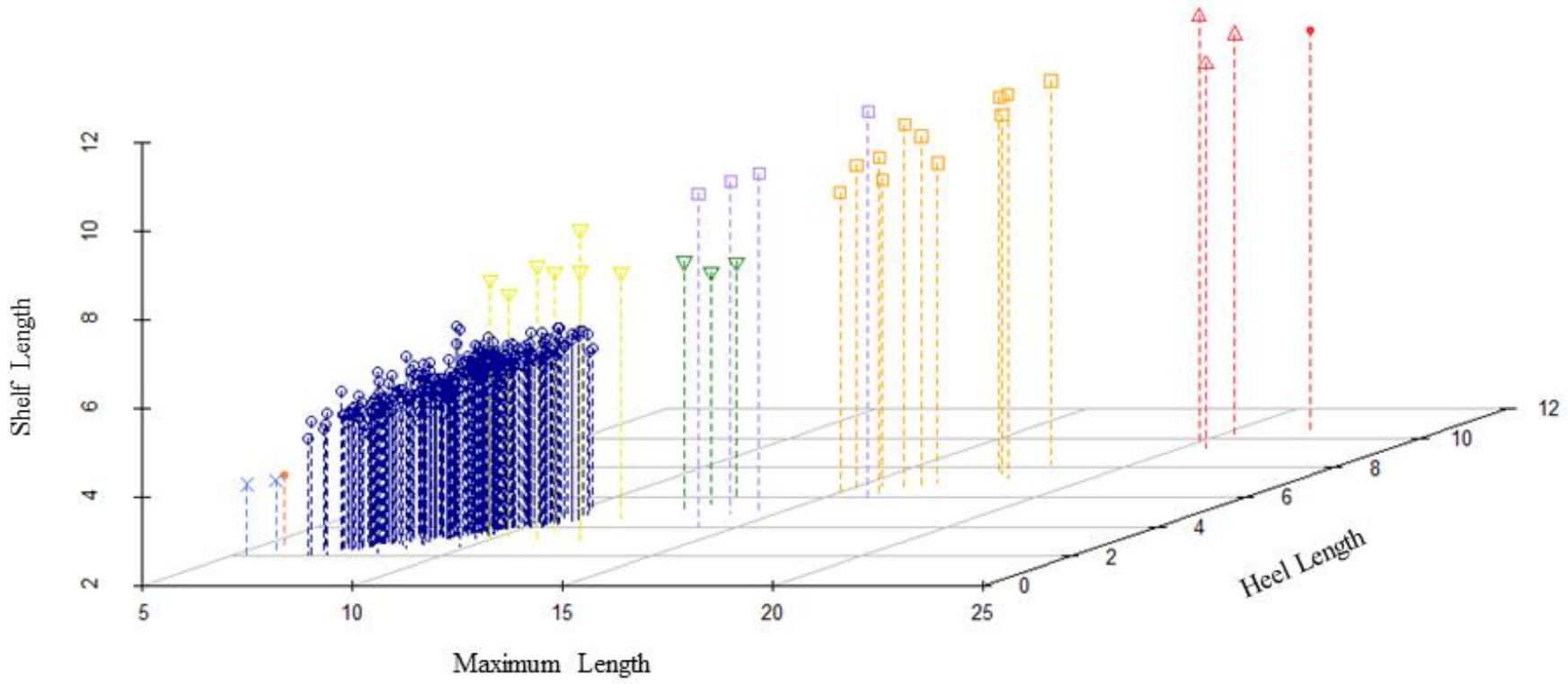

Figure 20. 3D scatterplot of the calcaneus with group size. Taxonomy is represented by colors: *P. armandvillei* (red), *P. theodorverhoeveni* (orange), *Spelaeomys* (purple), *Hooijeromys* (green), unknown (yellow), *K. rintjanus* and *P. naso* (dark blue), and small *Rattus* spp. (light blue). Known *P. armandvillei* (red; right) and *R. exulans* (orange; left) specimens are represented by closed circles.

Table 4. Humerus: Averages and standard deviations for each attributed murine species.

Taxa	AP Distal Depth	AP Capitulum Thickness	Anterior Articular Br.	Posterior Articular Br.	AP Min Articular Thickness
Papagomys armandvillei	6.090 ± 0.056	6.105 ± 0.077	9.495 ± 0.091	6.465 ± 0.063	4.340 ± 0.353
Papagomys theodorverhoeve	5.530 ± 0.374	5.261 ± 0.463	7.944 ± 0.607	5.225 ± 0.268	3.480 ± 0.358
Spelaeomys florensis	5.463 ± 0.381	5.110 ± 0.628	8.126 ± 0.597	5.486 ± 0.599	3.620 ± 0.690
Hooijeromys nusanteggara	4.686 ± 0.540	4.061 ± 0.491	6.328 ± 0.650	4.316 ± 0.268	2.722 ± 0.314
Unknown	4.161 ± 0.408	3.719 ± 0.258	5.567 ± 0.532	4.069 ± 0.288	2.500 ± 0.226
Komodomys sp. BIG	3.603 ± 0.324	2.876 ± 0.233	4.221 ± 0.237	2.975 ± 0.198	1.746 ± 0.118
Komodomys sp. SMALL	2.956 ± 0.270	2.379 ± 0.156	3.543 ± 0.196	2.552 ± 0.179	1.581 ± 0.091
Rattus sp.	2.350 ± 0.219	1.843 ± 0.121	2.762 ± 0.176	1.972 ± 0.160	1.231 ± 0.085

Table 5. Calcaneus: Averages and standard deviations for each attributed murine species.

Taxa	Max Length	Max Breadth	Heel Length	Shelf Length	Mid pt. to Heel Lg
P. armandvillei	20.526 ± 0.249	12.630 ± 0.721	9.563 ± 0.313	11.160 ± 0.495	13.570 ± 0.450
P. theodorverhoeveni	16.642 ± 1.072	9.485 ± 0.873	6.927 ± 0.634	9.812 ± 0.690	10.367 ± 0.724
S. florensis	14.675 ± 1.006	9.54 ± 0.961	4.920 ± 0.817	9.845 ± 0.589	8.190 ± 0.872
H. nusanteggara	12.830 ± 0.419	6.790 ± 0.689	5.466 ± 0.207	7.410 ± 0.170	7.720 ± 0.399
Unknown	11.128 ± 0.799	6.926 ± 1.330	3.508 ± 0.515	7.968 ± 0.511	5.657 ± 0.572
Komodomys sp.	8.921 ± 0.904	4.984 ± 0.486	3.480 ± 0.608	5.557 ± 0.441	5.109 ± 0.725
Rattus sp.	5.580 ± 0.395	3.130 ± 0.197	2.086 ± 0.091	3.605 ± 0.035	3.330 ± 0.395
Taxa	Mid pt. to Cuboid Lg	Mid Heel Br.	Mid Heel Ht	Post. Heel Br.	Post. Heel Ht
P. armandvillei	7.430 ± 0.497	5.080 ± 0.430	6.173 ± 0.310	5.076 ± 0.070	5.173 ± 1.547
P. theodorverhoeveni	6.527 ± 0.574	3.617 ± 0.440	5.183 ± 0.347	3.798 ± 0.371	5.189 ± 0.526
S. florensis	6.962 ± 0.530	3.152 ± 0.553	4.757 ± 0.468	3.362 ± 0.519	4.705 ± 0.491
H. nusanteggara	5.393 ± 0.090	2.960 ± 0.285	3.513 ± 0.384	2.820 ± 0.250	3.593 ± 0.388
Unknown	5.700 ± 0.323	2.654 ± 0.228	3.495 ± 0.557	2.705 ± 0.007	3.383 ± 0.298
Komodomys sp.	3.968 ± 0.397	2.220 ± 0.324	2.624 ± 0.313	2.199 ± 0.308	2.627 ± 0.304
Rattus sp.	2.715 ± 0.091	1.175 ± 0.120	1.600 ± 0.197	1.205 ± 0.176	1.640 ± 0.183

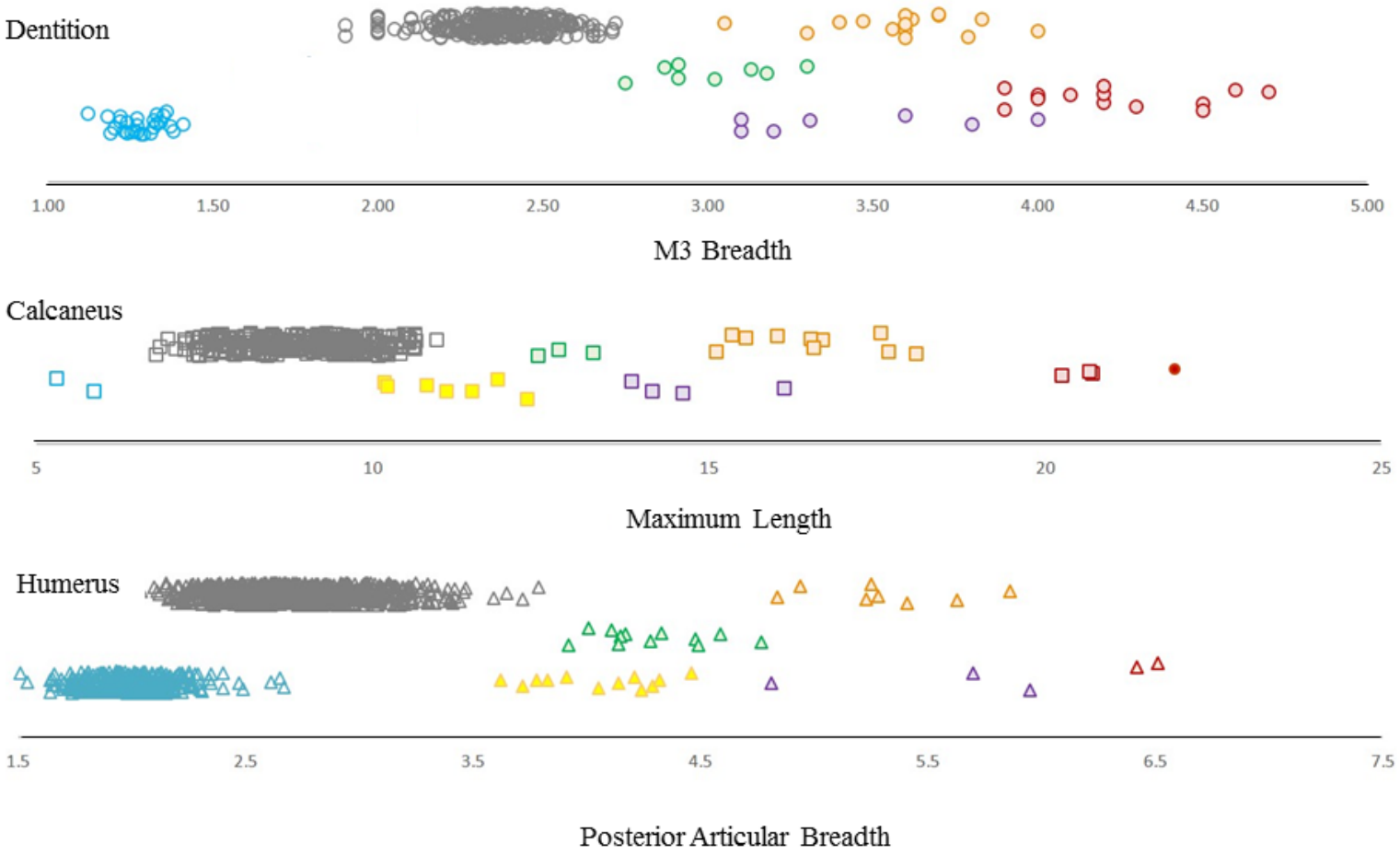

Figure 21. Size comparisons between dentition (circles), calcaneus (squares) and humerus (triangles). Taxonomy is represented by colors: *P. armandvillei* (red), *P. theodorverhoeveni* (orange), *Spelaeomys* (purple), *Hooijeromys* (green), unknown (yellow), *K. rintjanus* and *P. naso* (grey) and small *Rattus* spp. (light blue).

Figure 22. Hypothesized humeri from Sector XXI at Liang Bua: (A) Giant (*P. armandvillei*) (B) Huge (*P. theodorverhoeveni)* (C) Huge (*Spelaeomys*) (D) Large (*Hooijeromys*) (E) Large ("Unknown").

Figure 23. Hypothesized calcanei from Sector XXI at Liang Bua: (A) Giant (*P. armandvillei*) (B) Huge (*P. theodorverhoeveni*) (C) Huge (*Spelaeomys*) (D) Large (*Hooijeromys*) (E) Large ("Unknown").

Table 6. Calcaneal SHR index (shelf to heel ratio) of murines from Liang Bua compared to known semi-aquatic (*Hydromys*), terrestrial (*Leopoldamys*) and arboreal rats (*Crateromys*).

	SHR	
	Mean	SD
P. armandvillei	0.879	0.052
P. theodorverhoeveni	0.706	0.049
H. c.f. *nusatenggara*	0.738	0.041
S. florensis	0.498	0.061
Unknown	0.443	0.082
Komodomys sp.	0.625	0.095
R. exulans / R. hainaldi	0.627	0.048
Hydromys sp.	1.182	0.070
Leopoldomys sp.	0.777	0.019
Crateromys sp.	0.750	0.015

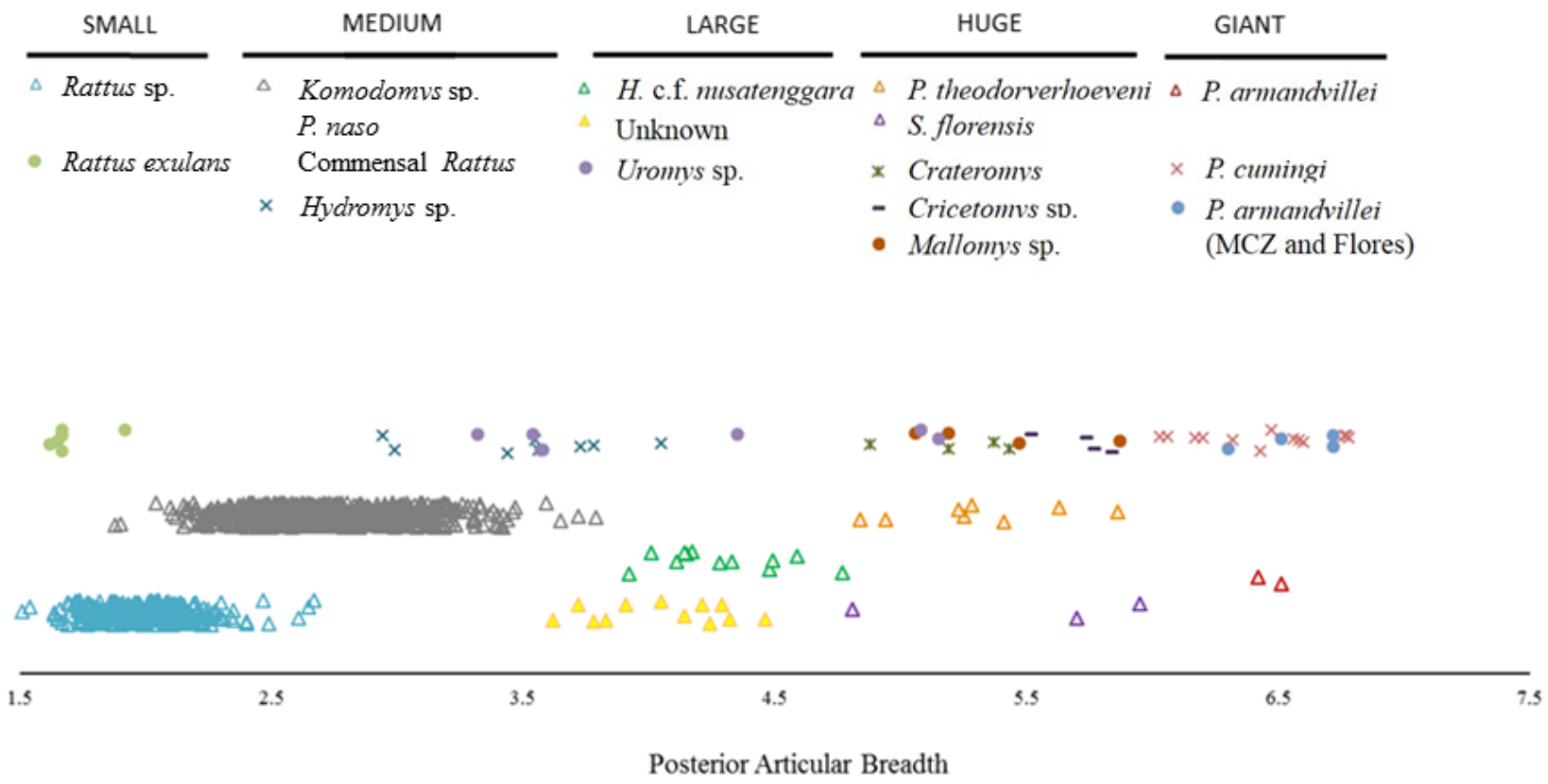

Figure 24. Humerus: Relative size distribution of fossil and extant taxa of various age ranges.

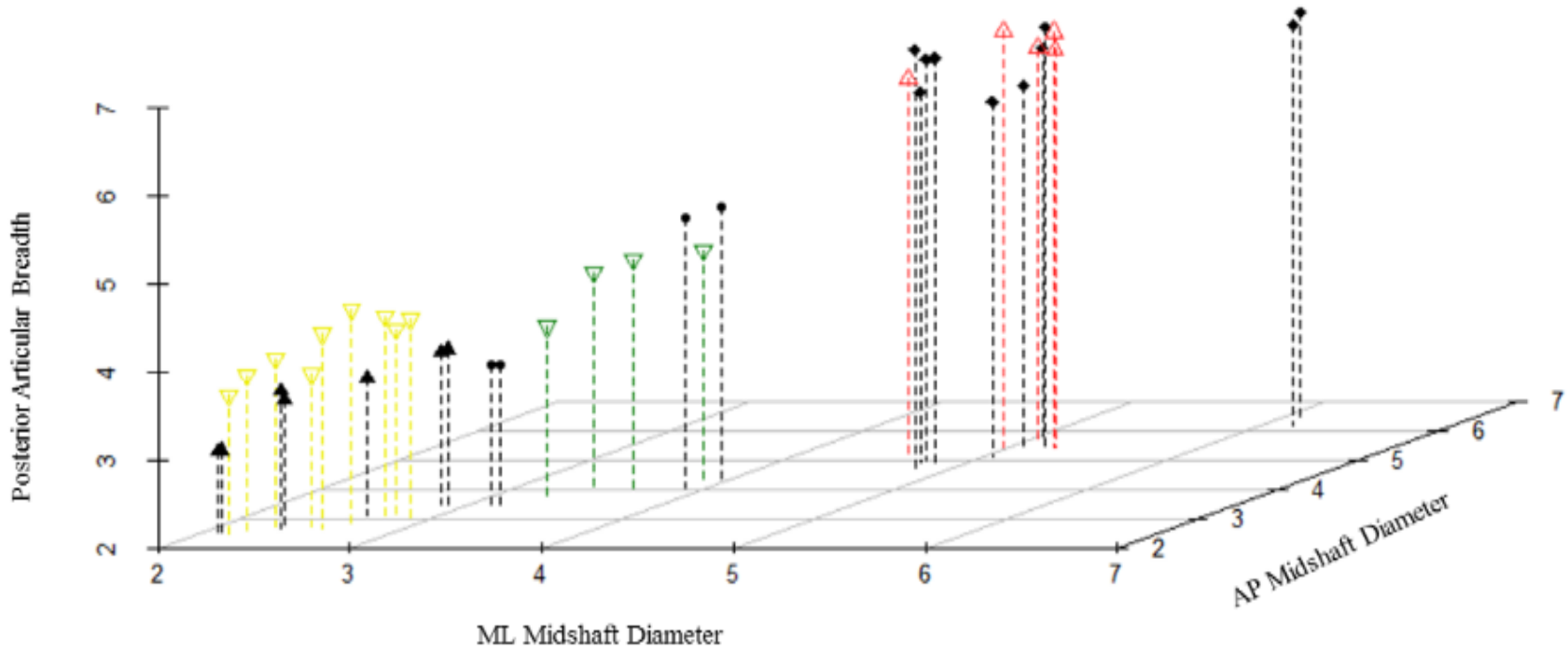

Figure 25. 3D scatterplot of the humeri at various developmental stages comparing *Phloeomys cumingi* (black diamonds), *Uromys caudimaculatus* (black circles) and *Hydromys chrysogaster* (black reverse triangle) with *P. armandvillei* (red triangles), *Hooijeromys* (green reverse triangles) and unknown (yellow reverse triangles) from Liang Bua.

Table 7. Percent increase in various dimensions of the humerus from juveniles (no epiphyseal fusion) to adult (full epiphyseal fusion).

Variable	*Phloeomys*	*Uromys*	*Hydromys*
Max Length	20.9	26.5	21.4
ML Midshaft	21.8	29.6	25.4
AP Midshaft	22.7	12.7	30.5
ML Distal Width	9.4	37.6	22.7
AP Distal Depth	9.5	43.2	16.3
AP Capitulum Thickness	9.5	40.4	24.8
Length Medial Condyle	18.6	44.6	33.1
Anterior Artic. Breadth	5.1	35.6	19.3
Posterior Artic. Breadth	0.4	55.1	21.0
AP Min Thickness	0	28.3	18.1

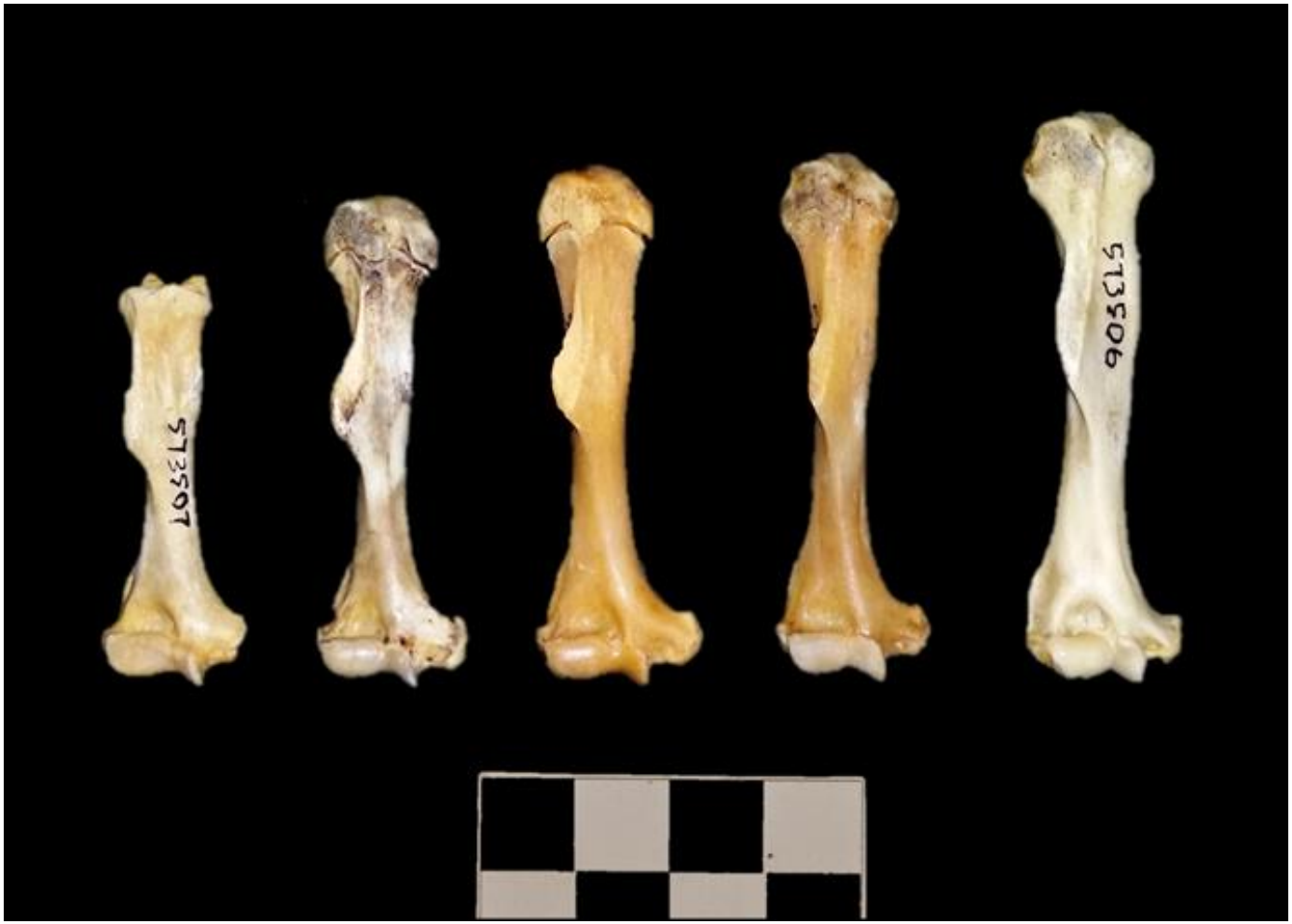

Figure 26. *Phloeomys cumingi* humeri at various stages of development.

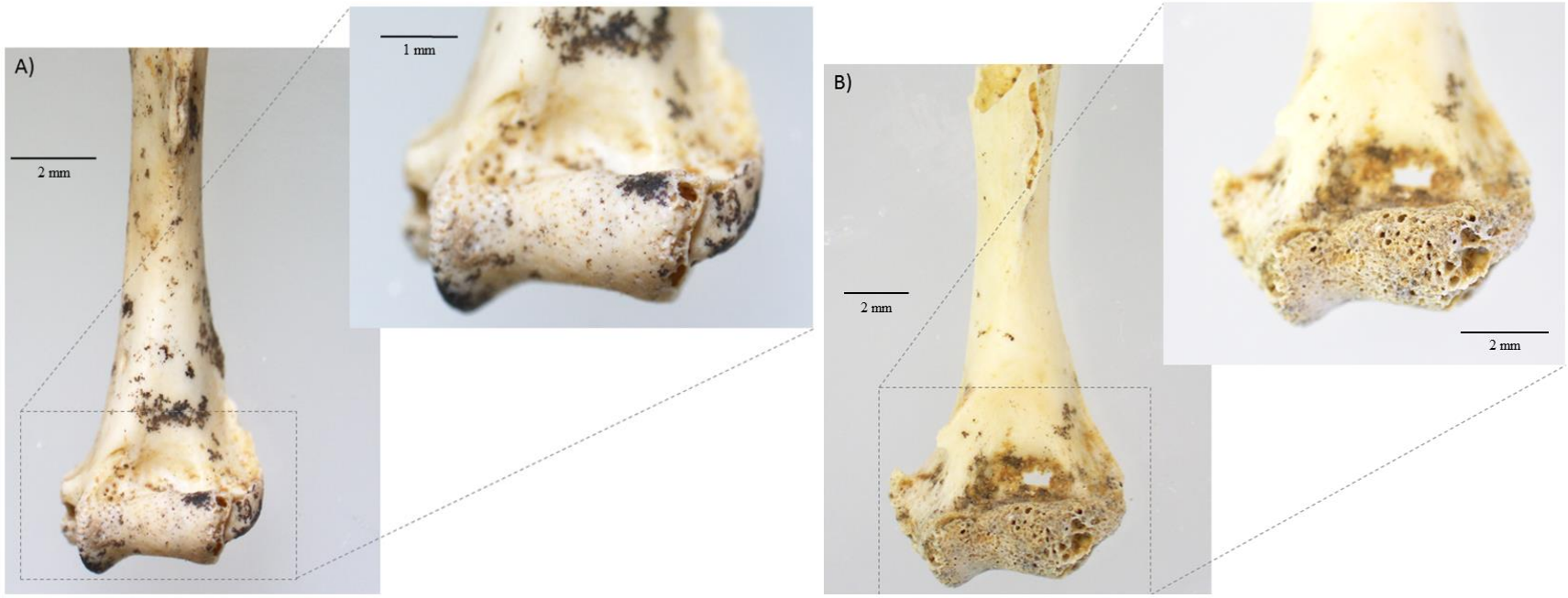

Figure 27. Examples of digestion on the humeral distal articular surface (A) Low (B) Moderate.

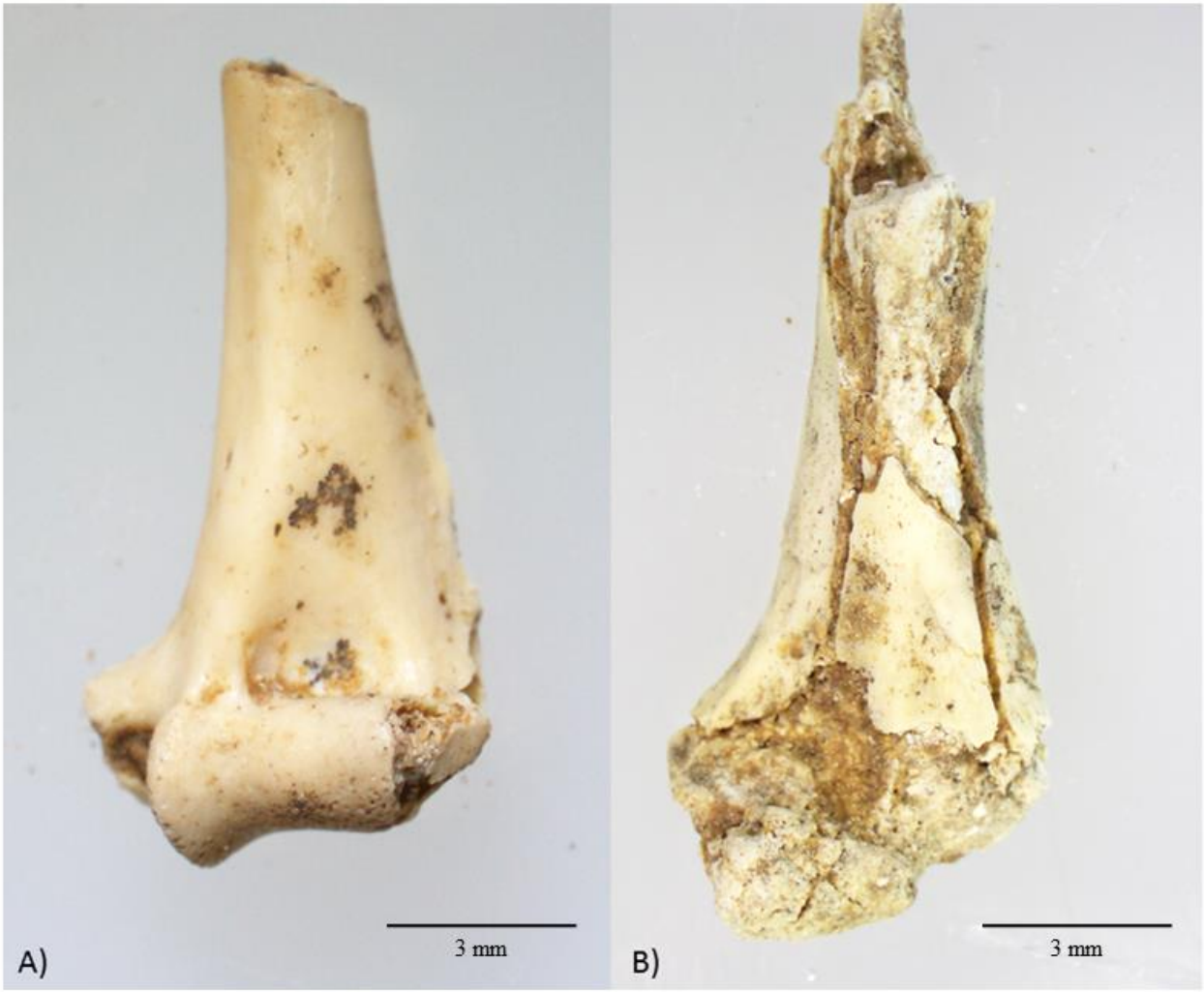

Figure 28. Examples of weathering damage to bone surface (A) BWS 1 (B) BWS 4.

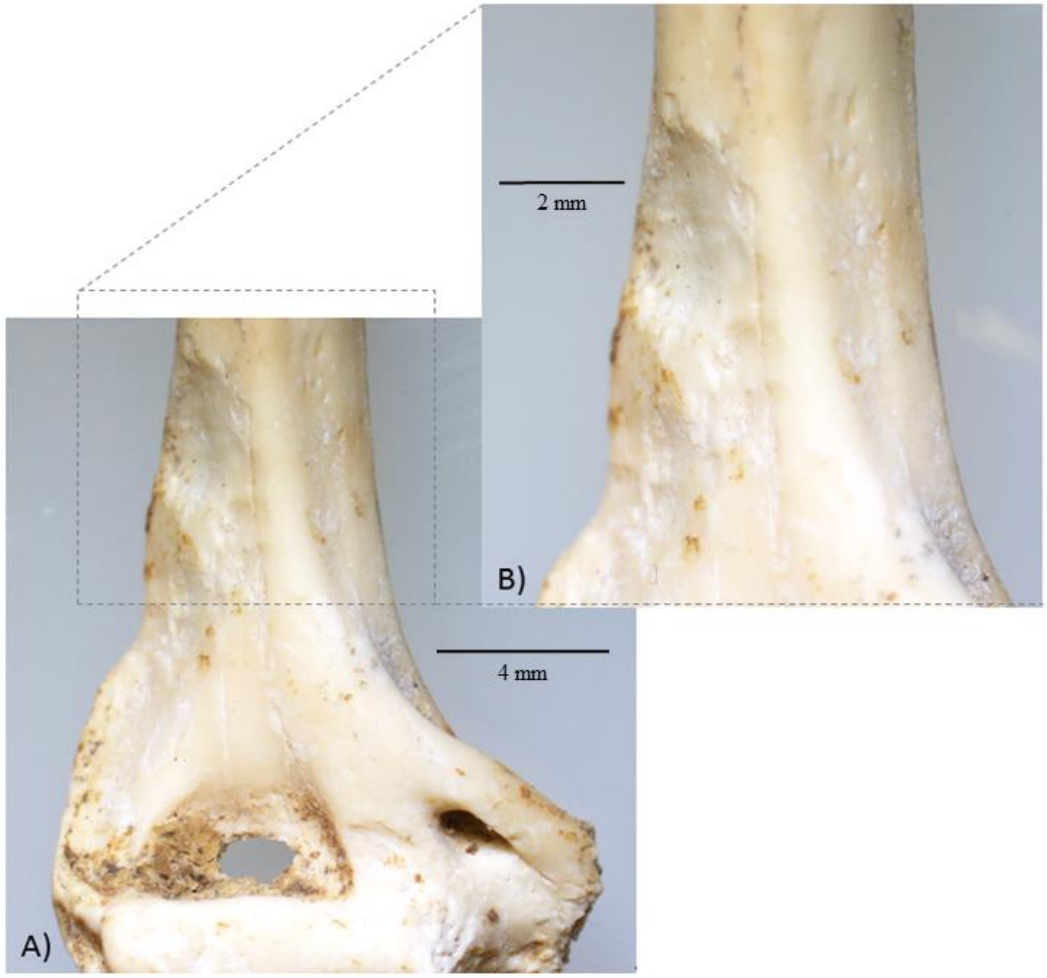

Figure 29. Examples of bone modification from rodent teeth (A-B)

Figure 30. Examples of bone modification from an unknown predator (A-B) (C) Arrows indicate bone cracking.

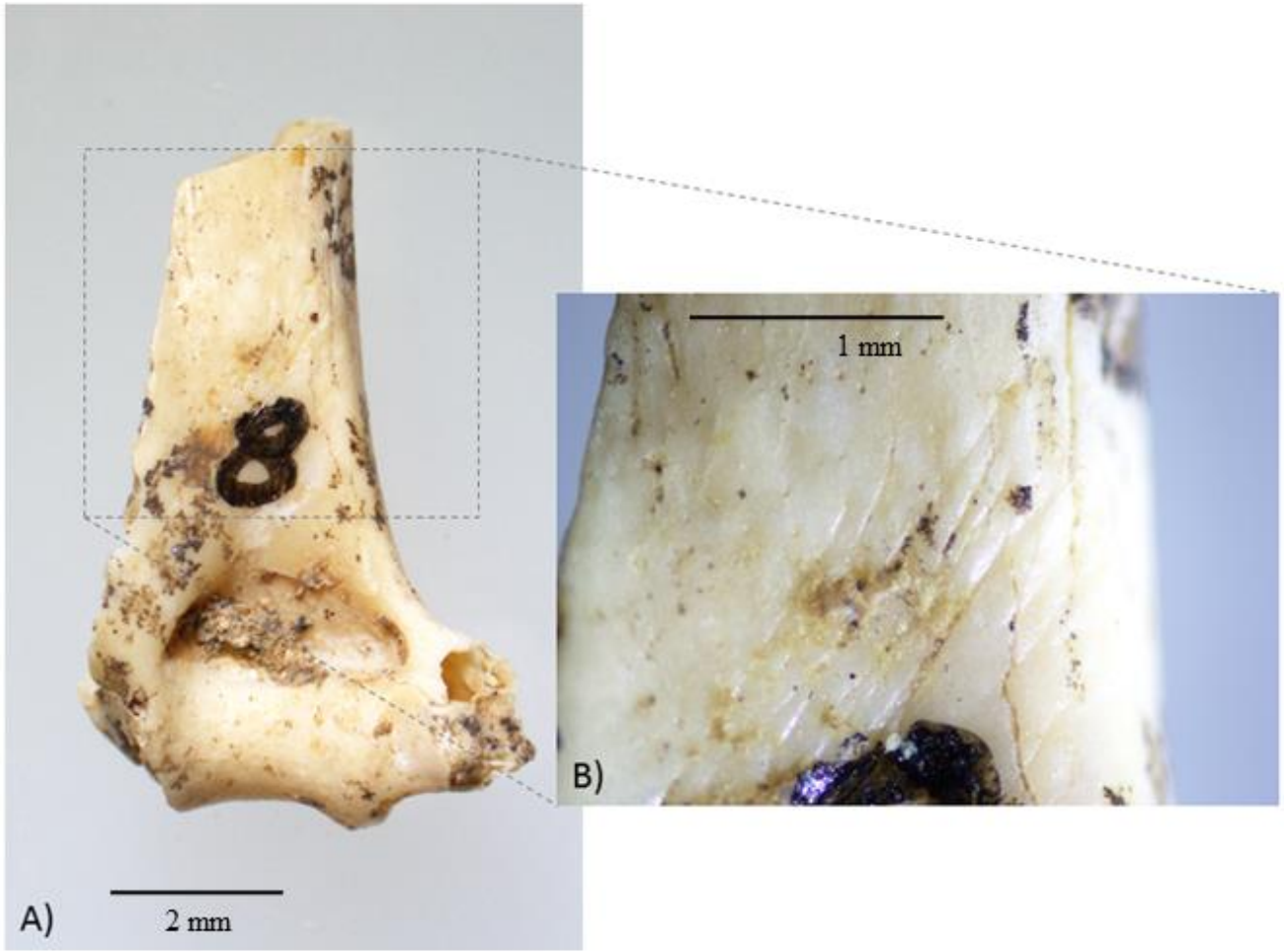

Figure 31. Example of additional bone modification showing oblique marks on the distal, posterior portion of the diaphysis (A-B)

Table 8. Humerus taphonomic summary: Breakage, digestion, and weathering stages organized by spit and Holocene and Pleistocene.

	Holocene		Pleistocene			
Breakage pattern	1-10	11-20	21-30	31-40	41-50	51-60
Complete	8	19	13	216	81	1
Proximal	4	7	4	148	48	5
Distal	6	34	13	593	151	22
Total	18	60	30	957	280	28
Digestion						
None	3	13	10	176	54	5
Low	19	54	24	841	313	21
Medium	0	3	1	72	16	0
High	0	0	0	6	0	0
Total	22	70	35	1095	383	26
Weathering (BWS)						
Stage 0	6	24	4	96	10	0
Stage 1	11	25	23	755	343	21
Stage 2	0	5	2	99	28	5
Stage 3	0	0	0	4	0	0
Total	17	54	29	954	381	26

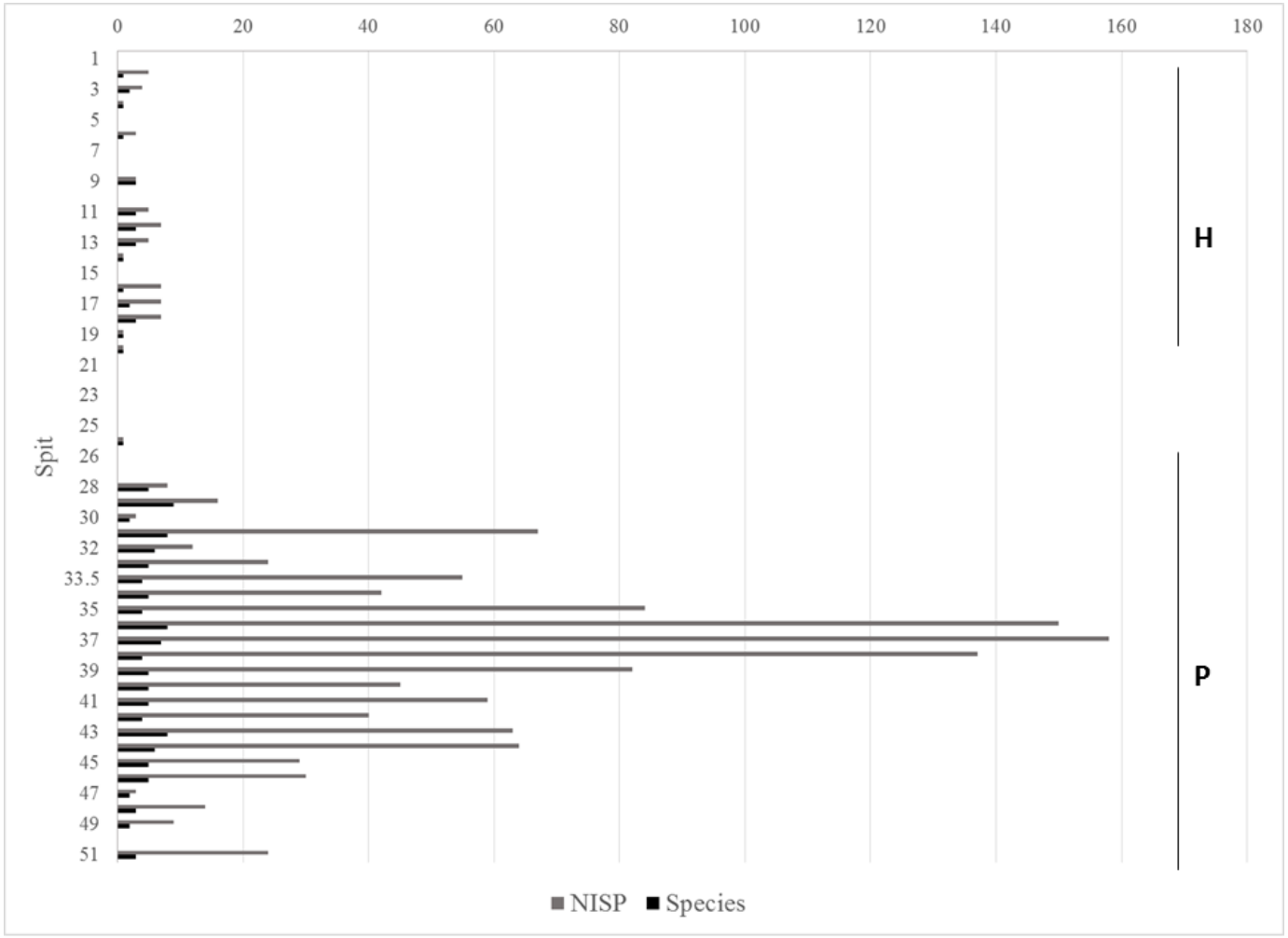

Figure 32. Rat species abundance recorded by depth. Light grey bars indicate number of identified specimens (NISP). Black bars indicate number of species recorded at a certain depth. ‘H’ and ‘P’ correspond to Holocene and Pleistocene deposits.

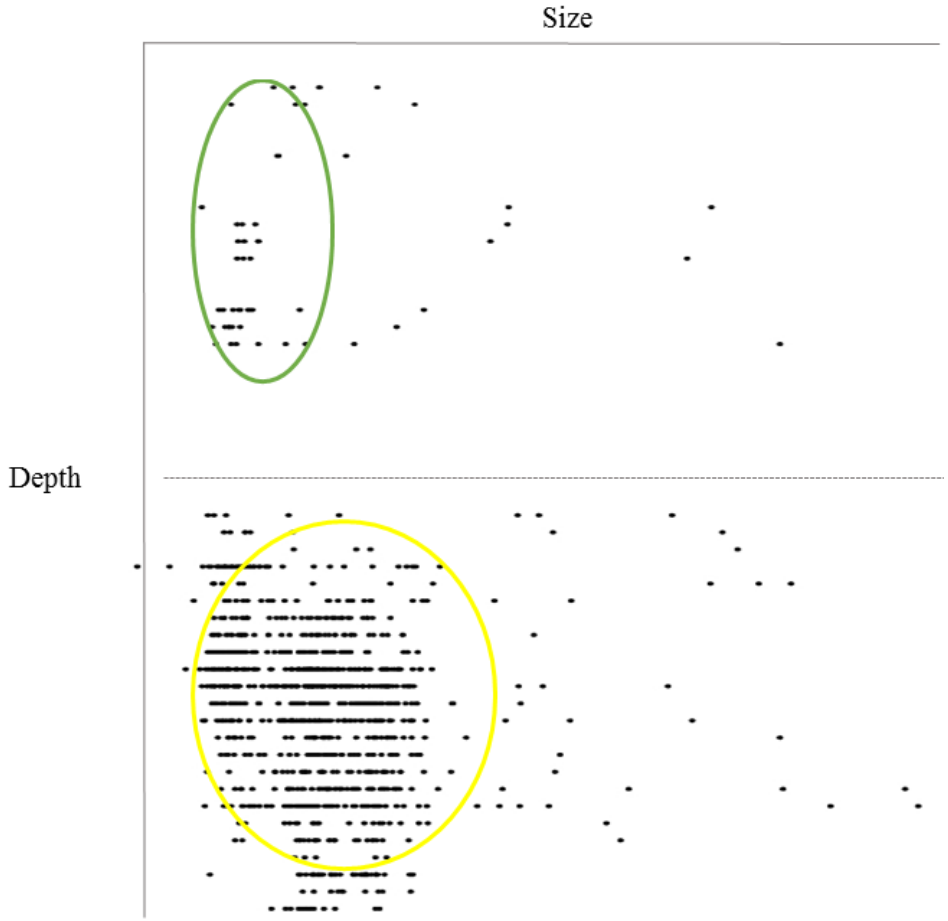

Figure 33. Jitter plot of fossil humeri illustrating hypothesized size groups of *Tyto* spp. prey body size ranges. Dashed line separates Holocene from Pleistocene deposits.

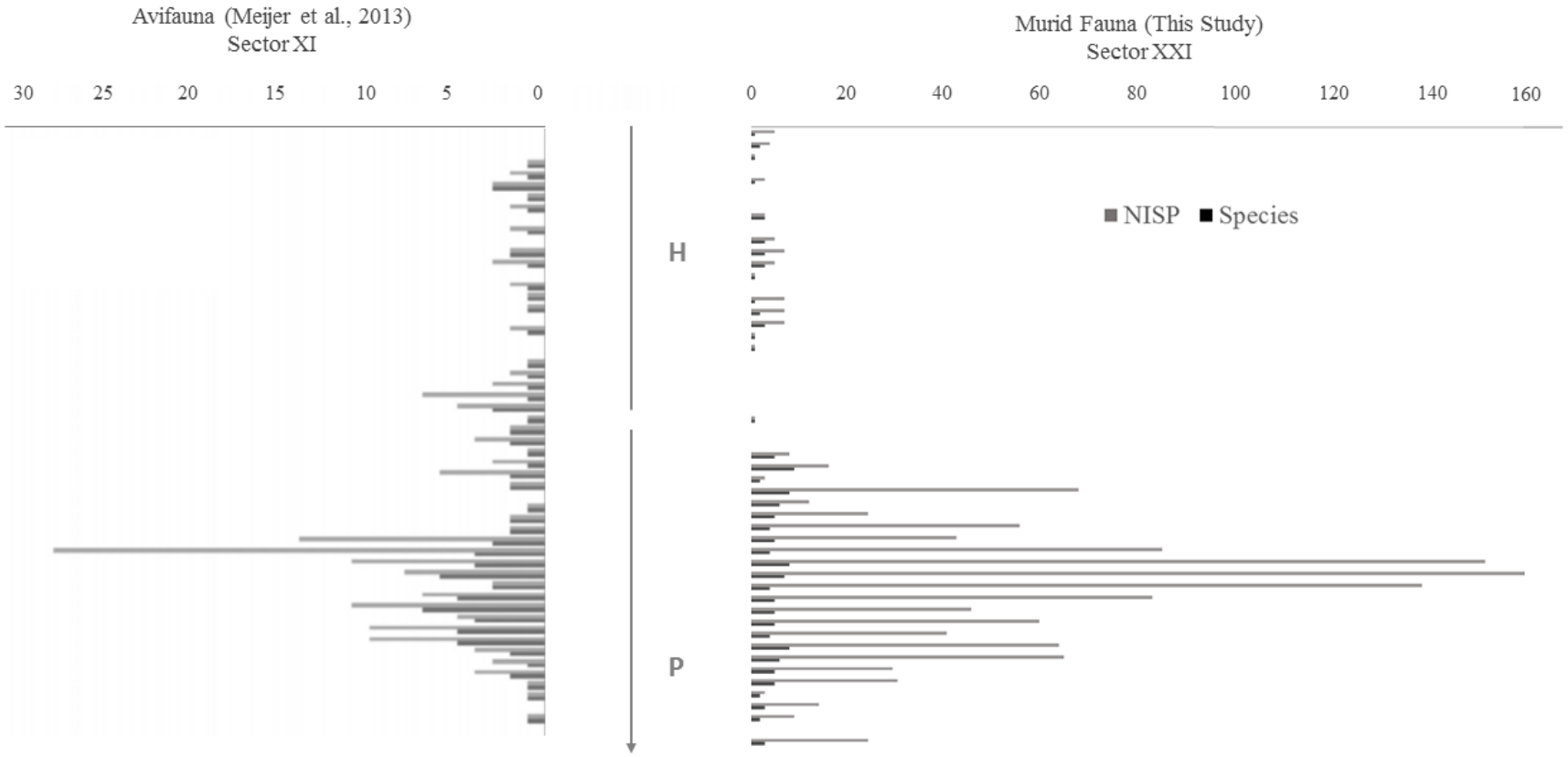

Figure 34. Relative comparisons of number of identified specimens (NISP) and number of identified species between avifauna from Sector XI (modified from Meijer et al., 2010) and murine postcrania from Sector XXI.

Table 9. Number of identified specimens and percentage of abundance (in parentheses) of dentition, humeri and calcanei between Holocene and Pleistocene deposits in Sector XXI.

	Holocene			Pleistocene		
Taxa	Dentition	Humerus	Calcaneus	Dentition	Humerus	Calcaneus
P. armandvillei	1 (7.1%)	1 (4.3%)		10 (6.8%)	3 (0.3%)	2 (0.8%)
P. theodorverhoeveni	2 (14.2%)	1 (4.3%)	1 (3.3%)	10 (6.8%)	9 (0.9%)	8 (3.1%)
S. florensis		1 (4.3%)		1 (0.7%)	1 (0.1%)	2 (0.8%)
H. cf. *nusatenggara*	2 (14.2%)	2 (8.6%)		1 (0.7%)	19 (0.2%)	5 (1.9%)
Komodomys sp.	2 (14.2%)	16 (69.5%)	2 (6.7%)	99 (67.3%)	658 (69.2%)	238 (92.6%)
P. naso				1 (0.7%)		
Rattus sp.	7 (50.0%)	2 (8.6%)		25 (17.0%)	260 (27.3%)	2 (0.8%)
Total	14	23	3	147	950	257