


Contributions to Mammalogy and Zooarchaeology of Wallacea

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A New Giant Shrew Rat (Rodentia: Muridae: Murinae) from Flores, Indonesia and a Comparative Investigation of its Ecomorphology

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ABSTRACT. We describe a new genus and species of large-bodied murine from archaeological deposits at Liang Bua, a limestone cave in western Flores, East Nusa Tenggara, Indonesia. Among a large assemblage of murine remains, several mandibular elements recovered from mostly Holocene sediments show a distinct anatomy, with a long and robust jaw, massive proodont incisors, and relatively small molars. These morphological features are unusual among murines but most similar to terrestrial and carnivorous species of the Indo-Pacific, colloquially referred to as shrew rats (Philippines, Sulawesi) or moss mice (New Guinea), and indicate a potential carnivorous dietary adaptation, perhaps specializing in a vermivorous diet. The size of the mandible indicates that this murine is the largest shrew rat yet known. Although presumed extinct, targeted field research is needed to determine if this rat still lives on Flores today.

ABSTRAK [Bahasa Indonesia]. Kami mendeskripsikan genus dan spesies baru murine bertubuh besar dari deposit arkeologi Situs Liang Bua, sebuah gua kapur di Flores bagian barat, Nusa Tenggara Timur, Indonesia. Di antara himpunan besar sisa-sisa murine, beberapa elemen rahang bawah yang sebagian besar ditemukan dari sedimen Holosen menunjukkan anatomi yang berbeda, dengan rahang yang panjang dan kokoh, gigi seri proodont sangat besar, dan geraham yang relatif kecil. Ciri-ciri morfologi ini tidak biasa di antara murine, tetapi sangat mirip dengan spesies terestrial dan karnivora dari bahasa sehari-hari Indo-Pasifik yang disebut sebagai tikus celurut (Filipina, Sulawesi) atau tikus lumut (New Guinea) dan menunjukkan adanya potensi adaptasi diet karnivora, mungkin mengkhususkan diri dalam diet vermivora. Ukuran rahang bawah juga menunjukkan bahwa murine ini adalah tikus celurut terbesar yang pernah diketahui. Meskipun dianggap punah, penelitian lapangan yang ditargetkan diperlukan untuk menentukan apakah tikus ini masih hidup di Flores saat ini.

Keywords: Island Southeast Asia, Liang Bua, murine rodents, extinction, rodent anatomy

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Introduction

The Indonesian island of Flores was once home to several endemic species of murine, which are currently known are preserved in the island's archaeological and fossil records (Fig. 1) (Hooijer, 1957; Musser, 1981; Musser *et al.*, 1986; Kitchener *et al.*, 1991a,b; Kitchener & Yani, 1998; Kitchener *et al.*, 1998; Locatelli *et al.*, 2012, 2015; Veatch *et al.*, 2019). The oldest murine record on the island includes as yet unidentified *ca.* 1.4-million-year old giant murine remains from the site of Tangi Talo in the So'a Basin of central Flores (van den Bergh *et al.*, 2022). Remains of a moderately large taxon, *Hooijeromys nusatenggara* (Musser, 1981), as well as a single molar provisionally identified as *Spelaeomys florensis*, have been recovered at other sites in the So'a Basin and are dated to between *ca.* 880 and 650 thousand years ago (ka) (Musser, 1981; Brumm *et al.*, 2010, 2016; van den Bergh *et al.*, 2022). *Spelaeomys florensis*, along with *Papagomys theodorverhoeveni* and *Paulamys naso*, were first described based on dentognathic material from Liang Toge, a cave excavated in 1954 and 1960 with deposits dated to within the past *ca.* 4–3 ka (Jacob, 1967; Hooijer, 1957; Musser, 1981; Musser *et al.*, 1986). Fragmentary material identified as the giant murine of Flores, *Papagomys armandvillei*—an extant species that has been known for some time (Jentink, 1892; Sody,

1941)—was also recovered from Liang Toge (Hooijer, 1957). A lower left mandible with an intact tooththrow from the Liang Toge murine assemblage was also identified as *Komodomys rintjanus*, an extant species currently inhabiting four satellite islands of Flores: Rinca, Padar, Lembata, and Pantar (Musser & Boedi, 1980; Musser, 1981; Musser & Carleton, 2005; Thomson *et al.*, 2018). Extant specimens of *Paulamys cf. naso* and *Rattus hainaldi*, other Flores endemic murines, were collected during mammalian surveys of the island (Kitchener *et al.*, 1991a,b; Suyanto, 1998; Kitchener & Yani, 1998; Kitchener *et al.*, 1998). Finally, although it is presently widely dispersed around the world, *Rattus exulans* may also originally have been a Flores endemic (Schwarz & Schwarz, 1967; Thomson *et al.*, 2014). Of all these species, only *Papagomys armandvillei*, *Paulamys naso*, *Rattus hainaldi*, and *Rattus exulans* are known with certainty to survive on the island today (Jentink, 1892; Musser, 1981; Kitchener *et al.*, 1991a,b; Kitchener & Yani, 1998; Kitchener *et al.*, 1998; Suyanto, 1998; Thomson *et al.*, 2014).

In his seminal review of the Flores endemic murines, Musser (1981) hypothesized that these and other species from the surrounding islands represent the descendants of three major taxonomic groups or radiations in the region: (I) Old endemics, (II) *Rattus*-like murines, and (III) the genus *Rattus*. Musser (1981) concluded that none of the endemic murines of Flores belonged to Group III and all *Rattus* species on the island were commensals that were recently introduced by humans. However, the subsequent discovery of *Rattus hainaldi* suggests that at least one non-commensal species of *Rattus* lives on Flores and thus, all three groups are or were once represented on the island. In contrast, Musser (1981) considered *Papagomys*, *Hooijeromys*, *Komodomys*, and *Paulamys*, all of which share a *Rattus*-like morphology, to belong to Group II. Although *Papagomys* shares similar

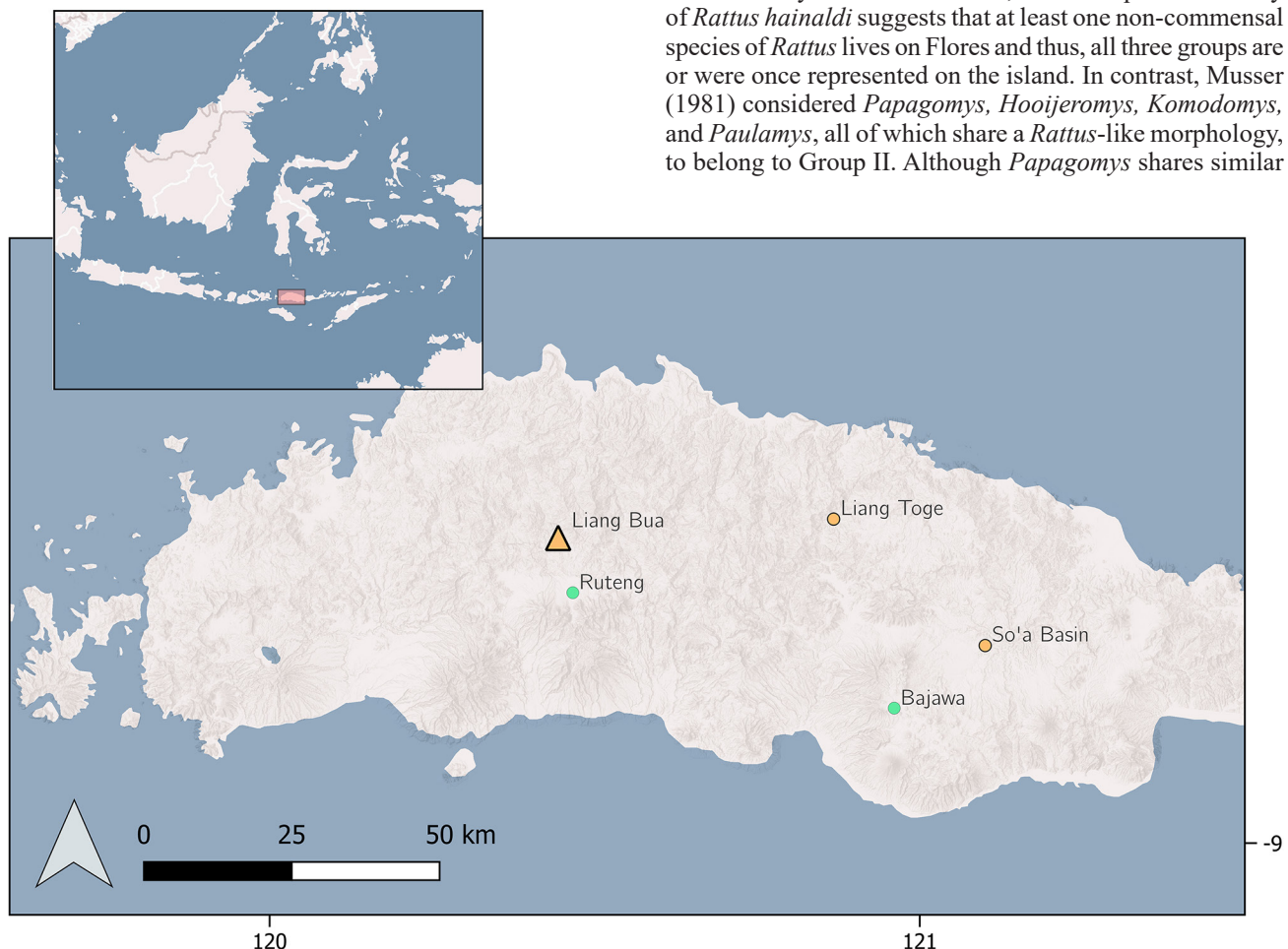


Figure 1. Map of Flores within the Indonesian archipelago showing the location of archaeological sites (yellow) in the western and central parts of the island mentioned in text. The nearest large towns are shown in green.

Table 1. The endemic^a murines of Flores (modified from Veatch *et al.* [2019]).

Species	Body mass (g)	Body size category	Extant ^a	Known or presumed diet ^b	Known or presumed behaviours ^b	Known or presumed habitat preferences ^b
<i>Papagomys armandvillei</i>	1200–2500 ^c	giant	yes	leaves, fruits, insects	terrestrial, burrowing	closed, semi closed
<i>Papagomys theodorverhoeveni</i>	600–1600 ^d	huge	uncertain	fruits, insects	terrestrial	closed, semi closed
<i>Spelaeomys florensis</i>	600–1600 ^d	huge	uncertain	leaves, flowers, buds	arboreal	closed
<i>Hooijeromys nusatenggara</i>	300–600 ^d	large	uncertain	unknown	terrestrial	open, semi open
<i>Komodomys rintjanus</i>	100–200 ^e	medium	yes	unknown	terrestrial	open, semi open
<i>Paulamys naso</i>	100–200 ^f	medium	yes	fungi, insects, snails, earthworms, fruits	terrestrial, burrowing	closed, mossy
<i>Rattus hainaldi</i>	40–100 ⁱ	small	yes	unknown	terrestrial, nesting	commensal
<i>Rattus exulans</i> ^h	40–100 ⁱ	small	yes	omnivore	terrestrial	commensal

^a Known from Flores and/or satellite islands of Komodo, Rinca, Padar, Pantar, and Lembata.

^b Based on information in Musser (1981), Musser & Boeadi (1980), Kitchener *et al.* (1991a,b), and Suyanto (1998).

^c Based on data in Musser (1981) and three extant specimens with known body masses (1495–2285 g) in the collections of the Zoological Museum in Bogor, Indonesia.

^d Based on molar sizes and other information in Musser (1981).

^e Based on molar sizes and other information in Musser & Boeadi (1980) and Musser (1981).

^f Based on molar sizes and other information in Musser (1981) and Musser *et al.* (1986) and one extant specimen with a known body mass of 120 g (Kitchener *et al.*, 1991a,b).

^h Although currently widespread, this taxon may have originally been endemic to Flores (Thomson *et al.*, 2014).

ⁱ Based on body weights and other information of *Rattus exulans* in Tamarin & Malecha (1972), but applies to small *Rattus* sp. generally.

dental features with *Lenomys* from Sulawesi (Musser, 1981) and was once taxonomically associated with *Mallomys* (Tate, 1936; Simpson, 1977), the most comprehensive molecular study to date places it as the most divergent branch within a division of the Rattini tribe that also includes *Bullimus*, *Bunomys*, *Eropeplus*, *Lenomys*, *Halmaheramys*, *Komodomys*, *Paulamys*, *Sundamys*, *Taeromys*, and “*Rattus*” *timorensis* (Rowe *et al.*, 2019). Similarly, the overall cranio-dental and external morphology of *Paulamys* greatly resembles that of *Bunomys* from Sulawesi (Musser, 1981; Musser *et al.*, 1986; Kitchener *et al.*, 1991a) such that some studies have referred to it as *Bunomys naso* (Kitchener *et al.*, 1998; Kitchener *et al.*, 1998). Its resemblance therefore suggests a close relationship with some endemic Sulawesi genera (e.g., *Bunomys*, *Taeromys*, *Frateromys*, *Eropeplus*, and *Lenomys* [Handika *et al.*, 2021]) indicating that its ancestor might have dispersed from Sulawesi to Flores (Musser *et al.*, 1986; Kitchener *et al.*, 1991a, 1998; Kitchener *et al.*, 1998). Molecular phylogenies also strongly support a close relationship between *Komodomys rintjanus* and “*Rattus*” *timorensis* (Thomson *et al.*, 2018; Rowe *et al.*, 2019). Lastly, *Rattus hainaldi* was recently confirmed as a member of the *Rattus* clade with a close relationship with *Rattus macleari* from Christmas Island (Thomson *et al.*, 2018). Considering Musser’s (1981) hypotheses, the available morphological and molecular data suggest that members of Group II colonized Flores independently at least two or three times. Finally, *Spelaeomys florensis* is the only Flores representative of Group I and is characterized by distinctively large, cylindrical tear-drop shaped cusps that resemble murines from New Guinea, such as *Mallomys* (Musser, 1981; but see Pagès *et al.*, 2016 for discussion of convergent dental characters among Murinae). The complex hypsodont molars of *Spelaeomys* indicate that this animal potentially occupied a more arboreal niche, consuming insects, buds, and flowers, compared to the other terrestrial

and largely herbivorous endemics with the exception of the omnivorous *Paulamys*, which consumes fungi, insects, snails, fruit, and earthworms from wet, forested habitats (Musser, 1981; Kitchener *et al.*, 1998).

Dentognathic remains from all of the above-mentioned endemics have been recovered from sediments at Liang Bua (Table 1), an archaeological cave site located in western Flores (Fig. 2) (Musser *et al.*, 1986; van den Bergh *et al.*, 2009; Locatelli, 2011; Locatelli *et al.*, 2012, 2015; Veatch, 2014; Veatch *et al.*, 2019; Veatch, 2021; Tocheri *et al.*, 2022). With a stratigraphic sequence spanning the past *ca.* 190 ka, Liang Bua preserves a large assemblage of murine remains (*ca.* 223,000 anatomical elements and counting) (Sutikna *et al.*, 2016, 2018). Since a majority of this assemblage consists of postcranial remains, species identification based on morphology alone is challenging, but linear measurements have shown that dentognathic and postcranial elements are divisible into five body size classes ranging from giant (*ca.* 1,200–2,500 g) to small (*ca.* 40–100 g) (Veatch, 2014; Veatch *et al.*, 2019). These body size classes generally correspond to murine habitat preferences and have been used to identify significant palaeoecological changes through time, including at *ca.* 60 ka and *ca.* 3 ka, corresponding with volcanic activity and the emergence of farming at Liang Bua, respectively (Veatch *et al.*, 2019). Thus, the endemic murines of Flores contribute important local palaeoenvironmental information that is critical for reconstructing both natural and human induced past ecologies.

In this study, we describe a new genus and species of large-bodied murine based on mandibular remains recovered at Liang Bua in mostly Holocene sediments. This taxon shares various morphological similarities with insectivorous but phylogenetically unrelated murine rodents that evolved independently on Sulawesi, the Philippines, and New Guinea, colloquially known either as “shrew rats” or “moss mice” (Rowe *et al.*, 2016; Helgen & Helgen, 2009). Shrew rats and

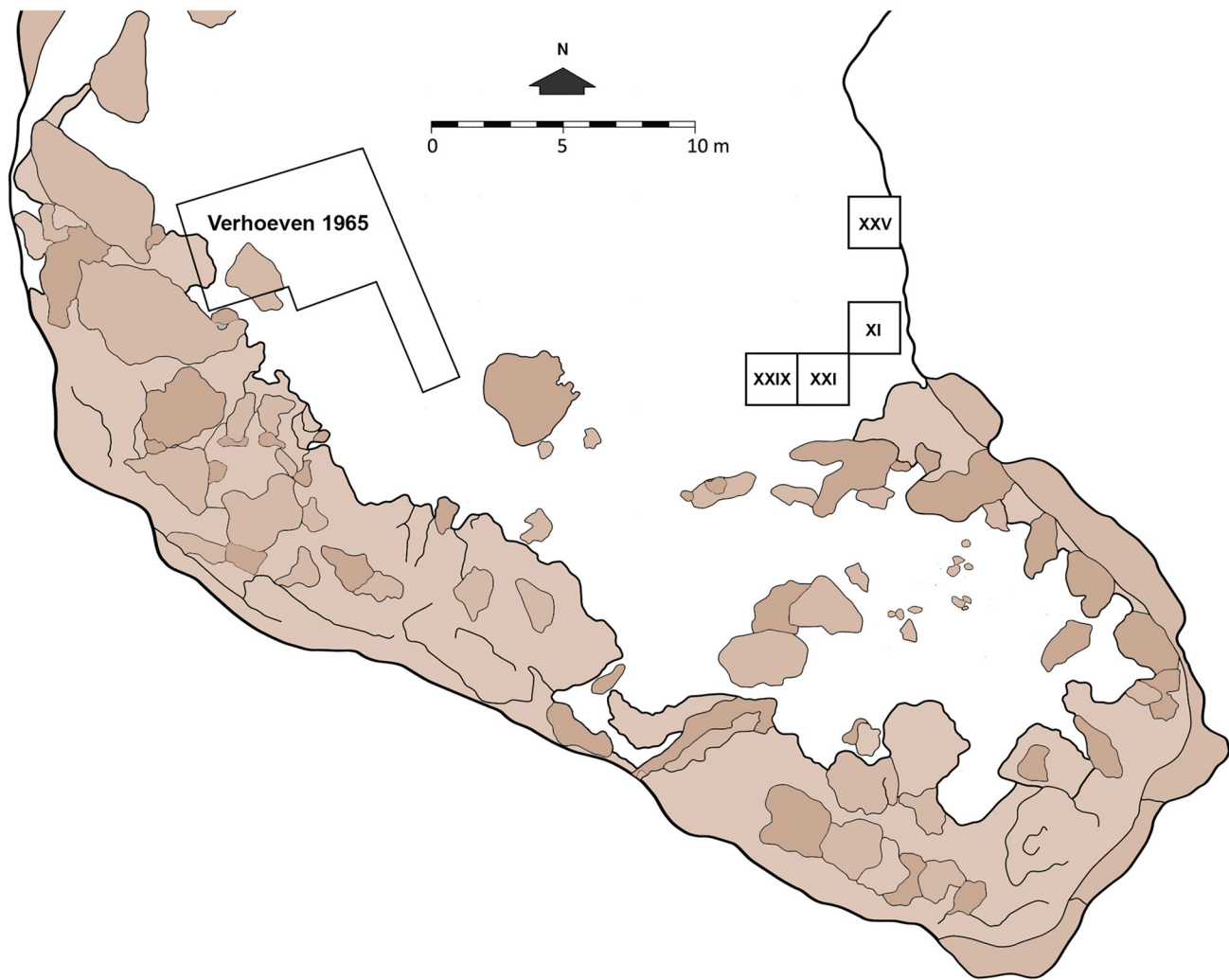


Figure 2. Plan of Liang Bua showing the locations where specimens of *Lawomys rokusi* have been recovered. Roman numerals denote specific 2×2 m excavation areas and the larger polygon at left shows the area excavated by Theodor Verhoeven in 1965.

moss mice are terms associated with murines that generally inhabit tropical evergreen forests, adopt a carnivorous diet, and occupy a range of ecological niches usually filled by shrews. These murines sometimes evolve traits reflecting these dietary niches, including a reduced number of molars, simplified occlusal pattern, longer and narrower snout, larger and more complex olfactory turbinals, small molar size relative to the size of mandible and maxilla, and proodont incisors reflecting an insectivorous or vermivorous diet (Musser, 1982; Musser & Heaney, 1992; Musser & Durden, 2014; Helgen & Helgen, 2009; Martinez *et al.*, 2018; Charles *et al.*, 2013). This adaptation repeatedly appears in the highly diversified Murinae with at least six major carnivorous lineages found within (1) the Echiothrix Division on Sulawesi, (2) the genus *Crunomys* found on the Philippines and Sulawesi, (3) the *Chrotomys* Division on the Philippines, (4) the *Hydromys* Division from Australo-Papua, (5) two species within the genus *Mus*, and (6) the *Praomys* Division in Africa (Supporting Information Appendix Table 1) (Heaney *et al.*, 2016; Rickart *et al.*, 2019; Musser & Durden, 2002; Esselstyn *et al.*, 2012; Esselstyn *et al.*, 2015; Helgen &

Helgen, 2009; Rowe *et al.*, 2016). The identification and description of an endemic shrew rat from Flores not only reveals a greater species and ecomorphological diversity on the island and in Wallacea, but may also contribute towards understanding past and current anthropogenic impacts on murine extinction.

Materials and methods

Comparative specimens used in this study ($n = 685$) are from collections at the American Museum of Natural History (AMNH, New York, USA), Australian Museum (AM, Sydney, Australia), London Natural History Museum (NHMUK, London, UK), Centre de Biologie pour la Gestion des Populations (CBGP, Montpellier, France), Delaware Museum of Nature & Science (DMNH, Delaware, USA), Field Museum of Natural History (FMNH, Chicago, USA), Harvard Museum of Comparative Zoology (MCZ, Massachusetts, USA), Louisiana State University Museum of Natural Science (LSUMZ, Baton Rouge), Muséum national

d'Histoire naturelle (MNHN, Paris, France), Museum Zoologicum Bogoriense (MZB, Cibinong, Indonesia), Museums Victoria (NMV, Melbourne, Australia), Naturalis Museum (RMNH, Leiden, Netherlands), Smithsonian's National Museum of Natural History (USNM, Washington DC, USA), and Western Australia Museum (WAM, Perth, Australia). Archaeological specimens (LB-MUR, n = 352) from Liang Bua derive from Holocene and Pleistocene deposits. Mandibular (total length) and dental measurements (molar lengths and widths) were taken with digital hand calipers to the nearest 0.01 mm. All authors are authorities of the new taxonomic names proposed.

Geometric morphometric procedures and simple jaw biomechanical proxies

Lateral view photographs of the mandible were taken for 664 specimens comprising 77 species (SI Table 2). The sample included 5 species from Flores, 21 species from the Philippines, 15 species from Sulawesi, and 32 species from the Australo-Papuan region representing 19 omnivorous, 26 carnivorous, and 19 herbivorous murids based on previous studies (SI Table 3). The skins and skulls of these specimens were carefully checked to avoid any taxonomic misidentifications.

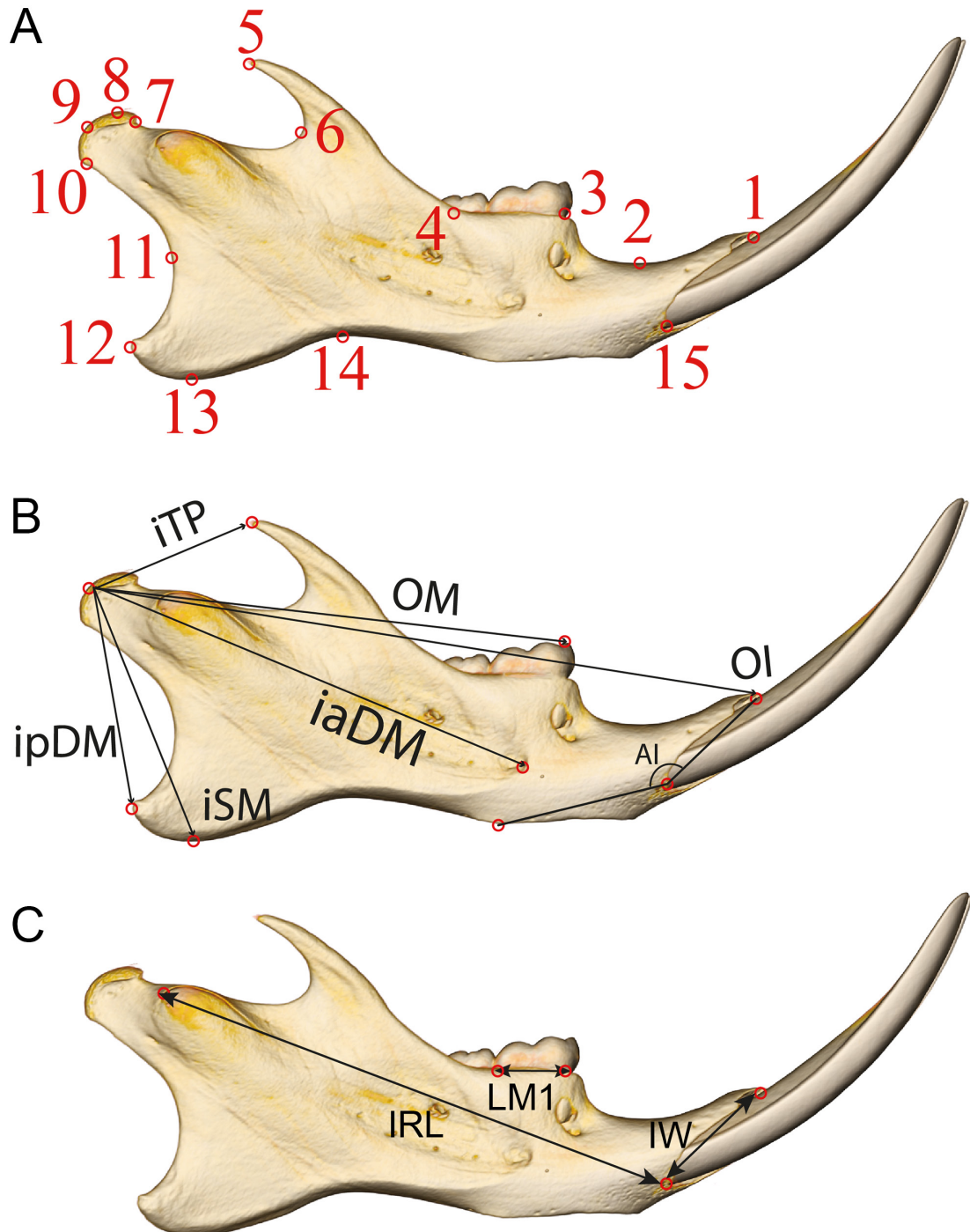


Figure 3. (A) Landmarks used in the 2D GMM analysis (see Fig. 8). (B) Distances used in the in-lever (i) and out-lever (O) analysis (see Fig. 10). (C) Dental measurements including length of the first molar (LM1), incisor width at the alveolus (IW), and internal incisor length (IRL) (see Figs 10 and 11).

Following Fabre *et al.* (2017), 15 landmarks were placed on each mandible image (Fig. 3a) and two-dimensional geometric morphometric (2DGM) methods (Bookstein, 1991; Slice, 2007; Adams *et al.*, 2013) were used to quantitatively assess mandibular shape variation as well as to identify the most divergent parts of the morphology among these island murid species. Landmark coordinates were analyzed using generalized Procrustes analysis (Rohlf & Slice, 1990) and centroid size was used as an indicator of overall size. A principal component analysis (PCA) was computed on superimposed coordinates (Dryden & Mardia, 1998) and extreme morphologies along each PC were computed to visualize the patterns of shape variation explained by each axis. A cluster analysis was also performed to further visualize the relationship between dietary groups (carnivorous, herbivorous, omnivorous, and unknown). An analysis of covariance (ANCOVA) was performed using centroid size as a covariate to test the effects of diet (carnivorous vs. omnivorous, carnivorous vs. herbivorous, omnivorous vs. herbivorous) (SI Table 4), and a MANOVA was performed using PC scores to assess the effects of diet (carnivorous vs. omnivorous + herbivorous) and size (calculated as the natural logarithm of jaw centroid size) (SI Table 5).

A simple biomechanical proxy based on four in- and two out-lever distances was used to evaluate functional differences explained by the observed shape variation (Fig. 3b). The four in-lever distances included: (1) the lateral temporalis lever-arm based on the distance between the coronoid and condylar processes (iTP); (2) the posterior deep masseter lever-arm based on the distance between the angular posterior tip and the condylar process (ipDM); (3) the superficial masseter lever-arm based on the distance between the angular ventral tip and the condylar process (iSM); and (4) the anterior deep masseter lever-arm based on the distance between the condylar process and the anterior insertion of the deep masseter (iaDM). The two out-lever distances include: (1) the distance between the condylar process and the anterior tip of the first lower molar (OM) and (2) the distance between the condylar process and the tip of the incisor alveolus (OI). A PCA was performed on the log-shape ratios of these lever arm distances to explore the relationship of these distances among murine species. A MANOVA was also performed on these in- and out-lever distances to test the effects of diet as described above (SI Table 6).

Additional comparisons were made to explore the relationship between the relative size of the first lower molar and the incisor (Fig. 3b,c). First, the length of the lower first molar (LM1) and the angle from the most ventral ramus to the tip of the incisor alveolus (AI) was compared against centroid size to explore the relationship between relative molar size and the mechanical position of the incisor, respectively. Second, ratios between incisor width, length, and molar length relative to centroid size were logged and compared to understand the trade-off between relative molar and incisor size between dietary groups.

Lastly, single and multiple linear regression analyses were used to estimate body weights of Flores taxa by taking the natural logarithm of both mandibular centroid size and known body mass (g) of museum specimens ($n = 128$) according to known diet. All statistical computations were performed using RStudio (2021.09.2).

Results

Systematics

Muridae Illiger, 1811

Type genus *Mus* Linnaeus, 1758.

Lawomys gen. nov.

urn:lsid:zoobank.org:act:C0D7C82A-47C6-4944-91A0-1587CC7B449B

Diagnosis: A murine of large body size with mandibular features unlike all known endemic murines on Flores or in the Indo-Pacific region (Figs 4 and 5). It is distinguished by the following features: a large mandible (measurable specimens are *ca.* 42–43 mm in length without the incisor and *ca.* 18–19 mm in height); prominent condyloid and angular processes with a broadly concave posterior margin between them; a condyloid process joint that extends along the entire dorsal ridge; a small coronoid process; large mental and mandibular foramina with a weakly developed retromolar fossa ridge; the alveolar sheath enclosing most of the lower incisor is encased entirely within the body of the dentary and extends from the anterior portion of the dentary to the base of the condyloid process; the molars are tiny relative to the size of the mandible; the first lower molar is the largest tooth and is anchored by two roots; the lower first molar is egg-shaped and resembles a basin in which the buccal and lingual edges of the cusps are smooth and continuous creating a bowl-like structure, the anterior lamina being the most reduced; its occlusal morphology is very simple with low, blunt cusps forming three distinct transverse laminae; the first lamina contains reduced anterolingual and anterolabial cusps that coalesce when worn; the protoconid and metaconid are somewhat coalesced but retain identifiable morphologies within the second laminae; the hypoconid and entoconid are distinctive from one another yet blend together to form a “bow-tie” shaped occlusal surface when worn; there is also a greater separation between the second and third laminae where a noticeable yet shallow cleft separates the two compared to the first and second; the second lower molar is anchored by two large roots but is markedly shorter than the first molar yet similar (slightly smaller) in breadth; its occlusal surface is simple like the first molar with a basin-like structure creating a smooth edge around the tooth; the protoconid and metaconid are identifiable within the first lamina as are a morphologically simple hypoconid and entoconid within the second lamina; the third lower molar is likely anchored by two fused roots (based on the shape of the alveolus as this molar has not yet been recovered) (Fig. 5); the lower incisor is large relative to the size of the mandible (measurable specimens have breadths between *ca.* 1.7–2.6 mm at the alveolus) and long, extending internally through the ramus and terminating at the condyloid process; the incisor is also wide and deep, especially at the alveolus; enamel forms most of the ventrolabial surface of the incisor ($\frac{1}{3}$ to $\frac{1}{2}$ of the lingual surface), the outer surface of which is smooth and lacks any anterior grooves or distinctive features; the incisal wear pattern is lengthy and continuous with no “lip” or abrupt termination.

Type species. *Lawomys rokusi* sp. nov., a new species from Flores, Indonesia.

Included species. The type species only.

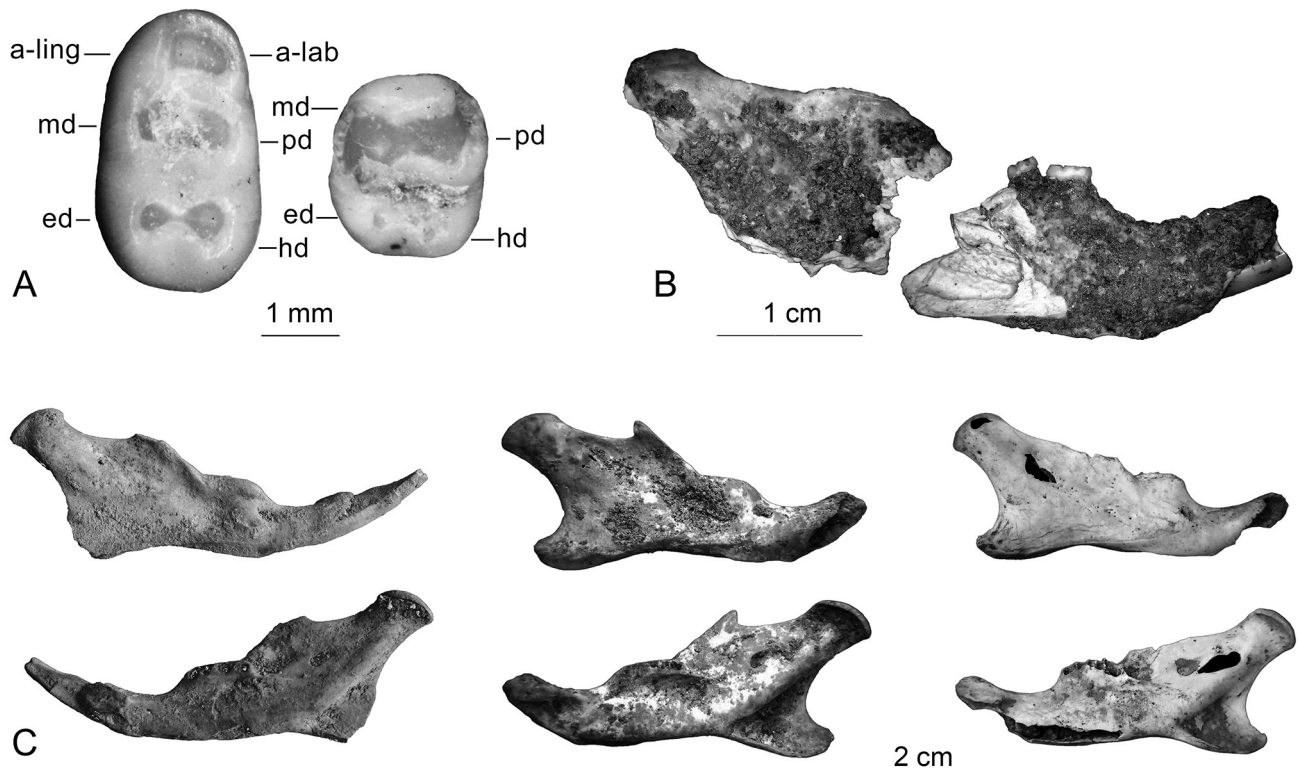


Figure 4. (A) *Lawomys rokusi* holotype first (at left) and second (at right) right molar occlusal surfaces (*a-ling*, anterolingual cusp; *a-lab*, anterolabial cusp; *md*, metaconid; *pd*, protoconid; *ed*, entoconid; *hd*, hypoconid). (B) *Lawomys rokusi* holotype right mandible showing the posterior break behind the second molar exposing the internal incisor alveolus and the posteriorly rotated second molar. (C) Three mandibles (all shown as from the right side) attributed to *Lawomys rokusi* (from left to right: LB-MUR-6488, LB-MUR-6484 [mirrored], LB-MUR-6485; top row, lateral view; bottom row, medial view).

Etymology. The genus name combines the word *Lawo*, from the Manggarai language meaning “rat”, with the suffix—*mys*, Greek for mouse or rat. Manggarai is an Indigenous language spoken in western Flores, including at Liang Bua, the type locality.

Lawomys rokusi sp. nov.

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Figs 4, 5, 7A, 12, 13, 16

Diagnosis. There is only one species in the genus; thus, the specific and generic diagnoses are the same.

Holotype. LB-MUR-6482 (held in Organisasi Riset Arkeologi, Bahasa, dan Sastra, referred to hereafter as ORARBASTRA, in Jakarta, Indonesia) is a partial right mandible with the dentary of an adult animal, preserving the first (LB-MUR-6491) and second (LB-MUR-6492) molars as well as the incisor (LB-MUR-6490) (broken at the alveolar opening). The specimen is broken along the ramus posterior to the second molar exposing the incisor canal (Fig. 4). The fracture surface of the break indicates it occurred recently, perhaps during excavation and/or wet sieving, with a separate refitting fragment retaining the condyle and ramus (LB-MUR-6483). It was recovered from Sector XXI (Fig. 2) between 75 and 85 cm depth from the cave surface floor. Approximately 90% of the bone surface is covered in matrix with slight manganese staining along the bone and

incisor enamel surface. In the holotype, the second molar is slightly rotated back artificially in the jaw, such that the tooth now slopes downward posteriorly rather than sitting in the natural plane of the original molar row (Fig. 4). There is damage to the anterior portion of the second molar where the outer enamel surface has been broken off.

Paratypes. A total of 11 relatively intact dentaries (Table 2; Fig. 4) and two additional dentary fragments: LB 33, left ramus, young adult; LB 36, right ramus, adult; LB 37, right ramus, adult; LB 86, right ramus, adult (all deposited in Naturalis Biodiversity Center in Leiden, Netherlands); LB-MUR-6488, right ramus with incisor (LB-MUR-6489), adult; LB-MUR-6484, left edentulous ramus, adult; LB-MUR-6485, right edentulous ramus, adult; LB-MUR-6487, fragment of right ramus, adult; LB-MUR-6486, fragment of left ramus, adult; LB-MUR-2759, left ramus with incisor (LB-MUR-2760), adult; LB-MUR-4846, left ramus with incisor (LB-MUR-4847), adult; LB-MUR-5372, left edentulous ramus, adult; LB-MUR-5415, right edentulous ramus, adult (all deposited at ORARBASTRA). The specimens at Naturalis (labelled simply as “LB”) were collected during excavations of Liang Bua in 1965 (Musser *et al.*, 1986) whereas those at ORARBASTRA were collected during more recent excavations between 2010 and 2019 (Sutikna *et al.*, 2016, 2018).

Type locality. The holotype, paratypes, and referred material were all recovered at Liang Bua (8.534167°S 120.460278°E), Flores, Indonesia.

Table 2. Specimens identified as *Lawomys rokusi* excavated at Liang Bua with dental and mandibular measurements (mm) where possible.

Specimen ^a	Element	Side	Age	Sector	Spit	Unit	alm1-3	b _i	d _i	br_m ₁	lg_m ₁	br_m ₂
LB 33	mandible	left	young adult	Verhoeven	—	8C	7.1	1.7	—	—	—	—
LB 86	mandible	left	adult	Verhoeven	—	8C	7.0	2.2	—	—	—	—
LB 37	mandible	right	adult	Verhoeven	—	8C	7.2	2.0	—	—	—	—
LB 36	mandible	right	adult	Verhoeven	—	8C	7.3	2.2	—	—	—	—
LB-MUR-2759 LB-MUR-2760	mandible incisor	left	adult	XI	15	8A/8B	7.6	1.9	3.8	—	—	—
LB-MUR-4846 LB-MUR-4847	mandible incisor	left	adult	XI	10	8C	—	2.1	—	—	—	—
LB-MUR-5372	mandible	left	adult	XI	2	8C	—	—	—	—	—	—
LB-MUR-5415 ^b	mandible	right	adult	XI	16	8A/8B	7.9	—	—	—	—	—
LB-MUR-5835	incisor	left	adult	XI	22	8A/6	—	1.8	3.6	—	—	—
LB-MUR-6482 (holotype)	mandible	right	adult	XXI	8	8A/8B	7.1	—	—	—	—	—
LB-MUR-6490 LB-MUR-6491 LB-MUR-6492 (holotype assoc.)	incisor m1 m2	right	adult	XXI	8	8A/8B	—	—	—	1.9	3.2	1.9
LB-MUR-6483 (holotype refit)	mandible	right	adult	XXI	8	8A/8B	—	—	—	—	—	—
LB-MUR-6484	mandible	left	adult	XXI	7	8C	7.2	—	—	—	—	—
LB-MUR-6485	mandible	right	adult	XXV		8A/6	7.3	—	—	—	—	—
LB-MUR-6486	mandible	right	adult	XXV		8A/6	—	—	—	—	—	—
LB-MUR-6488 LB-MUR-6489	mandible incisor	right	adult	XXIX	11	8B	7.3	2.6	4.7	—	—	—
LB-MUR-6487	mandible	right	indet.	XXV	11	8C	—	—	—	—	—	—
summary	—	—	—	—	—	—	7.3 ± 0.26	2.1 ± 0.28	4.0 ± 0.56	1.9	3.2	1.9
range	—	—	—	—	—	—	(7.0–7.9)	(1.7–2.6)	(3.6–4.7)	—	—	—
number	—	—	—	—	—	—	10	8	3	1	1	1

^a Specimens from ORARBASTRA abbreviated as: LB-Taxa-ID; specimens from RMNH labelled simply “LB”.

^b Sampled for stable isotopes.

Note. Univariate statistical summary consists of the mean ± 1 SD, observed range in parentheses, and size of sample. Abbreviations: *alm1-3*, alveolar length of mandibular molar row; *b_i*, breadth of incisor; *d_i*, depth of incisor; *br_m*, breadth of molar; *lg_m*, length of molar.

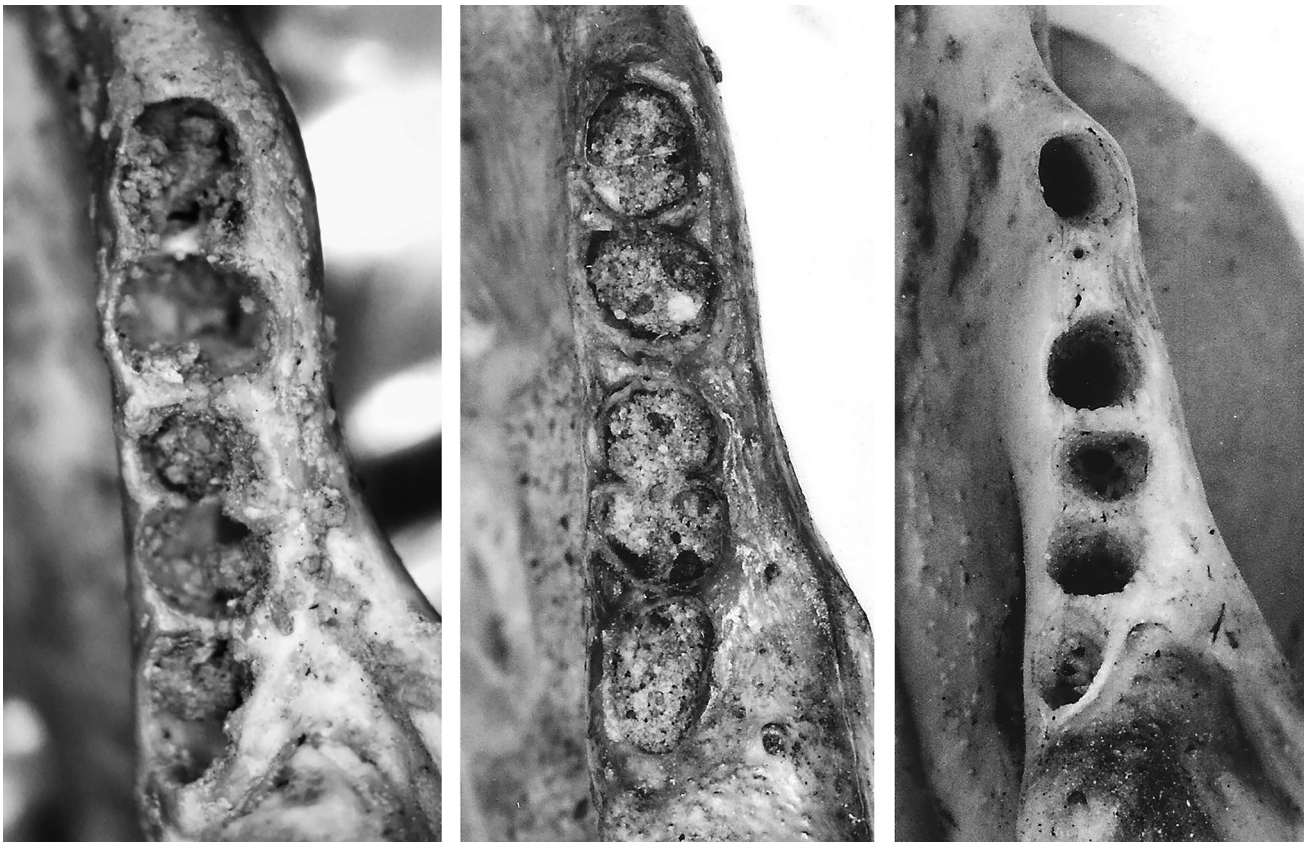


Figure 5. Alveoli of right lower tooththrows of two specimens of *Lawomys rokusi* (left, LB-MUR-6484; middle, LB 36) compared with a specimen of *Chrotomys mindorensis* (right, AMNH 12972). Specimens scaled to same size.

Age. The holotype, paratypes, and referred material all derive from Holocene sediments, although three specimens may be slightly older (i.e., terminal Pleistocene) given specific stratigraphic uncertainties. However, we suspect that targeted re-examination of the entire murine assemblage from Liang Bua will likely result in the identification of this new species in the older layers of the site as well.

Referred specimen. LB-MUR-5835, an isolated right lower incisor.

Etymology. The specific epithet honours zooarchaeologist Rokus Due Awe (Fig. 6), who was born 20 March 1942 in a small hamlet called Gisi (or Kampung Gisi) located in the Mataloko Subdistrict of the Ngada Regency (East Nusa Tenggara, Indonesia). To his family and childhood friends, he was affectionately known as “Due”, but to his many colleagues from Indonesia and around the world whom he met through his love of archaeology, he was “Pak Rokus”. He first became interested in archaeology when he participated in Theodor Verhoeven’s surveys and excavations in the early 1960s. Verhoeven was a Catholic missionary and archaeologist who taught ancient Latin and Greek at the Mataloko Seminary while Rokus was a student in elementary school. After graduating from high school in 1962, Rokus began to assist Verhoeven in his archaeological exploration of Flores. In 1963 and 1964, they conducted surveys and excavations in central Flores at the So’a Basin, recovering *Stegodon* remains at Boaleza and Lembah Menge, for example, as well as other areas further to the north, including Wangka, Teong, Liang Rundung, Liang Mbikong, and Liang Toge.

In July of 1965, Rokus walked more than 50 km over several days from his home in Mataloko to Liang Bua to meet Verhoeven. Together, they excavated Liang Bua for the first time, recovering large numbers of stone artifacts, faunal remains, and pottery, as well as several modern human burials. After finishing their excavations, Rokus and Verhoeven travelled to Reo, on the north coast, and took a small boat west to Labuan Bajo, where they excavated at Liang Momer in August. In 1966, Rokus helped Verhoeven survey Timor at Belu and Watu Besi. As the 1970s approached, Verhoeven retired and returned to the Netherlands while Rokus studied history at the Institut Keguruan dan Ilmu Pendidikan (Institute of Teacher Training and Education, a campus of the University of Cendana, Kupang) in Ende, Flores, and graduated with his baccalaureate degree in August 1973.

After completing his studies, Rokus went to Jakarta to meet Raden Pandji Soejono, who was the head of the Department of Prehistory at Djawatan Arkeologi (now known as ORARBASTRA). Verhoeven had mentioned Rokus in his previous correspondence with Soejono about the archaeology of Flores. In 1975, Rokus received a permanent job as civil servant at Djawatan Arkeologi and returned to Flores the following year with Budiarto Aziz to conduct an archaeological assessment of Liang Bua for Soejono. Rokus then participated in multiple excavations at the site between 1978 and 1989, as well as later between 2001 and 2014. He was the first person to correctly identify the hominin bones and teeth that ultimately became part of the hypodigm of *Homo floresiensis* following the discovery of the famous partial skeleton (LB1) in 2003 (Morwood *et al.*, 2004; Brown



Figure 6. Rokus preparing specimen labels for bones excavated at Liang Bua. Photograph taken 10 July 2007.

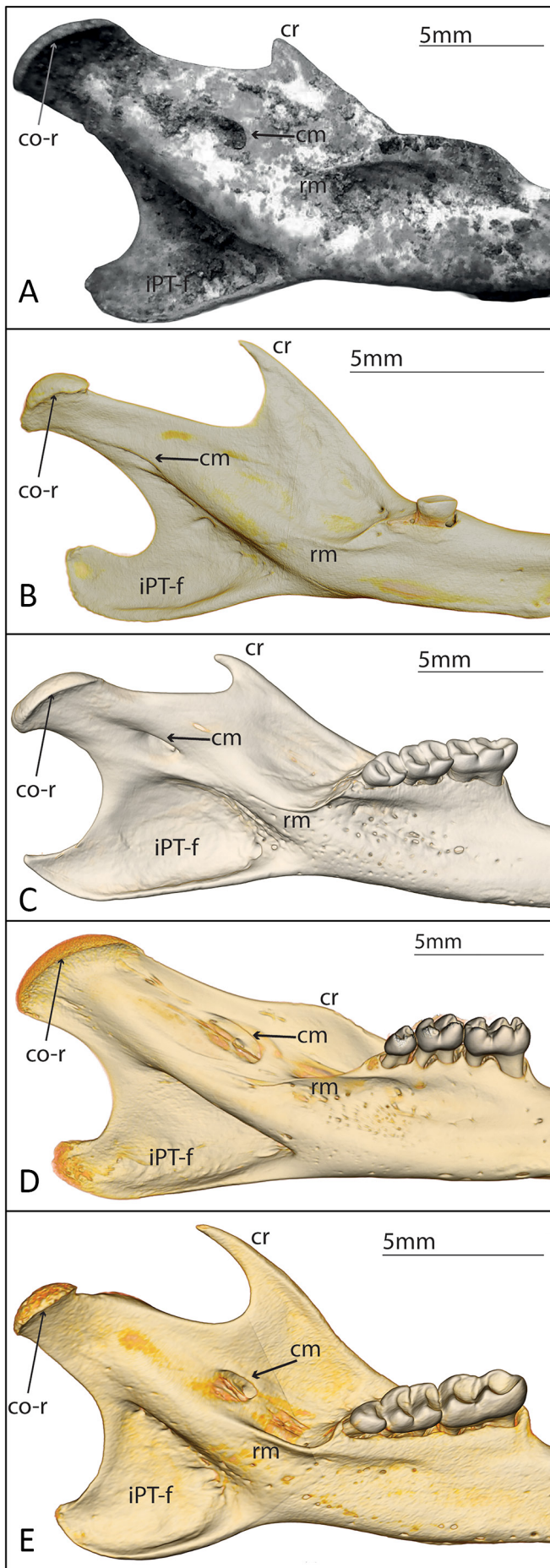
et al., 2004). Rokus' deep passion for and dedication to archaeology as well as the study of faunal remains resulted in his involvement in archaeological research across the entire Indonesian archipelago right up until his untimely death on May 18th, 2015. We pay tribute to his life's work and significant contributions to Indonesian archaeology by naming a unique endemic Flores murine in his honour.

Description and comparisons

Mandibular morphology

Lawomys shares several mandibular traits with other shrew rats from the Indo-Pacific. For example, *Lawomys* has a tiny coronoid process similar to some of the Sulawesi shrew rats from the Echiothrix Division (cf. *Echiothrix*, *Paucidentomys*, *Hyorhinomys*, *Tateomys*, and *Melasmothrix*). In contrast, shrew rats from the Philippines (tribe Chrotomyini: *Chrotomys* Division) and New Guinea (tribe Hydromyini: *Hydromys* Division) have a more developed coronoid process (Fig. 7). The coronoid process constitutes the origin of the lateral temporalis muscle, which is likely extremely reduced in these Wallacean shrew rat lineages. Another trait found in several Indo-Pacific shrew rats is a relatively large mandibular condyle joint, with an articular surface that extends across its entire dorsal edge (Fig. 7). In most murids, the articular facet is localized on the anterodorsal edge of the condyle, as in *Pseudohydromys ellermani* (Fig.

7B). However, in some worm-eating murids this articular surface extends to the outer edge of the condylar process. The medial ridge of this facet is similarly developed in *Chrotomys* and *Rhynchomys* in the Philippines as well as *Echiothrix* and *Hyorhinomys* in Sulawesi (Fig. 7C–E). In association with this large articulation, a large incisor canal bulges on the lateral side of the mandibular condyle in *Lawomys*, a trait also observed in *Chrotomys*, *Hyorhinomys*, and to a lesser extent in *Echiothrix*. This feature is also seen in some New Guinea species such as *Pseudohydromys ellermani* and *P. fuscus*. The large retromolar fossa of *Lawomys* is also found in *Echiothrix* as well as in *Rhynchomys* and *Chrotomys*, but it is not as developed as in *Hyorhinomys stuempkei* (Fig. 7C,E). This trait is unusual in murids and reflects the large surface insertion of the medial temporalis muscle. On the medial side, the mandibular foramen (Fig. 7) has a similar position and morphology, dorsal to the incisor bulge and posteroventrally to the coronoid process. This foramen, which is well developed in *Lawomys*, allows the passage of the mandibular branch of the trigeminal nerve. Its shape, size, and position in conjunction with large proodont lower incisors are like that seen in worm-eating rats (e.g., *Chrotomys* and *Hyorhinomys*). The morphology of this foramen is rather divergent in *Pseudohydromys* in which it is slit-like and closer to the condyle and its posteroventral border (Fig. 7B). On the medial side of the angular process in *Lawomys*, the internal pterygoid fossa is large and the angular shape overall is once again very similar to that of *Chrotomys*



and *Hyorhinomys*. Another diagnostic trait found in *Lawomys* concerns the masseteric ridge (Fig. 7). The anterior part of this ridge extends rather anteriorly and inserts more ventrally as compared to typical murids. Such a morphological state is only found in the most derived forms of worm-eating shrew rats. Perhaps due to its large body size, *Lawomys* is characterized by a well-developed anteriorly positioned ridge reflecting large anterior and posterior deep masseters.

Mandibular 2D geometric morphometrics and lever-arm distances

The mandibular morphology of *Lawomys rokusi* was quantitatively compared to that of other murids from the oceanic islands of Flores, Sulawesi, Sunda, Luzon, as well as Australo-Papua using 2DGM and visualized through a PCA (Fig. 8). Species with dorsoventrally narrower jaws load on the positive side of PC1, which explains 30.0% of the variance. These taxa exhibit an angular process extending posteriorly to the condyloid process, an elongated and narrow anterior portion of the jaw, and proportionally shorter coronoid and angular processes. *Lawomys* loads negatively on PC1 along with murine jaws that are dorsoventrally higher and characterized both by massive condyloid and angular processes, a condyloid process that expands posteriorly to the angular process, and a proportionately wider ramus including the coronoid and angular processes. Along PC1, the positive end mainly includes carnivorous murids such as vermivorous *Rhynchomys* and *Tateomys* while the negative end has more mixed species with lineages belonging to herbivorous (e.g., *Papagomys armandvillei* and *Komodomys rintjanus*), omnivorous (e.g., *Rattus hainaldi* and *Lorentzimys nouhuysi*), and carnivorous lineages (*Hyorhinomys stuempkei* and *Pseudohydromys* spp.) (Fig. 8). PC2, which explains 24.6% of the variance, distinguished carnivorous murids that cluster more negatively by having jaws with a more proodont lower incisor and a thinner angular process that is well circumscribed from their larger and longer condyloid process. Large herbivorous murids cluster more positively on PC2 due to jaws that have a more opisthodont lower incisor with a wider angular process as well as a shorter and wider condyloid process. *Lawomys* clearly stands apart on this axis and plots close to carnivorous *Pseudohydromys* (cf. *P. ellermani*, *P. occidentalis*, *P. pumehanae*), *Echiothrix* (*E. centrosa*, *E. leucura*), *Hyorhinomys stuempkei*, and *Chrotomys* (*C. whiteheadi*, *C. mindorensis*, *C. silaceus*, *C. sibuyanensis*). Along PC3, which explains 16.6% of the variance, mandibles with reduced coronoid and angular processes and an elongated condylar region plot toward the negative end whereas mandibles that have a shorter condyle along with longer coronoid and angular processes plot toward

Figure 7. Morphological comparison of the medial side of the mandible showing the location of features mentioned in text (*cr*, coronoid process; *cm*, mandibular foramen; *ipt-f*, internal pterygoid fossa, *co-r*, condyloid ridge; *rm*, retromolar fossa ridge) between (A) *Lawomys rokusi* LB-MUR-6484, (B) *Pseudohydromys ellermani* NHMUK ZD1953.277, (C) *Echiothrix leucura* NHMUK ZD1897.1.2.46, (D) *Hyorhinomys stuempkei* NMV C37198, and (E) *Chrotomys mindorensis* FMNH 222107.

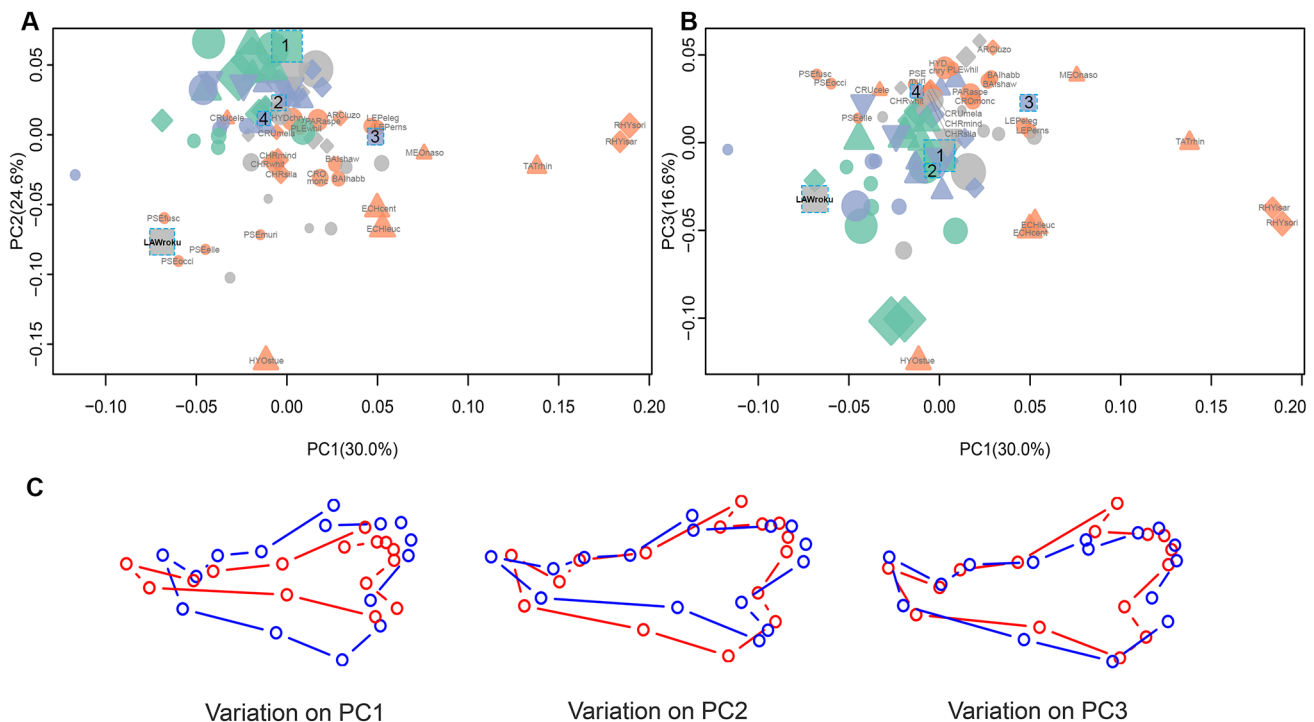


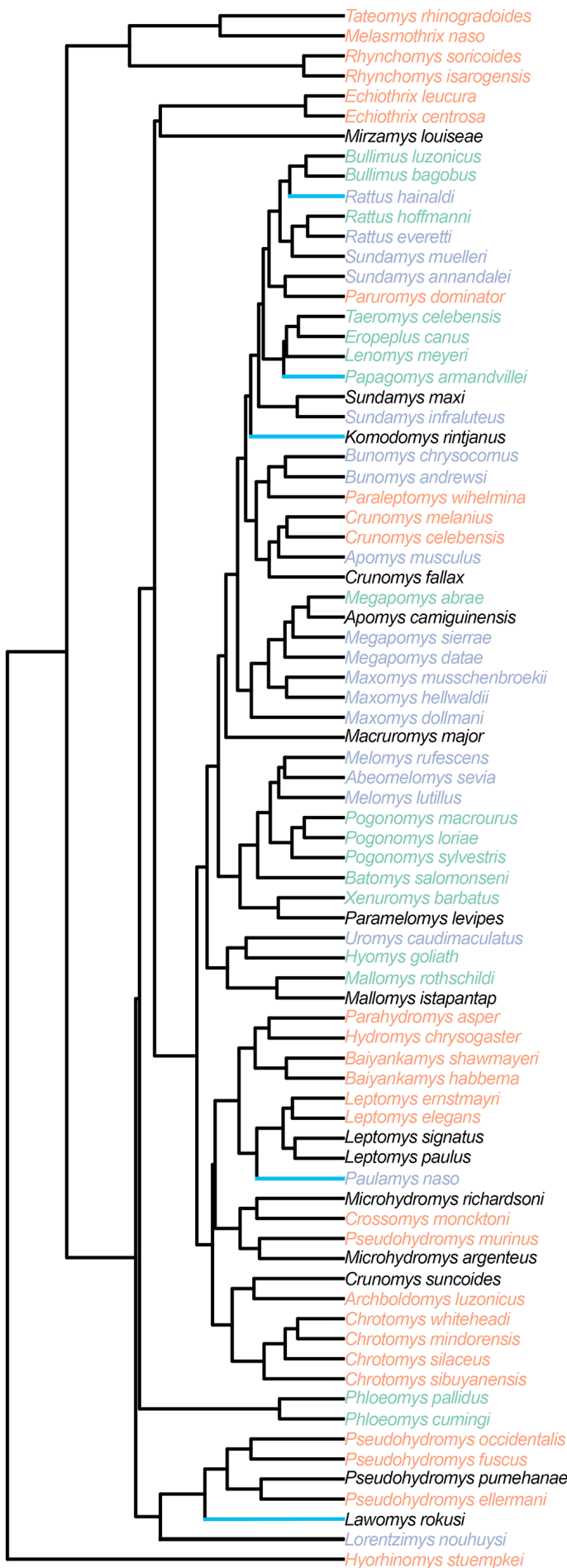
Figure 8. (A–B) Principal components analysis of 2DGMM comparing murid jaw shape and (C) shape profiles for principal component 1–3 showing the mandibular configuration on the extreme positive (red) and negative (blue) ends. Genus and species names are abbreviated (e.g., ECHcent) for carnivorous murids only. The relative size of the symbol corresponds to species body size. Shapes denote locality; triangles = Sulawesi, circles = New Guinea, diamonds = Philippines, reverse triangles = Sunda, and squares with blue dotted outlines = Flores. Colours denote diet; peach = carnivorous, green = herbivorous, blue = omnivorous. Flores taxa are denoted by number; 1 = *Papagomys armandvillei*, 2 = *Komodomys rintjanus*, 3 = *Paulamys naso*, and 4 = *Rattus hainaldi*.

the positive end. *Lawomys rokusii* stands apart from the carnivorous cluster on the positive end of PC3 by having both a short coronoid process and a large condyloid process like the Sulawesi shrew rats (e.g., *Echiothrix* spp.). Overall, the PCA of jaw shape data reveals significant ecomorphological differences among dietary categories which is confirmed by ANCOVA results on centroid size ($F = 15.55$; $P < 0.0001$, SI Table 4) and MANOVA analyses ($F = 5.4$; $P < 0.0001$, SI Table 5). Interestingly, a cluster analysis based on Procrustes distances indicated a similar mandibular ecomorphology between *Lawomys* and multiple *Pseudohydromys* species, with the *Lorentzimys* omnivorous lineage recovered adjacent to *Lawomys* and *Pseudohydromys* (Fig. 9).

A comparison between jaw centroid size (logged), length of the lower first molar (logged), and the incisor angle shows some interesting trends in murid dietary and morphological adaptations (Fig. 10A,B). Centroid size tracks overall jaw size, with larger mandibles plotting towards the positive end and smaller mandibles plotting towards the negative end of this axis. Similar patterns emerge for the length of the lower first molar (large molars plot positively and smaller molars plot negatively along this axis) (Fig. 10A) and the angle of the incisor (proodont incisors plot positively and opisthodont incisors plot negatively along this axis) (Fig. 10B). With regard to relative molar size, herbivorous and omnivorous murines with larger jaws tend to have proportionally large molars while carnivorous murines with small jaws tend to have small molars with some genera showing an unusually small molar size relative to centroid size (e.g., *Pseudohydromys*, *Rhynchomys*, and *Echiothrix*

(Fig. 10A). *Lawomys* stands apart by having a large jaw size with proportionately small molars (also see Fig. 8). Similar patterns emerge with incisor angle (Fig. 10B). Omnivorous murids range in body sizes but retain more opisthodont incisors (except for *Paulamys naso*) while herbivorous murids that tend to be smaller in body size tend to have opisthodont incisors and the larger sized taxa have a range of incisor angles (Fig. 10B). Conversely, the incisor angle in smaller carnivorous murids is proodont while the incisor angle in larger carnivorous murids range widely. Again, *Lawomys* separates itself with a large body size and more proodont incisors. Overall, *Lawomys* is an outlier as compared to omnivorous and herbivorous murid species and is morphologically similar to *Hyorhinomys*, *Rhynchomys*, *Echiothrix* and *Pseudohydromys* by having a small lower molar relative to its jaw centroid size. Considering the Flores murines, all of these taxa are scattered across each axis (Fig. 10A,B). *Rattus hainaldi* and *Komodomys rintjanus* cluster both within the overlapping omnivorous (*Sundamys maxi* and *S. infraluteus*) and herbivorous (*Bullimus bagobus* and *B. luzonicus*) clusters in the middle of the morphospace, while *Papagomys armandvillei* clusters with other large herbivorous species from Sulawesi (*Eropeplus canus*, *Lenomys meyeri*, *Taeromys celebensis*). Lastly, *Paulamys naso*, an omnivore based on stomach contents of captured specimens (Kitchener *et al.*, 1998), is clearly positioned among carnivorous species from the Indo-Pacific region.

The PCA of log-shape ratio of in-lever and out-lever distances reveals significant ecomorphological differences among dietary categories (Fig. 10C,D) (Table 3) ($F = 5.75$;



$P < 0.0001$, SI Table 6). Explaining 70.0% of the variance, PC1 separated murids with relatively longer distances between the coronoid and condylar processes (0.90), shorter distance between anterior part of the masseteric ridge and condylar process (-0.20) and those with relatively longer jaw molar and incisor out-levers (-0.26 and -0.26, respectively [numbers indicate the shape variable's correlation, or loading, with the principal component]). This shape difference along this axis is particularly salient among carnivorous murids, such as moss mice (*Pseudohydromys*) and worm-eating shrew rats (*Hyorhinomys* and *Echiothrix*) plotting along the positive end, which have shorter log shape ratios of the lower incisor and molar out-levers (-0.26 and -0.26, respectively) and longer in-lever distance ratios for the anterior deep masseter (-0.20), compared to vermivorous *Rhynchomys* spp. and *Tateomys rhinogradoides*, which plot on the negative end of this axis (Fig. 10C,D). *Lawomys rokusi* clusters on the positive end of PC1 together with the New Guinean moss mice (*Pseudohydromys* and *Microhydromys*) and two Sulawesi shrew rats (*Hyorhinomys* and *Echiothrix*) as well as one omnivorous species (*Lorentzimys nouhuysi*) showing an elongation on the posterior end of the mandible compared to the anterior region. PC2 explains 23.4% of the variance and distinguishes some carnivorous murids with relatively longer incisor and molar out-levers (-0.31 and -0.48, respectively) as well as longer in-lever distance ratios of the anterior deep masseter (-0.13) and superficial masseter (-0.14). In comparison, most herbivorous and omnivorous species display longer ratios of lateral temporalis muscle (0.70) and posterior deep masseter in-levers (0.37). On this axis, *Lawomys rokusi* clusters again with one omnivorous (*Lorentzimys nouhuysi*) and some carnivorous murids (*Pseudohydromys* species), but has a lever-arm pattern that is shared by both herbivorous, omnivorous, and some carnivorous murids (e.g., *Hydromys chrysogaster* and *Crunomys* species) reflecting a relatively short mandible and an overall larger and taller ramus.

Lastly, a comparison was made showing the trade-off between molar length and incisor size relative to centroid size (Fig. 11). These scatterplots show that the relative size of the lower first molar and lower incisor are more uniform among herbivorous and omnivorous murids while carnivorous murids show a range of adaptations, including worm eating rats with small molars and small lower incisors (e.g., *Rhynchomys*) or with small molars and large lower incisors (e.g., *Chrotomys*, *Echiothrix*, *Pseudohydromys*, and *Hyorhinomys*), water-rats with large molars and small lower incisors, or some animals with both large molars and incisors (e.g., *Paraleptomys*). *Lawomys* plots outside of the herbivorous and omnivorous cluster due to a combination of a large lower incisor and a small lower first molar, similar to *Hyorhinomys*, *Pseudohydromys*, *Chrotomys*, and *Echiothrix* (Fig. 11).

Figure 9. A cluster analysis using Procrustes distances showing the nearest neighbour based on 2DGM results. Colours denote diet; peach = carnivorous, green = herbivorous, blue = omnivorous. Branches highlighted in blue indicate species endemic to Flores. The clustering indicates phenetic similarity and not phylogenetic relationship.

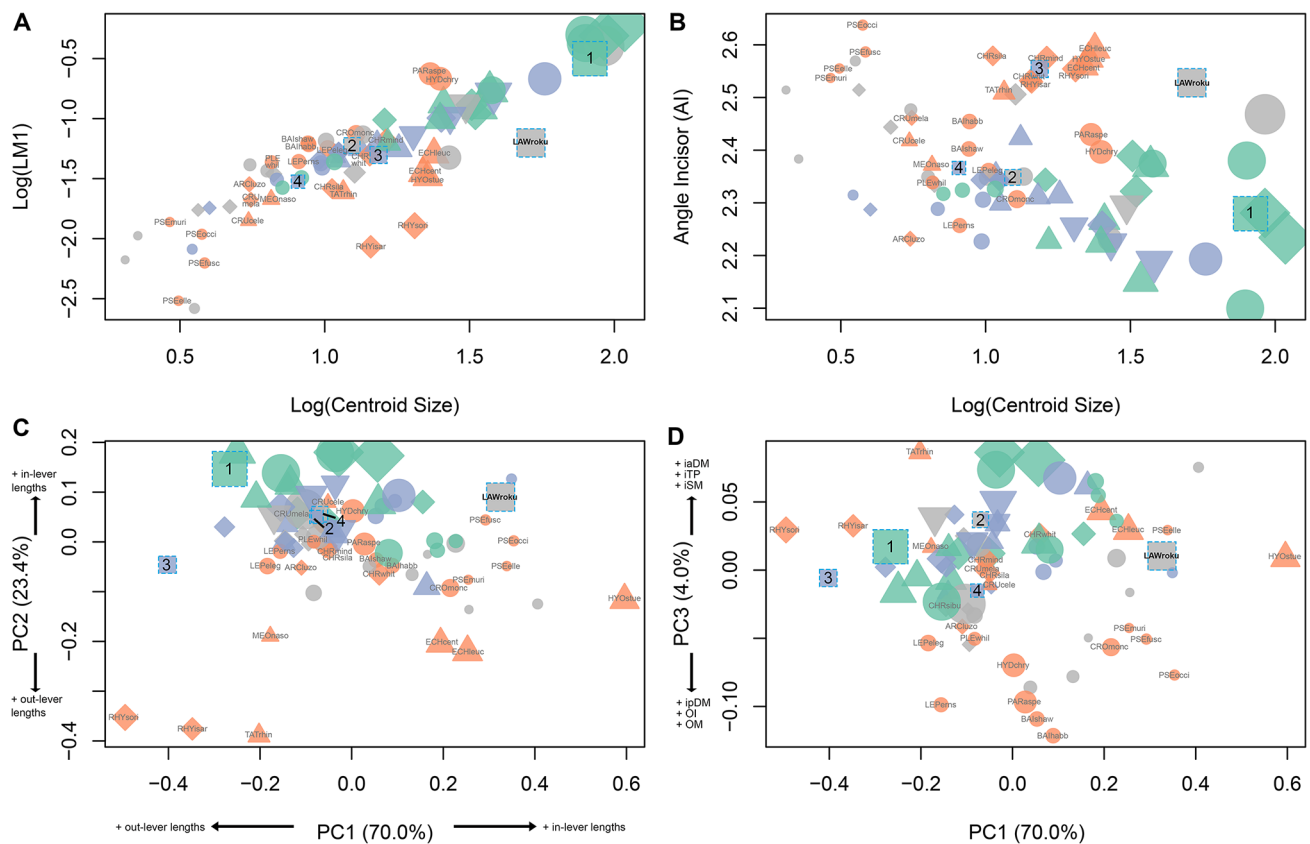


Figure 10. (A) The logged value of the jaw centroid size against the logged value of the lower first molar length (LM1) and (B) an angle measuring incisor orientation (AI). (C–D) Principal components analysis of the in-lever and out-lever distances. Description of variable loadings are provided along each PC. Genus and species names are abbreviated (e.g., ECHcent) for carnivorous murids only. The relative size of the symbol corresponds to species body size. Shapes denote locality; triangles = Sulawesi, circles = New Guinea, diamonds = Philippines, reverse triangles = Sunda, and squares with blue dotted outlines = Flores. Colours denote diet; peach = carnivorous, green = herbivorous, blue = omnivorous. Flores taxa are denoted by number; 1 = *Papagomys armandvillei*, 2 = *Komodomys rintjanus*, 3 = *Paulamys naso*, and 4 = *Rattus hainaldi*.

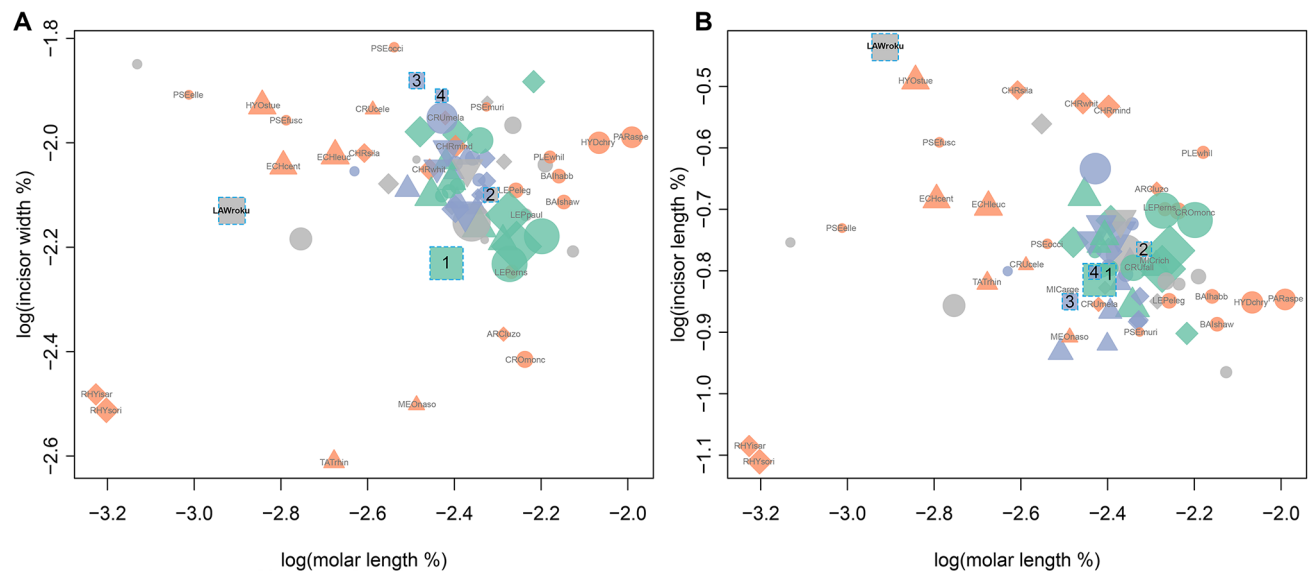


Figure 11. The relationship between molar length relative to centroid size (logged) against (A) incisor width relative to centroid size (logged) and (B) incisor length relative to centroid size (logged). Genus and species names are abbreviated (e.g., ECHcent) for carnivorous murids only. The relative size of the symbol corresponds to species body size. Shapes denote locality; triangles = Sulawesi, circles = New Guinea, diamonds = Philippines, reverse triangles = Sunda, and squares with blue dotted outlines = Flores. Colours denote diet; peach = carnivorous, green = herbivorous, blue = omnivorous. Flores taxa are denoted by number; 1 = *Papagomys armandvillei*, 2 = *Komodomys rintjanus*, 3 = *Paulamys naso*, and 4 = *Rattus hainaldi*.

Table 3. PCA loadings of in-lever and out-lever variables shown in Fig. 10C and 10D.

Variable	Abbreviation	PC1	PC2	PC3	PC4	PC5	PC6
lateral temporalis	iTP	0.890	0.200	0.025	-0.025	-0.006	0.408
posterior deep masseter	ipDM	-0.073	-0.382	-0.645	0.264	0.443	0.408
superficial masseter	iSM	-0.045	-0.700	0.293	-0.113	-0.493	0.408
anterior deep masseter	iaDM	-0.224	0.119	0.664	0.198	0.538	0.408
condyle to lower first molar	OM	-0.268	0.283	-0.182	-0.804	0.037	0.408
condyle to incisor alveolus	OI	-0.281	0.480	-0.154	0.481	-0.519	0.408

Dental morphology

The cusp pattern on both molars is extremely simple with a relatively wide and tube-like dentine wear shape. The most striking difference between *Lawomys* and all other murines from the Indo-Pacific is that the outer enamel of both molars forms a continuous outer surface similar to that in *Chrotomys*, yet three distinct laminae are maintained on the first molar as in *Hyorhinomys* (Fig. 12). The first molar's wear pattern is also generally concentrated towards the midline of the tooth but with heavy wear on the anterolabial cusp compared to the anterolingual cusp (Fig. 12). While the cusps in the first and second lamina coalesce, the dentine maintains separation and appears more transverse, unlike other shrew rats such as *Pseudohydromys*, *Chrotomys*, *Crunomys*, *Echiothrix*, and *Tateomys*, while the third lamina has a similar "bow-tie" wear pattern as in *Echiothrix* and *Hyorhinomys* (Musser & Durden, 2014; Esselstyn *et al.*, 2015). The second and third laminae have a very shallow separation between rows compared to all other shrew rats but resemble the laminae configuration in *Hyorhinomys* (Esselstyn *et al.*, 2015). Moreover, the first and second molars lack the posterior cusp and auxiliary cusplets, creating a simple occlusal pattern overall with little similarity with those of other shrew rat genera from the Philippines, Sulawesi, and New Guinea.

The enamel on the anterior aspect of the second molar in the holotype is broken, obscuring the cusp pattern on the first lamina, but the hypoconid and entoconid in the second lamina maintain separation and are barely worn. The second lamina is not as thick as in *Chrotomys* or *Echiothrix* and is more transversely oriented compared to *Pseudohydromys* (Fig. 12).

Judging from the relatively tiny and simple morphologies of the first and second molars, the occlusal traits of the third molar in *Lawomys* are likely simpler than those of other shrew rat taxa in which the third molar is known (e.g., *Archboldomys*, *Melasmothrix*, *Tateomys*), and is presumably reduced to a tiny and very simple peg-like structure (Musser, 1969; Musser & Durden, 2014). As observed in other murines where the third molar is similarly reduced, such as in *Leptomys* and *Chrotomys* (Rickart *et al.*, 2005; Musser *et al.*, 2008), it is normally present but occasionally congenitally absent (Charles *et al.*, 2011; Catzeflis *et al.*, 2017).

Compared to the Flores murines, *Lawomys* has the simplest occlusal pattern, both in terms of additional cusps, auxiliary cusplets, and cusp shape (Fig. 13). The thick, tube-like dentine wear pattern shown on the first molar of *Lawomys* shows some resemblance to the dentine wear shape on the first molar of *Paulamys*, but otherwise, *Lawomys* remains distinct in all other comparisons. Strikingly, the *Lawomys* mandible is of similar size to those of *Papagomys*

armandvillei and *Spelaeomys florensis*, which have the largest mandibles of the Flores murines, yet the breadths of the first and second molars in *Lawomys* are similar in size to those of the smallest *Komodomys* and small *Rattus* species, respectively (Fig. 13). Overall, additional molars with other degrees of wear are needed to determine how the occlusal morphology of *Lawomys* compares with that of other shrew rats and murines from the Indo-Pacific, but the features preserved in the holotype suggest that *Lawomys* maintained an extremely simple occlusal pattern for its size compared to other shrew rat taxa in the region and all other Flores murines. Moreover, the dissimilarity between *Lawomys* and the other Flores murines suggests that it occupied a different niche, possibly consuming earthworms or similar foods that do not require occlusal complexity.

Body size estimates

Compared to Flores taxa, the mandible of *Lawomys* overlaps in size with *Papagomys armandvillei* and *Spelaeomys florensis* suggesting a similar body size (Fig. 14). Indeed, regression analyses used to test if mandibular centroid size reasonably predicts the body masses of murid and shrew rat taxa suggest that *Lawomys* weighed *ca.* 623 g ($R^2 = 0.94$; $F(1, 126) = 1950$; $p < 0.001$), making it larger than any shrew rats endemic to the Indo-Pacific region (Table 4). When considering diet, and assuming *Lawomys* was carnivorous, *Lawomys* is predicted to range between *ca.* 1245–1594 g (Table 4). Most terrestrial shrew rats are typically smaller in body size with the largest living species (*Echiothrix leucura*) weighing *ca.* 310 g (Musser & Durden, 2014). Some species of water rats, such as *Hydromys chrysogaster*, can reach a similar body size (e.g., AMNH 154358, *ca.* 580 g) but water rats tend to have relatively smaller jaws, smaller incisors, and larger first and second molars. On Flores, the body mass estimate for *Lawomys* is comparable to those for *Papagomys theodorverhoeveni* and *Spelaeomys florensis* but larger than *Hooijeromys nusatenggara* and the other smaller endemics (i.e., *Paulamys naso*, *Komodomys rintjanus*, *Rattus hainaldi*).

Discussion

Flores murid diversification and the relationship of *Lawomys rokusi*

Large oceanic and mountainous islands such as Luzon, Mindanao, and Sulawesi, as well as the Australo-Papuan continental island shelf are rich in murid diversity (Rickart *et al.*, 2011; Heaney, 1998; Heaney *et al.*, 2011; Musser &

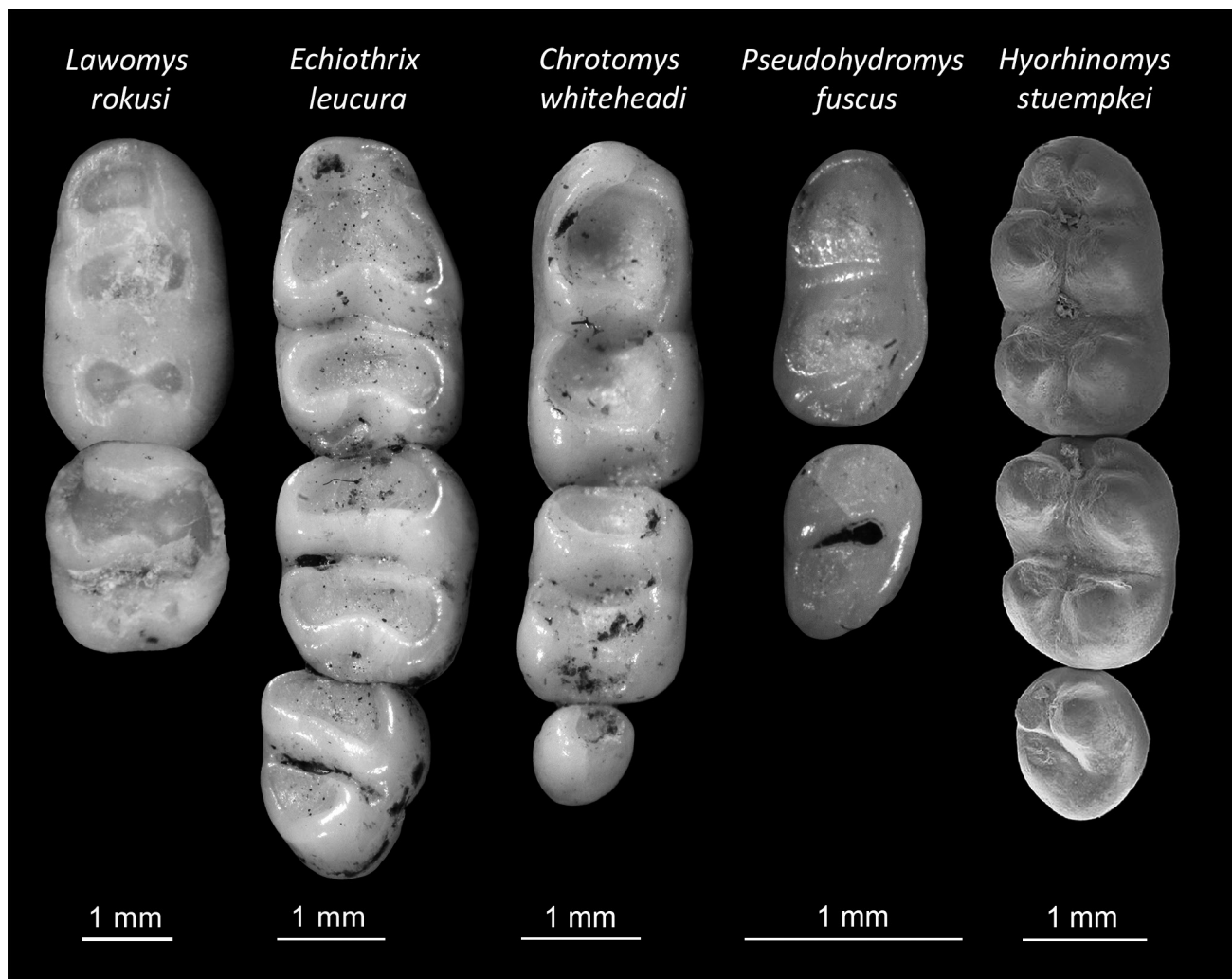


Figure 12. Comparison of the lower right tooththrow between *Lawomys rokusi* (LB-MUR-6488), *Echiothrix leucura* (NHMUK ZD 797.1.2.45; mirrored), *Chrotomys whiteheadi* (NHMUK ZD 95.8.2.20; mirrored), *Pseudohydromys fuscus* (NHMUK ZD 53.301), and *Hyorhinomys stuempkei* (LSUMZ 37060, SEM image modified from Esselstyn *et al.* [2015]).

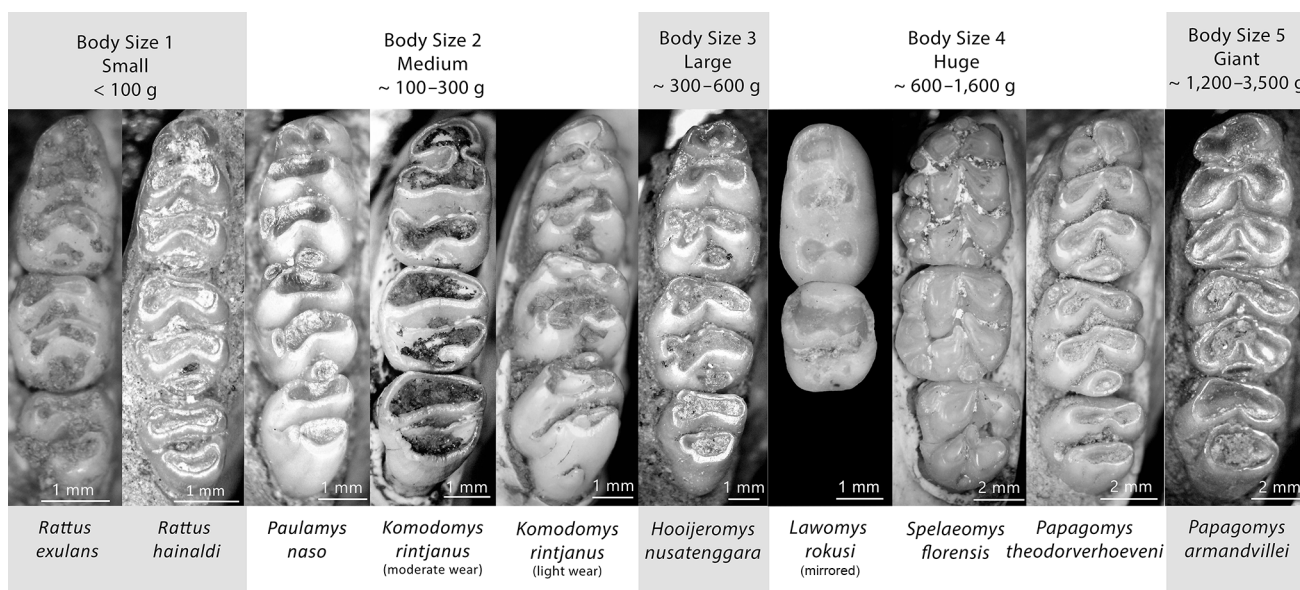


Figure 13. Left lower tooththrows of Flores murines from Liang Bua scaled to approximately the same size to show occlusal patterns. Delineations of murine body size ranges are also shown.

Table 4. Body mass predictions (g) for available Flores taxa based on linear regression models for the total comparative sample (All, Fig. 15a) and according to dietary groups (Fig. 15b, SI Table 2). The body mass range includes the predictive values for all dietary types. Where possible, the range of known body masses are included.

Taxa	Predicted mass (g)						Known body mass range
	All	Herbivorous	Omnivorous	Vermivorous	Insectivorous	Range	
<i>Papagomys armandvillei</i>	1146	1037	1508	2866	3450	1037–3450	1495–2285 ^b
<i>Lawomys rokusi</i>	623	564	771	1245	1594	563–1594	—
<i>Komodomys rintjanus</i>	97	88	100	98	152	88–152	—
<i>Paulamys naso</i> ^a	128	116	136	144	216	116–215	122 ^a
<i>Rattus hainaldi</i>	56	50	54	46	75	46–75	81 ^c
Regression statistics							
R ²	0.939	0.973	0.959	0.968	0.9307		
Adj. R ²	0.938	0.972	0.958	0.964	0.9289		
F(df)	(1,126) = 1950	(1,39) = 1417	(1,34) = 806	(1,8) = 242.3	(1,39) = 523.7		
Res. standard error	0.096	0.198	0.212	0.127	0.073		
p	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001		

^a Specimen WAM M32000 included in regression analyses with a known weight of 122 g.

^b Specimens include MZB 12716 (2285 g), MZB 12719 (1495 g), and MZB 19528 (2200 g).

^c Holotype WAM M32877 from Kitchener *et al.* (1991b).

Durden, 2014; Breed *et al.*, 2020). These regions not only display a high alpha diversity for murids, but are also rich in ecological and morphological diversity (Rowe *et al.*, 2016, 2019). Despite having fewer species, Flores harbors an ecomorphologically rich murid community, which is illustrated by the murid jaw morphospace (Figs 8–11). Herbivorous guilds are represented by the giant body-sized *Papagomys* and the medium-sized *Komodomys* genera. The omnivorous guild is represented by *Rattus hainaldi* and may also include *Rattus exulans* as a native species (see Thomson *et al.*, 2018). *Paulamys naso* was also categorized as omnivorous based on stomach contents but retains many features similar to carnivorous murids based on the murid jaw morphospace (Figs 8–11). Complete mandibles of *Hooijeromys nusatenggara* and *Spelaeomys florensis* have yet to be recovered and included in our analyses, but Musser’s (1981) dental comparison with *Bandicota indica* suggests that *Hooijeromys* was likely carnivorous and that *Spelaeomys* was likely omnivorous consuming vegetation and insects similarly to *Lenomys*. Morpho-functional traits or anatomical trait combinations place *Lawomys* as a carnivorous murid, with highly proodont incisors, tiny lower molars, large condyloid process, and a combination of both small lower molar and large incisors relative to jaw size, all of which are classic characteristics of shrew rats (Helgen & Helgen, 2009; Musser & Durden, 2014; Esselstyn *et al.*, 2015) that have been proposed to be functionally relevant to define carnivorous diet in rodents (Renaud *et al.*, 2005; Samuels, 2009; Verde Arregoitia *et al.*, 2017). As demonstrated by our description and our quantitative analyses, “shrew rats” cannot be described by a uniform morphology and several studies have already reported contrasting adaptations, such as in Neotropical Ichthyomyini water rats (Voss, 1988), Australo-Papuan Hydromyini (Fabre *et al.*, 2017), or Sulawesi lineages (Rowe *et al.*, 2014, 2016). As such, the specific diet of *Lawomys* is difficult to assess as it also shares some functional and morphological features with some omnivorous and herbivorous lineages, e.g., illustrated

by its functional and shape proximity with the omnivorous genus *Lorentzimys* (Fig. 10).

It is more difficult to infer the evolutionary origin of *Lawomys* due to its unusual morphology. For example, *Lawomys* shares many mandibular traits with Sulawesi shrew rats (e.g., *Echiothrix* and *Hyorhinomys*) especially its large condyloid process, large and elongated proodont incisors, molar morphology, and tiny coronoid process. Interestingly, this combination of traits is not found in any Philippine shrew rat or New Guinean moss mouse, suggesting that *Lawomys* may be more closely related to Sulawesi shrew rats in the *Echiothrix* Division *sensu* Rowe *et al.* (2019). However, without a molecular framework, its phylogenetic relationship remains unclear because these morphological similarities may reflect convergence (see Renaud *et al.*, 2007). Moreover, results from the Procrustes clustering analysis suggest a close morphological similarity to *Pseudohydromys* from New Guinea, suggesting similar ecological adaptations and niche exploitation.

Most of the Flores species that have been sampled for phylogenetic analyses are in the Rattini clade and demonstrate relationships with related taxa from the Sunda Shelf, Sulawesi, the Moluccas, and the Philippines (Fabre *et al.*, 2013; Rowe *et al.*, 2019). *Paulamys naso* might have a phylogenetic link to the Sulawesi fauna as it has been morphologically classified with the Sulawesi endemic *Bunomys* genus (Musser *et al.*, 1986; Kitchener *et al.*, 1991a; Kitchener *et al.*, 1998), but it has not yet been genetically sequenced. Moreover, during the Miocene and Pliocene, Sulawesi was likely a nexus island facilitating the colonization of several Indo-Pacific islands (Rowe *et al.*, 2019). However, we have shown that morphologically and functionally, *Lawomys rokusi* is rather distinct from all Indo-Pacific murines. Indeed, our geometric morphometric and lever analyses indicate a jaw shape that is similar with the New Guinea moss mice (*Pseudohydromys*, *Microhydromys*, *Mirzamys*), which contrasts with our observations regarding discrete jaw characters. As a result, *Lawomys* clearly

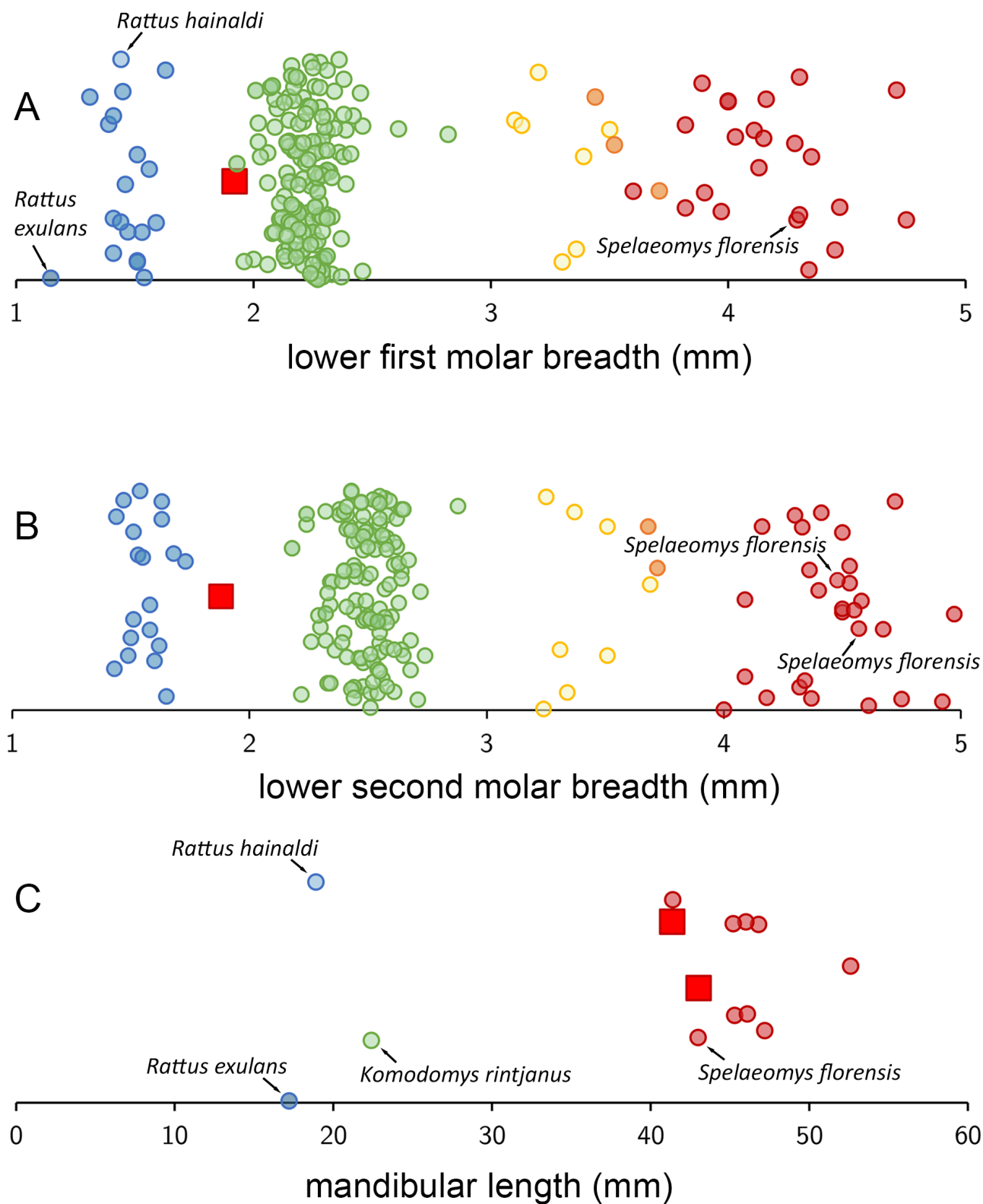


Figure 14. A comparison of molar and mandibular measurements between *Lawomys rokusi* (red square) and Flores taxa. Measurements include breadth of the lower first molar (A), lower second molar (B), and maximum length of the mandible (C). Samples of Flores taxa include archaeological and museum specimens grouped according to murine body size class (Veatch *et al.*, 2019), designating murines that are small-bodied (blue; *Rattus exulans*, *Rattus hainaldi*), medium-bodied (green; *Komodomy's rintjanus*, *Paulamys naso*), large-bodied (yellow; *Hooijeromys nusatenggara*), huge-bodied (orange; *Papagomys theodorverhoeveni*), and giant-bodied (dark red; *Spelaeomys florensis*, *Papagomys armandvillei*). All values are jittered along the Y axes.

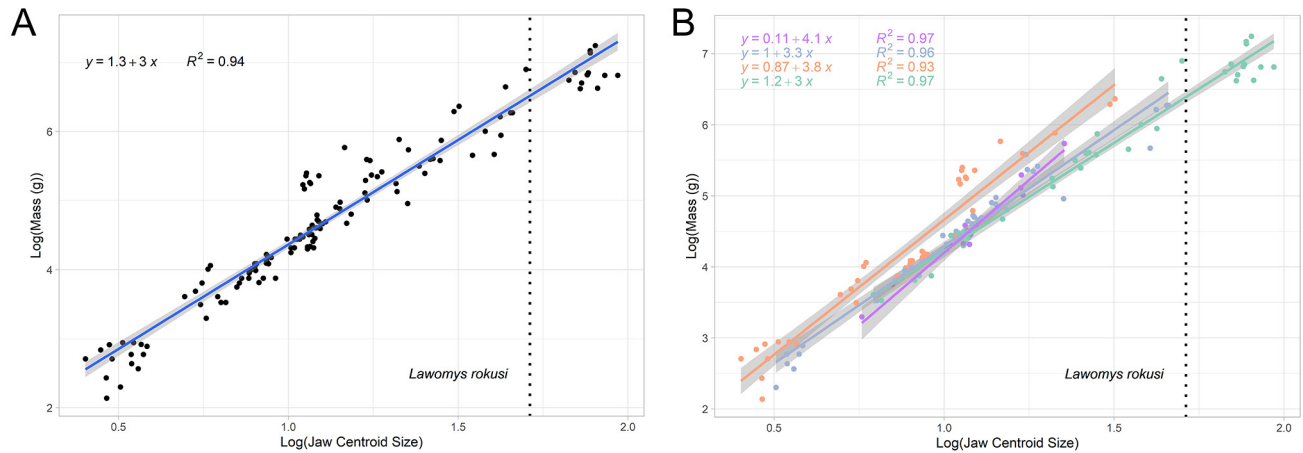


Figure 15. (A) Linear regression model showing the relationship between the natural log of jaw centroid size and known body masses (g) of murine taxa from the Indo-Pacific region (SI Table 3). The shaded region represents the 95% confidence interval. The dotted line represents the logged jaw centroid size for *Lawomys rokusi*. (B) Multiple linear regression models showing the same relationship as in (A) but grouped according to known diet (SI Table 3). Green = herbivorous, peach = insectivorous, purple = vermivorous, and teal = omnivorous.

stands as an outlier with a suite of discrete and quantitative morpho-functional traits that are quite different from any known genus. Its large size coupled with these unusual traits indicate an unusual and unique diet that is likely the result of *in situ* evolution on Flores whether via an independent colonization or via the diversification of the endemic Flores murid fauna. Further mammalian expeditions on Flores as well as ancient DNA studies might help to obtain further phylogenetic insights into its evolutionary relationships and biogeographical origin.

Ecomorphology

Lawomys shares several traits that are only found in worm-eating shrew rats from the Philippines and Sulawesi. The most significant of these traits is the large condyloid process with an extended joint surface, similar to *Hyorhinomys*, *Echiothrix*, *Chrotomys*, and *Rhynchomys* (Musser & Heaney, 1992; Musser & Durden, 2014; Esselstyn *et al.*, 2015). The condyloid surface is an indicator of jaw movement (Druzinsky, 2015), and as such the mandibular movements in these rodents might be extended due to this large articular surface. Shrew rats also tend to have elongated jaws leading to relatively longer out-lever arms both at the incisors and sometimes at the first lower molar as well. All lower incisors were broken but based on the size of the incisor within the jaw we expect the incisor to be very elongated as in *Chrotomys* or *Hyorhinomys* (see anatomical description and Figs 7 and 11). Conversely, bite force performances are usually proportional to the ratio of out-lever to in-lever lengths. Considering the long muscle in-lever lengths in *Lawomys* (Fig. 10), this elongation has some major biomechanical implications, as a shorter in-lever enables faster jaw closure and a longer in-lever enables a stronger bite at the first lower molar or the incisor. However, most insectivorous species are also characterized by faster movement at the incisor in relation to their short in-levers and long out-levers (Samuels, 2009; Fabre *et al.*, 2017; Renaud *et al.*, 2007; Michaud *et al.*, 2007; Missagia *et al.*, 2020), which is not the case in *Lawomys*. Indeed, *Lawomys* is characterized by high mechanical potential with long in-levers and shorter out-levers. However,

we note that we do not have access to true incisor out-lever length. Also, in-lever distances are proportionally longer in *Lawomys* as compared to Philippine and Sulawesi shrew rats, with an extreme elongation of the lateral temporalis in-lever.

Muscular attachments in *Lawomys* indicate important anatomical configurations. Firstly, *Lawomys* has a tiny coronoid process which is associated with one of the major jaw adductor muscles, the lateral temporalis (Anthwal *et al.*, 2015; Ginot *et al.*, 2018). The medial part of the temporalis muscle is inserted on both the medial side of the coronoid process and in the retromolar fossa. Thus, if the coronoid is small in *Lawomys*, the retromolar fossa is comparatively huge. The medial temporalis has a major role in pulling back the jaw both in other murids and cricetids (Satoh, 1997), and it might have a major role in pulling back the massive jaw of *Lawomys*. Secondly, *Lawomys* likely had a reduced superficial masseter based on a well-marked masseteric ridge that is positioned very ventrally. The deep and superficial masseters are usually the largest jaw muscles in murid rodents (Cox & Jeffery, 2011; Fabre *et al.*, 2017) with the superficial masseter having a functional role in protracting the jaw and in the jaw-closing power stroke in murids and cricetids (Satoh, 1997; Fabre *et al.*, 2017). As such, a ventral insertion as observed in *Lawomys* has strong consequences on the insertion area of the superficial masseter. Also, based on the development of the masseteric ridge, the deep masseter muscles of *Lawomys* are likely the major lateral component of the jaw adductor muscles. Such development of this ridge and associated muscle is unusual in worm-eating rats and more common in herbivorous species, as it is an indicator of powerful chewing and gnawing (Samuels, 2009). Indeed, based on cranio-mandibular morphology, these muscles are usually reduced in shrew rats (Samuels, 2009) and to a lesser extent in water rats (Fabre *et al.*, 2017), which appears to not be the case in *Lawomys*.

Lastly, the position of the coronoid and its elongated condyloid process are among the most distinctive features of *Lawomys rokusi*, a functional character also found in Papuan *Pseudohydromys* moss mice (Helgen & Helgen, 2009). Such a long temporalis in-lever length in relation to relatively shorter mandibles captured by out-lever lengths

likely indicate an increased mechanical advantage for the temporalis muscles, which usually has a reduced role in bite force for murids (Ginot *et al.*, 2019). Based on coronoid shape, we expect the lateral temporalis to be rather small in *Lawomys* reflecting a minor role in force production, which has been found to be important in water rats (Voss, 1988; Fabre *et al.*, 2017). Also, *Lawomys* has proportionally long in-lever ratio for masseter adductor muscles along with short out-lever ratios compared to most carnivorous murids with reduced masseter in-levers and elongated out-levers (Samuels, 2009). In other words, *Lawomys* has an unusually short anterior aspect of the ramus and an elongated ascending ramus compared to other carnivorous murids which usually exhibit the inverse configuration. Thus, *Lawomys* exhibits reduced mechanical potential in relation to gnawing and chewing (Missagia *et al.*, 2020; Maestri *et al.*, 2016; Renaud, 2005; Fabre *et al.*, 2017). As a result, *Lawomys* is rather unusual compared to other shrew rats as it shows high jaw mechanical advantage such that its morphological and functional position in the murid morphospace is closer to omnivorous or herbivorous murids.

Habitat and paleoenvironments

Flores murines present a wide range of adaptations suitable for various habitat types based on observations of living species (*Papagomys armandvillei*, *Komodomys rintjanus*, *Paulamys naso*, and *Rattus hainaldi*) (Musser & Boeadi, 1980; Musser, 1981; Kitchener *et al.*, 1991a,b), stable isotope analysis of *ca.* 700 ka-old *Hooijeromys nusatenggara* from Mata Menge (Brumm *et al.*, 2016), and palaeoecological data from Liang Bua (*ca.* 190 ka to present) (Veatch *et al.*, 2019; Veatch, 2021). *Komodomys rintjanus* and *Hooijeromys nusatenggara*, for example, are associated with more open, grass-dominated environments, whereas *Paulamys naso*, *Rattus hainaldi*, *Spelaomys florensis*, *Papagomys theodorverhoeveni*, and *Papagomys armandvillei* are associated with more closed, forest-dominated environments. Based on its current distribution across Flores, however, extant *Papagomys armandvillei* appears relatively versatile in terms of its habitat requirements, a feature that may have assisted its survival to present day. In the tropics and subtropics, species that rely especially on invertebrate prey, such as *Lawomys*, are also generally associated with forest or montane habitats. In the absence of other skeletal or digested remains that might indicate habitat preference, these inferred dietary adaptations suggest that *Lawomys* was probably associated with or relied heavily on closed, wet, and potentially mossy, habitats.

Remains of *Lawomys* at Liang Bua are thus far confined to Holocene sediments, although three elements may derive from the terminal Pleistocene (*ca.* 18–13 ka) given particular stratigraphic uncertainties. Based on current interpretations of the stratigraphy and chronology of the site (Sutikna *et al.*, 2016, 2018; Tocheri *et al.*, 2022), eight of the *Lawomys* mandibles were deposited within the past *ca.* 3 ka (Unit 8C), four between *ca.* 3 and 12 ka (Units 8B and/or 8A), and two along with an isolated incisor between *ca.* 5 and 18 ka (Units 8A and/or Unit 6) (Table 2). The specific agent responsible for the accumulation of *Lawomys* remains at Liang Bua is still uncertain but was likely either an avian or hominin predator or natural death. One mandible (LB-MUR-6485), for example, shows evidence of bird predation



Figure 16. An isolated lower incisor tentatively assigned to *Lawomys rokusi* with localized burning (carbonized) damage located at the tip of the tooth. Labial (top), lingual (middle and lower right), and occlusal (lower left) views are shown.

along both the lateral and medial surfaces of the mandible (Fig. 4). Alternatively, humans would have likely also sought after *Lawomys* as a food source (Veatch, 2021). For example, modern human activity at Liang Bua extends as far back as *ca.* 46 ka based on evidence of fire use and stone artifact raw material preference, and they likely included murines as part of their diet (Morley *et al.*, 2017; Sutikna *et al.*, 2018; Veatch *et al.*, 2019; Veatch, 2021). Moreover, paleoenvironmental reconstructions based on fourteen time-averaged speleothems from Liang Luar, a cave *ca.* 600 m from Liang Bua (Scroxton *et al.*, 2013, 2015; Westaway *et al.*, 2007, 2009), and one from Liang Neki located *ca.* 2 km from Liang Bua (Westaway *et al.*, 2007, 2009), suggest an increase in rainfall and wetter conditions beginning *ca.* 18 ka, which likely would have supported suitable habitats for animals like *Lawomys* around Liang Bua.

The greater number of elements identified as *Lawomys rokusi* after *ca.* 3 ka may be the result of anthropogenic factors. Pottery and polished stone adzes appear for the first time at Liang Bua *ca.* 3 ka and likely indicate a shift to sedentism and farming (Sutikna *et al.*, 2018). Although no cutmarks were identified to suggest that humans were responsible for accumulating *Lawomys*, one isolated incisor (LB-MUR-5835) tentatively attributed to this species shows localized carbonization from exposure to high temperatures along the tip of the tooth, indicating that this animal was directly exposed to fire (Fig. 16) (Veatch, 2021). Moreover, if human population sizes in the area were increasing as a result of sedentism and/or farming, then it may have resulted in increased predation pressures on endemic animals like *Lawomys* either from human hunters or the various non-endemic animals that they introduced (e.g., civets, pigs, and dogs) (Sutikna *et al.*, 2018).

Extinction or survival?

Several non-native murines—*Rattus rattus*, *Rattus argentiventer*, *Rattus norvegicus*, *Mus musculus*, and *Mus caroli*—are known from Flores but are almost certainly recently introduced commensal rodent species based on the archaeological and fossil records of Flores (Musser, 1981). The largest living endemic rat on Flores, *Papagomys armandvillei*, was first documented scientifically more than a century ago (Jentink, 1892; Musser, 1981) and it survives across much of Flores, including around Liang Bua. Other Flores murines were discovered much later and although some of these are also known to be extant (i.e., *Paulamys naso* and *Rattus hainaldi*) (Kitchener *et al.*, 1991a,b; Kitchener & Yani, 1998; Kitchener *et al.*, 1998), the rest are either apparently extirpated (*Komodomys rintjanus*) or believed to be extinct (*Spelaeomys florensis*, *Papagomys theodorverhoeveni*, and *Hooijeromys nusatenggara*) (Musser, 1981; Veatch *et al.*, 2019). *Lawomys* joins this latter group of presumably extinct taxa, and the causes of their disappearance within the past few thousand years is a question of interest.

Modern humans have long been posited as a major contributor and accelerator to the decline of faunal diversity in Southeast Asia, Wallacea, and Australo-Papua since their Late Pleistocene arrival in these regions (Roberts *et al.*, 2001; Barnosky *et al.*, 2004; Wroe *et al.*, 2004). However, the degree to which *Homo sapiens* is responsible for this decline remains a contentious issue with a noticeable bias towards megafaunal extinctions that often omit the outcomes for small mammals and other animals (Barnosky *et al.*, 2004; Louys *et al.*, 2007, 2017; Wroe *et al.*, 2013; Meijer *et al.*, 2015). At Liang Bua, dentognathic evidence indicates that all of the Flores endemic murines are present in the most recent stratigraphic unit (8C, < ca. 3 ka), so the presumed extinction and extirpation of four and one of these taxa, respectively, clearly occurred relatively recently. The fact that modern humans were present fairly continuously at Liang Bua for the past ca. 46 ka suggests that this endemic murine fauna survived not only any ecological disruptions and/or changes that may have occurred during the Late Pleistocene and Holocene but also the initial and continuous impacts of modern humans on the island (Sutikna *et al.*, 2018; Veatch *et al.*, 2019). Instead, it appears that human sedentism and farming with concomitant increases in population size on Flores may have caused increased predation of murines and/or the alteration, reduction, or destruction of murine habitats. Further mammalogical surveys on Flores and its adjacent satellite islands are desperately needed to determine whether any of the murine species observed in the relatively recent archaeological records of the island but are presumed extinct may in fact still survive today.

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Supplementary information

Supplementary information—SI Tables 1–6—are published separately as a *figshare* dataset (see Veatch *et al.*, 2023).

<https://doi.org/10.6084/m9.figshare.24549559>

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