Contributions to Mammalogy and Zooarchaeology of Wallacea

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Title-page image—Wallacean mammalogy and archaeology side by side: the skulls of a Flores giant rat (*Papagomys armandvillei*, left) and the "hobbit" (LB1, the type specimen of *Homo floresiensis*, right), from the archaeological site of Liang Bua on the island Flores in Indonesia. Image created by E. Grace Veatch.

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Wallacean Mammalogy and Zooarchaeology: Remembrances and a Renaissance

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The richness of life is not distributed haphazardly across the globe, but instead exhibits profound, non-random patterns. Numbers of species of insects, trees, and frogs, for example, abound in tropical localities, like in Brazil or the Congo, but not in Siberia or the Yukon. Species uniqueness, or endemism, peaks on large, long-isolated islands, like Madagascar or the Philippines. And different continents often have profoundly different assemblages of organisms. These types of observations regarding major patterns in the distribution of life, and their implied histories, formed the original foundation of the science of biogeography. Among the most important developers of this science was Alfred Russel Wallace, one of the architects of evolutionary biology.

One of Wallace's many fundamental biogeographic insights was the realization that the fauna of the "Malay Archipelago", extending from the Malay Peninsula to New Guinea, much of which is now encompassed within the modern nation of Indonesia, can be demarcated into zones of marked Asian and Australian character. (This was an insight based on firsthand fieldwork, collecting biological specimens for museums.) These zones of regional influence merge and meld along the island chain, but nevertheless a particularly sharp demarcation runs between the islands of Borneo and Sulawesi in the north, and Bali and Lombok, in the south. This demarcation is now known as the "Wallace Line" (Wallace, 1869, 1876; Fig. 1), and others later built on these Wallacean insights to identify additional "lines" of biogeographic significance in the archipelago (Fig. 1). We now understand more fully that the profound distinctions in the archipelago result from differential histories of continental connection and movement, with the islands of Sumatra, Java, and Borneo being part of Sundaland—the Asian continental shelf, and New Guinea an extension of the Australian, or Sahulian, continent. The area in between consists of the large island of Sulawesi and the oceanic archipelagos known as the Lesser Sundas (Nusa Tenggara) and the Moluccas (Maluku). These long-isolated islands constitute a geologically complex region that serves both as a zone of faunal transition between the two great continental faunas, as well as a realm unto itself with remarkable endemism. Today this region is called Wallacea by biogeographers, and it is rich in animal life, including mammals.

Most work on mammals in the Wallacean region has focused on Sulawesi, the largest and most centrally located island in the zone. Initial biological exploration on the island demonstrated that the fauna was a mix of mammals of both Asian and Australian genesis, with the island's forests home to native bats, rats, squirrels, shrews, monkeys, tarsiers, civets, pigs, and bovids, as well as marsupials—arboreal possums called cuscuses. Early, sporadic work by European collectors and taxonomists gave way to more systematic expeditionary collecting by British and American collectors in the twentieth century (Musser *et al*., 2010). This work illuminated the remarkable diversity and endemism of Sulawesi's mammals and led in particular to proliferation in knowledge of the island's rich native murine rodent fauna (e.g., Musser, 1969, 1982, and many similar contributions). From the mid twentieth century, palaeontological excavations on Sulawesi also began to reveal aspects of the deeper Quaternary history of the island's mammals, including the past presence of now-extinct megafauna such as proboscideans and large pigs (Hooijer, 1958, 1975, and many other contributions). This was accompanied by other discoveries of extinct megafauna on islands in Nusa Tenggara, including Sumba, Flores, and Timor, especially of species of the proboscidean genus *Stegodon* (Hooijer, 1975).

Much better known than the mammals of Wallacea are its birds (Rheindt *et al*., 2020), which are more colourful, more vocal, easier to find by day, and most importantly were more economically lucrative targets for early natural history collectors working in the region (Coates & Bishop, 1997). Wallacean fruit-eating bats (family Pteropodidae), from tiny blossom bats to massive flying foxes, were commonly collected by early European traders and expeditioners alongside birds and are thus the mammals best represented in historical museum collections. Because of this, much of their distributional patterns of occurrence became reasonably well documented by the turn of the twentieth century (Andersen, 1912) and more firmly fleshed out by the end of the century (Corbet & Hill, 1992; Flannery, 1995). Nevertheless, much remains to be published about the taxonomy of Wallacea's fruit-eating bats, and these species have been largely untouched by the revolution in systematics enabled by integrative approaches involving both molecular phylogenetic and modern morphometric methodologies.

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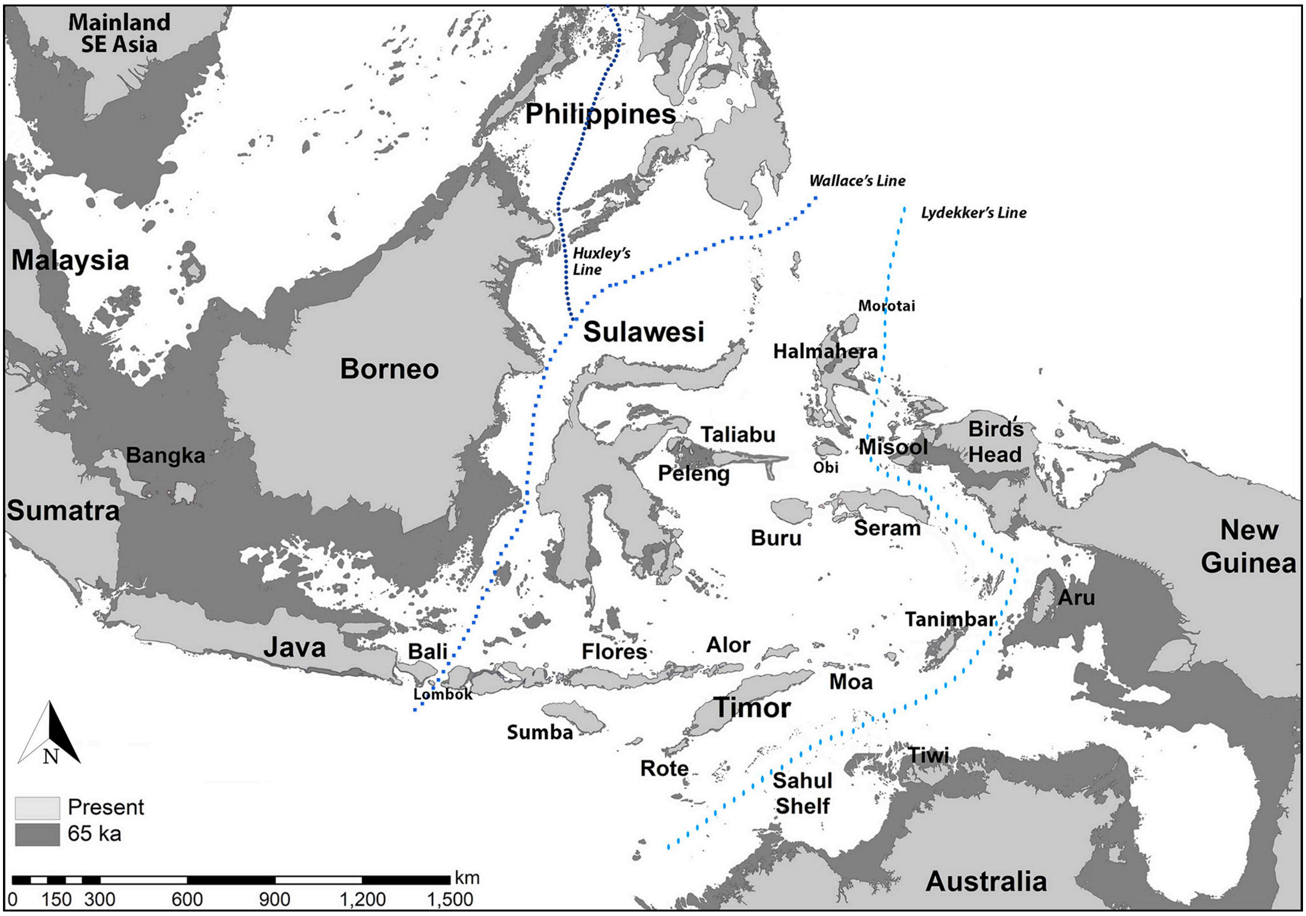

Figure 1. Regional map of Wallacea, showing the Huxley, Wallace and Lydekker lines. The extent of the continental shelves at 65 ka (accounting for uplift) is indicated by dark grey shading. This map is a modified version of the map appearing in Kealy *et al*. (2018) and has been edited and reproduced with permission.

(Taxonomic revision in these species forms the basis of another volume, currently in preparation for publication.)

Outside Sulawesi and apart from fruit-eating bats, mammals in Wallacea have remained less well known to science. It is these species, represented especially by murine rodents and insectivorous bats, that form the subject matter of many of the contributions in this volume. Our reports in this volume are drawn mainly from two streams of work. One is from modern mammal specimens collected during fieldwork in the Moluccas and Nusa Tenggara since the Second World War, including major initiatives led by the eminent biologist Boeadi in Indonesia and the collecting efforts of Tim Flannery and Darrell Kitchener from Australian museums, along with more recent efforts (see below). The other involves important archaeological excavations undertaken since the mid twentieth century, and especially since the 1990s, on the islands of Timor, Flores, and Morotai, especially by Indonesian and Australian archaeologists including Thomas Sutikna, Rokus Due Awe, Michael Morwood, Peter Bellwood, and Sue O'Connor, among others. This work has taken on greater interdisciplinary interest as archaeological discoveries have increasingly shown the importance of Wallacean islands in hominin and modern human history, and particularly since the discovery of the endemic hominin *Homo floresiensis* on Flores (Brown *et al*., 2004; Morwood *et al*., 2004). Joint insights from modern mammalogy and the study of zooarchaeological remains illuminating past mammal faunas form an especially powerful approach for understanding the ecology and evolution of Wallacean mammals across deep time and constitute a central motivation for the studies in this volume.

Across this deep history, the islands of Wallacea have been impacted by human activities, resulting in removal of rainforest, major land-use changes, hunting of native and endemic wildlife, and the introduction of non-native species like commensal rodents, livestock, and crops. More recently, and especially today, these impacts have taken on an industrial dimension, with logging, fires, mining, and other large-scale environmental perturbations transforming these islands in the face of growing human populations and increasing economic demands. Anthropogenic climate change, with its myriad concomitant environmental effects, is already underway globally, and its changes will be felt across the world, including in Wallacea, especially in the decades ahead. Clearer understanding of past environmental changes and impacts, and the ongoing effects of these modern pressures, are fundamental to identifying which Wallacean mammal species are most in danger of extinction and in need of conservation measures to ensure their survival (Monk *et al*., 1997; Aplin & Helgen, 2010). There is much still to discover, and corresponding urgency in this work.

Remembrances

We dedicate this Special Issue to the memory of two close colleagues from Indonesia, both giants in their fields, who have passed away in recent years: the eminent zoologist Bapak Boeadi (1935–2021) and the eminent zooarchaeologist Bapak Rokus Due Awe (1942–2015).

Boeadi was born on 13 March 1935 and passed away on 2 August 2021. A mammalogist and herpetologist from East Java, Boeadi was the most renowned Indonesian zoologist of his generation. He published extensively on the vertebrate fauna of the entire Indonesian archipelago, produced important taxonomic revisions, and named many taxa. These include, among mammals, the rodent genus *Komodomys*, the marsupials *Dendrolagus mbaiso* and *Phalanger alexandrae*, the murine rodent *Rattus timorenesis*,

Figure 2. Boeadi (standing), with Tim Flannery (left) and other colleagues in the field, September 1992, on Supiori Island in Cendrawasih Bay (Papua Province, Indonesia)—home to the endemic giant rat *Uromys boeadii*.

and the pteropodid bat *Megaerops kusnotoi* (Musser & Boeadi, 1980; Kitchener *et al*., 1993; Flannery *et al*., 1997; Flannery & Boeadi, 1995; Hill & Boeadi, 1978), as well as a variety of frogs and reptiles. Various species have been named in his honour, including the Indonesian endemic mammals *Uromys boeadii*, a giant rat from Biak-Supiori (Fig. 2) in Cenderawasih Bay, western New Guinea (Groves & Flannery, 1994), and *Hipposideros boeadii*, a leaf-nosed (or roundleaf) bat from Sulawesi (Bates *et al*., 2007).

Boeadi worked extensively with many zoologists from outside Indonesia, including Tim Flannery, who partnered with him on a series of expeditions across Maluku and western New Guinea during the 1990s. In remembering Boeadi, Flannery writes:

It was my great good fortune, on my first visit to Indonesia, to encounter Boeadi. It was in the days before email, and I had decided to drop in to the Zoology Museum in Bogor on my way home to Sydney from researching Europe. When I asked at the museum's front desk to meet someone from the mammal section, Boeadi came to the desk and greeted me. I had arrived around lunchtime, and when I suggested that we could go somewhere for lunch he instantly agreed, leading me into a warren of tiny shops in the market opposite the Museum's main gate. We settled into a dimly-lit and distant corner of a Chinese restaurant where he ordered a dish of pork, explaining that he had resorted to this out-of-the-way place so that none of his workmates might see him.

Boeadi was one of the sunniest and most enthusiastic people I ever met, and he cheerfully shared his life story with me. He had grown up in East Java, and by the time he was in his early teens WW2 was finished and the Indonesians were fighting the Dutch for independence. At the age of 14 Boeadi had become an itinerant cigarette seller, a profession that allowed him to play a role in the struggle for independence. Lugging his supply of cigarettes, he would slip through the Dutch lines with messages for the Indonesian freedom fighters on the other side. That year was also the year of Boeadi's circumcision, a ceremony which in Java is done at adolescence. Boeadi was determined to avoid having the operation done in the village with the other boys. So he saved the money he earned by selling cigarettes to pay for a circumcision done in a hospital, under anesthetic.

As we ate lunch that day, Boeadi also spoke of his career as a wildlife researcher—of trapping Sumatran rhinos and tigers for various breeding programs, of sleeping in remote jungle trees as tigers stalked below, and of climbing to the eternal snows of Mt Jaya in Papua as part of the 1963 military expedition sent to climb to the highest in Indonesia. He still had the letter from President Suharto (which he later showed me) requesting him to instruct the soldiers in jungle survival. He vividly recalled teaching these young, mostly Muslim men how to catch, kill and cook snakes and other wild sources of food.

We had soon set up a partnership that allowed us to do ground-breaking fieldwork in Maluku Utara and Papua. It was a period of relative freedom of travel, though tensions were prone to break out, especially during the First Gulf War, which some Muslims interpreted as an attempt by the West to take over Muslim heartlands. Without Boeadi's sage advice and care in mediating with bureaucrats and villagers, the fieldwork would have been impossible.

By the time we were doing our fieldwork Boeadi had been training researchers and conducting fieldwork throughout Indonesia for decades. He was held in the highest esteem, for not only was he the "guru" of many wildlife officials, but he was regarded as the grand old man of Indonesian mammalogy.

My fieldwork in Indonesia would have simply been impossible without Boeadi. He facilitated the granting of research permits, acquired the necessary surat jalans to work in eastern Indonesia, and obtained export permits. He was also an expert field hand who was never happier than when in the forest, cooking a delicious bush meal or skinning and preparing specimens. He was also a wonderful companion whose never-failing sense of humour made even the most difficult of circumstances bearable.

Boeadi contributed to a number of jointly authored papers, among which was one the naming a spectacular new tree-kangaroo from Papua, Dendrolagus mbaiso. *The Australian Museum had borrowed the holotype to allow for its description, and when I* *returned it to the Zoology Museum in Bogor, Boeadi had organized a small ceremony which included my meeting the Director of the institution, an honour I had not had before. It was perhaps Boeadi's way of ensuring that my reputation as a friend of the Bogor Museum would endure beyond his time.*

When our fieldwork ceased, it became difficult to remain in contact. Boeadi's wife Emma passed away, and he was cared for by an aged housekeeper who spoke only Sundanese. She also had few teeth, which made her difficult to understand on the phone. But we continued to exchange Christmas cards for many years. Boeadi was one of the most important, and most generous colleagues I've ever had. I miss him greatly.—Tim Flannery

The other colleague we remember with this Special Issue is Rokus Due Awe. Rokus was born in Flores and spent a lifetime dedicated to archaeological excavation and zooarchaeological investigation in Indonesia. From the 1960s onward, Rokus was involved in excavations at the world-renowned fossil sites in the So'a Basin and at Liang Bua on Flores. Liang Bua eventually was to yield evidence of a rich vertebrate fauna, including many species of extinct endemic rats, as well as *Homo floresiensis*, for which Liang Bua is the type locality (Brown *et al*., 2004). Rokus was the first person to correctly identify the original specimens of *Homo floresiensis*, and he co-authored the major papers documenting these finds. His life and contributions are memorialized further by Veatch *et al.* (2023) in this volume in their description of a new genus and species of gigantic "shrew rat" from Flores named in his honour. This subfossil rat, thus far known only from Liang Bua deposits, is ecomorphologically very different from any rodent previously named, characterized by a large and relatively robust jaw but miniscule molars.

A Wallacean mammal "renaissance"?

During the last decade or so, mammalogical work in Wallacea has seen a spurt in activity. This is especially true in Sulawesi, where this spurt has been energized by new fieldwork and integrative systematic revisions of small mammals, led especially by Jacob Esselstyn, Kevin Rowe, Anang Achmadi, and colleagues—enabled too, until recently, by the late Guy Musser (e.g., Esselstyn *et al*., 2012, 2015; Musser *et al*., 2010). This has led to the documentation of a remarkable number of new species and genera of Sulawesian mammals (e.g., Esselstyn *et al*., 2021). These taxonomic descriptions have demonstrated not only that Wallacean faunas remain incompletely inventoried, but also, as in the discovery of remarkable new genera like *Hyorhinomys* and *Paucidentomys*, that major new ecomorphological "ways of being a mammal" are still out there to be documented. (This type of documentation is continued in this volume especially with the description of a new giant rat genus from Flores: Veatch *et al*., 2023). Much has also been happening outside Sulawesi. For example, until relatively recently, the nonvolant mammals of the Moluccas were known mainly by a single expeditionary effort undertaken on Seram in 1920 (Thomas, 1920); many Moluccan islands are woefully unexplored for their biodiversity, including for mammals. One of the islands essentially unexplored by mammalogists previously is Kofiau, the subject of mammalogical surveys reported by Wiantoro *et al*. (2023) in this volume. Kofiau is biogeographically important in being an oceanic island with both Papuan and Moluccan zoogeographic affinities. Only one species of mammal was previously recorded from the island, a number now brought to 20 species by surveys reported in the paper. Fabre *et al.* (2023) in this volume also summarise results from recent fieldwork from Moluccan islands, including Obi, Halmahera, and Buru. This work has documented several new species of *Rattus*, which are presented within a comprehensive integrative taxonomic review of Moluccan *Rattus*. This same fieldwork has also documented previously overlooked taxa and populations in other Moluccan rodent genera, including *Melomys* and *Halmaheramys*, reported in earlier papers (Fabre *et al*., 2013, 2017, 2018). Mammalogical inventories of islands in Nusa Tenggara also remain incomplete, and Parnaby & Helgen (2023) in this volume report additional important fieldwork from Timor-Leste, reporting the re-discovery of the long-eared bat genus *Nyctophilus* for the first time after a hiatus of 200 years. This discovery is reported in the context of revisionary work on the genus *Nyctophilus*, an Australo-Papuan genus that just penetrates Wallacea. All of the papers in this volume emphasize the importance of new and ongoing fieldwork in the region toward better understanding Wallacean faunas, their deeper histories, and their connections to Asia and Australia.

An increasing motivation for studying wild mammals, and to inventory mammalian biodiversity, is to understand the parasites and pathogens they may harbour, especially where those may be of significance to human and veterinary welfare. Research on the role played by mammals as vectors of infectious disease has increased worldwide since the Second World War and has taken on new urgency in the 21st century as the importance of understanding zoonotic pathogens, including those with potential for pandemic impact, has become clearer (Cook *et al*., 2020). One paper in this volume, by Mursyid *et al*. (2023) provides the most comprehensive view yet obtained for the occurrence of trypanosome parasites in Wallacean mammals, based on sampling of hundreds of specimens of bats, shrews, rats, and squirrels across an elevational gradient in central Sulawesi. This provides an important foundation for work of this kind, which is only beginning in the region. Very little is known about parasites and pathogens of species elsewhere in the Moluccas, especially in rodents, but the recent discovery of new virus of medical and veterinary interest in a previously overlooked Moluccan murine, *Melomys* sp. cf. *burtoni* from Halmahera (Alfano *et al*., 2016), indicates the importance of embarking on this work with greater concentration.

The modern faunas of Wallacea, documented by fieldwork in existing and historical habitats, are framed in important resolution by studies of the deep past, and zooarchaeology is a field that has recently burgeoned in visibility in Wallacea recently. In these studies, it has been rats, which numerically dominate the material from some of the most important excavation sites, that take centre stage. In this volume, Aplin *et al*. (2023) and Veatch *et al*. (2023) document newly described species of murine rodents from Morotai and Flores, respectively, in the context of important taxonomic and ecomorphological comparisons. This brings to completion the naming of the various rat taxa previously identified in Morotai and Flores subfossil deposits, complementing other recent work from Sumba (Turvey *et al*., 2017) and Timor (Aplin & Helgen, 2010). Most of the subfossil rats of Timor, however, remain unnamed—a major unfinished task in Wallacean zooarchaeology, and the subject of another forthcoming revision. Taxonomic documentation of these small mammal faunas enables better understanding of insular patterns of evolution and extinction and the spread for commensal and invasive species. It also allows for clearer understanding of past environments and ecological associations in the past, considered increasingly valuable to studies in palaeoanthropology and archaeology (see Louys *et al*., 2023; and Veatch *et al*., 2023, in this volume). Indeed, Wallacea has increasingly drawn focal attention in studies of deep human history with the firm demonstration that hominins have histories extending many hundreds of thousands of years, or longer, on islands like Flores and Sulawesi (e.g., Brumm *et al*., 2016; van den Bergh *et al*. 2016), and that various Wallacean islands have been important in the history of modern humans, such as for migration (Kealy *et al*., 2018), cultural expression (Brumm *et al*., 2021), and genomic introgression (Teixeira *et al*., 2020).

In our view, scientific explorations of mammal faunas in Wallacea, both modern and ancient, have only just begun—all while we move into a world in which their future is fraught. Perhaps the most important insight from this volume is the urgent need to undertake fieldwork to understand if various species that have not been documented in decades (like the two new species of *Rattus* described here from Taliabu) or much longer (like new subfossil species described here from Morotai and Flores) are still extant, like we have shown here for *Nyctophilus* on Timor. Hopefully some of them are still extant, giving us a chance to better enable their long-term conservation in a changing world. Overall, we take great joy in delivering these current contributions to knowledge of mammalogy and zooarchaeology in the region, in collaboration with many excellent colleagues, and we remember others that have come before us and have now departed the stage.

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Corrigendum

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The figure caption should read.

Figure 2. Boeadi (standing), with Tim Flannery (left) and other colleagues in the field, September 1992, on Supiori Island in Cendrawasih Bay (Papua Province, Indonesia)—home to the endemic giant rat *Uromys boeadii*. (photo: Alexandra Szalay).

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Rediscovery of the Long-eared Bat Genus *Nyctophilus* (Chiroptera: Vespertilionidae) in Timor and a Reassessment of *Nyctophilus timoriensis*

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ABSTRACT. The only previous record of the Long-eared bat genus *Nyctophilus* from the island of Timor is a specimen collected by the Baudin expedition in 1803, used to describe *Nyctophilus timoriensis* by Geoffroy (1806). However, its geographic attribution to Timor is contentious because of uncertainty regarding the characteristics and the identity of the type material of *timoriensis*, and because no further specimens from Timor have been available until now. Here, we report on three specimens of *Nyctophilus* collected in 2003 at Maubisse, in the mountains of Timor-Leste (East Timor), which we tentatively assign to *N. timoriensis*. We present a revised concept of *N. timoriensis* based on a re-interpretation of the original description and illustration, as well as examination of the suspected holotype. Our assessment differs from the prevailing view of *timoriensis* as representing a large-bodied *Nyctophilus* with a rudimentary snout mound (similar to the Australian species *N. major* Gray, 1844, with which it has often incorrectly been synonymized). Instead, *N. timoriensis* is a medium-sized species with an enlarged snout mound, closely resembling *N. heran* Kitchener *et al.,* 1991, from Lembata Island, Indonesia, and *N. geoffroyi* Leach, 1821, of mainland Australia and Tasmania. Further revisionary work is needed to resolve the taxonomy and relationships of these similar species.

ABSTRAK [Bahasa Indonesia]. Catatan tentang kelelawar bertelinga panjang, genus *Nyctophilus* dari Pulau Timor, sebelumnya hanya diketahui dari spesimen yang dikoleksi dalam ekspedisi Baudin pada tahun 1803, yang selanjutnya digunakan untuk mendeskripsikan spesies *Nyctophilus timoriensis* oleh Geoffroy pada tahun 1806. Namun, pemahaman distribusi geografis spesies ini di Timor masih diragukan karena adanya ketidakpastian terkait dengan karakter dan identitas spesimen tipe dari spesies *N. timoriensis*, dan tidak tersedia spesimen yang lain dari Timor. Dalam makalah ini, kami melaporkan tentang tiga spesimen kelelawar *Nyctophilus* yang dikoleksi pada tahun 2003 dari Maubisse, pegunungan di Timor Leste, yang sementara ini kami masukkan ke dalam kelompok *N. timoriensis*. Kami mempresentasikan revisi dari pemahaman tentang spesies *N. timoriensis* berdasarkan pada penafsiran ulang terhadap deskripsi dan ilustrasi awal dalam penamaan spesies, serta eksaminasi spesimen yang diduga sebagai holotipe. Penilaian kami berbeda dengan pemahaman yang saat ini berlaku terhadap *timoriensis* sebagai representasi dari kelelawar *Nyctophilus* yang memiliki ukuran tubuh besar dengan tonjolan moncong yang mengalami rudimentasi (mirip dengan spesies dari Australia, *N. major* Gray, 1844, yang seringkali disalahartikan sebagai sinonim).

Keywords [English]: Baudin expedition; *Nyctophilus timoriensis*, Charles Alexandre Lesueur, Timorese bat inventory, Indonesian bat fauna
Keywords [Bahasa Indonesia]: ekspedisi Baudin, *Nyctophilus timoriensis*, Charles Alexandre Lesueur, inventarisasi kelelawar Timor, kelelawar Indonesia
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Sebaliknya, *N. timoriensis* adalah spesies dengan ukuran tubuh sedang dengan tonjolan moncong yang membesar, sangat mirip dengan *N. heran* Kitchener *et al*., 1991, dari Pulau Lembata, Indonesia, dan *N. geoffroyi* Leach, 1821, dari daratan Australia dan Tasmania. Upaya revisi lebih lanjut diperlukan untuk menyelesaikan taksonomi dan hubungan kekerabatan dari spesies-spesies yang mirip tersebut.

REZUMU [Tetum]: Rejistu úniku kona-ba niki ho tilun naruk, husi jéneru *Nyctophilus*, iha illa Timor, maka espésime (ezemplár) ida ne'ebé rekolle husi Baudin, iha ninia espedisaun iha tinan 1803, ne'ebé uza husi Geoffroy (1806) hodi halo deskrisaun kona-ba *Nyctophilus timoriensis*. Maske nune'e, ninia atribuisaun jeográfika ba Timor kontroversa (iha hanoin ne'ebé la hanesan) duni, tanba la iha serteza kona-ba karakterístika no identidade husi materiál tipu *timoriensis* nian, no tanba to'o agora la iha ezemplár tan Timor nian. Iha estudu ida ne'e ami aprezenta ezemplár *Nyctophilus* tolu, ne'ebé rekolle iha tinan 2003, iha Maubisse, iha Timor-Leste ninia foho sira, ne'ebé ami atribui ho provizóriu (la definitivu) ba *Nyctophilus timoriensis*. Ami aprezenta konseitu ne'ebé revee ona kona-ba N. timoriensis, bazeia ba interpretasaun foun kona-ba deskrisaun no ilustrasaun orijinál sira, no mos ba *holótipo* (ezemplár ne'ebé uluk uza hodi halo deskrisaun) suspeitu nian. Ami nia avaliasaun la hanesan ho ida seluk ne'ebé iha to'o agora, ne'ebé hatudu *N. timoriensis* hanesan *Nyctophilus* ho isin boot, ho ibun (nunun) rudimentár, (hanesan espésie australiana *N. major* Gray, 1844, ho ne'ebé kompara sala dala barak). Duké hanesan ne'e, *N. timoriensis* maka espésie ho tamañu médiu, ho nia ibun (nunun) luan, hanesan loos ho *N. heran* Kitchener *et al*., 1991, husi illa Lembata, Indonézia, no ho *N. geoffroyi* Leach, 1821, husi Austrália kontinentál no Tazmánia. Presiza halo revizaun tan hodi rezolve taksonomia no relasaun entre espésie hanesan sira ne'e.

Introduction

The French naturalist Étienne Geoffroy Saint-Hilaire described a long-eared bat species, *Vespertilio timoriensis*, based on a specimen or specimens collected from Timor during the Baudin expedition (Geoffroy, 1806). The species was later transferred to the genus *Nyctophilus*, erected by Leach (1821a). The Baudin expedition was based at Kupang Bay (now the Indonesian city of Kupang) on the western end of the island of Timor during August–November 1801 and April–July 1803 (Péron & Freycinet, 1807–1816). Jackson *et al.* (2021) gave the collection date of *Vespertilio timoriensis* as between 6 May and 3 June 1803.

Subsequent authors for the ensuing half century (e.g., Desmarest, 1821; Temminck, 1840; Giebel, 1855), including his son, Isadore Geoffroy Saint-Hilaire (I. Geoffroy, 1832), credited Geoffroy's (1806) documentation of this species from Timor. However, in the two centuries following the Baudin expedition, the presence of *Nyctophilus* in Timor has at times been doubted, in large part because no further material had been reported since the original account by Geoffroy (1806). More recently, Kitchener *et al*. (1991) confirmed the occurrence of *Nyctophilus* in the Lesser Sunda Archipelago in the late twentieth century, designating a newly collected specimen from the neighbouring island of Lembata, Indonesia immediately north of Timor, as the holotype (and thus far only known specimen) of *Nyctophilus heran* Kitchener, How, & Maharadatunkamsi, 1991. Kitchener *et al.* (1991) considered it likely that the genus also occurred in Timor.

Here we confirm that the genus *Nyctophilus* occurs in Timor. Three specimens of long-eared bats (genus *Nyctophilus*) collected in 2003 from Maubisse, montane Timor-Leste (East Timor) were documented in a report by Polhemus & Helgen (2004) to the Government of Timor-Leste. Until now the identity of these specimens has remained uncertain. In this paper we describe the Maubisse material and provide a morphological evaluation of their taxonomic status relative to the taxa they most resemble: *N. heran* from Indonesia, and the Lesser Long-eared Bat *N. geoffroyi* Leach, 1821a, from Australia and Tasmania. Our task is impeded by the unresolved taxonomy of the forms currently assigned to *N. geoffroyi*. The taxonomic status of *N. timoriensis* has long been confused, largely because it is a poorly defined entity in the literature and because the name has been applied to a variety of taxonomic concepts in the past (see below). Here, alongside review of the new material of *Nyctophilus* from Timor, we present a revised concept of the morphology of *N. timoriensis* sensu stricto, based on a re-interpretation of Geoffroy's original description and illustration.

Taxonomic history

As noted above, some doubt that Geoffroy's *timoriensis* came from Timor prevailed especially during the late nineteenth and twentieth centuries (e.g., Tate, 1941; Goodwin, 1979), though Thomas (1914) noted that the record might be valid and that further specimens might come from Timor. Scepticism seems to have originated from Tomes (1858a), who believed that È. Geoffroy's locality was an error, citing two reasons. First, many bat specimens from Timor were then held by museums in Europe yet no further *Nyctophilus* had been obtained from that island. Second, Tomes states that he had examined specimens from Western Australia, which he considered to be "identical" to "the original" specimen of *timoriensis* in the Muséum national d'Histoire naturelle, Paris. Consequently, Tomes (1858a) applied the name *timoriensis* to the Western Australian specimens. His specimens were later shown by Thomas (1914, 1915a) to belong to *N. major*, a species attributed to an illustration published by J. E. Gray but first diagnosed by Thomas. Tomes (1858a) did not use the name *N. major* in his revision, either because he was unaware of the name (see Peters, 1861) or else did not consider *N. major* to be an available name. The Baudin expedition collected specimens from south-western Western Australia, adding to Tomes' suspicion that the *Nyctophilus* material had been incorrectly attributed to Timor.

Throughout the past century the name *N. timoriensis* has often been used for the largest members of the genus from across mainland Australia and Tasmania, while *N. major* was sometimes applied to bats from south-western Western Australia but usually treated as a synonym of *N. timoriensis*. Hill & Pratt (1981) documented a large-bodied species of *Nyctophilus* from New Guinea which they also assigned to *N. timoriensis*. The largest members of the genus were reviewed by Parnaby (2009), who recognized four species, two of them new: *N. major* Gray, 1844 from Western Australia, *N. sherrini* Thomas, 1915a from Tasmania, *N. corbeni* Parnaby, 2009 from eastern mainland Australia, and *N. shirleyae* Parnaby, 2009 from New Guinea. Parnaby (2009) suggested that the name *N. timoriensis* sensu stricto be restricted to *Nyctophilus* from Timor.

The taxonomic identity of *N. timoriensis* has remained unresolved. It has not previously been possible to equate *Vespertilio timoriensis* with any other known species of *Nyctophilus* on account of the brevity of Geoffroy's description, which provided few measurements and illustrations, and uncertainty regarding whether Geoffroy's type material remains extant. In the first taxonomic revision of *Nyctophilus*, Tomes (1858a) examined what he believed to be the type specimen of *timoriensis* but did not provide any description or measurements of that specimen. Instead, his concept of *N. timoriensis* was based on material from south-western Western Australia, from where he believed Geoffroy's material had actually originated. In the second revision of the genus, Thomas (1915a) apparently did not examine Geoffroy's material of *timoriensis* and treated *timoriensis* as a *nomen dubium*. He provided the first diagnosis for *N. major* Gray, 1844 and applied that name to the same material examined by Tomes from south-western Western Australian. Tate (1941) incorrectly based his concept of *timoriensis* on an alcohol preserved specimen with extracted skull in the Muséum national d'Histoire naturelle, Paris that he thought to be part of Geoffroy's original material, but is now understood to be a specimen of *N. sherrini* Thomas, 1915a from Tasmania not collected during the Baudin expedition (Parnaby, 2009).

Fifteen species of *Nyctophilus* are currently recognized (Simmons, 2005; Parnaby, 2009; Parnaby *et al*., 2021) and we are aware of additional undescribed species. These species roost in tree cavities, under loose bark, and in buildings, and some species also roost in foliage (Churchill, 2008). The genus is not known to regularly use subterranean roost sites, although occasional instances have been reported for several species (e.g., Bonaccorso, 1998). The ecology of most species remains poorly known but all feed on arthropods and range in body weight from about 3 to 20 g (Churchill, 2008). The genus is widely distributed and commonly encountered throughout Australia and Tasmania, where ten species are recognized (Van Dyck *et al*., 2013; Parnaby *et al*., 2021). Three of the four species recorded from the island of New Guinea are endemics (Bonaccorso, 1998; Parnaby, 2009). Few records of the genus are known from the Indonesian provinces of Papua and West Papua (the western half of the island of New Guinea) (Flannery, 1995; Helgen, 2007), where records extend as far west as Salawati Island (Lavery & Flannery, 2023). However, the dearth of records could be an artefact of survey intensity. The genus also occurs broadly in the south-western Pacific to the east of mainland New Guinea, but the few records of occurrence remain poorly resolved. A specimen (QM JM13100) reported from Sudest in the Louisiade Archipelago suspected to be *N. microtis* by Koopman (1982) was examined and is confirmed here to be closest to that species. One specimen is known from New Ireland (United States National Museum USNM 580082) in the Bismarck Archipelago (Bonaccorso, 1998), and the genus has been reported from Bougainville in the Solomon Islands Archipelago based on echolocation recording data (Junior Novera, pers. comm.). The only species known from New Caledonia, *N. nebulosus*, remains a poorly known endemic (Parnaby, 2008). There is an unconfirmed report of a long-eared bat from Vanuatu that could be a *Nyctophilus* (Steadman, 2006: 67) and a nineteenth century *Nyctophilus* specimen labelled "Fiji Islands" (Dobson, 1878) is of uncertain provenance (Helgen *et al*., 2009).

Phylogenetic relationships within *Nyctophilus* remain incompletely understood, and species diagnoses and the extent of within-species variation are poorly defined for all species. Consequently, delineation of species groups within the genus is also in a state of flux. Tate (1941) recognized a *geoffroyi* species group but did not provide diagnostic features other than citing Thomas (1915a) regarding the specialized nose-leaves. Parnaby (2009) proposed tentative species groups within *Nyctophilus* and defined the *geoffroyi* group as having a highly developed snout mound posterior to the nose-leaf, relatively inflated bullae, and a serrated longitudinal dorsal ridge on the distal portion of the glans penis. The serrated dorsal penile ridge is unique to the *geoffroyi* group, but whether it is invariably present in all populations subsumed within *N. geoffroyi* has not been determined. Kitchener *et al.* (1991) believed that *N. heran* most closely resembled *N. geoffroyi*. Parnaby (2009) tentatively placed *N. heran* in the *geoffroyi* group, noting that it resembled *N. gouldi* Tomes, 1858a and *N. daedalus* Thomas, 1915a in some respects and that the latter taxon is a likely composite of at least two species.

Eldridge *et al.* (2020) demonstrated that multiple species are likely included under "*N. geoffroyi*" as currently understood; see also Parnaby *et al.* (2021). They found species-level differences in average divergence of mitochondrial genes (*cytochrome B* and *cytochrome oxidase 1*) between samples from eastern NSW and those from the Pilbara and southwestern Western Australia. Whether the distributions of these divergent lineages overlap remains to be determined. Substantial morphological variation exists within "*N. geoffroyi*", both within regions and throughout its extensive geographic range throughout most of mainland Australia and Tasmania. Its status as one of the most widely distributed Australian mammal species (Van Dyck *et al.*, 2013) will need to be re-evaluated.

The taxonomic status of mainland Australian *N. geoffroyi* is relevant to our assessment of the status of Timor *Nyctophilus*. Assigning current nomenclature to the two putative species within *N. geoffroyi* demonstrated by Eldridge *et al.* (2020) will require further work because names cannot reliably be assigned solely from geography. Three subspecies of *N. geoffroyi* are often recognized based on Thomas (1915a) and Iredale & Troughton (1934), but their validity remains uncertain (Simmons, 2005) and their geographic limits poorly defined. A detailed morphological evaluation of their taxonomic status is needed, ideally matched with analysis of DNA sampled from type material. The three currently recognized subspecies are *N. g. geoffroyi* Leach from south-western Western Australia; *N. g. pacificus* Gray from south-eastern Australia and Tasmania; and *N. g. pallescens* Thomas from central and northern Australia.

Five names are currently recognized as synonyms of *N. geoffroyi* (Table 1). The type locality of three of these names remains unknown and their subsequent localization to regions of Australia have a doubtful basis. Tomes (1858a) restricted the type locality of *N. geoffroyi* (type locality "Australia") to south-western Western Australia because he believed that the holotype of *geoffroyi* broadly resembled his material from Albany. His decision should be viewed in the context that interspecific diagnostic criteria within the genus were poorly understood at the time, and he struggled to see external differences, other than size, between the most morphologically divergent species then known, *N. geoffroyi* and *N. timoriensis*. Peters (1861) stated that his two specimens of *Nyctophilus australis* were from an unknown locality. He speculated that they were probably from Western Australia, simply because he had received material from that region in the past. Krefft (1871) listed *N. australis* from NSW (but *N. geoffroyi* from "West Australia"), a view also held by Iredale & Troughton (1934) but for unspecified reasons. Thomas (1915a) suggested that the holotype of *Barbastellus pacificus* (= *Nyctophilus pacificus*, see Mahoney & Walton, 1988) possibly came from south-eastern Australia or Tasmania, apparently on the basis that the holotype resembled a specimen he had examined from eastern Victoria.

In view of the likely taxonomic complexity of the taxa involved, we here offer a preliminary morphological assessment that must await a comprehensive study using morphological and molecular techniques.

Methods

For this paper we have examined specimens in many museum collections. Institutional abbreviations are: **AM**, Australian Museum, Sydney; **NHMUK**, Natural History Museum, London; **NMV**, Museums Victoria, Melbourne; **ANWC**, Australian National Wildlife Collection, CSIRO, Canberra; **MNHN**, Muséum national d'Histoire naturelle, Paris; **MZB**, Museum Zoologicum Bogoriense, Bogor, Indonesia; **NCBN**, Netherlands Centre for Biodiversity, Naturalis Museum, Leiden; **NTM**, Museum and Art Gallery of the Northern Territory, Darwin; **ZMB**, Universität Humboldt, Zoologisches Museum, Berlin; **WAM**, Western Australian Museum, Perth. We have not examined all relevant type material but have relied on black and white photographs of type specimens of all five names applicable to the *geoffroyi* group (Table 1), and have drawn from the literature, with additional skull measurements of types in the Natural History Museum, London supplied by Glenn Hoye. We have also relied on the description and measurements of the holotype of *N. heran* given by Kitchener *et al.* (1991), which is registered as MZB 16001 (previously registered as WAM M.32252). Complete skulls are available for type specimens of only two of the five names relevant to mainland *N. geoffroyi,* viz. *pacificus* and *pallescens*, and we have included measurements of both in our analyses. The skull of the holotype of *geoffroyi* consists of a rostrum only, and the holotype skull of *geayi* is evidently lost. Of the two syntypes of *australis* in the ZMB, one has the skull *in situ*, while the extracted skull of the other has not been located.

Measurements were taken with vernier calipers to the nearest 0.05 mm as illustrated by Parnaby (2009). These measurements are taken in the same manner as Kitchener *et al*. (1991), who state that their measurements were taken as specified by Kitchener *et al.* (1986). However, whereas Kitchener *et al.* (1986) indicate that "palatal length" is taken anterior to the incisor, palatal length given by Kitchener *et al*. (1991) for *N. heran* approximates that given for CM^3, indicating that their measurement of palatal length was actually palatal-sinusal length. Abbreviations for measurements used in the text are: **GL**, greatest length of skull: from the most anterior extension of the premaxilla to the posterior of the lambdoidal crest; **CM^3**, length of maxillary toothrow: from anterior cingulum of canine to posterior cingulum of M^3; **C^1–C^1**, outer breadth across upper canines from cingula; **ANT**, anteorbital width, between infraorbital foramina; **PAL,** palatal length, from most anterior of premaxilla to most anterior extent of interpterygoid fossa; **sinPAL**, palatal-sinusal length, from the most posterior margin of the anterior palatal emargination to the most anterior margin of the interpterygoid fossa; **ZYG**,

Table 1. Synonymy of *Nyctophilus geoffroyi* Leach. Based on Mahoney & Walton (1988), Turni & Koch (2008) and original descriptions. An additional name applied to the synonymy of *N. geoffroyi*, "*Nyctophilus leachii*, Gray" is a *nomen nudum* because it was listed by Dobson (1878: 174) as a name written on a specimen label, as noted by Tate (1941).

Name originally proposed	Type locality	Type material
Nyctophilus geoffroyi Leach, 1821a	"Australia", restricted to Albany, south-western Western Australia by Tomes (1858a)	Holotype, NCBN
Barbastellus pacificus Gray, 1831	"The Australasian Barbastelle", "Islands of the Southern Pacific", suspected by Thomas (1915a) to be southeastern Australia or Tasmania	Holotype, NHMUK
Nyctophilus unicolor Tomes, 1858a	Tasmania	At least 3 syntypes, NHMUK, NCBN
Nyctophilus australis Peters, 1861	Unknown, "probably Western Australia"; suggested as Sydney by Iredale & Troughton (1934)	Two syntypes, ZMB
Nyctophilus geayi Trouessart, 1915	Nicholson River area, eastern Victoria	Holotype, MNHN, skull lost
Nyctophilus g. pallescens Thomas, 1913	Alexandria, Northern Territory	Holotype, NHMUK

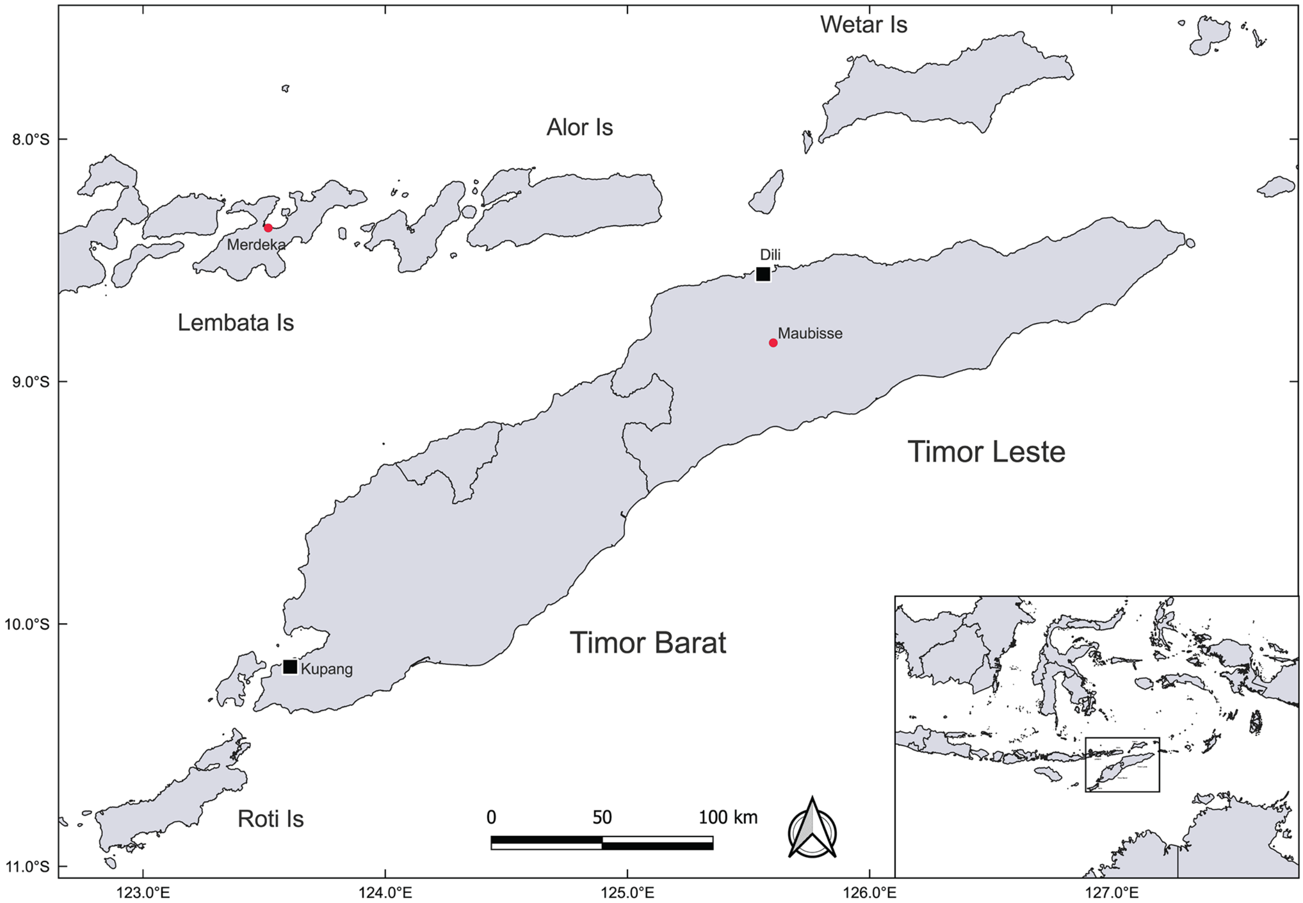

Figure 1. Map showing capture location of *Nyctophilus* in the township of Maubisse, Timor-Leste, and Merdeka, Lembata Island, Indonesia, type locality of *Nyctophilus heran*.

zygomatic breadth, maximum breadth across zygomatic arches; **INT**, least inter-temporal breadth; **M^3–M^3**, maximum breadth from left M^3 to right M^3, from labial cingula; **M^3L**, M^3 length measured at cingula; **M^3B**, maximum breadth of M^3 measured at cingula; **MESO**, maximum internal breadth of mesopterygoid fossa level with the hamular processes; **BRH**, braincase height: caliper blade positioned along basioccipital-basisphenoid bones and along the sagittal crest; **MAS**, maximum breadth across mastoids; **BTB**, least inter-bulla distance, least distance between each bulla; **BUL**, bulla length, from base of eustachian tube when present; **Baculum Length**, maximum length from most posterior tip of proximal arms to distal tip, taken perpendicular to the dorsal surface of the main shaft; **Baculum Breadth**, maximum breadth across proximal arms at their base; **Baculum Height**, maximum height from ventral extent of proximal arm to distal tip; **Ear Length**, taken from the junction of outer ear margin near the jaw.

Principal components analysis (PCA) and Unweighted Pair Group Method with Arithmetic mean (UPGMA) Cluster analyses were run using the Paleontological Statistics (PAST) software package (Hammer *et al.*, 2001), version 3.06. PCAs were run using both correlation and variance-covariance matrices, using only specimens with complete measurements. Standardized character coefficients were used ("Eigenvalue scale" was ticked) to explore the possible contribution of individual characters to each PC axis. UPGMA cluster analyses used Euclidean distance as the similarity metric.

CT scans were made using a Skyscan model 1174 micro CT scanner, using the following software packages: NRecon (version 1.5.1.5 © Skyscan, Belgium 2008) was used for reconstruction of 3D datasets from RAW CT x-ray images; 3D surface models used in illustrations were generated using CTAn Software (version 1.9.2.3, © Skyscan, Belgium 2003-8), and measurements of selected bacula were made using DataViewer (version 1.4.0.4 © Skyscan Belgium).

Nyctophilus from Maubisse

Three individuals of a species of *Nyctophilus* were collected by the second author during a mammal survey of Timor-Leste during November 2003 (Polhemus & Helgen, 2004). These were obtained from an elderly man in the town of Maubisse, elevation 4650 feet (1200 m), (8°50'26.6"S 125°36'6.9"E), Timor-Leste (Fig. 1). The resident stated that these bats lived in small colonies in the roofs of village houses. All three specimens are immature, based on the width of cartilaginous epiphyses in the wing joints. All three are stored in 75% ethanol and are registered in the Australian Museum, Sydney: AM M.37639, field number ET3, subadult female, body in alcohol, skull *in situ*, received 11 November 2003; AM M.38840, ET4, juvenile female, body in alcohol, skull extracted and in alcohol, received 11 November 2003; and AM M.38841, ET12, subadult male, body in alcohol, skull *in situ*, received 13 November 2003. Tissue samples from ET3 and ET12 were stored in 95% ethanol and were lodged with

Figure 2. AM M.37639 (ET3), subadult female *Nyctophilus*, from Maubisse, Timor-Leste, in life (photo: Dan Polhemus and Kristofer Helgen).

the South Australian Museum, Adelaide. Unlike the latter two individuals that were alive when received, ET4 was obtained dead and desiccated, limiting field measurements. Field measurements for ET3, ET4 and ET12 respectively, are: body weight, 5, —, 4.5 gm; total length (head-body and tail), 93, —, 85; tail length, 37, —, 36 mm; ear length (from notch), 25, —, 24 mm; forearm, 40, 39, 36 mm; tibia length, 17, 19, 17 mm; pes length (without claw), 8, 8, 7 mm. Skulls of M.38840 and M.38441 were extracted but only partially cleaned due to their fragility as they were not fully ossified. AM M.38840 is a newly volant juvenile female at a much earlier stage of development than the other two specimens and is not included in statistical analyses.

We provisionally assign the Maubisse individuals to *N. timoriensis* based on our revised concept of that species, detailed below. However, they also resemble mainland Australian *N. geoffroyi* and *N. heran* from Indonesia in cranial and dental characters, along with overall size, relatively large ears, uniform dark grey dorsal fur and paler white ventral fur, and having an enlarged post-nasal snout mound (Fig. 2). Our concept of *N. timoriensis* is a significant departure from previous interpretations and is presented below before further consideration of the identity of the Maubisse material.

A revised concept of *Vespertilio timoriensis* Geoffroy

Since the mid nineteenth century, Geoffroy's *timoriensis* has been viewed as one of the largest members of *Nyctophilus* and its identity has been closely intertwined with *N. major* Gray, 1844 from south-western Western Australia with which it has often been synonymized. We present a new concept of *timoriensis*, based on details of the illustration accompanying Geoffroy's description, a re-interpretation of measurements given in Geoffroy's account and a detailed examination of the basis for the prevailing view that *timoriensis* is one of the largest *Nyctophilus* species that resembles *N. major*. As set out below, we conclude that *timoriensis* is not conspecific with *N. major*, differing in important morphological distinctions that have previously been overlooked.

Figure 3. Illustration of the type specimen of *Vespertilio timoriensis* È. Geoffroy, 1806, reproduced from Plate 47 of Geoffroy's original account, showing tragus and snout features characteristic of the genus *Nyctophilus*. A post-nasal snout mound is evident within the red ellipse of the inset. Note that the black horizontal line is part of the original illustration and represents head length but is not a scale bar for the illustration. Scale bar (white) = 5 mm.

Geoffroy's account of *timoriensis*

The illustration of the head

A frontal drawing of the head (with the skull *in situ*) in Geoffroy's (1806) plate 47 is the sole illustration accompanying his description of *timoriensis* (reproduced in Fig. 3). Two aspects of this drawing have been overlooked in previous assessments of the status of this species. First, there is an elevated mound on the rear of the snout behind the narial foliations. The oblique ventral angle of the illustration obstructs a clear view of the dorsal snout region and a rudimentary post-nasal elevation, such as that characterizing *N. major,* would not be visible from this angle. The illustration resembles the distal part of the snout prominence of those *Nyctophilus* species in which the post-nasal mound is well developed, such as in *N. heran*, *N. gouldi* and *N. geoffroyi*. The snout mound in *Nyctophilus* consists of two separate bodies joined in the midline by an elastic membrane of variable extent. The bilobed structure is not seen in Geoffroy's illustration. However, it is likely that the artist did not have an accurate understanding of the shape of this structure, which might have shrunk in the specimen, and therefore was unable to accurately depict it. The small size of the illustration might be one reason these snout features have been overlooked, but the illustration contains an impressive level of detail. The enlarged snout mound is in sharp contrast to the low, rounded mound characteristic of *N. major*. This difference alone would suggest that *timoriensis* and *major* are not conspecific.

A second notable but overlooked feature of the illustration is a scale bar adjacent to the head of *timoriensis* on Geoffroy's plate 47. Geoffroy (1806: 205) states that head length is indicated by the scale line beside the head of each species illustrated. The head length line for *timoriensis* is *ca*. 17.5

mm long, measured on a hardcopy of the journal illustration. A comparison of his frontal and lateral illustrations of the head of "*V. nigrita*" on the same plate clearly indicates that "length" was measured along the long axis of the head and was not measured in another manner, such as from ear to ear.

We suspect that the head illustrations on Geoffroy's plate 47 are reproduced at life size, although he does not explicitly state so. Of the 19 species accounts in his paper, ear length is provided in the text only for *V. auritus* and his measurement of 33 mm is an exact match against his illustration, if ear length is taken from the notch as per modern measurements. If his illustration of the head of *timoriensis* is roughly life size, it is far too small to be a species the size of *N. major* but instead approximates a species the size of *N. geoffroyi*. Ear length measured from his illustration is *ca*. 22 mm, but the ears are not fully erect and could easily have attained about 25 mm. (Both of the latter ear measurements are not especially informative, as both fall within the expected range for many *Nyctophilus* including *N. geoffroyi* and *N. major*.)

Body measurements

Establishing the approximate body size of Geoffroy's type specimen of *timoriensis* relative to other species of the genus is fundamental to an interpretation of its possible identity, and therefore requires detailed examination. The prevailing view that Geoffroy's type was of one of the largest species of *Nyctophilus* originated from Tomes (1858a), yet as discussed below, only one of the measurements provided by Geoffroy (1806) implies a large-bodied species.

Three measurements are cited in Geoffroy's brief description of *timoriensis*, which he gave in millimetres: body length, 70 mm; tail length, 40 mm; and wingspan, 270 mm. These were the standard measurements given by Geoffroy (1806) for each species in his account of vespertilionid bats. Geoffroy provided a fourth measurement for *timoriensis*, head length of *ca*. 17.5 mm, as noted above. Geoffroy generally used three standard body measurements (head-body, tail, and wingspan) for bats in his other taxonomic papers (e.g., Geoffroy, 1810, 1813). Geoffroy (1806) does not indicate how these measurements were taken, which could differ somewhat from modern standard measurements. His revision was published in an early phase of French taxonomic research when standard measurements for bats were evolving; e.g., Desmarest (1821) used twice as many body measurements, and the taxonomic value of forearm length, now a fundamental measure of size, was not recognized until later (Geoffroy, 1832). Though we suspect that they would have been regarded at the time as having self-explanatory definitions, wingspan and body length could have been measured in several ways that would result in significantly disparate measurements.

Wingspan

The simplest interpretation of wingspan is a straight-line distance between wing tips of the extended wing. Alternatively, wingspan might have been measured along the bones of the leading edge of the wing, thus avoiding underestimates in specimens for which the wings could not be fully extended. Perhaps Geoffroy used both methods, depending on whether the specimen had fully extended wings, a procedure progressively adopted by Tomes throughout 1858. In his revision of *Nyctophilus*, Tomes (1858a, read 12 January) gave "expanse of the wings" for some species, while for others he cites "expanse of the wings, following the phalanges". In a subsequent paper, Tomes (1858b: 125, read March 9th) explains that to overcome this problem with wingspan measurement he used a thread placed along the bones of the wing to the shoulder, adding the distance between shoulders. We are uncertain what method was adopted by Geoffroy (1806) in his description of *timoriensis* but for at least one species in his account (Geoffroy, 1806) he seems to have measured wingspan as a straight-line span between wing tips, as revealed by his life-size illustration of one of his syntypes of *Vespertilio emarginatus* (= *Myotis emarginatus*). Although he does not cite a wingspan measurement for that species in the text, a comparison with the measurements of the type specimens examined by Tomes (1858c) suggests a straight-line measurement. The linear wingspan that we measured from a hard copy of Geoffroy's figure for *emarginatus* is *ca*. 258 mm and wingspan measured along the bones of the leading edge of the wing is *ca*. 306 mm. Geoffroy does not indicate which of his specimens of *emarginatus* was illustrated, but our linear wingspan measurement of 258 approximates the value 254 mm given by Tomes (1858c) for the specimen from Abbeville (the lectotype) and a wingspan of 267 mm for the Charlemont specimen.

Geoffroy's wingspan measurement of 270 mm would seem to be too small for a species the size of *N. major*. It falls at the upper range for wingspan given by Churchill (2008) of 208–275 mm (n = 22, mean = 245) for the small-bodied species *N. geoffroyi* from northern Australia, and at the lower end of the intermediate-sized *N. daedalus* (275–323 mm, mean = 300, n = 61). Few wingspan data are available for *N. major major* from south-western Western Australia other than from Bullen & McKenzie (2002), who cite a mean of 349.5 mm (n = 8) but do not provide maximum or minimum measurements. Bullen & McKenzie (2001) provide a mean wingspan of 321.9 mm (standard deviation = 10.8 mm, n = 11) for *N. major tor*, from which we estimate the sample range to fall within 290–354 mm (based on 3 standard deviations from sample mean) but that form has a significantly smaller body size than *N. major major*. An important consideration is that wingspan taken along the bones of the leading edge of both wings will exceed the straight-line span between wingtips. Consequently, had Geoffroy measured the *timoriensis* wingspan along the leading wing edge, the straight-line span would be appreciably less than 270 mm, further indicating a relatively small-bodied specimen.

Head length and tail length

Head length measured on a study skin might seem a fairly imprecise measurement, although perhaps less so if the skull was *in situ*, as indicated in Geoffroy's illustration. Nevertheless, the head length measurement given by Geoffroy suggests that his specimen might not have been as large as *N. major*. Geoffroy's measurement of 17.5 mm ("8 lines"; 1 line = 2.1 mm) is smaller than the "10 lines" given by Tomes for his two specimens of *N. major*, yet falls within the range of species regarded by Tomes to be of small and intermediate body size (given as 7.5–9 lines), i.e. *N. geoffroyi* and *N. gouldi*. The range for GL of *N. major major* (18.8–20.7 mm, n = 20, Parnaby, 2009) also implies that Geoffroy's *timoriensis* might belong to a relatively smaller-bodied species. Tail length (40 mm) is a relatively uninformative discriminator between species of *Nyctophilus*, e.g., Geoffroy's measurement of 40 mm falls within the range of both the small-bodied *N. geoffroyi* and the large-bodied *N. corbeni* (see Churchill, 2008). (This applies regardless of whether tail length is measured from the root of the tail, or from the vent as for Churchill, 2008).

Body length

The different interpretations of "body length" need to be considered, given that we do not know how this measurement was taken and that modern concepts of the term might not have applied in the early 19th century. We assume Geoffroy's "body length" included the head, and thus equates to "head-body length". The latter interpretation was applied by Desmarest (1821), who gave Geoffroy's body length of 70 mm for *timoriensis* as "length of body and head". Body length was presumably taken from nose tip to base of tail on a stuffed specimen. An alternative interpretation could be that it was taken from the ear tips, because in long-eared bats such as *Plecotus* and *Nyctophilus*, the ears project forward well past the nose tip. However, for the one species for which Geoffroy (1806) provided ear length in the text in addition to "body" length (*Plecotus auritus*, a species with exceptionally long ears), it is apparent that he measured body length from snout tip and not to the projecting ear tip.

Head-body measurements for small mammals are generally reported as a linear measurement and have been for more than a century, but it is possible that Geoffroy measured head-body length along the body contours of the dorsal surface along the midline, as was often done with skin mounts of large mammals, at least in the latter half of the nineteenth century. Our dorsal measurement on the apparent type of *timoriensis* taken along the spine (67 mm, Anja Divljan pers. comm. 2019) is a close match to the 70 mm given in the original description.

A body length of 70 mm is the only measurement give in Geoffroy's description that matches a large species such as *N. major*, but only if this represents a linear measurement. If so, 70 mm would seem to exclude all but the largest species of *Nyctophilus*. Geoffroy's head-body measurement would be some 5 mm longer if he had measured from the rear of the body, rather than the current practice of measuring from the vent. Head-body measurements provided by Churchill (2008) show that small and intermediate-sized species of *Nyctophilus* do not exceed about 50 mm. Head-body measurements are available only for three adult female and two male *N. major major*, as the species is poorly represented in collections. These field measurements of snout-vent length were taken from specimens now in the AM and range from 56–62 mm. However, Churchill (2008) provides snout-vent measurements of 50–75 mm (n = 33) for *N. corbeni* which is of comparable size to *N. major*. We compared body measurements given in fourteen nineteenth century accounts of *timoriensis* published in the decades after Geoffroy's description (see below) in the hope that subsequent authors might have re-measured Geoffroy's type but all appear to be re-iterations of his account. There is no indication that any of those authors had examined Geoffroy's material, contrary to Parnaby (2009), who mistakenly believed that Temminck (1840) had done so. Some accounts are short (Griffith, 1827; I. Geoffroy, 1832) while others seem to provide identical measurements when accounting for possible error from conversion to mm from the variety of European definitions of the inch of that time (Desmarest, 1819, 1821; Lesson, 1827; Fischer, 1829, 1830; Temminck, 1840; Giebel, 1855, 1859; Wagner, 1840, 1855; Fitzinger, 1872).

Reconciling Geoffroy's measurements

To summarize, the only clear indication of large body size, Geoffroy's measurement of 70 mm for head-body length, seems to clash with other measurements given in his account. The wingspan of 270 mm would appear to be too small for such a large body length. Perhaps the wings were not fully extended on the type specimen, but the smaller body size implied by wingspan is supported by the head length measurement provided by Geoffroy, and the small size of the head illustration, which we suspect was reproduced at approximately life size. As noted above, we suspect that the head-body length reported by Geoffroy (1806) seems disproportionally large because it is measured as an arc length along the dorsal contours of the prepared specimen, and not as a linear measurement as usually reported today.

The account of *N. timoriensis* by Tomes (1858a)

The entrenched view that *timoriensis* is a large-bodied species similar to *N. major* that arose from Tomes (1858a) has remained unchallenged. Significantly, Tomes (1858a) had examined "the" original specimen of *timoriensis* in Paris, but his statement that it was "absolutely identical" to his *Nyctophilus* specimens from south-western Western Australia is not tenable in light of modern understanding of morphological variation in *Nyctophilus*. As previously mentioned, Tomes did not recognize differences in external morphology, other than size, between *N. geoffroyi* and *N. major* (for which he used the name *timoriensis*), which are distinctive species. His account is bereft of a description or measurements of the Paris type specimen and we suspect that his assessment of *timoriensis* was based only on external features of the apparent type skin. In particular, Tomes seemed unaware of the diagnostic value of the relative size and structure of the snout mound, which he does not cite as a character for differentiating *N. geoffroyi* from *N. major*, two species that exhibit opposite extremes of development of that character. Most of the material available to Tomes consisted of dry skins, in which snout morphology might have been difficult to assess. A full appreciation of the diagnostic value of snout morphology in the genus was first recognized by Thomas (1915a), who assembled a large collection of fluid-preserved *Nyctophilus* on loan from the Australian Museum, Sydney.

Further doubt regarding Tomes' emphatic judgement that *timoriensis* and *major* were "identical" or at least of similar body size arises from a comparison of Geoffroy's measurements with those of Tomes (Tomes himself did not make that comparison.) When compared to Tomes's measurements of his four species, head-body length of 70 mm (= 2 inch 9 lines) is the only one of Geoffroy's four measurements that unequivocally fits the largest *Nyctophilus* recognized by Tomes, i.e. the southwestern Western Australian material that Tomes called *N. timoriensis*. As noted above, Geoffroy's remaining three measurements (tail length, wingspan, and head length), when compared to measurements provided by Tomes, fit the species considered to be *intermediate* in size by Tomes, i.e. *N. gouldi*, and *N. unicolor* from Tasmania (currently a synonym of *N. geoffroyi*). Tomes appeared to place some credence in wingspan as a character, as it was the only measurement directly cited by him when discussing size differences between his species. Had Tomes compared the wingspan of 270 mm given by Geoffroy against wingspan measurements for his own material, the intermediate size suggested by that measurement would have been apparent. Wingspans given by Tomes are: *geoffroyi* 9–10 inches (228–254 mm), *gouldi* and *unicolor*, *ca*. 10–11 inches (254–279 mm), and *timoriensis* from Western Australia, 12.75–13.5 inches (324–343 mm). Tomes measured wingspan for *timoriensis* as "expanse of the wings, following the phalanges" which is not equivalent to measurements of the remaining three species, measured as "expanse of the wings", implying a direct tip to tip measurement. His measurements of *ca*. 323–343 mm are much larger than Geoffroy's 270 mm, even when accounting for the fact that wingspan measured along the bones of the leading edge of the wing will be greater than a direct span between wing tips.

In conclusion, we suggest that the concept of *timoriensis* as a large-bodied species has a far weaker foundation than previously thought and it seems more likely to be of intermediate size in the genus. The concept of *timoriensis* as a large bodied species rests largely with the outdated assessment by Tomes (1858a) and on the body measurement of 70 mm given in Geoffroy's account. Although Tomes examined Geoffroy's original specimen, he based his understanding of *timoriensis* on specimens from south-western Western Australia from Gould's collection, one of which was later designated the type (lectotype) of *N. major* by Thomas (1914). In effect, Tomes published the first diagnosis of what was later to become known as *major*, but under the name *timoriensis*. A further source of confusion arose because Tomes did not mention the name *major* anywhere in his paper. This omission was noted by Peters (1861), who proposed, in a footnote, that *major* should therefore be placed in the synonymy of *timoriensis*. Perhaps Tomes did not consider *major* to be a published name. The fact that *N. major* remained undiagnosed throughout the nineteenth century has also contributed to the erroneous conflation of *timoriensis* with *major*. The first diagnosis of *N. major* was provided by Thomas (1915a). The written account of *N. major* and the accompanying illustration of an animal from southwestern Western Australia was published by Gray (1875) but that illustration, accompanied with the name *Nyctophilus major*, was published separately and widely circulated privately in the 1840s (the publication date of *major* has been determined to be 1844 by Mahoney & Walton, 1988). Gray (1875) did not provide measurements or a description of *N. major*. His brief account consisted solely of a statement that he could not determine what species of *Nyctophilus* should be applied to his previously published plate.

The suspected holotype of *timoriensis*

Jansen (2017) noted that for birds collected by the Baudin expedition, none of the specimens have original field tags attached, and no original tags are known to have survived. Jansen indicates that original specimen data was communicated by the naturalists Peron and Lesueur to MNHN taxidermists and transcribed to pedestal bases. We suspect that the same applies to the Baudin mammal material, and we note that the identity of the type specimen of *timoriensis* is uncertain. The earliest registers of bird and mammal specimens in the MNHN that assign specimen numbers began in the early 1840s (Jackson *et al*., 2021), and it is possible that the identity of Geoffroy's original material might have become confused before the 1840s.

The specimen currently labelled the holotype of "*Nyctophilus timoriensis*" is CG1990-36 in the MNHN. Although forearm length is not given in the original description, this specimen is a medium-sized *Nyctophilus* with forearm length of 43 mm. It is a puppet skin (see Fig. 4a,b) from which the skull has been extracted at an unknown date and is now apparently lost (Figs 4c–e). Three other numbers are associated with the skin. The first published attribution of type status to this specimen is the catalogue of bat type specimens by Rode (1941), stated that the skull was lost and who might have assigned the number 217 to the skin. We have not found any other reference in the literature to the skull. The skin has 884 written in old ink on the right wing, to the left of which is some partially obliterated writing (Fig. 4f). There were no tags associated with the skin when examined in Sydney by HP in 1990. Later in 1990, Michel Tranier inventoried the MNHN collection and apparently registered the specimen as CG1990-36 and concluded that there were no other specimens in the collection that could be Geoffroy's type material (see Parnaby, 2009). It appears that Tranier also added numbers to an old board label that could have originated from the 19th century when the species was referred to *Plecotus* (Fig. 4g). A tag now attached to the specimen, presumably by Tranier, has an additional number 160a, evidently an old pedestal number (Fig. 4h). That number is listed in the *Nouveau Catalogue des Galeries* (New Catalogue of Galleries for skin mounts) (Jackson *et al*., 2021), which commenced around the 1840s. We do not know the source of the pedestal number 160a. Perhaps it originated from the initial taxidermy procedures immediately following the Baudin expedition, as described for bird specimens by Jansen (2017).

We are unable to definitely establish that CG1990-36 is Geoffroy's original specimen, but we have no reason for rejecting it, other than the incongruent head-body length of 70 mm. However, detecting a mis-matched skin of a similar-sized *Nyctophilus* species is hampered by the poor condition of the skin. Our measurements of the putative type wingspan and tail length are consistent with Geoffroy's (1806) account: our wingspan measurement of 264 matches his 270 mm given that part of the wing tip is missing (Fig. 4) and our measurement of tail length, taken from the base of the body, equates to his 40 mm. Thomas (1914) reported a forearm length of 42 mm for the alleged type of *timoriensis*, taken by Trouessart at MNHN. This is a close match with our measurement of 43 mm taken on the putative type CG1990-36. Crucially, we have not been able to determine the nature

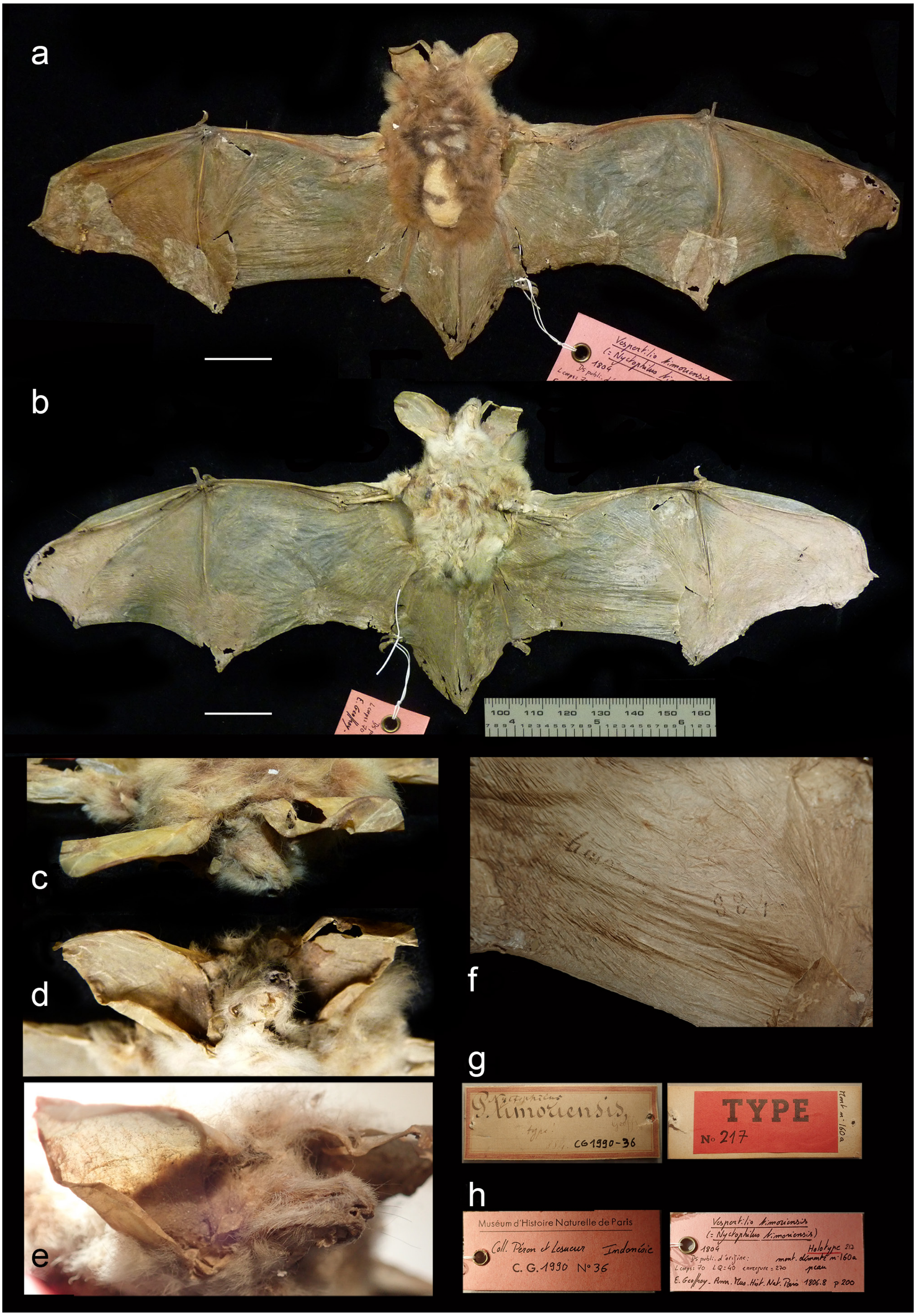

Figure 4. MNHN CG1990-36, study skin with skull extracted, alleged holotype of *Vespertilio timoriensis* È. Geoffroy, 1806. (*a*), skin dorsal view, scale bar = 2 cm (photo: Ken Aplin); (*b*), skin ventral view, scale bar = 2 cm (photo: Ken Aplin); (*c*), dorsal view of snout (photo: Ken Aplin); (*d*), oblique view of snout showing nose-leaf (photo: Ken Aplin); (*e*), lateral view of snout (photo: Anja Divljan); (*f*), old writing and numerals on ventral surface of left plagiopatagium (photo: Anja Divljan); (*g*), front and reverse view of associated, presumed 19th century tag (photo: Anja Divljan); (*h*), front and reverse view of contemporary skin tag (photo: Anja Divljan).

of the post-nasal elevation, which is hidden in the shrivelled skin folds. Finally, we note that Geoffroy (1806) did not state the number of *timoriensis* specimens that he examined, but he does not mention more than one and it has generally been assumed that his description was based on a single type specimen. Parnaby (2009) mistakenly believed that there were two specimens; his confusion arose from a statement by Temminck (1840) to that effect, but Temminck was instead referring to material of *Vespertilio peronii* I. Geoffroy, 1832. On balance, we accept that MNHN CG1990-36 is possibly Geoffroy's original specimen of *timoriensis*.

Comparisons with Maubisse specimens

Nyctophilus timoriensis sensu stricto

The Maubisse specimens share several features with our revised concept of Geoffroy's *N. timoriensis*: both are of medium body size, with a conspicuously developed post-nasal mound, similar to species such as *N. geoffroyi*, *N. heran*, and *N. gouldi*. The largest Maubisse specimen, though not fully mature, is of medium body size for the genus as reflected by a forearm length of 40 mm compared with 43 mm for the suspected *N. timoriensis* holotype. Field head-body measurements for male AM M.38841 and female AM M.37639 from Maubisse approximate that of the suspected type specimen (56 and 50 mm vs. *ca*. 53 mm).

Nyctophilus heran and *N. geoffroyi*

Our comparison with these two species focuses on the Maubisse male AM M.38841, given that sexual size dimorphism occurs within *Nyctophilus* (males averaging smaller) and that the unique specimen of *N. heran* and the holotypes of *geoffroyi* and *pallescens* included in our analyses are all males. Measurements of an extensive series of *N. geoffroyi* from throughout Australia indicates that Tasmanian animals average larger than those from mainland Australian. Tasmanian specimens are excluded from further consideration here, given that mainland Australian "*N. geoffroyi*" is a composite of at least two species (Eldridge *et al.*, 2020) and the taxonomic status of Tasmanian populations has not been assessed. Our analyses treat *N. geoffroyi* as one entity because we did not identify any obvious geographic or morphological groupings in the morphometric data.

The Maubisse specimens undoubtedly most resemble *N. geoffroyi* and *N. heran* in overall morphology rather than any other species of the genus (other than *N. timoriensis*) based on the following combination of external, cranial and bacular characters:

1 Overall body size is medium within the genus.
2 The post-nasal prominence is well developed, consisting of two elevated mounds tapering to their distal tips and joined in the midline by an elastic membrane, forming the "Y" shape characteristic of *N. geoffroyi* (see Fig. 5).
3 The external ears are large relative to body size, and joined in the midline for a substantial proportion of the length of the ear and general colour of body fur is a mouse-brown dorsally, with much paler ventral fur.
3 The auditory bullae are large relative to skull size (Fig. 6).
4 Baculum shape is consistent with 12 specimens of *N. geoffroyi* examined from mainland Australia and resembles that of the holotype of *N. geoffroyi pallescens* illustrated by Hill & Harrison (1987). A slight groove is evident in the distal tip of M.38841 (Fig. 7). It is not clear if this represents incomplete ossification in this subadult animal, but a similar indentation is apparent in the holotype baculum of *N. geoffroyi pallescens*. Baculum length of AM M.38841 falls within the range for 12 specimens *N. geoffroyi,* and height and breadth are smaller in this subadult animal (Table 2). Baculum morphology of

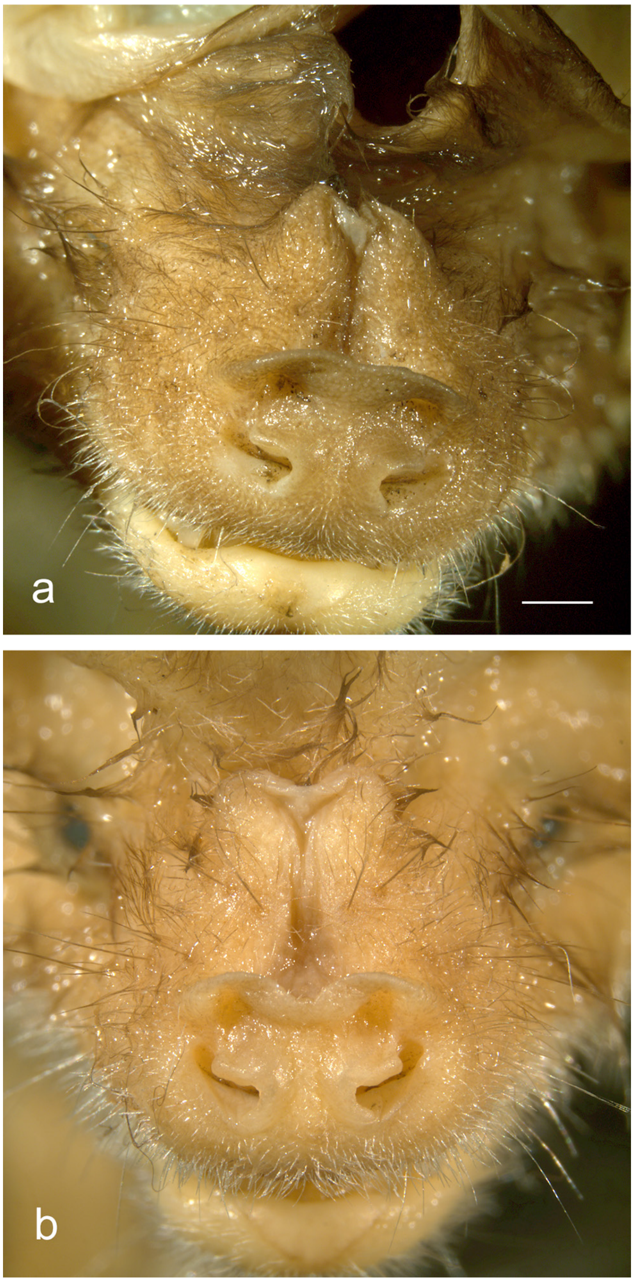

Figure 5. Snout morphology of (*a*) subadult female *Nyctophilus* from Maubisse (AM M.37639, ET3), and (*b*) an adult male *N. geoffroyi* from Napier Downs Station, Kimberleys, Western Australia (AM M.22122) (imaging: Sue Lindsay). Scale bar represents *ca.* 1 mm.

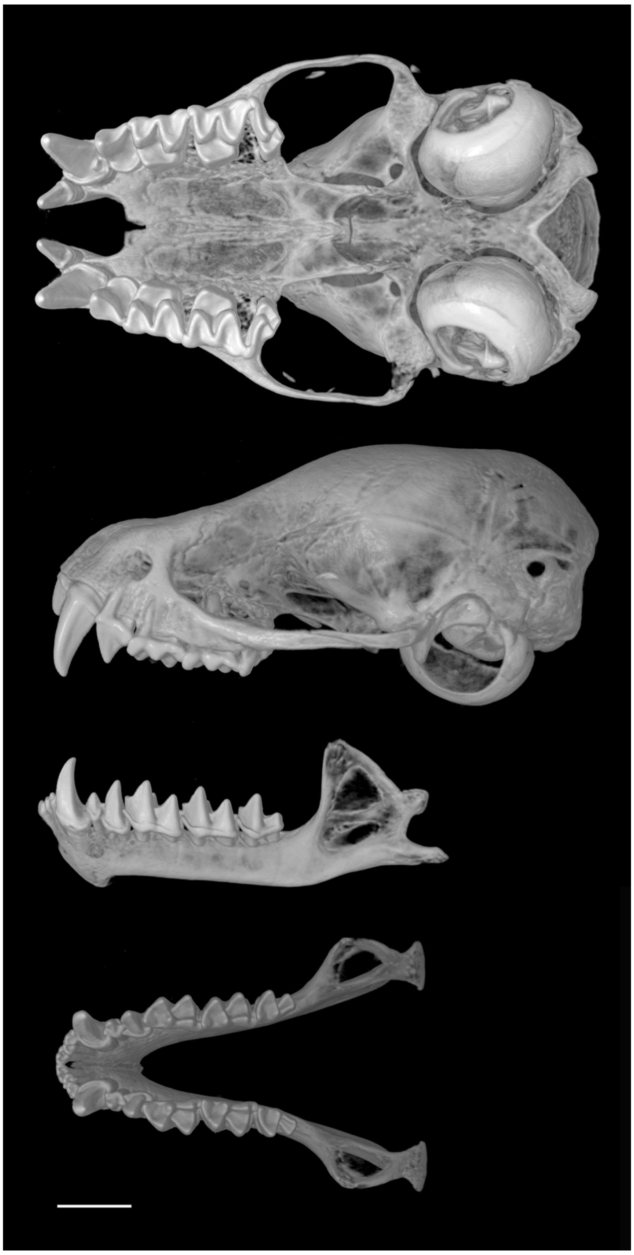

Figure 6. Micro CT scans of skull and dentary of AM M.38841. Scale bar represents *ca.* 2 mm. (images: Fred Ford).

N. heran remains imperfectly defined (Kitchener *et al*., 1991).

The Maubisse male M.38841 is compared against the following differences between *N. heran* and *N. geoffroyi* cited by Kitchener *et al.* (1991):

1. *Nyctophilus heran* has smaller and less inflated bullae relative to skull length. The bullae of *N. heran* are smaller and less inflated than *N. geoffroyi*. In absolute size, BUL of *N. heran* falls within the size range for *N. geoffroyi*. However, the larger skull size of *N. heran* results in relatively smaller and less inflated bullae, as illustrated in a plot of BUL vs GL (Fig. 8a) and BTB vs MAS (Fig. 9). The bullae of M.38841 appear to be relatively larger than those of the holotype of *N. heran* as evident in the lateral skull view (compare Fig. 6 with figure 2 of Kitchener *et al.,* 1991), in which M.38841 is far more typical of *N. geoffroyi*. However, BUL of M.38841 is at the low end of the size range for *N. geoffroyi* (Table 2) and a bivariate plot of BUL vs GL (Fig. 8a) indicates that relative to GL, BUL is smaller relative to most specimens of *N. geoffroyi*. Kitchener *et al.* contrast the smaller ratio BUL/GL of the holotype of *N. heran* (0.233) compared to the smallest ratio of 0.247 in their sample of six male *N. geoffroyi*. The ratio of 0.232 for M.38841 is similar to that of *N. heran* but this ratio ranged from 0.225–0.314 in our sample of 53 adult male skulls of *N. geoffroyi* from throughout mainland Australia. However, the ratio exceeded 0.237 in all but one of the 53 males that we measured, and the trend for a relatively larger BUL in *N. geoffroyi* is clear.
2. *Nyctophilus heran* has a more sharply angled anterior edge of the mesopterygoid fossa. The anterior edge of the mesopterygoid fossa is gently curved toward the base of the post-palatal spine in M.38841 (Fig. 6), similar to *N. geoffroyi*, but in contrast to the more linear margin in the holotype of *N. heran*. We have examined photographs of the holotype skulls of *pallescens* and *pacificus*, both of which resemble that of M.38841. However, this feature is not invariant, and occasional mainland Australian *N. geoffroyi* specimens had angled edges.
3. *Nyctophilus heran* has a more pronounced post-palatal spine. The post-palatal spine of M.38841 is relatively shorter, similar to that of the holotypes of *pallescens* and *pacificus* and other *N. geoffroyi* specimens examined, compared to *N. heran*.
4. Hypocones on M^1 and M^2 more developed in *N. heran*. The hypocones of M.38841 are present but are relatively undeveloped. Kitchener *et al.* (1991) state that the hypocones are more developed than in *N. geoffroyi* and we assume that hypocone

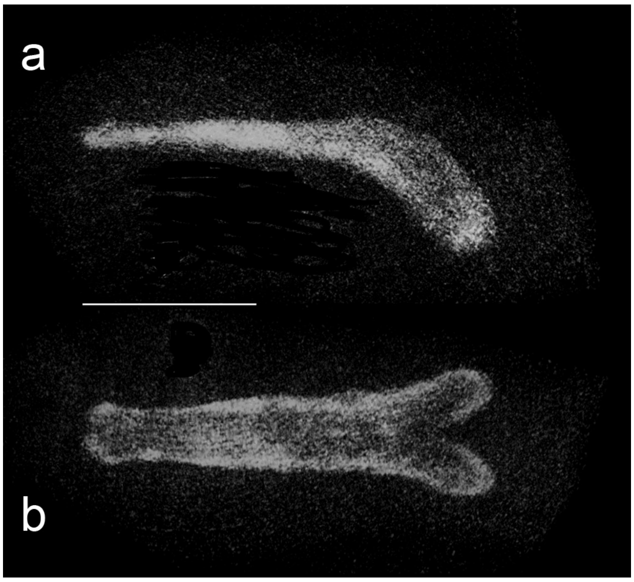

Figure 7. Micro CT scan of baculum of AM M.38841. (*a*) lateral view; (*b*) dorsal view. Distal end of bone faces left. Scale bar represents *ca.* 2 mm (images: Fred Ford).

Table 2. Selected cranial and external measurements of AM M.38841 from Maubisse, Timor-Leste, and the holotypes of *N. heran*, *pacificus*, and *pallescens*, compared to male *N. geoffroyi* from the Australian mainland. * Measurements from Kitchener *et al.* (1991).

Character	AM M.38841 (ET12) subadult male	*N. heran* holotype male *	*pacificus* holotype BM84.410 male	*pallescens* holotype BM7.1.4.1 male	*N. geoffroyi* adult male, Australian mainland	
					range	n
GL	15.23	16.70	16.1	15.75	14.5–16.3	74
CON	14.44	—	—	—	13.5–15.4	78
ZYG	9.12	10.64	9.90	9.24	8.6–10.0	77
ANT	4.12	4.73	4.78	4.53	4.1–4.8 *	6
INT	2.97	3.76	3.40	3.45	3.1–3.7	64
C^1–C^1	4.00	4.54	4.53	4.18	3.7–4.8	68
CM^3	5.61	6.05	5.36	5.63	4.9–6.0	78
M^3–M^3	6.21	6.97	6.37	6.13	4.9–6.6	64
PAL	7.28	—	6.97	7.12	6.4–7.3	29
sinPAL	5.47	6.02	—	—	5.4–5.8	5
MESO	1.80	2.05	1.55	1.56	1.4–1.8 *	6
BUL	3.66	3.90	3.62	3.76	3.6–4.1	49
BTB	1.65	1.64	—	—	1.0–1.6	45
MAS	8.35	8.89	8.30	7.64	7.5–8.6	78
BRH	5.59	6.18	4.97	5.40	4.5–5.7	75
M^{3}B	1.72	1.75	1.65	1.65	1.4–1.7 *	6
M^{3}L	0.72	0.74	0.60	0.60	0.6–0.7 *	6
BAC length	2.39	—	—	—	2.4–2.8	12
CM$_3$	6.01	6.53	—	—	5.8–6.0 *	—
EAR	24.0	23.4	—	—	20.6–28.0	100
FA	36	39	37	34	30.8–37.7	132
HB	41	52	—	—	43–47	19
Tail L	36.0	40.7	—	—	35–43	18
WT	4.5	7.6	—	—	4–6	19

development in the latter species is variable, given that they are absent in the *N. geoffroyi* that we examined. We are unable to evaluate this further because we cannot clearly discern hypocone morphology from the illustrations of *N. heran* given by Kitchener *et al.* (1991), although it appears that they are more developed than those of M.38841. We note that the latter authors did not include this character in their diagnosis of the species. Cusp terminology used by those authors is possibly the same as in figure 2 of Kitchener & Caputi (1985).

5 *Nyctophilus heran* has a relatively longer third commissure on M^3. The third commissure is relatively much shorter in M.38841 compared with *N. heran*. Kitchener *et al.* (1991) suggest that the greater development of the third commissure has resulted in a greater M^3 width than that of *N. geoffroyi*, however M^3 length and breadth of M.38841 approximates that given for *N. heran*, and the likely level of measurement error suggests that M^3 is effectively the same size as the holotype of *N. heran*, both of which fall at the upper end of the range for the six *N. geoffroyi* measured by Kitchener *et al.* (1991).

6 *Nyctophilus heran* has a less rounded distal end on the glans penis.

7 Dorsal crest on the glans penis is absent in *N. heran*. The external morphology of the glans penis of M.38841 resembles that of the holotype of *N. heran* (see fig. 4 of Kitchener *et al.,* 1991), rather than that of *N. geoffroyi*, in having a broadly rounded distal tip, and no dorsal crest.

8 Larger absolute size of *N. heran.* The holotype of *N. heran* is clearly larger in overall size than mainland Australian *N. geoffroyi* of equivalent sex, as noted by Kitchener *et al.* (1991). This is evident, for example, in bivariate plots of ZYG vs GL (Fig. 8b) and GL vs FA (Fig. 8c), in which *N. heran* falls well outside *N. geoffroyi* but close to *N. daedalus*. We have added the latter species to these plots as a yardstick to the magnitude of interspecific differences that can occur for *Nyctophilus* species. The four examples of larger skull and dental dimensions cited by Kitchener *et al.* (1991) are GL, ZYG, BRH and CM^3, all of which are corroborated by our much larger sample sizes (Table 2).

Morphometric comparisons with *N. heran* and mainland Australian *N. geoffroyi*

Skull and external measurements of M.38841 fall within the size range of mainland Australian adult male *N. geoffroyi* for most dimensions (though smaller than the range for INT). However, given the specimen is subadult, it likely has

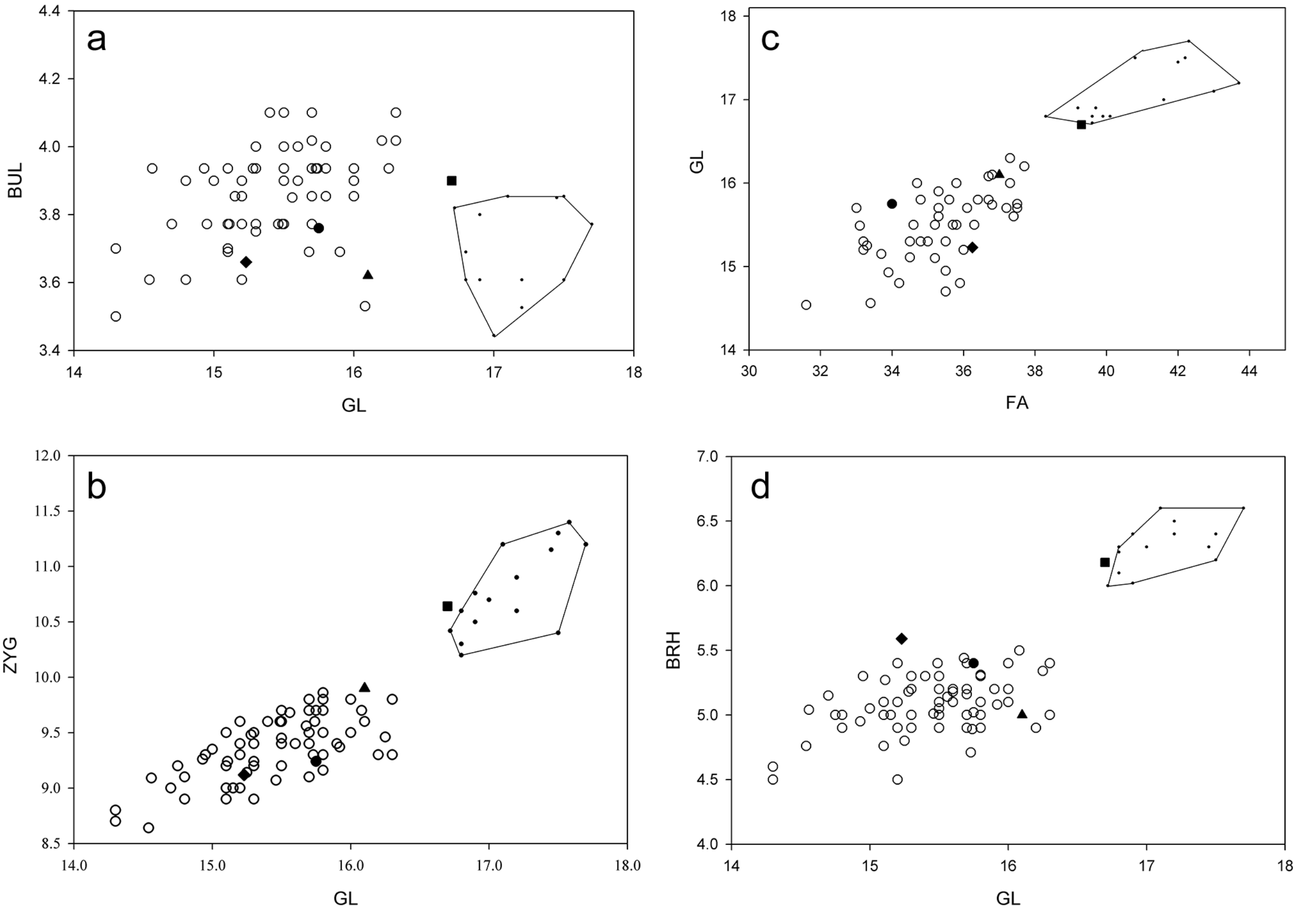

Figure 8. Bivariate plots of adult male *Nyctophilus*: (*a*) BUL vs GL (n = 71 for *N. geoffroyi*); (*b*) ZYG vs GL (n = 79 for *N. geoffroyi*); (*c*) GL vs FA (mm) for male *Nyctophilus geoffroyi* (n = 50), and (*d*) BRH v GL (n = 75). Symbols are: *N. geoffroyi* from throughout mainland Australia (○); holotype of *Nyctophilus geoffroyi pallescens* (●); holotype of *Nyctophilus geoffroyi pacificus* (▲); holotype of *N. heran* (■); subadult male M.38841 from Maubisse, Timor-Leste (♦); *N. daedalus* are small dots bounded by polygon, for a comparison with a similar-sized species.

not attained fully adult size, compromizing morphometric comparisons overall. In contrast, this specimen is at the upper size limit of specimens measured in this study, for sinPAL, BTB and M^3B, for which it approaches the size of *heran* (Table 2). AM M.38841 falls within the range of variation of *N. geoffroyi* as illustrated in bivariate plots of BUL, ZYG, and BRH vs GL, GL vs FA (Fig. 8a–d), and EAR vs FA (Fig. 10). In contrast, the holotype of *N. heran* falls outside the range of *N. geoffroyi* in these plots and exceeds the upper range of mainland *N. geoffroyi* for most characters other than BUL and EAR, which fall within the range (Table 2).

Table 3. Standardized character coefficients on the first three PC axes based on 9 skull and dental measurements of 75 adult male specimens of *N. geoffroyi*, the holotype of *N. heran* and M.38841 from Timor-Leste.

	Character	PC 1	PC 2	PC 3
character loadings	GL	0.634	0.000	–0.551
	CM^3	0.245	–0.079	–0.309
	C^1–C^1	0.247	–0.133	–0.125
	ZYG	0.412	0.076	0.645
	INT	0.114	–0.063	0.130
	M^3–M^3	0.354	–0.368	0.142
	BRH	0.193	0.886	0.012
	MAS	0.352	0.019	0.294
	BUL	0.090	–0.214	0.214
Eigenvalue		0.511	0.055	0.046
% variance		71.106	7.620	6.424

A comparison of M.38841 with *N. geoffroyi* and *N. heran* was explored further in a principal components analysis based on 9 skull and dental dimensions of 75 mainland Australian adult male *N. geoffroyi*. Separate analyses using a correlation matrix and a variance-covariance matrix yielded similar trends, with the holotype of *N. heran* a clear outliner in both. The PCA explained 59.6 and 12.1% of variance on the first and second PC axes respectively, compared to 71.1 and 7.6% in the variance-covariance analysis and we only present results of the latter. The first three PC axes account for a substantial percentage of the measurement variance (Table 3) and character coefficients suggest the first PC axis is dominated by overall size, while PC 2 contrasts BRH, with M^3–M^3 and BUL. A plot of PC scores on the first two PC axes, and on PC 1 vs. PC 3 (Fig. 11) indicate that scores for AM M.38841 fall within the range of *N. geoffroyi*, while those of the holotype of *N. heran* are an outlier on the first two axes but not on PC 3. A minimum spanning tree fitted to each specimen in the PCA plots (not shown) revealed that the holotype of *N. heran* is a clear outlier on a plot of PC 1 vs. PC2, and PC 1 vs. PC 3, while that of the Maubisse male falls within the range of variation of *N. geoffroyi*.

We further compared skull and dental measurements of *N. heran* and M.38841 with the same sample of mainland

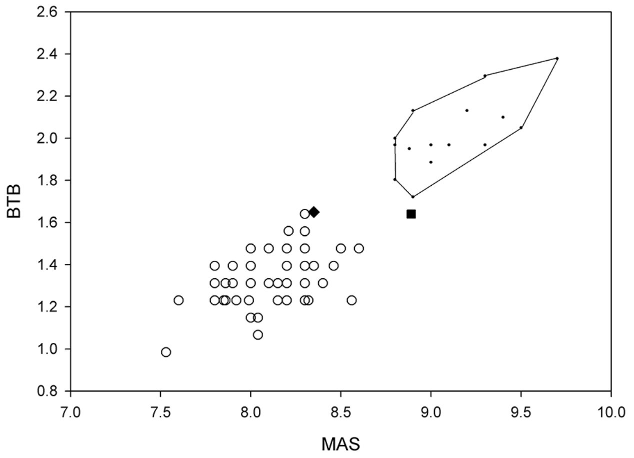

Figure 9. Plot of BTB vs MAS, for adult males: *N. geoffroyi* (n = 50) from throughout mainland Australia (○); holotype of *N. heran* (■); subadult male M.38841 from Maubisse, Timor-Leste (♦); *N. daedalus* (n = 15) are small dots bounded by polygon, for a comparison with a similar-sized species.

Australian *N. geoffroyi* in dendrograms from UPGMA cluster analyses using euclidean distance as a measure of similarity. The holotype of *N. heran* formed an outgroup to both M.38841 and all mainland *N. geoffroyi* in all 10,000 boot-strap replications, in which there was little or no support for subgroupings within *N. geoffroyi* and M.38841 was an outgroup to mainland *N. geoffroyi* in 37% of replications (not shown). This suggests that no meaningful substructure was detected within *N. geoffroyi* and M.38841 with this character set using this technique.

The subadult female specimen M.37639 was at the most advanced growth stage of the three Maubisse specimens and falls at the upper end of the size range of 70 adult female mainland Australian *N. geoffroyi* as shown in a plot of Ear Length vs. FA (Fig. 10). Its measurement of C^1–C^1 of 4.26 mm falls within the range of 3.8–4.8 mm of 70 adult female *N. geoffroyi* from mainland Australia.

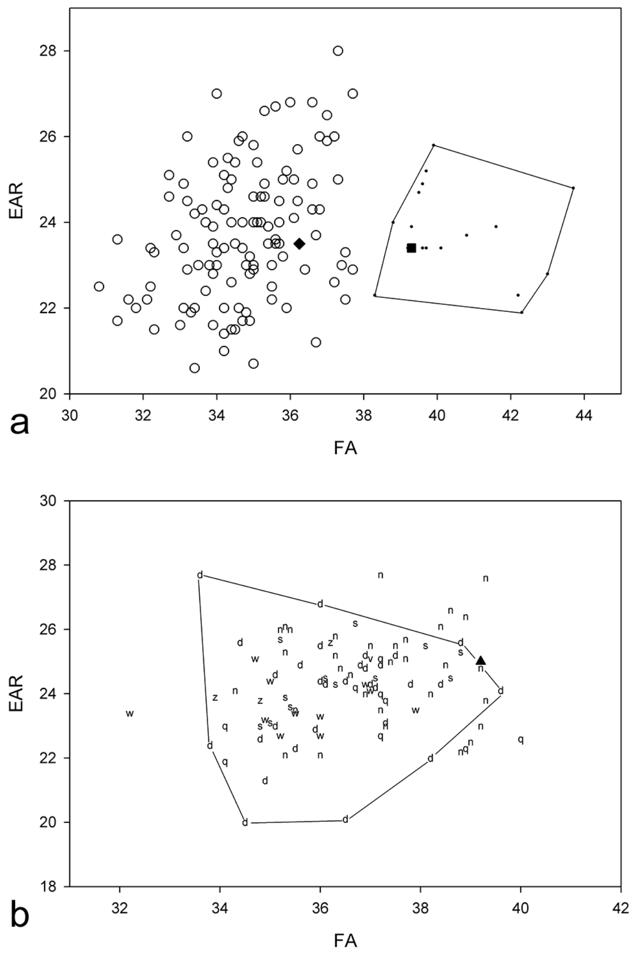

Figure 10. Plot of Ear vs FA (mm) of *Nyctophilus*: (*a*) males: adult male *N. geoffroyi* (n = 122) from throughout mainland Australia (○); holotype of *N. heran* (■); subadult male M.38841 from Maubisse, Timor-Leste (♦); *N. daedalus* (n = 18, small dots) are bounded by polygon, for a comparison with a species of similar size to *N. heran*. (*b*) Adult female *N. geoffroyi* from throughout mainland Australia (n = 99); subadult female M.37639 from Maubisse, Timor-Leste (▲). Locality codes for *N. geoffroyi* are: central Australia (c); NSW (n), Queensland (q); Victoria (v), northern Western Australia and northern Northern Territory (z). Thirty specimens from Danggali, SA (d), are bounded by a polygon, indicating extent of within locality variation relative to total variation.

Summary of species comparisons

Seven potentially diagnostic criteria are available to compare the Maubisse male with *N. geoffroyi* and the original description of the holotype of *N. heran*. The character states shared by the three entities are summarized in Table 4. The Maubisse male has a unique combination of characters shared with both *N. heran* (glans penis morphology and BTB) and *N. geoffroyi* (skull and dental morphology). This suggests that the Maubisse animals could be a separate taxon. The Maubisse male has only three of the seven criteria in common with the holotype of *N. heran*, but four with *N. geoffroyi*.

Ontogenetic changes in size and shape potentially influence at least three of the five criteria this specimen

Table 4. Characters of Maubisse *Nyctophilus* specimens shared (+) with *N. heran* and *N. geoffroyi* complex.

Character	M.38841 Maubisse	*N. heran* holotype	*N. geoffroyi* complex
Glans penis with rounded distal tip	+	+	—
Glans penis without dorsal ridge	+	+	—
BTB exceeds 1.6 mm	+	+	—
M^3 third commissure relatively short	+	—	+
Mesopterygoid fossa with rounded anterior margin	+	—	+
Posterior palatal spine not enlarged	+	—	+
Relatively large auditory bullae	+	—	+

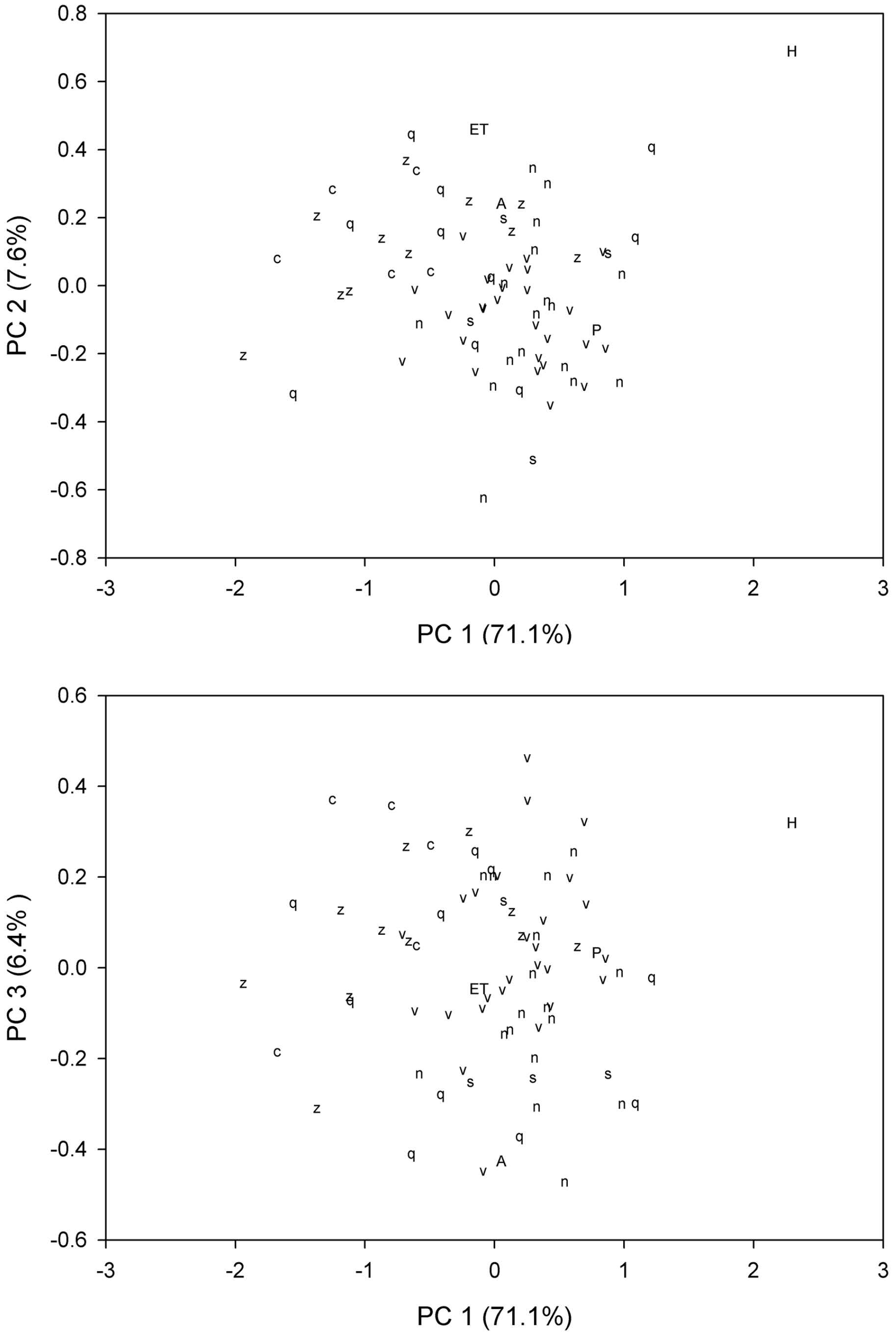

Figure 11. Plot of PC scores for the first three axes of a PCA based on 9 skull and dental measurements of 75 adult male specimens of *N. geoffroyi*; AM M.38841 from Maubisse (ET), holotype specimens of *pacificus* (P), *pallescens* (A) and the holotype of *N. heran* (H). Mainland Australian *N. geoffroyi* symbols designate specimen localities: central Australia (c); NSW (n), Queensland (q); Victoria (v) and northern Western Australia and northern NT (z).

shares with *N. geoffroyi*. The relatively enlarged bullae, which are very characteristic of *N. geoffroyi*, possibly result from differential skull growth. If the cranial cavity and auditory regions attain near adult dimensions earlier than rostral dimensions, the Maubisse male might be a subadult specimen of *N. heran* irrespective of its relatively large bullae. Further support for this interpretation stems from the large absolute size of BTB, for which the Maubisse male matches that of *N. heran* and exceeds the largest of 45 male *N. geoffroyi* (Table 2). However, this is contradicted by BUL of the Maubisse male, which is at the lower end of the range of *N. geoffroyi* and is substantially smaller than *N. heran*. Although the Maubisse male could have skull proportions not shared with either *N. heran* or *N. geoffroyi*, these differences potentially result from differential growth rates of bullae relative to the cranial vault. This could be resolved when adult material becomes available from Timor, and additional material enables an assessment of intraspecific variation in *N. heran*. Although the overall size of the Maubisse male falls within the range of *N. geoffroyi* for most individual dimensions and also in the PCA based on skull and dental dimensions, the animal is at a fairly early stage of development based on the extent of fusion of the wing epiphyses and it might not have attained full adult size. The relative length of the post-palatal spine is similarly problematic, and further growth in the length of this structure cannot be discounted. However, we suspect that the anteriorly more rounded shape of the mesopterygoid fossa of the Maubisse male reflects the adult state.

Discussion

Our primary aim was to evaluate the taxonomic status of new specimens of *Nyctophilus* collected in Timor-Leste but this first required a re-examination of Geoffroy's description of *timoriensis*, the only previously reported material of *Nyctophilus* from Timor. Our re-interpretation of Geoffroy's illustration of *timoriensis*, combined with a review of the few measurements given in his original description, indicate that *timoriensis* is not conspecific with *N. major* and we see no reason to doubt that Geoffroy's original material of *timoriensis* was obtained while the Baudin expedition was stationed in Timor.

A new concept of *N. timoriensis* that arose from our review of the taxonomic literature is of a species with an enlarged post-nasal mound that is similar in relative size to species with the maximum development of that structure, such as *N. heran*, *N. geoffroyi* and *N. gouldi*, and not a rudimentary structure of *N. major* as previously implied. There is little evidence for the entrenched view that *N. timoriensis* is of similar body size to the large-bodied *N. major* and it is more likely to be of intermediate body size for the genus. Further, the suspected holotype of *N. timoriensis* is a closer match in body size to our revised concept of *N. timoriensis* than it is to *N. major*.

The possibility that more than one species of *Nyctophilus* occurs on the island of Timor needs to be considered, particularly given that the Baudin expedition might have obtained *Nyctophilus* from the lowlands in contrast to our montane material. No island that is not connected to the Sahul Shelf (the continental shelf containing New Guinea, mainland Australia, and Tasmania), like Timor, has yet been shown to support more than one species of the genus (e.g., Lembata, Sudest, New Ireland, Bougainville, New Caledonia) and there is no clear indication of multiple species in the specimens available from Timor. However, it is doubtful that adequate survey effort with appropriate techniques has been undertaken in these regions to be confident that only one species is present. Although the specimens from Maubisse provide a general correspondence in morphological features, including body size and snout morphology, with Geoffroy's description of *timoriensis* from the Baudin expedition, confident assignment of the Maubisse specimens to *N. timoriensis* is premature (discussed below). However, we tentatively assign the Maubisse material to *N. timoriensis* until further material becomes available.

Four factors hindered our assessment of the Maubisse material in the preliminary morphological analysis presented here. First, the immature status of the three specimens complicates interpretation of diagnostically valuable skull proportions, due to potential age-related differential growth of cranial components. It also diminishes the value of absolute cranial and external measurements which can be important in defining species of this genus. Bullae size is a possible exception, assuming that basicranial structures attain adult size earlier than other regions of the skull. Differences in absolute size separating the mensural range for characters between similar *Nyctophilus* species are typically small, often only one or two mm, yet can be consistent and diagnostic. Consequently, the size difference, for example in GL, of about one mm between *N. heran* and our largest male *N. geoffroyi* could be significant. Second, intraspecific variation remains undefined in *N. heran*, known from the unique holotype. The extent of variability of key diagnostic criteria, such as the dorsal penile ridge and molar cusp morphology, within mainland Australian *N. geoffroyi* has also not been adequately assessed, nor have species limits within what is currently regarded as "*N. geoffroyi*". Third, we have not made direct comparisons between our material and the holotype of *N. heran* but have relied on the original description and illustrations. Finally, large numbers of *N. geoffroyi* exist in museum collections, the majority from southern Australia, but we used readily available specimens with intact skulls which had already been extracted from bodies, with a resultant relatively small sample size.

Overall, Geoffroy's description and illustration, and the Maubisse material, show closest morphological resemblance to *N. heran* and *N. geoffroyi*. The Maubisse male M.38841 exhibits characters that are diagnostic of both *N. heran* and *N. geoffroyi*, as currently understood. External morphology of the glans penis is a diagnostic feature for *Nyctophilus* species, and two penile characters (rounded distal end and absence of a dorsal ridge) clearly align M.38841 with *N. heran* and suggest that they are not conspecific with *N. geoffroyi*. Overall, our morphological assessment, particularly the shape of the glans penis, suggests that the Maubisse material is distinct from the *N. geoffroyi* complex. The Maubisse male fell outside our material of mainland *N. geoffroyi* in our cluster analyses of cranial characters, being larger than all *N. geoffroyi*. Conversely, M.38841 resembles *N. geoffroyi* but differs from *N. heran* in the diagnostically important shape of the mesopterygoid fossa and post-palatal spine, provided it had attained the adult condition for those characters. The more angular mesopterygoid fossa of *N. heran*, judging from fig. 2 of Kitchener *et al.* (1991), more closely resembles eastern Australian *N. gouldi* and the smaller form of *N. daedalus* from northwest Western Australia than it does *N. geoffroyi*. The lateral skull profile and relatively large bullae of M.38841 are very characteristic of *N. geoffroyi*, and if that specimen had attained adult proportions, it would be a significant distinction from *N. heran*.

Genetic comparisons seem to indicate a close relationship between *N. timoriensis*, as represented by the Maubisse sample, and *N. heran*, its closest geographic neighbour; analysis of two mitochondrial genes and one nuclear gene showed that samples from the holotype of *N. heran* and the Maubisse animals clustered together to the exclusion of all other *Nyctophilus* species, and are probably conspecific (Belinda Appleton, pers. comm. to first author, 2008). However, these comparisons remain unpublished and the original tissue samples for these specimens may no longer be available. Though this provides an indication that *N. timoriensis* and *N. heran* are closely related and likely conspecific, firmer understanding of species limits in this group should arrive via analyses that sample larger segments of the genome in as many specimens as possible.

Table 5. Bat species recorded from the island of Timor, indicating endemic taxa (E). Based on Polhemus & Helgen (2004), Simmons (2005), our interpretation of the taxonomic literature combined with inspection of world collections by the second author, and research by our colleagues as indicated. *

Taxon	Timor endemic?	Remarks
Fruit-bats (Pteropodidae)		
Acerodon mackloti mackloti (Temminck, 1837)	—	
Cynopterus terminus Sody, 1940	E	Variably considered a subspecies *Cynopterus titthaecheilus terminus*, e.g., Simmons (2005), or a full species, e.g., Schmitt *et al*. (2009).
Cynopterus nusatenggara Kitchener & Maharadatunkamsi, 1991	—	Recorded from West Timor (Ruedas *et al*., 2019).
Dobsonia moluccensis (Quoy & Gaimard, 1830)	—	Recorded by Polhemus & Helgen (2004) based on a nineteenth century specimen, suspected to be extinct on Timor.
Dobsonia peronii peronii (Geoffroy, 1810)	—	
Eonycteris spelaea (Dobson, 1871)	—	
Macroglossus minimus lagochilus Matschie, 1899	—	
Nyctimene keasti Kitchener in Kitchener, Packer & Maryanto (1993)	—	The few Timorese records are usually assigned to *N. cephalotes* (Pallas, 1767); considered more likely to be *keasti* by Kitchener, Packer & Suyanto (1995: 138).
Pteropus griseus (Geoffroy, 1810)	—	
Pteropus lombocensis salottii Kitchener, in Kitchener & Maryanto, 1995	E	*P. lombocensis* first reported from Timor by Kitchener & Maryanto (1995); endemic subspecies.
Pteropus vampyrus edulis (Geoffroy, 1810)	—	
Rousettus amplexicaudatus (Geoffroy, 1810)	—	
Sheathtail-bats (Emballonuridae)		
Saccolaimus saccolaimus (Temminck, 1838)	—	
Taphozous melanopogon Temminck, 1841	—	
? Taphozous achates Thomas, 1915b	—	Probably occurs in Timor, see Kitchener *et al.* (1993: 80).
Horseshoe-bats (Rhinolophidae)		
Rhinolophus keyensis parvus Goodwin, 1979	E	Endemic subspecies, previously included in *R. celebensis* Andersen, 1905.
Rhinolophus montanus Goodwin, 1979	E	Previously included as a subspecies of *R. philippinensis* Waterhouse, 1843 but elevated to species by Csorba (2002).
Rhinolophus timorensis Goodwin, 1979	E	Often included as a subspecies of *R. canuti* Thomas & Wroughton, 1909 but likely to be a full species (Helgen, 2004).
Rhinolophus sp. cf. *philippinensis* Waterhouse, 1843	—	Captured in Timor-Leste, taxonomic status under investigation (Armstrong, 2007).
Leaf-nosed bats (Hipposideridae)		
Hipposideros bicolor hilli Kitchener in Kitchener *et al.* (1996)	E	Subspecies endemic.
Hipposideros crumeniferus (Lesueur & Petit, 1807). *incertae sedis*	—	Entity of uncertain taxonomic status, suspected to be *H. cervinus* (Gould, 1854) or a closely related taxon by Oey & van der Feen (1958) and Hill (1963).

Table 5. *Continued …*

Table 5. *Continued.*

Taxon	Timor endemic?	Remarks
Hipposideros diadema diadema (Geoffroy, 1813)	—	
Hipposideros sumbae rotiensis Kitchener & Maryanto, 1993	E	Recorded from Timor by Kitchener & Maryanto (1993).
Bent-wing bats (Miniopteridae)		
Miniopterus macrodens Maeda, 1982	—	Past records of *M. schreibersii* (Kuhl, 1817) from Timor are likely to be this species but species taxonomy of *Miniopterus* from Timor remains confused. Maeda (1983) demonstrated that *macrodens* and *magnater* Sanborn, 1931 are distinct but often treated as a subspecies, *M. magnater macrodens*.
Miniopterus blepotis Temminck, 1840	—	Requires confirmation. Past records of *M. schreibersii* (Kuhl, 1817) from Timor might include this species (Ibáñez & Juste, 2019), possibly along with past records of *M. oceanensis* Maeda, 1982.
Miniopterus pusillus Dobson, 1876	—	Subspecies from Timor uncertain, see Kitchener & Suyanto (2002: 26).
Miniopterus shortridgei Laurie & Hill, 1957	—	Recorded by Kitchener & Suyanto (2002). Previous authors assigned Timor specimens to *M. australis* Tomes, 1858b.
Vespertilionid bats (Vespertilionidae)		
Harpiocephalus sp.	?	Captured in Timor-Leste by Pavey & Milne (2004), generic identity determined by Armstrong & Konishi (2012); taxonomic status under investigation (Kyle Armstrong, pers. comm. 2020).
Kerivoula sp.	?	Captured in northern Timor-Leste (Pavey & Milne, 2004); subsequent records from the south coast, Timor-Leste (Armstrong & Konishi, 2012). Taxonomic status under investigation (Kyle Armstrong, pers. comm. 2020).
Murina sp.	?	Captured in northern (Pavey & Milne, 2004) and south coast Timor-Leste (Armstrong & Konishi, 2012). Taxonomic status under investigation (Kyle Armstrong, pers. comm. 2020).
Myotis adversus (Horsfield, 1824)	—	First recorded from Timor by Kitchener *et al.* (1995).
Myotis muricola (Gray, 1847)	—	Captured by Hisheh *et al.* (2004).
Nyctophilus timoriensis (Geoffroy, 1806)	?E	Probably endemic. Obtained by Baudin expedition of 1802–1804, at Kupang. Specimens from Maubisse, Timor-Leste might be this species.
Pipistrellus sp. cf. *papuanus* Peters & Doria, 1881 **	—	Previously recognized as *P. tenuis* (Temminck, 1840) but taxonomic status of *P. papuanus* from Timor is uncertain.
Scotophilus collinus Sody, 1936	—	Treated as a synonym of *S. kuhlii* (Leach, 1821b) or *S. temminckii* (Horsfield, 1824), prior to the taxonomic revision of Kitchener *et al*. (1997).
Scotorepens sanborni (Troughton, 1937)	—	See Kitchener *et al.* (1994).
Tylonycteris robustula Thomas, 1915c	—	

* We note that Kitchener & Maryanto (1995) include *Pteropus alecto* in the Timorese bat fauna based on a specimen from "island of Timor" that Kitchener, Packer & Maharadatunkamsi (1995) assigned to *P. alecto ?gouldi* based on a specimen from "island of Timor" for which they provide no further data.

** We concur with Hill (1992) who does not recognize *Pipistrellus javanicus* from the island of Timor.

In conclusion, sequencing studies are required to establish whether the Maubisse specimens, the holotype of *N. heran* and the suspected holotype of *N. timoriensis* are conspecific. Analysis of tissue samples from the suspected holotype of *N. timoriensis* is a high priority given that we cannot exclude the possibility that the specimen is not Geoffroy's original. Further resolution of the identity of the *Nyctophilus* from Timor and Lembata also warrants a comprehensive morphological and genetic study of the genus more broadly. It is currently hindered by the unresolved taxonomic status of the taxa, other than *N. timoriensis*, with which they should be compared. This includes the species composites of both *N. geoffroyi* from mainland Australia (Eldridge *et al.*, 2020) and *N. daedalus* from northern Western Australia (Parnaby, 2009).

Timor has a relatively depauperate mammal fauna with low species endemicity and no extant endemic mammal genera (Hill, 1992) but had a much richer prehistoric endemic rodent fauna (Aplin & Helgen, 2010). The Timorese bat fauna remains poorly known and the unresolved taxonomic status of a large proportion of species probably masks what we anticipate is a higher level of endemism. It includes elements derived from both the Australian and Asian regions and considerable endemism occurs at the subspecies level and above for bats within the Outer Bandic Island Arc, which includes Timor (Kitchener & Suyanto, 1996). As we could not find an up to date list of the bat fauna of the island of Timor, we have compiled one from our interpretation of the taxonomic literature, combined with museum material examined by the second author (Table 5). The species taxonomy of the Timor bat fauna remains unresolved for many species and we have included past nomenclature to assist interpretation of the literature. The absence of widespread Australasian insectivorous bat genera such as *Otomops* and *Chaerephon* suggest that the current tally of about 37 bat species could increase with further survey work. In particular, those insectivorous species that do not roost in caves, and are therefore more likely to have been overlooked, are likely to be under-represented.

The presence of a number of unique mammal taxa in the Timorese fauna highlights the urgent need for conservation and restoration of the country's remaining native forests and wildlife, including detailed studies of taxonomy, geography, and ecology of the mammal fauna. Priorities for further survey work in Timor are the lowland rainforests of the eastern tip of Timor and montane habitats at 2000–3000 m in the central highlands, as these areas are very poorly known biologically, but are likely to yield additional endemic species. Specialist bat surveys should include routine capture using bat traps ("harp traps"), mistnets of suitable mesh size for small insectivorous bats, and retention of museum voucher specimens in addition to echolocation call surveys.

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Appendix. Specimens of *Nyctophilus geoffroyi* (n = 75) used in multivariate statistical analyses and specimens of *N. daedalus* (n = 16) used in bivariate plots.

Nyctophilus geoffroyi

Northern Territory (10 specimens). AM M.34418, AM M.34420–21, Dunmarra; AM M.34424–25 Bushy Park, NE of Alice Springs; ANWC CM2435 Alice Springs, 2 miles NW; ANWC M05976 Ellery Water Hole, 59 miles W of Alice Springs; NTMU3100 (M808), Studholme Hills; NTM U3104 (M380), Katherine; NHMUK 7.1.4.1, holotype of *Nyctophilus geoffroyi pallescens* Thomas, Alexandria Station. **Queensland** (10 specimens). M.35513 and M.35514, Cape York; AM M.34481 Brisbane environs; AM M.34482 Mt Nebo; AM M.12968 42 km SE of Normanton; AM M.3908 Millmerran, near Toowoomba; ANWC CM2103 Mt Isa, Spear Ck; ANWC CM4019 Mt Isa, 20 mile S; QM JM5393 Babbiloora Stn.; NTM U3106 (M5183), Sandringham Station. **South Australia** (4 specimens). AM M.34467–34469, Danggali Conservation Park; NMV C5180, Purnong. **Western Australia** (7 specimens). AM M.22120, 11 km W of Inglis Gap, King Leopold Ranges; AM M.22125, 10 km SW of Napier Downs Station, Kimberleys; AM M.22129, 20 km SW of Marillana Station, Pilbara Region; AM M.22133, AM M.22135, 27 km NE of Tom Price, Pilbara Region; AM M.34430, Gogo Station, Fitzroy Crossing; NTM U3096 (M217), Labi Labi. **New South Wales** (18 specimens): NMV C3167, Barham; AM M.14012, Putty, Wollemi National Park; AM M.3379, Mandurama, via Blayney; AM M.342, Mt Kosciusko; AM M.35517 Mumbulla State Forest, 7 km E of Mumbulla Mountain; AM M.3742, Micalago Station, Michelago; AM M.4442, Berrima; AM M.5115, Bombala; AM M.5122, Fairfield, Sydney; AM M.7297, Bringagee; AM M.8040, Lake Popilta, 83 miles SSE of Broken Hill; AM M.9390, Murrumbidgee River, upper reaches, 3.5 miles from Tantangara Dam; ANWC CM590, 24 km N of Griffith; ANWC M04990–991, M04993, M04995, M04997, Lake Cowell. **Victoria** (25 specimens). AM M.34920–922, AM M.51374, Daylesford; AM M.34888, Bruthen; AM M.34897, AM M.34899, AM M.34902–903, AM M.34905, Sunset Country; AM M.34906, Zumstein, Grampians; NMV C18122, Phillip Island; NMV C24876, Surrey Hills, Melbourne; NMV C2623, Meredith; NMV C3093, Little Desert, south of Kiata; NMV C3161, Gorae West, Portland; NMV C3736, Heathmere, near Portland; NMV C3753, South Blackburn, Melbourne; NMV C4015, Murrayville, 3 miles NE; NMV C431, Monbulk; NMV C4360, Lake Meran; NMV C4362, East Buchan; NMV C5169, Ballarat; NMV C5175, Windsor; NMV C5177, Gunbower. **Unknown locality**. NHMUK 84.410, holotype of *Barbastellus pacificus* Gray, “Islands of the Southern Pacific”.

Nyctophilus daedalus

Western Australia. (9 specimens). AM M.22126, AM M.22128 Corktree Bore, Pilbara region; AM M.49931–932, Weeli Wolli Spring; WAM M.14097, Drysdale River National Park; WAM M.22558, Martins Well; WAM M.30586, Millstream Station; WAM22356, WAM M.22358, Cadgeput Springs. **Northern Territory.** (7 specimens). ANWC C7592, Deaf Adder Creek Valley; AM M.9411, NHM 1897.4.12.8 (holotype), Daly River; AM M.13351, Roper River, Mataranka; AM M.34451–52, West Alligator R., junction Highway; AM M.34453, Daly River Rd, 28 km NNE of Nauiya.

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The Mammal Fauna of Kofiau Island, off Western New Guinea

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Abstract. Kofiau's terrestrial mammal fauna shares many taxa with oceanic islands lying close to New Guinea. Its fauna is distinctive in possessing a mixture of Moluccan near-endemics, such as *Pteropus chrysoproctus*, along with Melanesian species, like *Dobsonia beauforti*, that reach their westernmost limit on Kofiau. Very little has been published on the terrestrial vertebrate fauna on Kofiau compared to the adjacent islands. This paper presents two surveys of the terrestrial mammal fauna of Kofiau Island, undertaken in 2011 and 2019, increasing the number of species recorded from the island from 1 to 20: one rodent, two marsupials and 17 bats.

Abstrak [Bahasa Indonesia]. Fauna mamalia terestrial di Pulau Kofiau memiliki kemiripan dengan pulau-pulau di sekitar kawasan Papua dan Papua New Guinea. Mamalia terestrial di pulau ini sangat khas yang merupakan campuran dari spesies dengan sebaran terbatas di Kepulauan Maluku, seperti *Pteropus chrysoproctus*, sampai dengan spesies dari Kawasan Melanesia seperti *Dobsonia beauforti* yang mencapai batas paling barat Pulau Kofiau. Sampai saat ini, publikasi tentang fauna vertebrata terestrial di Pulau Kofiau masih sangat sedikit dibandingkan dengan pulau-pulau lain di sekitarnya. Makalah ini menyajikan hasil survei mamalia terestrial di Kofiau yang telah dilakukan pada tahun 2011 dan 2019, dan menunjukkan adanya peningkatan jumlah spesies yang tercatat di pulau ini, dari satu menjadi 20 spesies yang terdiri dari satu spesies hewan pengerat, dua spesies hewan berkantung dan 17 spesies kelelawar.

Introduction

Kofiau Island is a relatively large (144 sq. km) landmass in Southwest Papua Province, Indonesia, which lies around 30 km west of the New Guinean continental shelf (Fig. 1). Being surrounded by water over 200 m deep, it was not connected with New Guinea during the last glacial maxima (Diamond *et al*., 2009). Its maximum elevation is 288 m, though most of the island consists of a coralline platform that is raised a few metres above sea level. The uplifted marine limestone plateau is undated, as are the two volcanic hills that project above it (Diamond *et al.,* 2009).

Keywords: Raja Ampat, biogeography, bat echolocation, biodiversity survey
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Kofiau is part of the Raja Ampat islands group. The largest islands of the group are Misool, Salawati, Waigeo, and Batanta. Misool and Salawati are continental land-bridge islands, while Batanta and Waigeo were not connected with the mainland during periods of low sea level, though they were separated only by a narrow channel, and were connected with each other. Both the continental land-bridge islands have relatively rich mammal faunas, including macropodids and other marsupials typical of the New Guinea lowlands. Waigeo/Batanta have a more limited non-volant mammal fauna, but are home to an endemic marsupial, the phalangerid *Spilocuscus papuensis*. Kofiau and Gag are oceanic islands that are separated from the continental shelf by a wide expanse of sea. At 56 sq. km Gag Island is the smallest and most isolated major island in the group, lying around 80 km due north of Kofiau. Thirteen mammal species have been recorded on Gag (Maryanto & Kitchener, 1999; Maryanto *et al*., 2010), comprising seven pteropodid bats (*Pteropus neohibernicus*, *P. conspicillatus*, *P. personatus*, *Nyctimene* sp. cf. *albiventer*, *Dobsonia beauforti*, *Macroglossus minimus* and *Syconycteris australis*), two emballonurid bats (*Emballonura alecto* and *Mosia nigrescens*), and four murid rodents (*Rattus tanezumi*, *R. exulans*, and *R. nikenii,* and an unidentified murine with a white tail-tip). Of these, the presence of both an apparent endemic (*Rattus nikenii* Maryanto, Sinaga, & Maharadatunkamsi, 2010) and the North Moluccan endemic *Pteropus personatus* is noteworthy (Wiantoro & Maryanto, 2016).

Very little has been published about the vertebrate fauna of Kofiau Island. Only the avifauna has received close attention, and even that is poorly documented relative to that of adjacent landmasses (Ripley, 1959; Diamond *et al.*, 2009). Kofiau's avifauna comprises 78 species, including two endemic allospecies—the Kofiau Paradise Kingfisher (*Tanysiptera ellioti*) and the Kofiau Monarch (*Symposiachrus julianae*), and 5 endemic subspecies (Diamond *et al.,* 2009). It is, according to Diamond *et al.* (2009) "typical of the Papuan region's oceanic islands". This paper represents the first study that documents the terrestrial mammal faunal on the island (Table 1).

Kofiau's marine mammals have received more attention than the terrestrial mammal fauna. Twelve cetacean species have been recorded from the Kofiau Marine Protected Area, which surrounds the island (Ender *et al.*, 2014), including the spinner dolphin (*Stenella longirostris*), pantropical spotted dolphin (*Stenella attenuata*), common bottlenose dolphin (*Tursiops truncatus*), Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), Fraser's dolphin (*Lagenodelphis hosei*), Risso's dolphin (*Grampus griseus*), short-finned pilot whale (*Globicephala macrorhynchus*), killer whale (*Orcinus orca*), Bryde's whale (*Balaenoptera edeni*), sperm whale (*Physeter macrocephalus*), false killer whale (*Pseudorca crassidens*) and pygmy killer whale (*Feresa attenuata*).

Prior to this report, the only existing published terrestrial mammal record for Kofiau was a single museum specimen of *Pteropus chrysoproctus* (Flannery, 1995; see below).

Table 1. List of mammals recorded for Kofiau.

Taxa	Kofiau local name	Nature of record
Diprotodontia		
Phalangeridae		
Phalanger orientalis	Rambau	photograph
Petauridae		
Petaurus sp. cf. *breviceps*	Mantuan	local report
Rodentia		
Muridae		
Melomys sp.	Intowek	local report
Chiroptera		
Pteropodidae		
Pteropus chrysoproctus	Mambikaf	historic voucher sighting
Dobsonia beauforti		voucher
Rousettus amplexicaudatus		voucher
Macroglossus minimus	Mamquai	voucher
Nyctimene sp. cf. *albiventer*	Mamquai	voucher
Paranyctimene raptor		voucher
Syconycteris australis		voucher
Emballonuridae		
Emballonura sp. cf. *alecto*		bat detector
Mosia nigrescens		voucher, bat detector
Vespertilionidae		
Myotis sp. cf. *stalkeri*		sighting, bat detector
Miniopteridae		
Miniopterus sp. cf. *australis*		bat detector
Hipposideridae		
Aselliscus tricuspidatus		voucher, bat detector
Hipposideros diadema		bat detector
Hipposideros sp. cf. *maggietaylorae*		voucher
Hipposideros ater		voucher
Rhinolophidae		
Rhinolophus sp. cf. *euryotis*		bat detector
Molossidae		
Chaerephon jobensis		bat detector

Materials and methods

Here we report the results of two independent investigations of Kofiau's mammal fauna. The first, undertaken by one of us (SW) occurred in December 2011 when a bat survey was undertaken over two consecutive nights using a four-bank harp trap and a mistnet in two uninhabited areas in the central (1.184°S 129.847°E) and west coastal parts of the island (sites marked by stars on Fig. 1). This survey resulted in the recording of 10 species of bat, as documented by voucher specimens deposited at the Museum Zoologicum Bogoriense in Cibinong, Indonesia (Table 2). The second investigation, on 2 October 2019, occurred when the *Spirit of Enderby,* carrying 42 tourists visited Kofiau and two of us (TF and DB) took the opportunity to record what we could of the island's mammals. Evidence was gathered for the presence of 20 terrestrial mammal species (1 phalangerid marsupial, 1 petaurid marsupial, 1 murid rodent, 7 pteropodid bats, 1 rhinolophid bat, 4 hipposiderid bats, 2 emballonurid bats, 1 miniopterid bat, 1 vespertilionid bat, 1 molossid bat, see Table 1).

In 2011, during the first night of bat trapping, one mistnet and harp trap were deployed in the secondary forest close to the coast. The mistnet was set up from 6 pm until midnight, while the harp trap was left overnight. Periodic checks were done on both types of traps. During this survey, one of us (SW) found a lot of fallen ripe mango under the wild mango trees along the trail from the beach to the sampling site. It was mango fruit season in the island. On the second night, we moved the mistnet and harp trap to the other sampling site which was dominated by mangrove vegetation. There was no rain on the first night, however, light rain fell on the second night.

Just prior to the 2019 visit some rain had fallen on Kofiau. Throughout September, however, the region had experienced a severe dry season. We saw large numbers of tall, leafless (possibly dead) trees, and the *Terminalia catappa* trees were in the process of shedding red leaves. The expedition stopped at two locations: (1) Kampong Deer, on Deer Islet off the north coast, and the adjacent mainland; and (2) an islet off the largely uninhabited south coast of Kofiau (1.216757°S 129.737884°E, see circle on Fig. 1). At both locations, most of the 42 passengers participated in an opportunistic survey for mammals.

Location 1: Kampong Deer and adjacent coast of Kofiau. The expeditioners undertook a 20-minute walk on the mainland of Kofiau directly opposite Kampong Deer. The group was led from the coast to Jenyan Lake by Naftali, a ranger with a Nature Conservancy funded conservation initiative. He confirmed the presence of *Phalanger orientalis*, and the absence of bandicoots, on Kofiau. The only mammal sighting made during the walk was a group of 4 scats, consistent with those of a juvenile *P. orientalis*, found on a palm spathe on a path through young regrowth. At Kampong Deer, using Flannery (1995) as a source of illustrations, Josias, the Kepala Kampong, was questioned about Kofiau's mammals.

Table 2. Measurements from captured bat species from the expedition conducted by MZB (SW) in 2011. All length measurements in millimetres (mm). Means, with range in parentheses.

Species	n	Weight (g)	Head and body length	Tail length	Ear length	Tragus length	Forearm length	Tibia length	Hindfoot length
Aselliscus tricuspidatus	1♀	2.5	40	24	11	—	40	14	5
Dobsonia beauforti	1♂1♀	170 (150.0–190.0)	150 (135–165)	26 (24–29)	24 (22–25)	—	111 (110–112)	46 (44–49)	23 (22–24)
Hipposideros ater	1♀	5	49	30	17	—	43	18	6
Hipposideros sp. cf. *maggietaylorae*	1♂	—	—	32	16	—	50	22	10
Macroglossus minimus	3♂	13 (12.0–14.0)	49	—	14 (13–15)	—	38 (38–39)	14 (12–15)	11 (10–11)
Mosia nigrescens	1♀	2	37	9	10	4	34	12	6
Nyctimene sp. cf. *albiventer*	1♂2♀	29 (26.0–30.0)	82 (73–86)	21 (18–26)	14 (11–15)	—	55	20	12 (11–13)
Paranyctimene raptor	3♂4♀	30 (25.0–35.0)	82 (78–86)	20 (17–24)	13 (12–15)	—	56 (53–59)	21 (20–21)	13 (12–13)
Rousettus amplexicaudatus	1♀	67	108	18	18	—	83	35	20
Syconycteris australis	2♂2♀	16 (15.0–16.0)	67 (65–70)	—	15 (14–16)	—	43 (41–44)	17 (15–18)	12 (11–12)

MZB registration numbers:
Aselliscus tricuspidatus: MZB 35057
Dobsonia beauforti: MZB 35096, MZB 35097
Hipposideros ater: MZB 35118
Hipposideros sp. cf. *maggietaylorae*: MZB 35119
Macroglossus minimus: MZB 35112, MZB 35113, MZB 35064
Mosia nigrescens: MZB 35071
Nyctimene sp. cf. *albiventer*: MZB 35091, MZB 35092, MZB 35093
Paranyctimene raptor: MZB 35065, MZB 35068, MZB 35101, MZB 35102, MZB 35098, MZB 35099, MZB 35100
Rousettus amplexicaudatus: MZB 35117
Syconycteris australis: MZB 35067, MZB 35081, MZB 35082, MZB 35083

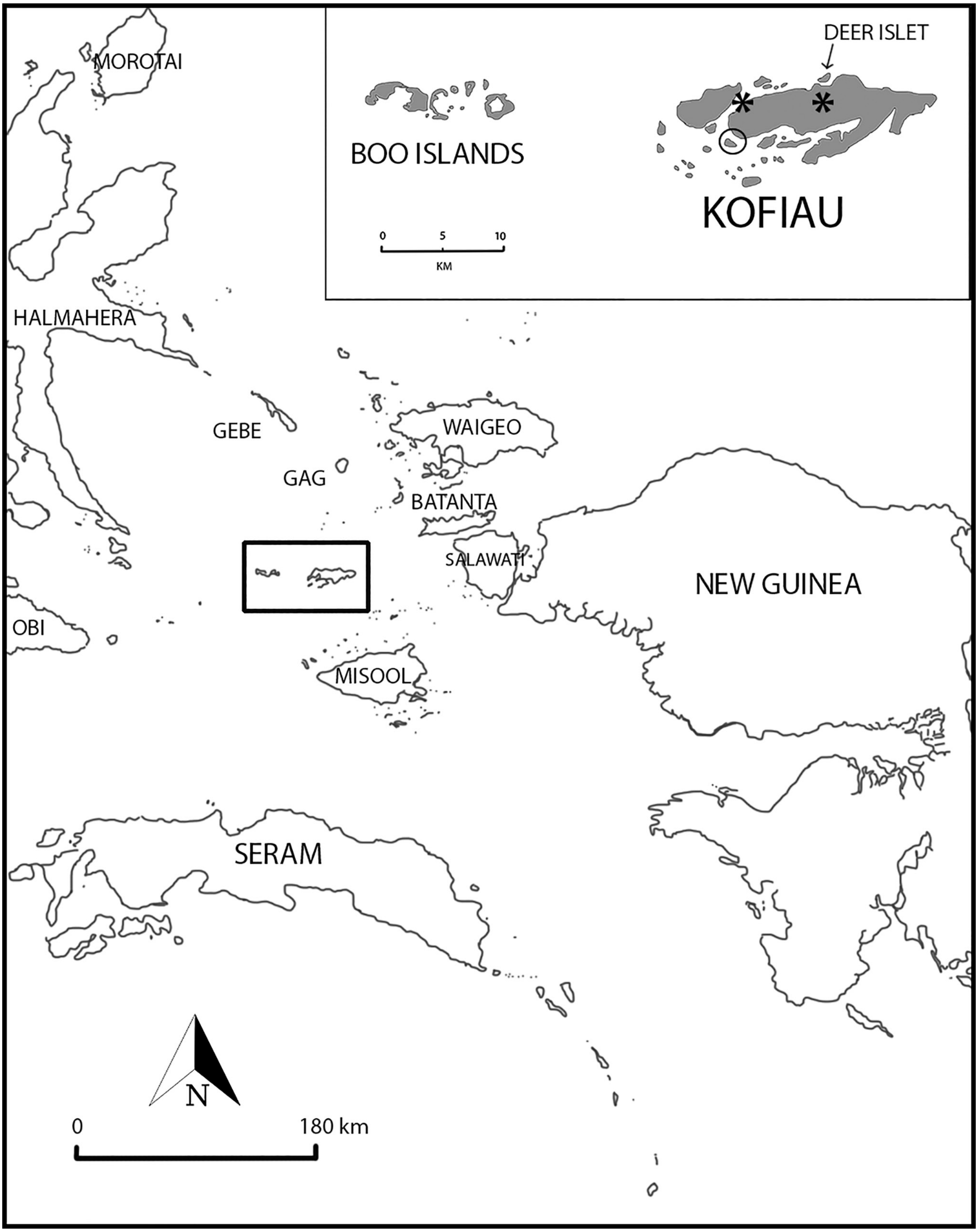

Figure 1. Map of Kofiau Island and wider region. The stars denote survey locations from 2011 and the small circle indicates the south coast islet survey location in 2019.

Josias incidentally noted that the nearest cave inhabited by bats was *jauh sekali* (very far away) from Kampong Deer, as well as confirming the presence of several species (see below), and the absence of some species we had suspected might occur on Kofiau.

Location 2: Islet off the south-west coast of Kofiau. Observations were conducted between approximately 6 pm and 7 pm, from four Zodiacs. DB had a bat detector and torch, TF had Swarovski X10 binoculars. Attention was focussed on bats. Little bat activity was noted until around 6.30 pm, when a flowering *Syzygium* tree (jambu) was located growing adjacent to the shore, and several fruit bats were seen flying in the vicinity. At least eight species of echolocating bat were identified from the bat detector recordings. Bat echolocation calls were recorded at a resolution of 256 kHz with a Wildlife Acoustics Echo Meter Touch 1 connected to an Apple iPhone. Calls were inspected in Adobe Audition CS6 version 5.0.2 and identified based on the similarity of calls documented from Papua New Guinea (Armstrong & Aplin, 2011, 2014; Leary & Pennay, 2011; Armstrong *et al.*, 2015; Armstrong, 2017; see these references also for call type nomenclature used herein).

Results

The terrestrial mammal fauna of Kofiau

Diprotodontia Owen, 1866

Phalangeridae Thomas, 1888

Phalanger orientalis orientalis (Pallas, 1766). Common throughout the island. Two juvenile females (both large pouch young) were being held in the village at the time of our visit. Both individuals were photographed by expeditioners, one of which is shown in Fig. 2. Based on our examination of their external morphology, they are not distinguishable from individuals from mainland New Guinea.

Phalanger orientalis is widespread and abundant in the northern lowlands of New Guinea and adjacent islands, as well as in the Raja Ampat Islands, Seram, Buru and Timor (Flannery, 1995). It has been introduced to Timor, and probably to many other islands in its distribution, including possibly Kofiau.

Petauridae Bonaparte, 1838

Petaurus* sp. cf. *breviceps Waterhouse, 1838. Sugar gliders were confirmed by Josias as being present in coconut plantations and elsewhere. None were seen by members of the 2019 expedition. As currently constituted, it is one of the most widespread of marsupials, occurring from southeastern Australia to New Guinea, New Ireland, Halmahera and many smaller islands. However, *Petaurus breviceps* is almost certainly a species complex in the New Guinea region (Helgen, 2007), as has recently been demonstrated for the Australian portion of its formerly recognized range, which is now classified in 3 distinct species, *P. breviceps*, *P. notatus*, and *P. ariel*. Previously, sugar gliders have been recorded on Salawati and Misool in the Raja Ampats. *Petaurus* may have been introduced by humans to some Melanesian and particularly to Moluccan islands (Flannery, 1995).

Rodentia Bowdich, 1821

Muridae Illiger, 1811

***Melomys* sp**. After careful examination of a photograph, and a description of the creature given by TF, Josias confirmed that a species of *Melomys* resembling *M. rufescens* occurs on Kofiau. *Melomys rufescens* is widespread in the New Guinea lowlands as well as on adjacent islands, but several similar island endemics also occur in Melanesia, e.g., *M. matambuai* on Manus, and *M. bougainville* in the Solomon Islands (Flannery, 1995). Other species of *Melomys* occur throughout the Moluccas, including the widespread species *Melomys lutillus* in Halmahera and a variety of endemic taxa in Seram, Obi, the Tanimbars, and Talaud Islands (Flannery, 1995; Helgen, 2003; Fabre *et al*., 2017).

Chiroptera Blumenbach, 1779

Pteropodidae Gray, 1821

Nyctimene* sp. cf. *albiventer (Gray, 1863). This taxon represents a species complex and requires systematic revision (Helgen, 2007; Aplin & Armstrong, 2021). It has been recorded on Salawati, Waigeo and Batanta in the Raja Ampats, as well as on Gebe, Halmahera, New Guinea and nearby islands (Flannery, 1995). It was recorded during the 2011 survey but was not encountered in 2019. However, a photograph of *Nyctimene albiventer* was recognized by Josias (Kepala Kampong), who commented that it roosted in foliage on Kofiau.

Paranyctimene raptor Tate, 1942. Seven individuals of *Paranyctimene* were captured during the 2011 survey, but the taxon was not recorded in 2019. The genus is widespread below around 1,000 m in elevation in New Guinea and has been recorded from Salawati and Waigeo in the Raja Ampat group (Wiantoro, 2011). The two currently recognized species of *Paranyctimene, P. raptor* and *P. tenax*, are difficult to distinguish (Bergmans, 2001).

Macroglossus minimus (Geoffroy, 1810). This is an extremely widespread species of blossom bat, being recorded from Thailand and Vietnam through to the Solomon Islands and Australia. It is one of the most commonly mistnetted species in lowland Melanesia. It was recorded from the Boo Islands near Kofiau by Kompanje & Moeliker (2001). This species was captured in a mistnet in the 2011 survey. In 2019, between 6.30 and 7.00 pm, blossom bats probably representing both *Macroglossus* and *Syconycteris* (which were not possible to distinguish in the spotlight) were present in abundance, feeding on the blossoms of a *Syzygium* that was growing on an islet just south of Kofiau. Feeding frequency dropped from its initial high rate by around 6.50 pm.

Syconycteris australis (Peters, 1867). This species is distributed in eastern Australia, New Guinea and nearby islands, as well as on Salawati and Batanta in the Raja Ampat group, and on Halmahera, Gebe, Seram, and Buru in the Moluccas (Flannery, 1995). This species was captured in a mistnet during the 2011 survey and probably sighted by spotlight feeding on a flowering *Syzygium* growing on an islet just south of Kofiau, in 2019.

Figure 2. Juvenile *Phalanger orientalis*, Kampong Deer (Location 1), Kofiau.

Dobsonia beauforti Bergmans, 1975. This species is endemic to the Raja Ampat group. It occurs on Batanta, Gebe, Salawati, Gag and Waigeo, and is possibly present on Misool (Mildenstein, 2016). It is otherwise known only from the Biak-Supiori group in Cenderawasih Bay. It has been recorded roosting in caves, and also under fallen logs (Flannery, 1995). It was captured in a mistnet in the 2011 survey. In 2019 around a dozen individuals likely to be this species were seen emerging from the forest in the vicinity of the flowering *Syzygium*, before flying at low elevation (2–3 m) towards another islet.

Rousettus amplexicaudatus (Geoffroy, 1810). This species has a wide distribution, from Myanmar through to Indonesia in southeast Asia, and on to New Guinea and satellite islands, eastwards to the Solomon Islands (Flannery, 1995). During the 2011 survey, this species was captured. In 2019, a few individuals, likely to be this species, were observed flitting around a flowering *Syzygium* growing on an offshore islet.

Pteropus chrysoproctus Temmick, 1837. Otherwise known only from the north and central Moluccan islands of Gebe, Obi, Buru and Seram and satellite islands, including Ambon, Gorong, and Pulau Panjang (Flannery, 1995; Tsang, 2016). A single medium-sized flying-fox with a yellowish mantle, identified as this species, was seen flying parallel to the coast at an elevation of about 10 m in the channel between the islet off the south coast and the main island of Kofiau. This species was first recorded on Kofiau over a century ago: the only museum specimen of a mammal previously reported from Kofiau is a single specimen of *Pteropus chrysoproctus* in the Naturalis Museum in Leiden, RMNH 38000, an adult female, mounted skin with skull. Matschie (1899: 14) and Jentink (1887) referred to the locality for this specimen as “Koffian”, and Andersen (1912: 261, 263) interpreted this as Keffing (= Seram Rei), an island in the Seram Laut group. However, according to labels associated with RMNH 38000 (an adult female, mounted skull and skin), the specimen was indeed collected on Kofiau by D. S. Hoedt in 1867 (or perhaps actually his assistant D. Hokum—Ripley, 1959) during a bird-collecting trip, and letters from Hoedt in the Leiden archives confirm the validity of this record (C. Smeenk, *in litt.*). There is thus no confirmed record of *P. chrysoproctus* from Seram Rei.

Rhinolophidae Gray, 1825

Rhinolophus* sp. cf. *euryotis Temminck, 1835. Recorded from Sulawesi to Timor, New Guinea and the Bismarck Archipelago, it also occurs on smaller islands in the region, including Batanta and Waigeo in the Raja Ampat group (Wiantoro, 2011). It roosts in caves and appears to be far more common in the Moluccas than on islands further east (Flannery, 1995). On Kofiau, long duration echolocation calls indicative of a species of *Rhinolophus* were detected with a characteristic frequency of 55 kHz, which is similar to *R. euryotis* in New Guinea (call type *55 lCF;* Armstrong & Aplin, 2017).

Hipposideridae Lydekker, 1891

Aselliscus tricuspidatus (Temminck, 1835). Temminck's horseshoe bat occurs from Halmahera in the west to New Guinea and on to the Solomon Islands and Vanuatu in the east (Flannery, 1995). In the Raja Ampat group, it has previously been recorded only from Waigeo (Meinig, 2002; Wiantoro, 2011). It was captured on Kofiau during the 2011 survey, and in 2019 was detected unambiguously based on its echolocation calls that have a shape typical of hipposiderids and a characteristic frequency between 115 and 120 kHz (call type *118 sCF*) (Fig. 3).

Hipposideros* sp. cf. *maggietaylorae Smith & Hill, 1981. This medium-sized hipposiderid has been recorded from the Bismarck Archipelago, New Guinea and some nearby islands (Armstrong & Wiantoro, 2021b; Flannery, 1995). Meinig (2002) and Wiantoro (2011) have recorded individuals provisionally assigned to this species from Waigeo and Batanta in the Raja Ampat group. A single specimen also provisionally referred to this species (pending a more detailed systematic review) was collected on Kofiau during the 2011 survey. Its echolocation calls were not recorded with the bat detector on the 2019 survey.

Hipposideros diadema (Geoffroy, 1813). This species is widely distributed from Thailand to New Guinea, Australia and the Solomon Islands, and has previously been reported from Batanta and Waigeo in the Raja Ampat group (Aguilar & Waldien, 2021). It was detected unambiguously based on its low frequency echolocation calls that have a shape typical of hipposiderids and a characteristic frequency typical of the species throughout its range (call type *55 mCF*; Leary & Pennay, 2011; Armstrong, 2017) (Fig. 3).

Hipposideros ater Templeton, 1848. This species occurs from India eastwards to the Philippines, Australia, New Guinea and the Bismarck Archipelago (Flannery, 1995; Armstrong, 2021a). It is uncommon in Melanesia. Meinig (2002) reports it from Batanta. A single specimen was captured on Kofiau during the 2011 survey.

Emballonuridae Gervais, 1855

Emballonura alecto (Eydoux & Gervais, 1836). This taxon has its centre of distribution on Borneo, the Philippines and Sulawesi. The nearest occurrences to Kofiau are on Gag Island and Seram (Armstrong & Wiantoro, 2021a). Members of the genus *Emballonura* produce distinctively shaped calls that resemble the short tonal calls of *Hipposideros* with a dominant second harmonic, but at much lower frequencies. The most likely candidate for call type *35 i.fFM.d* given the low frequency of the calls (relative to calls known from New Guinea and similar to *E. dianae*) is the relatively large-bodied *E. alecto* (Armstrong & Wiantoro, 2021a), to which we attribute these recorded calls.

Mosia nigrescens (Gray, 1843). This small sheath-tailed bat is distributed from Sulawesi, through New Guinea and to the Solomon Islands (Flannery, 1995). It roosts in the twilight zone of caves, as well as in vegetation and possibly in houses (Flannery, 1995), and occurs on many smaller islands in this region including Salawati, Batanta and Waigeo in the Raja Ampat group (Flannery, 1995). It was collected during the 2011 survey, and in 2019 was detected unambiguously on the basis of its distinctively shaped echolocation calls that have a characteristic frequency above 60 kHz (call type *63 i.fFM.d*) (Fig. 3).

Miniopteridae Dobson, 1875

Miniopterus* sp. cf. *australis Tomes, 1858. Recorded from Sumatra eastwards to Borneo, New Guinea, Australia and as far east as Vanuatu and New Caledonia, this widespread species has previously been reported from Batanta and Waigeo in the Raja Ampat group and nearby Gebe in the North Moluccas (Flannery, 1995; Meinig, 2002; Armstrong *et al*., 2021). Frequency modulated calls with a characteristic frequency of *ca.* 53 kHz and a terminal droop have been attributed to small species of bent-winged bat in Papua New Guinea (call type *53 st.cFM.d*) (Fig. 3). The revision of Indo-Australasian *Miniopterus* by authors SW and KNA did not include a sample from Kofiau Island, but this call type is likely attributable to an undescribed species of small *Miniopterus*.

Vespertilionidae Gray, 1821

Myotis* sp. cf. *stalkeri Thomas, 1910. This distinctive fishing bat has been recorded from the Moluccan islands of Gebe and Kai Kecil, as well as from Waigeo and Batanta in the Raja Ampat group (Meinig, 2002; Bouillard, 2021). Our tentative identification from Kofiau involves observation of a large insectivorous bat seen hawking within centimetres of the ocean surface off the south coast. The bat had narrow wings and appeared to be silvery in colour in torchlight. Although no calls were recorded from the bat detector while it was under observation, at least one, and possibly two, distinct echolocation call types, attributable to different species of *Myotis* were recorded at other times (call types *20 bFM* and *30 bFM*) (Fig. 3). Given that *Myotis* can vary their calls depending on their activity, it is possible that both calls derive from one species.

Molossidae Gervais, 1856

Chaerephon jobensis (Miller, 1902). Distributed across New Guinea, Seram, Yapen and New Britain and northern Australia (Flannery, 1995; Armstrong, 2021b), Kofiau is the smallest island this taxon has been recorded on. A single recorded sequence of very narrowband ("flat") echolocation

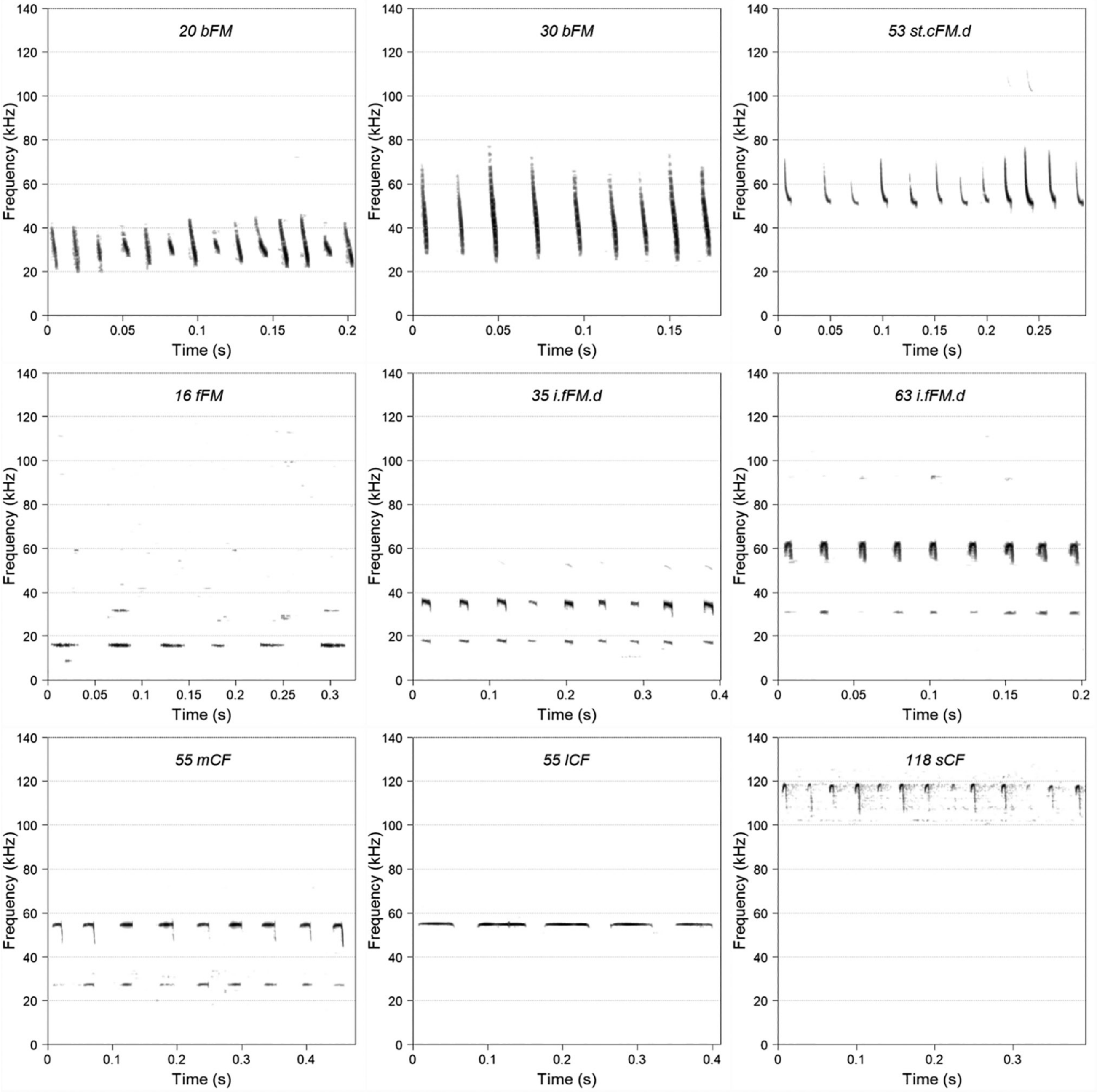

Figure 3. Representative echolocation call sequence portions of the species identified (time between pulses has been compressed). *20 bFM* and *30 bFM*: *Myotis* sp. cf. *stalkeri*; *53 st.cFM.d*: *Miniopterus* sp. cf. *australis*; *16 fFM*: *Chaerephon jobensis*; *35 i.fFM.d*: *Emballonura alecto*; *63 i.fFM.d*: *Mosia nigrescens*; *55 mCF*: *Hipposideros diadema*; *55 lCF*: *Rhinolophus euryotis*; *118 sCF*: *Aselliscus tricuspidatus*.

calls with a characteristic frequency at the fundamental of *ca.* 16 kHz (and weaker second harmonic at 32 kHz) most likely represents *C. jobensis* (call type *16 fFM*) (Fig 3).

Discussion

The records reported here bring the number of terrestrial mammals known from Kofiau from one, *Pteropus chrysoproctus,* to 20. Six species of the 20 recorded (*Macroglossus minimus*, *Syconycteris australis*, *Dobsonia beauforti*, *Rousettus amplexicaudatus*, *Mosia nigrescens* and *Aselliscus tricuspidatus*) were reported in both 2011 and 2019, by specimen collecting, direct observation, or by bat echolocation call recordings.

Several mammal species that are widespread on Melanesian islands were noted by local residents to be absent from Kofiau. These taxa were often known by Kofiau residents as occurring on other islands and could be unequivocally identified. The absent taxa include all bandicoots, *Hydromys* spp., and *Rattus praetor.* This last absence seems remarkable, because the species is widespread on Melanesian islands, but neither Josias (Kepala Kampong) nor other residents recognized images and descriptions of *Rattus praetor*, claiming that no large, harsh-furred rats existed on Kofiau. Josias also noted that spotted cuscuses (*Spilocuscus* spp.) were absent from Kofiau, but another villager told DB that a spotted cuscus did in fact occur on the island. These issues highlight the need for further work exploring the mammal fauna of Kofiau.

Our surveys reveal that the mammal fauna of Kofiau is typical of that of oceanic islands in having a very limited non-volant element. It is notable that there are no endemic taxa so far identified. This may be a function of the island's small size, but may also suggest that Kofiau might be a relatively young island, despite its endemic birds (see above). The island is however of interest in that it marks a zone of overlap between the distinctive Moluccan fauna, and the mammal fauna typical of non-land bridge islands lying near New Guinea. *Pteropus chrysoproctus* and *Myotis* sp. cf. *stalkeri* are principally Moluccan species that may reach their easternmost limit on Kofiau, while others, such as *Hipposideros* sp. cf. *maggietaylorae* and *Dobsonia beauforti*, are Melanesian taxa that reach their westernmost distributional limit on the island.

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Trypanosoma (Euglenozoa: Kinetoplastea) Infections in Rodents, Bats, and Shrews along an Elevation and Disturbance Gradient in Central Sulawesi, Indonesia

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Abstract. Surveillance of wildlife pathogens is critically important to the conservation of species and human health. However, few species of wildlife in biodiverse countries like Indonesia, especially endemic species in intact ecosystems, have been screened for most wildlife pathogens, including the abundant and diverse blood parasites in the family Trypanosomatidae. We used PCR and sequencing to screen for the presence of *Trypanosoma* infections in 616 native mammalian specimens (355 samples from 15 rodent species, 155 samples from 7 shrew species, and 96 samples from 12 bat species) collected in 2013 and 2018 along an elevation and disturbance gradient in and adjacent to Cagar Alam Gunung Dako, Toli-Toli, Central Sulawesi. We identified *Trypanosoma* infections with an average prevalence of 22.1% across all species, 21.7% in rodents, 30.3% in shrews, and 10.4% in bats. Infections were dominated by sequences similar to *T. cyclops* in the Theileri clade, which accounted for 86.6% of infections and are most likely native trypanosomes to Sulawesi. The second most common trypanosome sequences matched cosmopolitan and probably introduced trypanosomes in the Lewisi clade. They accounted for 9.7% of infections in all mammals but were only detected in rodents of the family Muridae where they accounted for 16.9% of infections. We also detected five infections in bats (50% of bat infections) by two trypanosomes from the

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Cruzi clade, one matching *T. dionisii* and the other unassignable to a named species but with sequence similarity to a diverse clade of trypanosomes found in Neotropical bats, Australian marsupials and rodents, and Malagasy lemurs. We found significant differences in prevalence of the Theileri clade (*T. cyclops*) among elevations with higher infection rates in more intact and healthier rainforest. While no health impacts are evident from infections by these Theileri clade (*T. cyclops*) trypanosomes, their infections across mammalian orders including rodents, bats, shrews, primates and marsupials suggest that they may infect humans and domestic livestock. Our discovery of infections of rodents on Mt. Dako by introduced trypanosomes from the Lewisi clade and infections of bats by *T. dionisii* and an unnamed trypanosome from the Cruzi clade warrant further surveillance of trypanosome infections in wildlife of Sulawesi.

Abstrak [Bahasa Indonesia]. Pengamatan tentang patogen sangat penting dalam dunia konservasi dan kesehatan manusia. Namun, hingga saat ini penelitian tentang keberadaan kebanyakan parasit satwa liar masih sangat sedikit sekali, terutama pada spesies endemik di ekosistem yang utuh di negara dengan tingkat keanekaragaman biodiversitas yang tinggi seperti Indonesia. Ini termasuk pada kelompok parasit darah famili Trypanosomatidae yang memiliki tingkat keberagaman yang tinggi dan melimpah. Kami menggunakan teknik PCR untuk mengidentifikasi keberadaan infeksi famili Trypanosomatidae pada 616 spesimen spesies mamalia asli (355 sampel dari 15 spesies Rodentia, 155 sampel dari 7 spesies celurut, dan 96 sampel dari 12 spesies kelelawar) yang dikoleksi pada tahun 2013 dan 2018 disepanjang lereng elevasi dan tingkat gangguan habitat di Cagar Alam Gunung Dako, Toli-Toli, Sulawesi Tengah dan daerah terdekat. Kami mengidentifikasi rata-rata tingkat prevalensi infeksi *Trypanosoma* sebesar 22,1% untuk semua spesies, 21,7% pada hewan pengerat, 30,3% pada celurut, dan 10,4% pada kelelawar. Infeksi *Trypanosoma* didominasi oleh sekuen yang mirip dengan *T. cyclops* di klade Theileri yang menyumbang 86,6% dari total infeksi dan diduga sebagai *Trypanosoma* asli Sulawesi. Sekuen denganurutan tingkat infeksi paling umum kedua teridentifikasi sebagai spesies cosmopolitan dan kemungkinan spesies *Tryponosoma* introduksi di klade Lewisi. Kelompok ini menyumbang 9,7% di semua mamalia dan terbatas pada kelompok hewan pengerat dari famili Muridae dimana mereka menyumbang 16,9% dari total infeksi. Kami juga mendeteksi lima infeksi *Trypanosoma* dari klade Cruzi pada kelelawar (50% dari total infeksi pada kelelawar), dimana satu sampel teridentifikasi sebagai *T. dionisii* dan sampel lainnya belum diberikan nama, tetapi hasil sekuen memiliki kesamaan dengan sub-klade Australia dan *Neobats*. Kami menemukan perbedaan tingkat prevalensi yang signifikan dari klade Theileri (*T. cyclops*) pada berbagai ketinggian habitat dengan tingkat infeksi tertinggi pada hutan hujan tropis yang lebih utuh dan sehat. Meskipun tidak ada dampak kesehatan yang terbukti dari infeksi oleh trypanosoma klade Theileri (*T. cyclops*), ditemukannya infeksi jenis tersebut pada beberapa Ordo Mamalia, termasuk pada kelompok hewan pengerat, kelelawar, celurut, primata, dan hewan berkantung mengindikasikan bahwa parasit tersebut kemungkingkan dapat menginfeksi manusia dan hewan ternak. Ditemukannya hewan pengerat yang terinfeksi *Trypanosoma* introduksi di Gunung Dako dari klade Lewisi dan infeksi kelelawar oleh *T. dionisii* serta beberapa species Trypanosoma dari *clade* Cruzi yang belum dinamai, menunjukkan bahwa pengamatan lebih lanjut terhadap infeksi trypanosoma pada satwa liar Sulawesim masih perlu dilakukan.

Introduction

Species in the genus *Trypanosoma* are protists in the family Trypanosomatidae (Euglenozoa: Kinetoplastea) (Kostygov *et al.*, 2021). All members of this family are known to be parasitic in vertebrates. *Trypanosoma*, in particular, are known to infect a wide range of vertebrates across almost all classes (Hamilton *et al.*, 2007; Botero *et al.*, 2013; Thompson *et al.*, 2014; Cooper *et al.*, 2017; Calzolari *et al.*, 2018). While trypanosome infections have been detected in fewer than 150 mammalian species, they probably infect all mammalian species, of which there are over 6000 (Thompson *et al.*, 2014; Winterhoff *et al.*, 2020). Within mammals, some *Trypanosoma* are exclusive to certain orders, such as *T. lewisi* which infects only rodents (Rodentia) and is associated with the spread of invasive rodents such as black rats, *Rattus rattus* (Pumhom *et al.*, 2014). Other species infect a wide range of mammals, such as *T. cruzi* which is most common in bats but also known to infect other mammals (Cooper *et al.*, 2017). However, most mammals have not been screened for trypanosomes, including widespread groups such as shrews. Many species of *Trypanosoma* are yet to be formally described and many infections are detected by DNA methods that cannot always assign samples to species. Thus, *Trypanosoma* species are routinely organized into major phylogenetic clades including the Theileri, Lewisi, Cruzi, and Brucei clades (Cooper *et al.*, 2017). The names of these clades are based on some of the most common and significant *Trypanosoma* species found in mammals (i.e., *T. theileri*, *T. lewisi*, *T. cruzi*, and *T. brucei*) but they include numerous other species many of which have not been formally described (Cooper *et al.*, 2017).

Some species of *Trypanosoma* cause clinical symptoms in humans such as *T. brucei*, which causes sleeping sickness and Chagas disease (Cooper *et al.*, 2017). In Indonesia, the disease trypanosomiasis, caused by the introduced species *T. evansi*, that originated in Africa, inflicts considerable losses to livestock such as horses, cows, and buffaloes (Wardhana & Savitri, 2018; Setiawan *et al.*, 2021). *Trypanosoma evansi* infects livestock around the world and has spread to almost all major islands in Indonesia including Sulawesi (Dieleman, 1986; Luckins, 1998; Setiawan *et al.*, 2021). *Trypanosoma* species in the Theileri clade and closely related to *T. cyclops* (Weinman, 1972), were detected recently on Sulawesi infecting endemic rodents with high prevalence (Winterhoff *et al.*, 2020). Given that the island of Sulawesi is located between the Asian and Australian continental shelves, it is particularly relevant to the biogeography

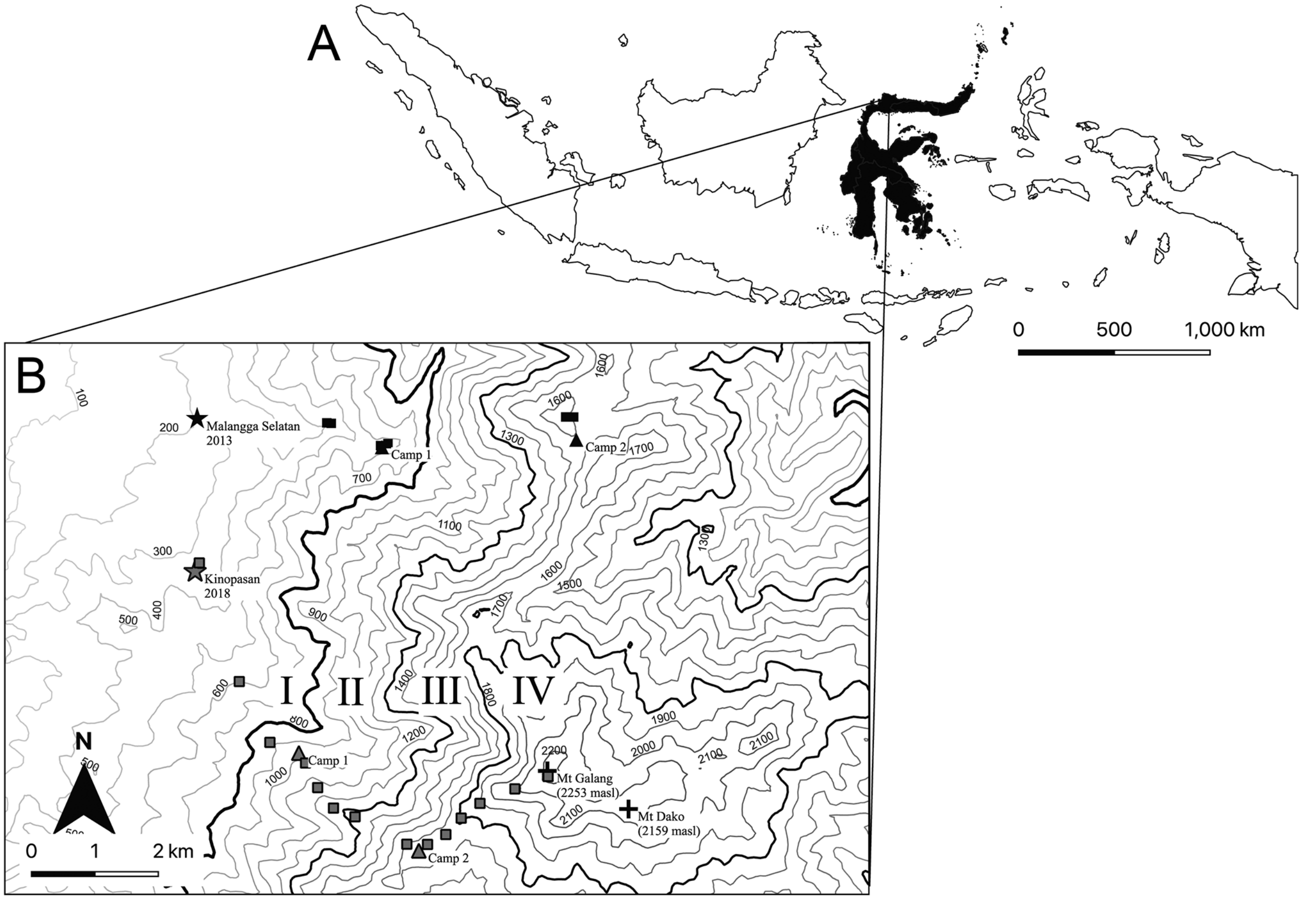

Figure 1. (*A*) Location of Gunung Dako Cagar Alam on Sulawesi Island Indonesia. (*B*) Detail of elevational transects surveyed in 2013 (black symbols) and 2018 (grey symbols). The villages of Malangga Selatan and Kinopasan are indicated with stars. Camps are indicated with triangles. The approximate centroids of traplines are indicated with squares. Topographic lines are marked at 100 m intervals. Elevational bins used in this study are labelled with roman numerals with topographic lines at 800, 1300, and 1800 m in bold.

and spread of pathogens between the continents, with *T. cyclops* an example. *Trypanosoma cyclops* was originally described from an infection in a Malaysian primate, *Macaca nemestrina* (Weinman, 1972) and has been detected with genetic methods from rodents and marsupials from Sri Lanka to Australia (Thompson *et al.*, 2014; Cooper *et al.*, 2017; Winterhoff *et al.*, 2020). They are most likely endemic to these areas, including across Indonesia, and are likely to infect a wide range of mammalian hosts. Species of trypanosomes that are spread by introduced rodents (e.g., *Rattus* spp.) in the Lewisi clade were also detected on Sulawesi and infecting endemic rodents, albeit at much lower prevalence than the endemic *T. cyclops* (Winterhoff *et al.*, 2020). Given the widespread distribution of invasive rodents across Indonesia and on the island of Sulawesi (e.g., *Rattus exulans*, *R. tanezumi*, *R. norvegicus*, and *Mus musculus*), *T. lewisi* is likely to be distributed throughout Indonesia.

Introduced parasites are threats to native species worldwide, especially island endemics. Some species of trypanosome cause diseases in wildlife leading to population declines. For example, *T. copemanii* infections are linked to the rapid decline of populations of an Australian marsupial, the woylie (*Bettongia penicillata*) (Thompson *et al.*, 2014). Zoonotic diseases threatening wildlife can emerge through "spill-over" or "spill-back" from invasive species and domesticated animals, especially when an infected population with a high pathogen prevalence comes into contact with a novel host population (Thompson, 2013). Transmission of diseases from introduced species to novel wildlife hosts also pose risks of emerging diseases infecting domestic animals and/or humans (Cleaveland *et al.*, 2001; Gortázar *et al.*, 2007; Martin *et al.*, 2011).

In this study, we used PCR and sequencing to identify trypanosome infections in native rodents, bats, and shrews on a protected mountain of Sulawesi where trypanosome communities have not been assessed. Notably, no *Trypanosoma* infection has ever been reported from shrews in Indonesia, and this is the first study to include these host species from Indonesia. To test if infection rates are correlated with forest disturbance or with proximity to humans and their commensal species, we sampled from village to peak along an elevation gradient spanning nearly 2000 m.

Material and methods

Sampling of small mammals

In this study we surveyed small mammals (rodents, bats, and shrews) in and adjacent to Cagar Alam Gunung Dako (Mount Dako Nature Reserve), Sulawesi, Indonesia (Fig. 1). The reserve is located in the Galang District of the Toli-Toli Regency at the northern end of the Central Sulawesi province. It has an area of 197 km^2 and surrounds the peaks of Mount Dako (2,159 m asl) and the slightly taller Mount Galang (2,253 m asl). Surveys were conducted in March 2013 and July 2018 along two elevational transects starting from the villages of Malangga Selatan and Kinopasan, respectively. Surveys were conducted using a combination of Sherman traps, snap traps, mistnets, and pitfall traps. We merged trap lines into four elevational bins (Fig. 1), reflecting a gradient of human impacts from village edge to the peak of Mt. Galang. The lowest elevational bin (300–800 m asl) was adjacent to villages, farms, and plantations. The second elevational bin was in secondary forest above active plantations (801–1300 m asl). The third (1301–1800 m asl) and fourth (1801–2225 m asl) elevational bins were in largely intact forest well inside the reserve. While preparing specimens, liver and other tissues were perfused with RNA later or ethanol and stored in liquid nitrogen until returning from the field (Table S1). Sampling was led by the Research Center for Biology, Indonesian Institute of Sciences (LIPI) with permits from the Indonesian Ministry of Technology and Higher Education (RISTEK), along with authorization from the Ministry of Environment and Forestry Indonesia (Central Sulawesi BKSDA). Procedures followed animal ethics permit MVAEC-15002.

Molecular detection and sequencing

To identify samples infected with *Trypanosoma*, we extracted genomic DNA from liver tissue using QIAextractor (DX reagents and plasticware), QIAGEN DNeasy blood and tissue kits, or Wizard SV 96 Genomic DNA Purification Systems following manufacturer's guidelines (QIAGEN Inc., Valencia, CA, USA; Promega, Madison, WI, USA). We used a universal set of trypanosome primers targeting *ca.* 906 bp fragments from the 18S gene region following the PCR protocol previously described (Winterhoff *et al.*, 2020). PCR reactions were screened using electrophoretic gels and those with visible bands in the correct size range were considered a positive infection. Each of these was purified using ExoSAP (USB Corporation, Cleveland, Ohio, USA) and sequenced on an Applied Biosystems 3730 Automatic DNA Sequencer (Applied Biosystems, Foster City, California, USA) using PCR primers. Successful sequences were identified to genus and species where possible using the nucleotide BLAST tool within the NCBI GenBank database. DNA sequences are available in GenBank under accessions OR036096–OR036228.

Statistical analysis

To examine how trypanosome infections were related to ecological factors, we tested the relationship between prevalence and elevation. We estimated trypanosome prevalence (number infected vs. non-infected) for each trypanosome clade with more than 10 infections (i.e., Theileri and Lewisi) in each elevational bin and tested for significant differences among bins using a Chi-square test of independence. In the case where significant differences were found among elevation bins, we used a Chi-square goodness of fit test to determine whether the number of infections within a bin was significantly different than random. For both tests, we used the "chisq.test" function from the "stats" package in R (version 3.6.3, R Core Team, 2020).

Results

We collected and screened 616 specimens from three mammalian orders for trypanosome infections (Table 1; Table S1). Ten samples with positive PCR bands (eight shrews, two rodents) failed to produce reliable sequences that could be assigned to a trypanosome clade. We excluded these from our sample sizes leaving 606 samples comprising 355 rodents (16 species), 155 shrews (7 species), and 96 bats (11 species). We detected identifiable trypanosome infections by sequencing in 134 samples including in seven species of rodents (*Bunomys chrysocomus, Frateromys fratrorum, Haeromys minahassae, Maxomys musschenbroekii, Rattus hoffmanni, Taeromys dominator,* and *T. taerae*), five species of shrews (*Crocidura balete, C. elongata, C. lea, C. nigripes, C. pseudorhoditis*), and six species of bats (*Cynopterus brachyotis, Macroglossus minimus, Rhinolophus celebensis, Rousettus celebensis, Thoopterus nigrescens,* and *Tadarida sarasinorum*). Excluding samples that failed at sequencing, the average prevalence across all samples was 21.9%. Shrews had the highest prevalence with 30.3% of specimens infected by *Trypanosoma* compared to 21.4% in rodents and 10.4% in bats.

Based on sequences of the 18s rDNA gene we identified infections by trypanosomes from three major clades (Cooper *et al.*, 2017); the Theileri, Lewisi and Cruzi clades (Table 2). Sequences of the Theileri clade matched closely (> 99% sequence similarity) to *T. cyclops*, originally described from Malaysian macaques, and previously detected in terrestrial leeches, frogs, marsupials and rodents from mainland Asia, Sulawesi, and Australia (Cooper *et al.*, 2017; Winterhoff *et al.*, 2020). These Theileri clade (*T. cyclops*) infections were the most common with a prevalence of 19.1% (116 infected individuals) across all samples we screened accounting for 87.2% of all infections. They were also the most common infection in each of the three orders infecting 30.3% of shrews, 18.0% of rodents, and 5.2% of bats.

Lewisi clade trypanosomes were the next most commonly detected infection accounting for 9.0% of infections and detected in 2.0% of samples. All infections were detected in rats and mice (family Muridae) where they comprised 15.8% of infections with 3.4% of individuals infected. We did not detect Lewisi clade infections in squirrels (family Sciuridae, n = 14). Lewisi clade sequences were nearly all identical and indistinguishable from several named species of *Trypanosoma* in the Lewisi clade with > 99% sequence similarity and which cannot be differentiated by 18s rDNA sequences alone. These included *T. lewisi*, *T. kuseli*, *T. otospermophili*, *T. musculi*, *T. microti* and *T. rabinowitschae* (see phylogeny in Winterhoff *et al.*, 2020).

Two Cruzi clade trypanosomes were detected in five bat samples with a prevalence of 5.2% among bats. One sample, infecting *Tadarida sarasinorum*, had 99% sequence similarity to *T. dionisii*, a close relative of *T. cruzi* and *T.*

Table 1. Sample sizes of mammalian species screened in this study, elevation range of samples, and number of samples where infections were detected. Samples with "sp." were not identified to species for this study. Generic taxonomy for murines follows Handika *et al.* (2021). Taxonomy for *Crocidura* follows Esselstyn *et al.* (2021).

					Infections		
Order	Family	Species	Elevation range (m asl)	Sample size	Theileri clade	Lewisi clade	Cruzi clade
Chiroptera	Hipposideridae	*Hipposideros* sp.	560–700	1	0	0	0
Chiroptera	Megadermatidae	*Megaderma spasma*	560–700	1	0	0	0
Chiroptera	Molossidae	*Tadarida sarasinorum*	1740–1750	3	0	0	1
Chiroptera	Pteropodidae	*Chironax melanocephalus*	560–1240	5	0	0	0
Chiroptera	Pteropodidae	*Cynopterus brachyotis*	939–1750	33	4	0	0
Chiroptera	Pteropodidae	*Macroglossus minimus*	939–965	3	1	0	0
Chiroptera	Pteropodidae	*Rousettus celebensis*	310–965	38	0	0	1
Chiroptera	Pteropodidae	*Styloctenium wallacei*	1560–1630	1	0	0	0
Chiroptera	Pteropodidae	*Thoopterus nigrescens*	310–330	5	0	0	1
Chiroptera	Rhinolophidae	*Rhinolophus celebensis*	310–1750	5	0	0	2
Chiroptera	Vespertilionidae	*Myotis* sp.	750–975	1	0	0	0
Chiroptera	**All families**	**all species**	**310–1750**	**96**	**5**	**0**	**5**
Eulipotyphla	Soricidae	*Crocidura balete*	1560–2170	4*	1	0	0
Eulipotyphla	Soricidae	*Crocidura caudipilosa*	560–1965	12	0	0	0
Eulipotyphla	Soricidae	*Crocidura elongata*	560–2170	30*	9	0	0
Eulipotyphla	Soricidae	*Crocidura lea*	750–1630	13*	8	0	0
Eulipotyphla	Soricidae	*Crocidura nigripes*	310–1850	35	8	0	0
Eulipotyphla	Soricidae	*Crocidura pseudorhoditis*	560–2170	60*	21	0	0
Eulipotyphla	Soricidae	*Crocidura quasielongata*	310–330	1	0	0	0
Eulipotyphla	**Soricidae**	**all species**	**310–2170**	**155**	**47**	**0**	**0**
Rodentia	Muridae	*Bunomys chrysocomus*	310–1390	31	2	0	0
Rodentia	Muridae	*Frateromys fratrorum*	750–1750	58*	17	1	0
Rodentia	Muridae	*Haeromys minahassae*	410–1630	2	0	1	0
Rodentia	Muridae	*Hyorhinomys stuempkei*	1560–1965	3	0	0	0
Rodentia	Muridae	*Margaretamys* sp.	2200–2230	1	0	0	0
Rodentia	Muridae	*Maxomys dollmani*	1240–1965	4	0	0	0
Rodentia	Muridae	*Maxomys hellwaldii*	410–450	1	0	0	0
Rodentia	Muridae	*Maxomys musschenbroekii*	550–2170	113	24	2	0
Rodentia	Muridae	*Rattus facetus*	550–2170	19	0	0	0
Rodentia	Muridae	*Rattus hoffmanni*	310–1750	45	2	8	0
Rodentia	Muridae	*Taeromys callitrichus*	560–700	2	0	0	0
Rodentia	Muridae	*Taeromys celebensis*	1740–1765	1	0	0	0
Rodentia	Muridae	*Taeromys dominator*	310–2230	27	4	0	0
Rodentia	Muridae	*Taeromys taerae*	975–2170	34*	15	0	0
Rodentia	Sciuridae	*Prosciurillus murinus*	310–1755	14	0	0	0
Rodentia	**all families**	**all species**	**310–2170**	**355**	**64**	**12**	**0**
all orders	**all families**	**all species**	**310–2170**	**606**	**116**	**12**	**5**

* Sample sizes exclude 10 samples with positive PCR bands that failed at sequencing.
Crocidura balete (n = 1), *C. elongata* (n = 4), *C. lea* (n = 2), *C. pseudorhoditis* (n = 1), *Frateromys fratrorum* (n = 1), and *Taeromys taerae* (n = 1).

erneyi (Schizotrypanum subclade of Espinosa-Álvarez *et al.*, 2018). The remaining four infections, detected in *Rhinolophus celebensis, Rousettus celebensis,* and *Thoopterus nigrescens*, had identical sequences but were more distantly related in the Cruzi clade (near Australian and Neobats subclades of Espinosa-Álvarez *et al.*, 2018) with 98% sequence similarity to *T. livingstonei*, *T. ralphi*, *T. grayi*, and *T. terrestris*, but not clearly assignable to any named species.

The average prevalence of any trypanosome infection varied across elevational bins with the highest prevalence at middle elevations (range 10.8–26.2%; Table 3). However, this pattern was driven primarily by the prevalence of Theileri clade (*T. cyclops*) infections (range 3.3–24.1%; Table 3). A chi-square test for independence showed that Theileri clade (*T. cyclops*) infections were not randomly distributed among elevational bins ($\chi^2 = 25.124$, $p < 0.0001$) and largely because infections in the lowest elevational bin (4 of 120 specimens) were significantly less than expected (chi-square goodness of fit, $\chi^2 = 18.97$, $p < 0.0001$). Infections were slightly but not significantly higher than expected at middle elevational bins and exactly as expected at the highest elevational bin.

Table 2. Sample sizes of hosts and prevalence of each trypanosome clade for each mammalian order. Sample sizes are counts whereas prevalences are percentages. Sample sizes exclude failed sequences noted in Table 1.

	Sample size			Theileri clade (*T. cyclops*)				Lewisi clade			Cruzi clade		
	♂	♀	na	♂	♀	na	all	♂	♀	all	♂	♀	%
Rodentia	175	175	5	28	35	1	18.0%	5	7	3.4%	0	0	0
Eulipotyphla	71	80	4	25	21	1	30.3%	0	0	0	0	0	0
Chiroptera	34	61	1	2	3	0	5.2%	0	0	0	4	1	5.2%
all orders							19.1%			2.0%			0.8%

For Lewisi clade infections, we calculated prevalence based on murid rodents alone as these trypanosomes only infected rodents in this family. While the highest rates of infections occurred at the lowest elevation (6 of 63 specimens; Table 3) and no infections occurred at the highest elevation, a chi-squared test for independence found that infections were only marginally significantly different from randomly distributed among elevational bins ($\chi^2 = 4.864$, $p = 0.182$). For the Cruzi clade, we calculated prevalence based only on bat specimens as these trypanosomes only infected bats. The small sample size of Cruzi infections precluded any statistical analysis. Of the five detections of Cruzi clade trypanosomes, three were at the lowest elevational bin and one each at the middle elevational bins but percent infections were consistently low, ranging from 3.7–6.5% of specimens. No bats were collected from the highest elevational bin hence prevalence could not be calculated.

Discussion

Our study demonstrates the breadth of *Trypanosoma* infections in native bats, shrews, and rodents on Sulawesi, Indonesia (Winterhoff *et al.*, 2020). Our sampling from Mount Dako, detected *Trypanosoma* infecting 17 mammalian species native to Sulawesi, including seven murid rodent species (50% of species), five shrew species (71% of species), and five bat species (45% of species). The trypanosome infections we detected fell within three of the four major *Trypanosoma* clades known to infect mammals: Theileri clade (*T. cyclops*) which contains trypanosomes endemic to placental mammals and marsupials in Malaysia, Sri Lanka and Australia (Hamilton *et al.*, 2005; Pumhom *et al.*, 2014); Lewisi clade which contains the invasive and globally distributed *T. lewisi*; and Cruzi clade which contains trypanosomes from Old and New World bats, South American mammals and Australian marsupials (Hamilton *et al.*, 2012). Consistent with Winterhoff *et al.* (2020), infections were dominated by the Theileri clade (*T. cyclops*), which accounted for > 86% of infections. Notably, we did not detect any trypanosomes from the Brucei clade, which contains the introduced *Trypanosoma evansi* known to infect cattle on Sulawesi (Setiawan *et al.*, 2021).

Theileri clade (*T. cyclops*) infections were present in all three host orders sampled indicating that all three are reservoirs for infection. Shrews exhibited the highest prevalence of Theileri clade (*T. cyclops*) infections being nearly two times higher than in rodents and nearly six times higher than in bats suggesting that native shrews are an important and unrecognized reservoir for infection. The occurrence of Theileri clade (*T. cyclops*) infections in three distantly related mammalian orders suggests that these trypanosomes infect a broad range of other mammalian species on Sulawesi. Prevalence of Theileri clade (*T. cyclops*) trypanosomes was highest in intact forest at mid-to-upper elevations lending further support to the notion that they are widespread parasites of endemic mammalian communities on Sulawesi (Winterhoff *et al.*, 2020). Documentation of widespread infection by Theileri clade (*T. cyclops*) trypanosomes across rodents, bats, shrews, primates and marsupials suggests that these trypanosomes can infect most other mammalian species including humans and domesticated animals. While Theileri clade (*T. cyclops*) trypanosomes were more prevalent at higher elevations on Mount Dako, they also were present at the lowest elevations where endemic host species overlap with humans and domesticated animals. Theileri clade (*T. cyclops*) trypanosomes have not been recorded in humans, domesticated animals or other introduced species on Sulawesi. However, atypical human cases of other *Trypanosoma* (e.g., *T. lewisi*) occur elsewhere in Southeast Asia (Pumhom *et al.*, 2015) and few relevant samples on Sulawesi have been screened for *Trypanosoma* with PCR methods that could detect the Theileri clade. A recent study screening 100 cattle on Sulawesi did not detect any Theileri clade sequences, while detecting three sequences of the introduced *T. evansi* (Setiawan *et al.*, 2021). However, these cattle were sampled in communities near the large urban centre of Makassar and far from native mammalian communities where Theileri clade (*T. cyclops*) is likely to be a reservoir. Cattle or other domesticated animals may be at greater risk of disease spillover where they are closer to intact and more diverse mammalian communities. Disease spillover from reservoir host species to naïve hosts can lead to higher virulence in naïve hosts compared to reservoir hosts, including diseases caused by *Trypanosoma* (Wyatt *et al.*, 2008; Truc *et al.*, 2013; Pumhom *et al.*, 2014). However, to our knowledge, no illness in humans, domesticated animals or wildlife has been associated with infection by the Theileri clade (*T. cyclops*). Consequently, further research is needed into the potential for disease transmission and associated health impacts to humans, domesticated animals, and wildlife from Theileri clade (*T. cyclops*) trypanosomes.

Consistent with previous sampling on Sulawesi, Lewisi clade trypanosomes were only detected in murid rodent species (Winterhoff *et al.*, 2020). Among the Lewisi clade, *T. lewisi* is a cosmopolitan rat-specific trypanosome, whereas

Table 3. Mammalian host sample sizes and prevalence of *Trypanosoma* and *Trypanosoma* clades in each elevational bin. Prevalence of any *Trypanosoma* and of the Theileri clade (*T. cyclops*) were calculated using sample sizes of all mammalian species. For the Lewisi clade, prevalence was calculated considering only sample sizes of murid species. For the Cruzi clade, prevalence was calculated considering only sample sizes of bats. Sample sizes exclude failed sequences noted in Table 1.

	Elevational bins (m asl)			
	I (300–800)	II (801–1300)	III (1301–1800)	IV (1801–2225)
sample size (all mammals)	120	97	336	53
prevalence *Trypanosoma* (all mammals)	10.8%	23.7%	26.2%	18.9%
prevalence Theileri clade (all mammals)	3.3%	21.6%	24.1%	18.9%
sample size (Muridae)	63	50	211	17
prevalence Lewisi clade (Muridae)	9.5%	2.0%	2.8%	0
sample size (Chiroptera)	46	23	27	0
prevalence Cruzi clade (Chiroptera)	6.5%	4.3%	3.7%	na

other Lewisi clade species are known to infect other rodent species (Hamilton *et al.*, 2005, 2007). Thus, it is likely that the Lewisi clade trypanosomes infecting endemic murid rodents on Sulawesi were introduced with introduced murid rodents (e.g., *Mus musculus, Rattus exulans, R. norvegicus* or *R. rattus;* Winterhoff *et al.*, 2020). Prevalence of Lewisi clade trypanosomes was highest at the lowest elevations sampled corresponding to areas of greatest human habitat disturbance. This also is consistent with it being introduced through the spread of introduced and commensal murid host species which are most common around human disturbance (Pumhom *et al.*, 2014; Salzer *et al.*, 2016). While none of these introduced rodents were sampled in this study they were observed in the village where limited trapping was conducted. Nearly 70% of Lewisi clade infections occurred in an endemic *Rattus* species (*R. hoffmanni*) including all infections at the lowest elevation. However, Lewisi clade infections were also detected in three other native murid host genera (i.e., *Frateromys*, *Haeromys* and *Maxomys*), whereas surveys on Mts Latimojong and Bawakaraeng detected Lewisi clade infections from endemic species of *Rattus* and *Bunomys* (Winterhoff *et al.*, 2020). In addition, Lewisi infections were detected in specimens collected in relatively intact forest within Mount Dako Cagar Alam (nature reserve) at elevations up 1750 m asl, where introduced murids were not detected, suggesting that these introduced trypanosomes are penetrating protected areas of Sulawesi. On Mount Bawakaraeng, Lewisi clade infections were also detected at the highest elevations (> 2800 m asl), but where human disturbance was also substantial and introduced *R. exulans* were present (Winterhoff *et al.*, 2020). Spillover of *T. lewisi* from introduced *Rattus* species to endemic murid rodents has been reported in other forest habitats including neighbouring landmasses in the Indo-Australian region (Dobigny *et al.*, 2011; Milocco *et al.*, 2013; Pumhom *et al.*, 2014; Salzer *et al.*, 2016). This transmission risk may have implications for native wildlife health, as virulence of *T. lewisi* may increase in naïve hosts or affect host susceptibility to other infections (Brown, 1915; Hoare, 1972; Averis *et al.*, 2009; Milocco *et al.*, 2013). Where introduced, the prevalence of *T. lewisi* in native rodent hosts can exceed the prevalence of native trypanosomes (Salzer *et al.*, 2016). However, the prevalence of Lewisi clade infections in endemic rodent host species of Mount Dako (this study) and two other mountains of Sulawesi (Winterhoff *et al.*, 2020) is much lower than for the Theileri clade (*T. cyclops*). Further research into the distribution patterns of Lewisi clade trypanosomes including penetration into intact native ecosystems and their potential epidemiological effects on native wildlife is required.

Our limited sampling of bats on Sulawesi suggest that bats are hosts to numerous undocumented species of Cruzi clade trypanosomes that occur at low prevalence and will require much greater sampling to detect. While most species of Cruzi clade trypanosomes infect bats exclusively, others infect a wide range of mammalian hosts (e.g., *T. cruzi* and *T. rangeli*; Espinosa-Álvarez *et al.*, 2018), and spillover effects to wildlife, humans or domesticated animals are possible (Maeda *et al.*, 2012; Dario *et al.*, 2016, 2017). Like Lewisi clade trypanosomes, we detected Cruzi clade trypanosomes in the most samples at the lowest elevations (n = 3), but they occurred across all elevations where bats were sampled with no statistical differences detected among elevations. We detected one sequence of the Cruzi clade that was nearly identical to *T. dionisii*, which is the first record of this cosmopolitan bat-infecting trypanosome from Indonesia. *Trypanosoma dionisii* has previously been detected in a broad range of bat species from North and South America, Africa, Europe, China, Japan and Australia, so its presence on Sulawesi is not surprising (Hamilton *et al.*, 2012; Espinosa-Álvarez *et al.*, 2018; Mafie *et al.*, 2019; Wang *et al.*, 2019; Austen *et al.*, 2020; Clément *et al.*, 2020). While *T. dionisii* is generally considered non-pathogenic in bats, it has the potential to infect other mammalian species including humans with unknown epidemiological effects (Maeda *et al.*, 2012; Dario *et al.*, 2016, 2017). The four other Cruzi clade sequences detected in this study were identical to each other but not clearly related to any known Cruzi clade species. They are closest to several species in the "Australian" and "Neobats" subclades (as defined by Espinosa-Álvarez *et al.*, 2018) that include trypanosomes found in Neotropical bats, Australian marsupials and rodents, and Malagasy lemurs. Further sampling is required to determine the taxonomy, prevalence, transmissibility, and implications of Cruzi clade trypanosomes in wildlife, in particular in bat hosts where their ecological traits, behaviours and global distribution increase the chances of parasitic spill-over to new host species (Melaun *et al.*, 2014; Lima *et al.*, 2015; Clément *et al.*, 2020).

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Supplementary information

Table S1. Mammalian specimens screened for *Trypanosoma.* All registration numbers from Museums Victoria (NMV)—published separately as a *figshare* dataset
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Review of Moluccan *Rattus* (Rodentia: Muridae) with Description of Four New Species

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Abstract. Four new species of *Rattus* are described from the Moluccan islands (Maluku) of Indonesia: *Rattus taliabuensis* and *R. feileri*, both from the island of Taliabu, and *R. halmaheraensis* and *R. obiensis* from the islands of Halmahera and Obi, respectively. These descriptions are presented as part of a taxonomic review of Moluccan *Rattus* based on all known specimens in museum collections worldwide. Morphological characters, molecular systematics, and geographical distributions are documented for each of these species. Using both morpho-anatomical and morphometric approaches, we found that the Maluku Islands support *Rattus* taxa with spiny fur and two distinct morphotypes (1) species with a long tail and short rostrum (*R. morotaiensis*, *R. halmaheraensis*, *R. obiensis*, *R. feileri*) and (2) species with a short tail and long rostrum (*R. taliabuensis*, *R. feliceus, R. ceramicus, R. elaphinus*). Most of the new Moluccan species belong to a clade that includes members of the *R. xanthurus* species group from Sulawesi and the Australo-Papuan *Rattus* lineages. Their phylogenetic relationships highlight the role of Wallacea as an important area for diversification of *Rattus* into the Australo-Papuan region. Finally, the morphologically distinctive taxon *Nesoromys ceramicus* from Seram was found to be sister species to *R. feliceus*, and we relegate *Nesoromys* into the synonymy of the genus *Rattus*. The close affinities between *R. ceramicus* and *R. feliceus* may be an example of *in situ* island speciation, which has not been observed for small mammals on other Maluku Islands.

Keywords: biodiversity, biogeography, Maluku, molecular systematics, morphology, Murinae, Rattini, Wallacea
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ABSTRAK [Bahasa Indonesia]. Empat spesies baru *Rattus* dideskripsi dari Kepulauan Maluku, yaitu *Rattus taliabuensis* dan *R. feileri* dari Pulau Taliabu, *R. halmaheraensis* dan *R. obiensis* masing-masing dari Pulau Halmahera dan Pulau Obi. Deskripsi spesies baru tersebut merupakan bagian dari reviu taksonomi *Rattus* dari Maluku berdasarkan semua spesimen yang ada di seluruh koleksi museum dunia. Selain spesies baru, juga didokumentasikan karakter morfologi, sistematika molekuler dan persebaran geografis *Rattus* dari Maluku. Dengan menggunakan pendekatan morfo-anatomi dan morfometri, kami menemukan bahwa Maluku memiliki taksa *Rattus* dengan rambut duri dan dua morfotipe yang berbeda yaitu (1) berekor panjang dan moncong pendek (*R. morotaiensis*, *R. halmaheraensis*, *R. obiensis*, *R. feileri*) atau (2) berekor pendek dan moncong panjang (*R. taliabuensis*, *R. feliceus, R. ceramicus, R. elaphinus*). Semua spesies baru dari Maluku termasuk dalam satu kelompok anggota *R. xanthurus*-group dari garis keturunan *Rattus* Sulawesi dan Australo-Papua. Hubungan kekerabatan mereka menunjukkan peran Wallacea sebagai jalur kolonisasi *Rattus* menuju ke kawasan Australo-Papua. Terakhir, *Nesoromys ceramicus* dari Seram yang secara morfologis berbeda, diketahui merupakan sister spesies dari *R. feliceus*. Oleh karena itu, kami mengusulkan agar genus *Nesoromys* ditempatkan di dalam genus *Rattus*. Kedekatan antara *R. ceramicus* dan *R. feliceus* kemungkinan merupakan contoh dari spesiasi pulau *in situ*, yang belum pernah diamati pada mamalia kecil di pulau-pulau lain di Maluku.

Introduction

The Maluku Islands, also known as the Moluccas and the "Spice Islands", form an archipelago within the Wallacean biogeographic region and comprise islands between Sulawesi and western New Guinea, from Morotai Island in the north to the Tanimbar Islands in the south (Monk *et al*., 1997). Sporadic inter-island ferry services, long and dangerous voyages, ethno-political conflicts, and the ever-increasing impact of human activities make Maluku a highly challenging area in which to organize fieldwork and study little-known insular taxa. As a result, only a few expeditions have been able to conduct surveys and collect specimens to elucidate its mammalian biodiversity. The difficulty of unravelling the evolutionary relationships and biogeography of Moluccan mammals is compounded by the scarcity of older voucher material scattered throughout natural history collections (Flannery, 1995; Helgen, 2003). Indeed, most of our knowledge of Moluccan mammals comes from the seminal work of Oldfield Thomas, which was based on mammals collected by Felix, Charles, and Joseph Pratt in coastal and central Seram (Thomas, 1920). In his 1920 report, Thomas described an endemic bandicoot, *Rhynchomeles prattorum*, and six endemic species of murine rodents from Seram. Two species, *Rattus feliceus* and *Stenomys ceramicus*, were the first endemic rats recorded from Maluku, and each has a distinctive morphology. This is especially true for "*Stenomys*" *ceramicus*, which has unusual short incisive foramina and an elongate bony palate. This species, later placed in the monotypic genus *Nesoromys* by Thomas (1922), has posed a conundrum for systematists, who have classified it either as a species of *Rattus* (Corbet & Hill, 1992; Flannery, 1995; Musser, 1981), as a member of a different, widespread genus *Stenomys* (Rümmler, 1938; Musser & Newcomb, 1983), or as the monotypic Seramese endemic genus *Nesoromys* (Ellerman, 1941; Helgen, 2003; Laurie & Hill, 1954; Misonne, 1973; Musser & Carleton, 2005).

It was not until 20 years after Thomas' report, during the Second World War, that new endemic Moluccan rats were named and described. Sody (1941) described *Rattus elaphinus* from Taliabu Island in the Sula Islands, and Kellogg (1945) described *Rattus morotaiensis* from Morotai Island in the North Maluku. These species have remained little known. *Rattus elaphinus* is a ground-dwelling rat restricted to the Sula Archipelago on Taliabu and (more recently documented on) Mangole Islands (Flannery, 1995). Musser & Holden (1991) discussed this species in their monograph on the Sulawesi rat *Rattus hoffmanni*, and Musser & Carleton (2005) subsequently proposed a phylogenetic affinity for *R. elaphinus* with the *Rattus leucopus* group of species from New Guinea and Australia. Since its original description from Morotai, *R. morotaiensis* has been reported from the islands of Halmahera and Bacan (Flannery, 1995), as well as Moti Island (Rowe *et al*., 2019; Roycroft *et al*., 2022). This spiny rat has a very long potentially prehensile tail (Flannery, 1995), a short rostrum, and distinctive cranial and dental morphology which led Musser & Carleton (2005) to place it, *incertae sedis*, in a "*Rattus* species group unresolved."

Rattus has traditionally been recognized as a large genus with broad taxonomic membership across Indo-Malayan and Australo-Papuan taxa (Corbet & Hill, 1992; Taylor *et al*., 1982). Despite extensive systematic revision within the genus overall, the Moluccan species of *Rattus*, together with *Nesoromys*, still represent a major problem within the classification of the genus *Rattus*, as few specimens have been available in museums and their taxonomic status has never been assessed using DNA sequence analysis. According to recent molecular results, the "Rattus Division" (*sensu* Musser & Carleton, 2005) is now divided into five clades (Fabre *et al*., 2013, 2018; Schenk *et al*., 2013), comprising an Asian and Sundaic *Rattus* clade, a Philippine clade including *Rattus everetti* and species of *Baletemys*, *Limnomys* and *Tarsomys* (Rowsey *et al*., 2022), a *Bandicota* + *Nesokia* monophyletic group, the *Diplothrix* lineage endemic to Japan, and an Australo-Papuan clade including *Rattus morotaiensis* (Fabre *et al*., 2013, 2018, Thomson *et al*., 2018, Rowe *et al*., 2019). The study by Thomson *et al*. (2018) reported > 4% *cytochrome b* (*Cytb*) divergence between *R. morotaiensis* populations from Halmahera and Morotai, suggesting that the Halmahera population may represent a distinct species, a topic we review below.

Reviewing the taxonomic status of endemic Moluccan rats is an important step towards improving our knowledge of the alpha diversity of Wallacean *Rattus*, as well as our understanding of the role that the Asian and Australo-Papuan regions have played as evolutionary cradles and theatres for rat speciation and evolution. Indeed, Wallacea is part of a faunal transition zone between Australo-Papua, the Philippines, Sulawesi, and the Asian continental shelf (Wallace, 1902; Ali & Heaney, 2021). The murine faunas of the Philippines, Lesser Sundas, and Sulawesi are clearly of

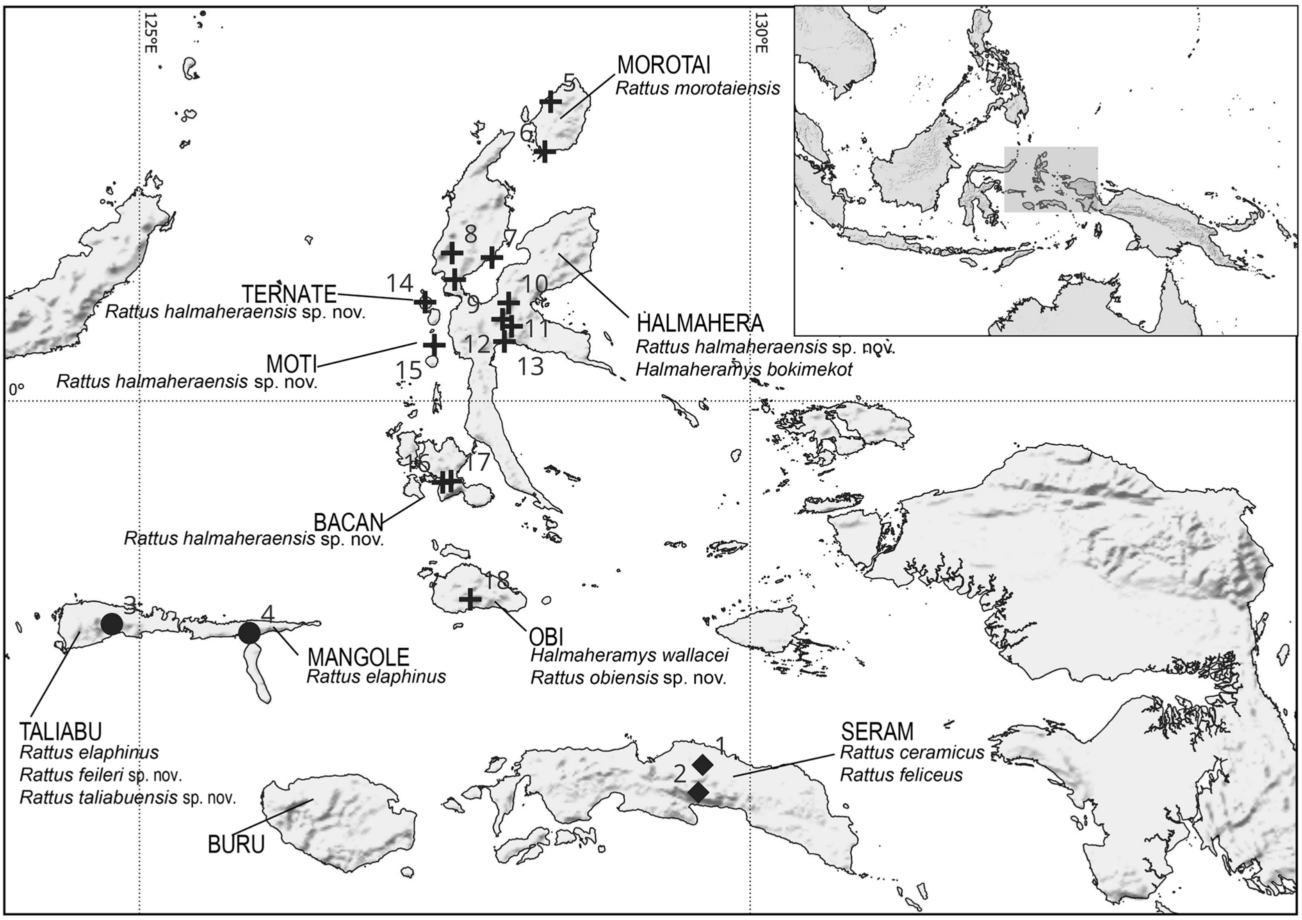

Figure 1. Distribution map for endemic species of the Rattus Division (*Rattus* and *Halmaheramys*) in the Moluccas (Maluku). Maps produced using the open SRTM database (https://www.cgiar-csi.org/data/srtm-90m-digital-elevation-database-v4-1) in the open source QGIS software (https://www.qgis.org/en/site/index.html).

Asian origin (Fabre *et al*., 2013; Heaney *et al*., 2013; Rowe *et al*., 2019). In contrast, murines arriving relatively recently from Asia appear to represent only a minor component of the faunas of the western (Taliabu, Mangole), southern (Seram) and northern Maluku Islands (Morotai, Halmahera, Bacan, Moti) (Musser & Holden, 1991; Fabre *et al*., 2013, 2018; Rowe *et al*., 2019). All other murine lineages documented in Maluku (species in the genera *Melomys* and *Hydromys*; Flannery, 1995; Fabre *et al*., 2017, 2018) belong to the Hydromyini sensu Rowsey *et al*. (2018, 2019), a clade that originated in the Australo-Papuan or Sahul region (Lecompte *et al*., 2008; Rowe *et al*., 2008; Roycroft *et al*., 2022). The Rattus Division was first defined morphologically by Musser & Carleton (2005) as one of many taxonomic "divisions" within the Murinae. More recent authors have delineated murine clades based especially via molecular phylogenetic comparisons (e.g., Lecompte *et al*., 2008; Pagès *et al*., 2010, 2016; Fabre *et al*., 2013, 2018), and we recognize these here at the taxonomic level of tribes. The tribe Rattini is a minor component within this region and is mainly of relatively recent Asian origin. Recent discoveries, such as the description of four species of the Moluccan endemic murine genus *Halmaheramys* (Fabre *et al*., 2013, 2018; Aplin *et al*., 2023), have highlighted that part of the Moluccan murine fauna is related to faunal elements of Asian rather than Sahulian origin, in particular the Sulawesian lineages *Bunomys*, *Lenomys*, *Frateromys*, *Eropeplus* and *Taeromys*, as well as the Philippine *Bullimus* and Sundaland *Sundamys* (Handika *et al*., 2021). In previous molecular studies, several Moluccan *Rattus* taxa were not placed in a phylogenetic framework, and therefore their affinities with Asian or Australo-Papuan faunas could not be assessed or clearly understood. Because of this lack of resolution, some researchers have suggested a potential affinity between Moluccan *Rattus morotaiensis* and Australo-Papuan *Rattus* lineages (Musser & Carleton, 1993, 2005; Musser & Holden, 1991; Fabre *et al*., 2013). This current view of Moluccan murine diversity persists largely due to a lack of knowledge of the molecular phylogenetic relationships among Rattini from this region. Factors such as the existence of very few specimens distributed among several museum collections around the world, the difficulty of organizing fieldwork in Maluku, and the difficulty of locating and capturing endemic taxa in highly disturbed habitats, which have proliferated in the region, have limited our knowledge of endemic Moluccan murines to date.

To address these questions, we obtained sequences of the mitochondrial gene *cytochrome b* (*Cytb*) and, where possible, some nuclear gene sequences representing all Moluccan *Rattus* species (except *Rattus elaphinus*, for which we could not yet recover sequence data). Fresh tissues were used when available, and the remaining samples were taken from traditional museum-preserved skin samples. Using these DNA markers, we then inferred phylogenetic relationships between these *Rattus* lineages and for another, previously unstudied genus from the Rattus Division—*Nesoromys*, endemic to Seram. Using this new phylogenetic framework, coupled with examinations of external and craniodental anatomies, a morphometric geometric approach, and detailed morpho-anatomical comparisons, we can now offer new diagnoses for members of the Moluccan Rattus Division. We describe two new, highly distinctive species of *Rattus* from Taliabu Island, as well as two new species of *Rattus* related to *R. morotaiensis* (*R. halmaheraensis* sp. nov. from Halmahera, Ternate, Bacan, and Moti, and *Rattus obiensis* sp. nov. from Obi; Fig. 1). We also show that *Nesoromys* is not a valid genus-level lineage within Rattini, but should be subsumed within *Rattus*, with its type species, *Rattus ceramicus*, representing a close sister lineage to *Rattus feliceus* within the broader group of Australo-Papuan *Rattus*. Analysis of these endemic Moluccan lineages enables us to better understand the importance of the Wallacean and Australian regions in the evolutionary history of *Rattus*, one of the most diverse mammalian genera worldwide, both in terms of species number and morphological variation.

Material and methods

Institutions and specimens

The research reported here is based on specimens held in the following institutions: The Australian Museum, Sydney (AM M); American Museum of Natural History, New York (AMNH); Field Museum of Natural History, Chicago (FMNH); Natural History Museum, London (NHMUK); Australian National Wildlife Collection, Canberra (ANWC); Museum Zoologicum Bogoriense, Cibinong (MZB); Nationaal Natuurhistorisch Museum Naturalis, Leiden (RMNH, Naturalis); Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde (SNSD); National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); Museums Victoria, Melbourne (NMV); and Western Australian Museum, Perth (WAM M). Specimens referenced by catalogue or field number in gazetteers, tables, text and figure captions are preceded by one of these acronyms (see Appendix 1 and Appendix 2).

Specimens were photographed using a Canon EOS7D DSLR camera equipped with a 100 mm macro lens. Scanning electron micrographs were also taken of the maxillary and mandibular occlusal surfaces of specimens of *R. morotaiensis*, *R. feileri* sp. nov. and *R. xanthurus*. Micro-CT images of the holotype of *R. obiensis* sp. nov. and two specimens of *R. halmaheraensis* sp. nov. (1 juvenile, 1 adult) were produced using an RX SkyScan 1076 (ISEM Institute, Montpellier, France). Measurements in millimetres reported for head and body length (HB), tail length (TL), hind foot length (including claws) (HF), ear length from notch (E) and weight in grams (WT) are those recorded by the collectors of museum specimens in their field notes. Skin measurements from newly collected specimens were taken with a metric ruler calibrated in millimetres; weight was measured with a Pesola balance calibrated in grams. Hair lengths in millimetres were taken from preserved museum skin specimens using a metric ruler. External measurements are reported only for adult animals (males with descended testes and females with enlarged nipples, and as demonstrated also by craniodental correlates for maturity, including as indicated by fully erupted dentition and obliteration of most cranial sutures and synchondroses, including ossification of the basioccipital-basisphenoid junction). Using a 0.01 mm graduated caliper, the following cranial and dental measurements described by Musser & Newcomb (1983) were taken from adult and subadult specimens (and a small number of juveniles representing *R obiensis* sp. nov., which is not yet represented by fully mature specimens): greatest length of skull (GLS), greatest zygomatic breadth (ZB), least interorbital breadth (IB), length of the rostrum (LR), breadth of the rostrum (BR), breadth of the braincase (BBC), length of the braincase (HBC), breadth of the zygomatic plate (BZP), length of the diastema (LD), postpalatal length (PPL), length of the bony palate (LBP), breadth of the bony palate at first molar (BBPM1), breadth of the mesopterygoid fossa (BMF); length of the incisive foramen (LIF), breadth across the incisive foramina (BIF), length of the auditory bulla (LB), crown length of the maxillary molar row (CLM1-3), and breadth of first upper molar (BM1). All measurements are given in millimetres (mm). Molar cusps and cranial structures are generally named according to the conventions established by Musser in numerous publications (e.g., Musser, 1981; Musser & Holden, 1991). The authority for the new species described below reflects the full author line of this paper.

Sequencing and assembly of the molecular data

Drawing on both NCBI specimens and new sequences, we included 130 extant species of the Rattus Division (Musser & Carleton, 2005; Appendix 2 Table 6) in our molecular phylogenetic comparisons, including species of *Abditomys*, *Baletemys*, *Bandicota*, *Diplothrix*, *Kadarsanomys*, *Nesokia*, *Palawanomys*, *Limnomys*, *Tarsomys*, *Rattus*, and *Nesoromys*. Biological specimens were obtained from both museums and fresh tissues from the above collections. In addition, we collected data from the National Center for Biotechnology Information (NCBI), selecting sequences from voucher specimens for which both mitochondrial and nuclear data were available (Table 6). We included the closest Rattini relatives as outgroups, i.e. representatives of most genera of Rattini (except the little known Philippine endemics *Anonymomys* and *Tryphomys*).

Samples from the six museum skin specimens (representing *Abditomys latidens*, *R. feliceus*, *R. feileri* sp. nov., *Rattus jobiensis*, *R. taliabuensis* sp. nov., and *Nesoromys ceramicus*) were stored in Eppendorf tubes and subsets of these were processed at the Degraded DNA Facility in Montpellier, France, which is dedicated to the processing of low quality/quantity DNA tissue samples. Ethanol preserved samples of fresh tissue were available for other sequenced taxa (*R. halmaheraensis* sp. nov. and *R. obiensis* sp. nov.; Table 6); DNA from these samples was extracted in a separate room of the laboratory to avoid contamination (LabEx CeMEB, Montpellier). DNA was extracted using the DNeasy Blood and Tissue Kit (QIAGEN) according to the manufacturer's instructions, with a final elution in water. The oldest samples were extracted in small batches and a negative control was included in each batch to monitor for possible contamination. We sequenced *Cytb* from all tissue preparations and 4 nuclear loci from the fresh tissue samples: *Brca1* (Breast cancer gene 1, exon 11), *Rbp3* (retinol binding protein 3, exon 1), *Ghr* (growth hormone receptor, exon 10), and *Rag1* (Recombination Activating 1) genes according to the detailed protocols of Rowe *et al*. (2008), Fabre *et al*. (2013, 2018) and Pagès *et al*. (2016). PCR products were processed at the Genoscope sequencing centre (Evry, France) using an ABI 3730xl automated capillary sequencer and the ABI BigDye Terminator v.3.1 sequencing kit. All sequences were analysed using CODONCODE ALIGNER software (CodonCode Corporation, Dedham, Massachusetts, USA). All genes were subsequently aligned using MACSE 1.2 (Ranwez *et al*., 2011).

A mito-nuclear supermatrix was constructed, incorporating sequence data from *Cytb*, *Brca1*, *Rbp3*, *Ghr*, and *Rag1*. We also included newly sequenced genes for 3 specimens of *Rattus halmaheraensis* sp. nov. from Halmahera, a sample of *Rattus* sp. cf. *halmaheraensis* from Moti (Rowe *et al*., 2019), and two *Rattus obiensis* sp. nov. from Obi. We combined these data into a nucleotide supermatrix consisting of 118 Rattini specimens containing both *Cytb* and coding nuclear exons (Table 6).

Phylogenetic analyses

Maximum likelihood inference was implemented on our mito-nuclear dataset using IQ-TREE 2.1.3 (Minh *et al*., 2020). Two character partitions (TIM2+F+I+G4 for codon position 1, 2, 3 *Cytb* and TRNEF+I+G for codon position 1, 2, 3 for RBP3 and GHR) were identified for this mito-nuclear dataset using IQ-TREE 2.1.3 (Minh *et al*., 2020) and the corrected Akaike information criterion. We used IQ-TREE 2.1.3 and the two selected evolutionary models to construct a phylogeny based on our supermatrix dataset. Robustness of nodes was assessed using nonparametric bootstraps (BP) with 1,000 replications. Bayesian inference was performed to account for the underlying heterogeneity of substitution patterns among genes, using the CAT mixture model (Lartillot & Philippe, 2004) implemented in PHYLOBAYES version 3.3f (Lartillot *et al*., 2009). Relative nucleotide exchangeabilities were estimated using the general time reversible (GTR) model (Rodriguez *et al*., 1990). To account for inter-site heterogeneity in nucleotide substitution rates, we used a gamma distribution with four discrete categories. For each dataset, two Markov chain Monte Carlo (MCMC) analyses were run with PHYLOBAYES for 10,000 cycles (approximately 8,000,000 generations), with trees sampled every ten cycles after discarding the first 1,000 as burn-in. Convergence was ensured when the maximum difference in posterior bipartition probabilities estimated by the two chains was less than 0.1. Node support was estimated by posterior probabilities (PP) computed from samples of 9,000 post-burn trees.

Log-shape ratios on skull and external measurements

Our external morphometric dataset for Moluccan *Rattus* consists of 4 body measurements: head-body (HB), tail (TL), hindfoot (HF) and ear (E) length, and two additional qualitative variables corresponding to species identification (8 species) and sex (male or female). External measurements were analysed using the log-shape ratio approach (Mosimann, 1970), following the R script of Claude (2013). Size was calculated for each specimen as the geometric mean of all measurements, which were then divided by size to obtain shape ratios. The logarithms of these values were used to calculate subsequent analyses. Principal component analysis (PCA) was performed on the four shape ratios. The effects of sex and species identification were tested with a multiple linear model on geometric size (ANCOVA), see Claude [2013] for protocol details). A multivariate analysis of variance (MANOVA) on the first three components was then calculated using non-zero eigenvalues. Explanatory variables were sex, size, and species. For this MANOVA, we also included interactions up to the third order.

Geometric morphometric procedures

Photographs were taken of 90 specimens representing 10 species listed in Appendix 1. Skins and skulls were carefully re-examined to verify correct identification. Dental wear patterns were used to assign specimens to age classes. To explore morphological variation in the skulls (see Fig. 17 for our landmarks): (1) 25 landmarks were taken on the ventral view of the skull (n = 72 specimens) and (2) 19 landmarks were taken on the dorsal view of the skull (n = 85 specimens), following the protocol of Camacho-Sanchez *et al.* (2017) and Fabre *et al*. (2018). A CANON 7D video camera equipped with an EF 100 mm f/2.8L macro lens and TPS dig2 software (Rohlf, 2015) were used to obtain landmark coordinates (details of our approach are available in Camacho *et al*. [2017]). Landmark coordinates were analyzed using a general Procrustes analysis (GPA—Rohlf & Slice, 1990). The logarithm of the centroid size was used as an indicator of size. A principal component analysis (PCA) was computed on superimposed coordinates (Dryden & Mardia, 1998) and the scores of the principal components (PCs) were used in the multivariate analyses of shape. We calculated extreme morphologies along each PC to visualize the patterns of shape variation observed on the first two PCs for dorsal and ventral views. An analysis of covariance (ANCOVA) was performed using centroid size as a covariate to test the effects of species, genus, and sex, and a MANOVA was performed using PC scores to assess the effects of species and sex factors, the size variable, and interactions up to third order as explanatory variables.

Results

Molecular phylogenetic results

Maximum likelihood analysis yielded the topology shown in Fig. 2. We calculated the molecular distance of *Cytb* using both the uncorrected pairwise distance (UPD) and the Kimura 81 nucleotide models (Table 1). Most Moluccan *Rattus* species have a *Cytb* divergence greater than 10% from close relatives, justifying their species status (see also morpho-anatomical descriptions, below). The smallest nucleotide species divergences were found between *R. ceramicus* and *R. feliceus* (*Cytb* UPD > 4%), and between the *R. ceramicus* + *R. feliceus* clade and the North Moluccan *Rattus halmaheraensis* sp. nov. from Halmahera and *R.* sp. cf. *halmaheraensis* sp. nov. from Moti (*Cytb* UPD > 6% range: 5–9%). In the first case, for *R. ceramicus* and *R. feliceus*, these two are highly morphologically distinct species living on the same island, such mitochondrial similarity could conceivably be due to possible introgression; in the second case, the endemic *Rattus* samples from Moti, although molecularly and morphologically divergent (Anang Achmadi, personal communication), may be conspecific and deserve more detailed anatomical examination in the future in order to be properly described.

Rattus ceramicus (previously placed in an endemic genus, *Nesoromys*, by some systematists) and *R. feliceus*, both Seramese endemics, are recovered as a monophyletic group with high statistical support (ML bootstrap (BP) = 100%, posterior Bayesian probability (PP) = 1) and a *Cytb* UPD > 4% (Table 1). This Seramese clade is the sister group to another moderately supported clade (BP > 80%) that includes all Australo-Papuan endemic *Rattus* and the North Maluku endemics *Rattus morotaiensis* from Morotai, *Rattus halmaheraensis* sp. nov. from Halmahera + *R.* sp. cf. *halmaheraensis* sp. nov. from Moti, and *Rattus obiensis* sp. nov. from Obi Island. These latter four Moluccan endemic lineages constitute four distantly related lineages, and no support for their potential sister relationships was found, probably due to our small gene sampling. The two new species from Taliabu (*Rattus feileri* sp. nov. and *R. taliabuensis* sp. nov.) represent molecularly divergent lineages (UPD > 6%, Table 1) that are recovered as basal to this broader Australo-Papuan *Rattus* clade (albeit without significant statistical phylogenetic support, and no nuclear genes have yet been sequenced for these two new Taliabu species).

Morphometric results

External and cranio-dental measurements for each species are presented in Tables 2, 3 and 4.

We performed a PCA on the four shape ratios (Fig. 3). Observations with missing measurements were excluded from this analysis. The first PC axis represents 50.5% of the shape variation, the second 35.6% and the third 13.9%. The first and second axes are strongly influenced by head-body length and tail length (Table 5). For example, species with relatively shorter tails and longer head-body lengths (*R. feliceus*, *R. ceramicus*, or *R. taliabuensis* sp. nov.) are separated on PC1 from species with longer tails and intermediate head-body lengths (*R. feileri* sp. nov., *R. morotaiensis*, *R. halmaheraensis* sp. nov., and *R. obiensis* sp. nov.). *Rattus taliabuensis* sp. nov. from Taliabu is close to the morphospace of the Seramese *R. feliceus*; both are large-bodied, spiny-furred rats with short tails. There is significant overlap within the morphospace of the allopatric species *R. halmaheraensis* sp. nov. and *R. morotaiensis* (Fig. 3), with *R. feileri* sp. nov. being a distinct outlier on PC2 and PC3. Most of the islands surveyed support large spiny-furred *Rattus* with a short tail (relative to head-body length), as well as a medium-sized species with a long tail. Halmahera, Obi and Morotai are exceptions, where large spiny-furred *Rattus* are seemingly instead replaced by endemic species of *Halmaheramys* in a similar ecological role (Fabre *et al*., 2013, 2018; Aplin *et al*., 2023). Seram is the only island with a distinctive lineage characterized by very short head-body length, short tail length and dark fur (*R. ceramicus*, adapted to high montane environments), but similar taxa may exist undiscovered in high altitude habitats on other Moluccan islands; these habitats remain largely unexplored for murines on high islands like Bacan, Halmahera, Morotai, and others. We used geometric size and an ANCOVA to estimate the effects on size of the species and sex explanatory variables. We also computed a MANOVA on the first three principal

Table 1. Uncorrected *cytochrome b* distances as percent sequence divergence (below diagonal) of Wallacean *Rattus*. Values derived from means of sequenced individuals for each species (Fig. 2 and Appendix 1).

	Taxa	1	2	3	4	5	6	7	8	9	10
1	*R. taliabuensis* sp. nov.	—									
2	*R. feileri* sp. nov.	0.10	—								
3	*R. feliceus*	0.10	0.11	—							
4	*R. ceramicus*	0.09	0.11	0.04	—						
5	*R. halmaheraensis* sp. nov.	0.05–0.10	0.06–0.10	0.05–0.09	0.05–0.09	(< 0.01)–0.07					
6	*R.* sp. cf. *halmaheraensis* sp. nov. (Moti)	0.07	0.08	0.07	0.06	0.01–0.02	—				
7	*R. obiensis* sp. nov.	0.10	0.10	0.10	0.09	0.05	0.04–0.07	—			
8	*R. facetus*	0.06–0.08	0.06–0.07	0.07–0.08	0.06–0.08	0.05–0.07	0.03–0.06	0.06–0.07	< 0.01		
9	*R. xanthurus*	0.06	0.06	0.07	0.07	0.07	0.03–0.06	0.06	0.02–0.03	—	
10	*R. morotaiensis*	0.05–0.06	0.05–0.06	0.05–0.06	0.05–0.06	0.04–0.05	0.04	0.04–0.05	0.04–0.05	0.04–0.05	0.01

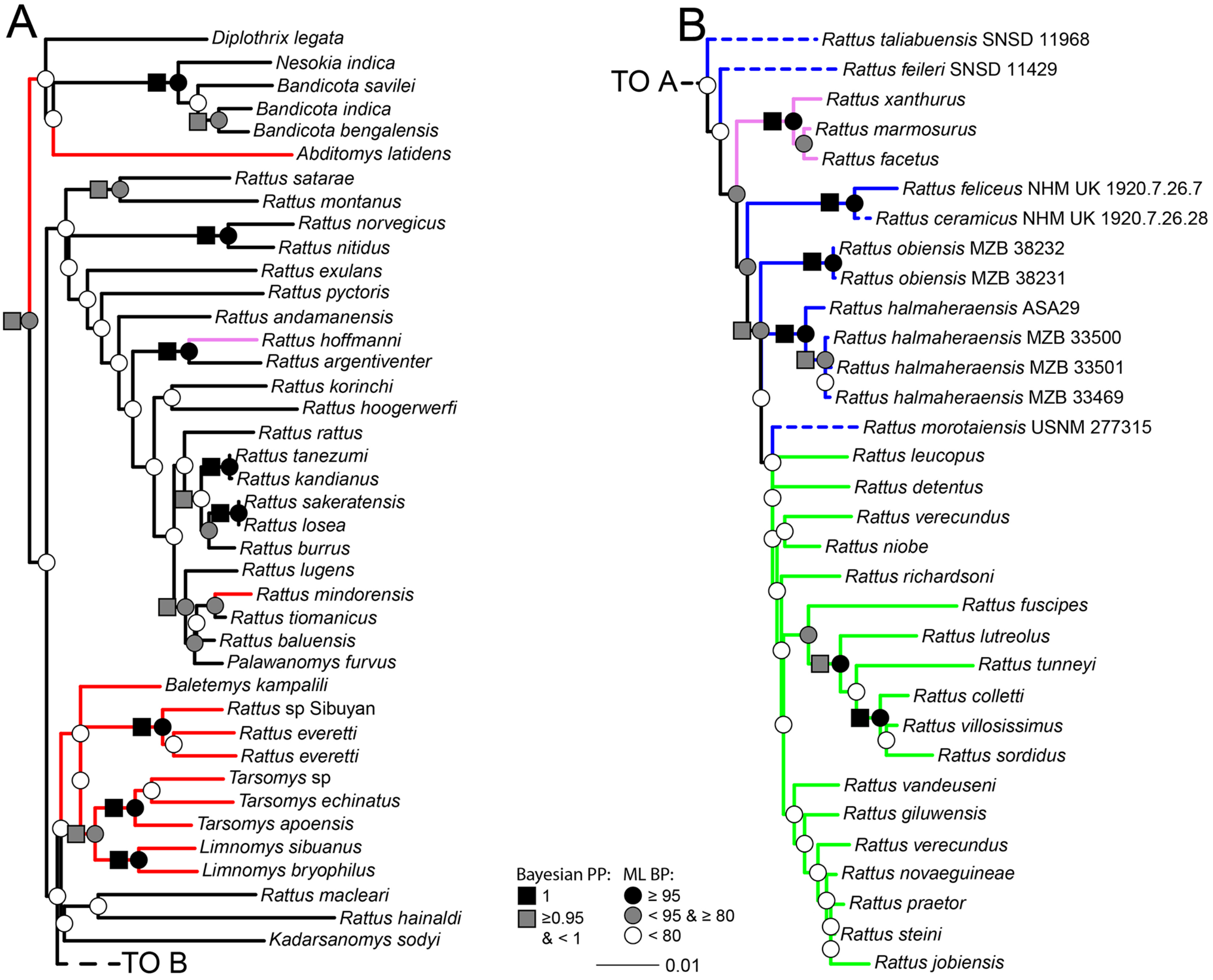

Figure 2. IQ-TREE maximum likelihood tree for the mito-nuclear supermatrix dataset. Branch support indicated by: black circles for ML bootstrap support ≥ 95%; grey circles for ML bootstrap support < 95% and ≥ 80%; and white circles for ML bootstrap support < 80%. Phylogenetic posterior probabilities (PP) are indicated by black squares for PP = 1 and grey squares for 1 > PP ≥ 0.95. Dotted branches indicate Moluccan *Rattus* species represented by *Cytb* sequences only. Geography and species are represented by different colours: Philippines = red; Sundaland and widespread = black; Sulawesi = pink; Maluku = blue; Australia and New Guinea = green.

components of shape variation with non-zero eigenvalues. The ANCOVA indicates a significant effect of species on the centroid size (Appendix 2 Table 7). The MANOVA model shows that both species and centroid size factors have a significant effect on our shape results (Appendix 2 Table 8). The MANOVA also showed a significant effect of sex on the external log shape ratio. We did not detect a significant interaction effect between sex, size and species within our dataset. No other significant second or third order interactions were found. No interaction was found between size and species, suggesting that allometries were similar between age groups of Moluccan *Rattus*.

Projection of individuals onto eigenvectors for the dorsal and ventral shape datasets (Fig. 4) shows that large to medium-sized terrestrial species (i.e., inferred to be terrestrial: *R. feliceus*, *R. taliabuensis* sp. nov, *R. elaphinus*, and *R. ceramicus*) and medium-sized long-tailed species (i.e., inferred to be arboreal or scansorial: *R. feileri* sp. nov., *R. morotaiensis*, *R. halmaheraensis* sp. nov., and *R. obiensis* sp. nov.) are well differentiated along PC1 and sometimes along PC2 and PC3 (Fig. 4).

For ventral shape analysis, PC 1 separated (1) short-tailed species with long rostra, proportionally narrower braincase, long molar rows, long incisive foramina, broad, small tympanic bullae, and a bony palate extending posteriorly to M3 (*R. feliceus*, *R. taliabuensis* sp. nov., *R. elaphinus*, *R. ceramicus*), from (2) long-tailed species with shorter incisive foramina, short and narrow rostra, shorter molar rows, a palate that does not extend very far posterior to M3, and a wider zygomatic arch and braincase (*R. feileri* sp. nov, *R. halmaheraensis* sp. nov., and *R. obiensis* sp. nov.). Interestingly, *R. morotaiensis* appears to lie between these two groups in terms of ventral shape morphology, with juveniles clustering toward the negative PC1 side and adults on the positive PC1 side. The ventral shape axis PC2 involved age-related variation and species differentiation (see *R. ceramicus* and *R. obiensis* sp. nov.), with negative values on this axis associated with juveniles having a wider braincase, a wider foramen magnum, larger auditory bullae and a wider posterior part of the zygomatic arch. The PC3 axis separated Seramese *Rattus* (*R. ceramicus* and *R. feliceus*) from other *Rattus* species, which have smaller

Table 2. Selected external measurements (mm) and body weight (g) of *Rattus* species from Maluku. Mean, range (in brackets) and sample size (after the brackets) are reported in each case. All specimens are adult except for the two specimens of *Rattus obiensis* sp. nov.

Taxa / islands	Sex	HB	TL	HF	E	WT	TL/HB (%)	HF/HB (%)
Seram								
Rattus ceramicus	♂	130.0 [125–135] 2	135 [130–140] 2	29.5 [29–30] 2	18 [18–18] 2	66.5	104	23
	♀	118	126	28	17	—	107	24
Rattus feliceus	♂	197.3 [167–225] 3	180 [175–185] 3	45.0 [44–46] 3	22 [22–22] 3	120	91	21
	♀	243.5 [200–287] 2	165 [165–165] 1	41.5 [40–43] 2	21 [20–22] 2	306 [272–345] 3	68	17
Taliabu								
Rattus elaphinus	♂	189.1 [161–215] 11	176 [154–188] 11	35.8 [34–38] 11	20.1 [18–22] 11	—	93	19
	♀	173.6 [128–212] 17	172.2 [136–201] 17	34.9 [32–38] 17	19.5 [17–22] 17	—	99	20
Rattus feileri sp. nov.	♂	176	237	40	17	—	134	23
Rattus taliabuensis sp. nov.	♂	234	165	43	24	—	71	18
Mangole								
Rattus elaphinus	♂	186.5 [173–200] 3	156 [156–156] 3	33.0 [33.0–34.6] 3	21.5 [19.6–22.5] 3	154.7 [123–197] 3	101	18
Morotai								
Rattus morotaiensis	♂	190.8 [167–221] 4	209.2 [20–216] 3	39.2 [38–41] 4	—	—	110	21
	♀	161.0 [148–184] 3	188 [165–213] 3	34.4 [30–35] 3	17	86	117	21
Halmahera								
Rattus halmaheraensis sp. nov.	♂	163.6 [161–215] 17	186.8 [154–188] 17	34.0 [34–38] 17	19.3 [18–22] 17	112.5 [49–159] 17	114	21
	♀	151.2 [119.4–175] 19	184.2 [158–221] 18	33.3 [30.7–37.2] 19	19.9 [18.2–22.3] 19	103 [51–146] 17	122	22
Bacan								
Rattus halmaheraensis sp. nov.	♂	200	224	39.5	18.7	158	112	20
Obi								
Rattus obiensis sp. nov.	juv.♀	119.0 [116–122] 2	157.0 [157–157] 2	27.8 [27.3–28.3] 2	16.8 [16.7–16.9] 2	37.5 [36–39] 2	132	23

Table 3. Descriptive statistics for cranial and dental measurements (mm) for *Rattus taliabuensis* sp. nov., *R. elaphinus*, *R. feliceus*, and *R. ceramicus*. Mean and observed range (in brackets) are listed. Abbreviations: ONL, occipitonasal length; ZB, greatest zygomatic breadth; IB, least interorbital breadth; LR, length of rostrum; BR, breadth of rostrum; BBC, breadth of braincase; HBC, height of braincase; BZP, breadth of zygomatic plate; LD, length of diastema; PPL, postpalatal length; LBP, length of bony palate; BBPM1, breadth of bony palate at first molar; BMF, breadth of mesopterygoid fossa; LIF, length of incisive foramina; BIF, breadth of incisive foramina; LB, length of auditory bulla; CLM1–3, crown length of maxillary molar row; BM1, breadth of first upper molar.

	Taliabu		Seram				
	R. taliabuensis sp. nov.	*R. elaphinus*	*R. feliceus*			*R. ceramicus*	
	SNSD 11968	RMNH 9799	NHMUK ZD 1920.7.26.7			NHMUK ZD 1920.7.26.29	NHMUK ZD 1920.7.26.30
Age	Adult	Adult	Adult	Adult	Adult	Adult	Adult
Sex	♂	♀	♀	♂♂	♀♀	♂	—
ONL	50.6	48.7	50.7	54.3 [54.3–54.3] 2	50.8 [50.7–50.9] 3	37.11	NA
ZB	24.3	22.4	23.9	23.9 [22.6–25.2] 2	23.6 [23.3–23.9] 3	—	—
IB	8.1	7.5	7.1	7.3 [7.2–7.4] 2	7.2 [6.7–7.7] 3	5.83	6.68
LR	16.7	15.8	16.8	17.4 [16.4–18.4] 2	16.9 [16.4–17.6] 3	13.27	14.29
BR	8.9	9.4	9.5	9.7 [9.3–10.0] 2	9.6 [8.9–10.4] 3	6.12	6.14
BBC	17.9	16.7	18.8	19.5	18.5 [18.1–18.8] 3	14.43	—
HBC	12.4	12.0	14.0	14.0	13.9 [13.8–14.0] 3	10.72	—
BZP	5.4	5.7	5.5	6.1 [5.6–6.5] 2	5.7 [5.5–5.8] 3	2.18	2.13
LD	13.8	13.9	14.4	13.7 [13.2–14.1] 2	14.4 [13.4–15.3] 3	11.06	10.06
PPL	17.3	15.5	15.7	18.2	15.8 [15.7–15.8] 3	10.15	—
LBP	10.5	10.1	11.3	11.5 [11.4–11.5] 2	11.7 [11.3–12.3] 3	10.16	9.55
BBPM1	5.2	5.0	5.3	5.3 [4.9–5.7] 2	5.2 [5.0–5.3] 3	—	5.05
BMF	3.6	3.2	4.7	4.2 [4.1–4.2] 2	4.3 [4.1–4.7] 3	—	—
LIF	9.5	9.2	9.6	10.7 [9.8–11.6] 2	9.5 [9.0–10.0] 3	5.73	5.62
BIF	3.9	3.1	3.8	3.5 [3.2–3.8] 2	3.6 [3.1–3.9] 3	2.40	2.23
LB	6.4	7.0	6.6	7.1	6.6	6.63	—
CLM1–3	8.2	6.8	8.4	8.6 [8.5–8.6] 2	8.5 [8.2–9.0] 3	5.96	5.91
BM1	2.2	2.2	2.5	2.6 [2.5–2.7] 2	2.5 [2.5–2.6] 3	1.87	1.94

auditory bullae, wider zygomatic arches and narrower rostra.

Dorsal shape analysis yielded a similar morphospace, but with less overlap between long-tailed and short-tailed rats. The PC1 axis separated (1) *Rattus* species with long rostra, wide lacrimal and zygomatic widths, and small braincases with a wide interparietal (*R. feliceus*, *R. ceramicus*, *R. elaphinus*, and *R. taliabuensis* sp. nov.) from (2) *Rattus* species with short rostra, narrow lacrimal and zygomatic regions, and larger braincases with a narrower interparietal (*R. feileri* sp. nov, *R. halmaheraensis* sp. nov., *R. morotaiensis*, and *R. obiensis* sp. nov.). On PC2, juveniles and small-bodied *Rattus* species (*R. ceramicus* and *R. obiensis* sp. nov.) were distinguished from adults of larger species. On PC3, *R. morotaiensis*, *R. halmaheraensis* sp. nov., *R. obiensis* sp. nov. and *R. feileri* sp. nov. clustered on the lower side of the axis, mainly due to their narrow rostra and braincase, as well as their reduced incisive foramina and molar row.

A univariate linear model (ANCOVA) was calculated on centroid size for both dorsal and ventral shape to understand the possible effects of species and sex (Appendix 2 Table 7). We also used a MANOVA on the principal components of shape variation with non-zero eigenvalues (Appendix 2 Table 8). Our ANCOVA results show that the centroid size of the skull was significantly influenced by the species factor in both our dorsal and ventral shape datasets. Regarding the ANCOVA results, the variation in ventral skull centroid size was also significantly explained by sex. For the dorsal and ventral shape MANOVA, both size and species factors were recovered as having a significant effect. We did not detect any significant interaction effect between sex, size, and species within our dataset. No other significant second or third order interactions were found. There was also no interaction between size and species, suggesting that allometry was similar between age groups of Moluccan *Rattus*. Overall, these results indicate that two distinct *Rattus* ecomorphotypes occur on the Maluku Islands, one with a scansorial/arboreal lifestyle (*R. morotaiensis*, *R. halmaheraensis* sp. nov., *R. obiensis* sp. nov., and *R. feileri* sp. nov.) the other largely terrestrial (*R. taliabuensis* sp. nov., *R. feliceus*). Using these morphometric approaches, we identified distinct clusters of species that converged with our previous phylogenetic conclusions. We conclude that dorsal, ventral or external characters carry signals that in combination allow us to recognize each of the newly described species ecomorphologically. In the next section we will focus on the discrete morpho-anatomical characters that allow the identification and diagnosis of each of these Moluccan *Rattus* species.

Table 4. Descriptive statistics for cranial and dental measurements (mm) for *Rattus feileri* sp. nov., *R. halmaheraensis* sp. nov., *R. morotaiensis*, and *R. obiensis* sp. nov. Mean and observed range (in parentheses) are listed. Abbreviations: ONL, occipitonasal length; ZB, greatest zygomatic breadth; IB, least interorbital breadth; LR, length of rostrum; BR, breadth of rostrum; BBC, breadth of braincase; HBC, height of braincase; BZP, breadth of zygomatic plate; LD, length of diastema; PPL, postpalatal length; LBP, length of bony palate; BBPM1, breadth of bony palate at first molar; BMF, breadth of mesopterygoid fossa; LIF, length of incisive foramina; BIF, breadth of incisive foramina; LB, length of auditory bulla; CLM1–3, crown length of maxillary molar row; BM1, breadth of first upper molar.

	Taliabu	Morotai			Halmahera			Pulau Obi	
	R. feileri sp. nov.	*R. morotaiensis*			*R. halmaheraensis* sp. nov.			*R. obiensis* sp. nov.	
	SNSD 11429	USNM 277312			AM M.23652			MZB 38231	MZB 38232
Age	Young adult	Adult	Adult	Adult	Young adult	Adult	Adult	Juvenile	Juvenile
sex	♂	♂	♂♂	♀♀	♂	♂♂	♀♀	♀	♀
ONL	41.6	42.6	39.9 [37.4–42.4] 2	39.9 [37.4–42.4] 2	38.0	39.5 [33.0–45.8] 21	38.9 [34.4–42.6] 18	30.6	30.7
ZB	21.7	21.2	20.3 [19–21.5] 2	20.3 [19–21.5] 2	18.4	20.2 [17.0–22.2] 21	19.1 [4.9–22.0] 18	15.8	15.3
IB	6.6	6.1	5.9 [5.3–6.4] 2	5.9 [5.3–6.4] 2	5.4	5.6 [5.1–6.3] 21	5.6 [5.2–6.2] 18	5.5	5.1
LR	11.4	12.1	11.5 [10.1–12.8] 2	11.5 [10.1–12.8] 2	11.5	12.5 [10.2–15.4] 21	12.4 [10.3–15.1] 18	10.0	9.0
BR	8.2	7.7	7.0 [6.3–7.7] 2	7.0 [6.3–7.7] 2	6.2	6.6 [5.5–7.5] 21	6.7 [5.9–7.6] 18	5.9	5.0
BBC	17.2	16.6	16.2 [15.8–16.6] 2	16.2 [15.8–16.6] 2	15.7	15.4 [14.1–16.6] 21	15.4 [14.4–16.3] 18	13.2	13.8
HBC	12.9	12.2	12 [11.5–12.5] 2	12.0 [11.5–12.5] 2	11.7	12.8 [12.2–13.6] 21	12.5 [11.8–13.2] 18	10.3	10.1
BZP	4.0	4.4	4.1 [3.8–4.4] 2	4.1 [3.8–4.4] 2	4.1	4.5 [3.4–5.5] 21	4.5 [3.5–5.6] 18	3.0	2.6
LD	12.2	12.5	11.6 [10.2–13] 2	11.6 [10.2–13] 2	10.3	11.7 [9.7–14.2] 21	11.0 [7.1–13.2] 18	8.7	8.7
PPL	15.8	14.8	12.9 [12.3–13.5] 2	12.9 [12.3–13.5] 2	12.1	13.2 [10.8–15.4] 21	13.0 [11.5–14.6] 18	10.0	10.8
LBP	7.5	9.8	8.7 [7.6–9.7] 2	8.7 [7.6–9.7] 2	7.9	8.4 [7.0–9.4] 21	8.4 [7.3–10.2] 18	14.4	14.2
BBPM1	4.2	4.0	4.2 [3.9–4.5] 2	4.2 [3.9–4.5] 2	3.5	4.0 [3.5–4.5] 21	3.9 [3.3–4.5] 18	3.3	3.1
BMF	2.6	3.1	3.1 [3–3.1] 2	3.1 [3–3.1] 2	2.8	3.8 [3.2–4.5] 21	3.8 [3.1–4.4] 18	2.7	2.5
LIF	8.2	7.1	7.7 [7.3–8] 2	7.7 [7.3–8] 2	6.7	6.6 [4.5–7.6] 21	6.6 [5.5–7.5] 18	5.1	5.2
BIF	2.8	2.4	2.4 [2.3–2.5] 2	2.4 [2.3–2.5] 2	2.5	2.3 [2.0–2.7] 21	2.3 [1.9–2.7] 18	2.0	2.1
LB	6.3	6.2	5.8	5.8	6.9	6.3 [5.6–7.1] 21	6.3 [5.8–6.9] 18	5.2	5.4
CLM1–3	7.1	—	6.5	6.5	6.9	6.2 [5.7–6.7] 21	6.3 [5.6–6.6] 18	5.0	5.0
BM1	2.2	2.0	1.9	1.9	2.1	1.9 [1.8–2.2] 21	2.0 [1.9–2.1] 18	1.5	1.5

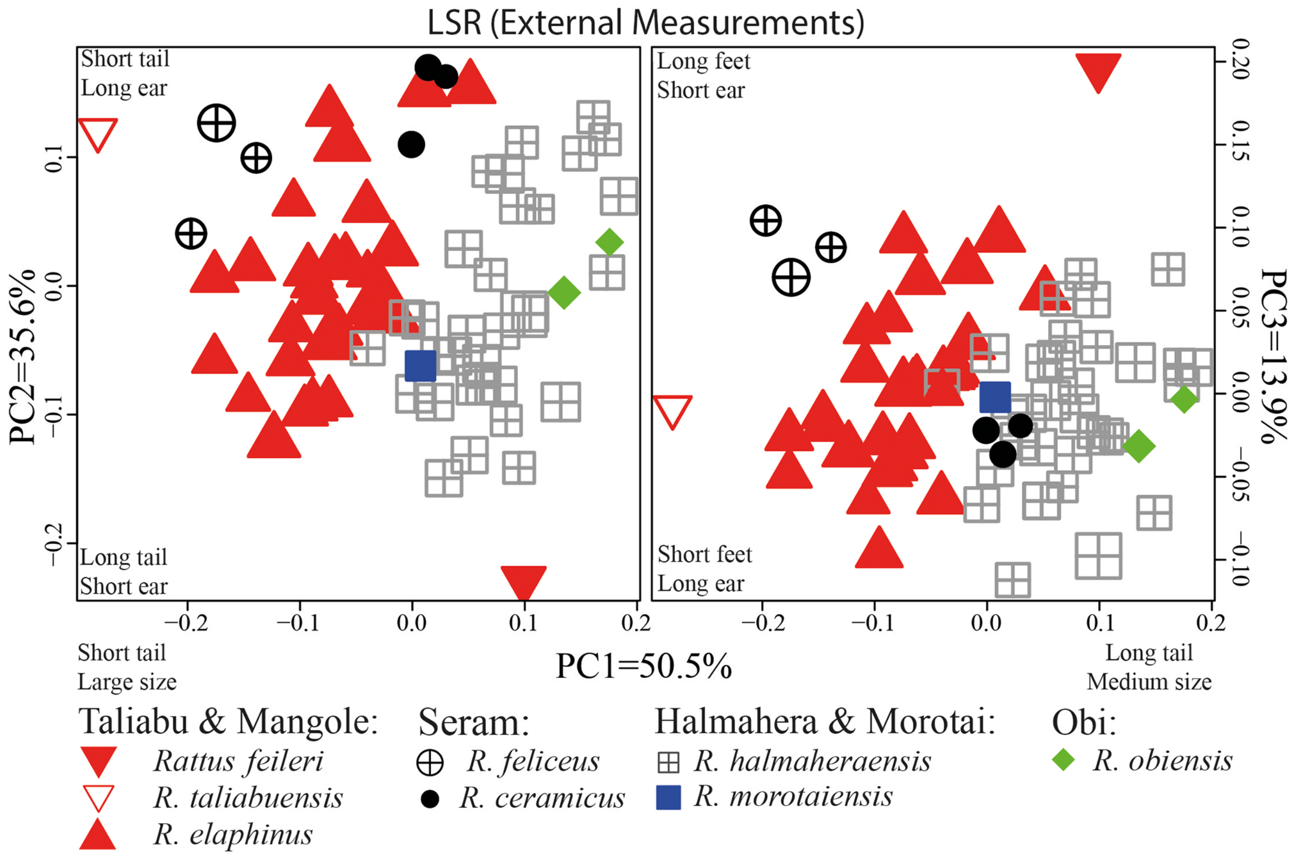

Figure 3. Principal component analysis of log-shape ratios of external measurements (PC1 to 3). Geography and species are represented by different colours and symbols (see legend). Taliabu and Mangole = red, Seram = black, Halmahera = grey, Morotai = blue, Obi = green.

Table 5. PCA loadings of log shape ratio of the external measurement variables shown in Fig. 3.

	PC1	PC2	PC3
head body length	–0.77	–0.36	–0.16
tail length	0.61	–0.62	0.01
foot length	–0.02	0.40	0.77
ear length	0.18	0.58	–0.62

Taxonomy of Moluccan *Rattus* species

Our diagnoses and comparisons involving morphological variation between species are based primarily on characteristics of external form, pelage texture and colour, and cranial and dental features. Certain characteristics are common to all species and are outlined below.

The pelage texture of *Rattus* species can be defined as spiny, bristly, harsh or soft-furred (cf. Emmons [2005: 254–255]). The length of the tail varies between species, both absolutely and relative to the length of the head and body. The tail is covered by overlapping rows of square scales; three hairs arise from beneath each scale, the hairs being approximately the length of a single tail scale. The palmar pads consist of three interdigital pads, one thenar pad and one hypothenar pad. Plantar pads consist of four interdigitals (middle pads 2 and 3 are in front of pads 1 and 4), a thenar and a hypothenar.

The basic skull conformation shared by all *Rattus* species discussed in our revision includes a gradually tapering rostrum, which is long and moderately broad in most species. The smooth sides are marked near the base of the rostrum by nasolacrimal capsules. The tips of the nasals are rounded, slightly protruding from the external nares, and their posterior margins are either level with the ends of the rostral processes of the premaxillae or extend slightly posterior to the premaxillary frontal suture.

The zygomatic plate is broad or narrow, depending on the species; its anterior margin is usually straight or convex, but always oblique, and joins the dorsal maxillary root to form a shallow or deep zygomatic notch between the anterior edge (zygomatic spine) and the side of the skull (in dorsal view). The posterior margin of the zygomatic plate is usually at the level of the first upper molar. The infraorbital foramen is large and narrow. The zygomatic arches arch outward and curve laterally to approximately the level of the molar row; the maxillary and squamosal roots of each arch are joined by a moderately long jugal. The squamosal root of each zygomatic arch originates low on the braincase but above the auditory bulla, and its posterior margin extends along the braincase to the occiput as a weak ridge.

The interorbital region is moderately broad. Its dorsolateral borders are defined by either shallow or prominent ridges that extend along the dorsolateral margins of the postorbital region and onto the braincase as shallow temporal ridges. The braincase is otherwise smooth, deep and either oval or square in dorsal view. The inner walls of the braincase are smooth, lacking squamosal-alisphenoid furrows. The sides of the braincase are vertical or nearly so. The occipital region is moderately deep, marked laterally

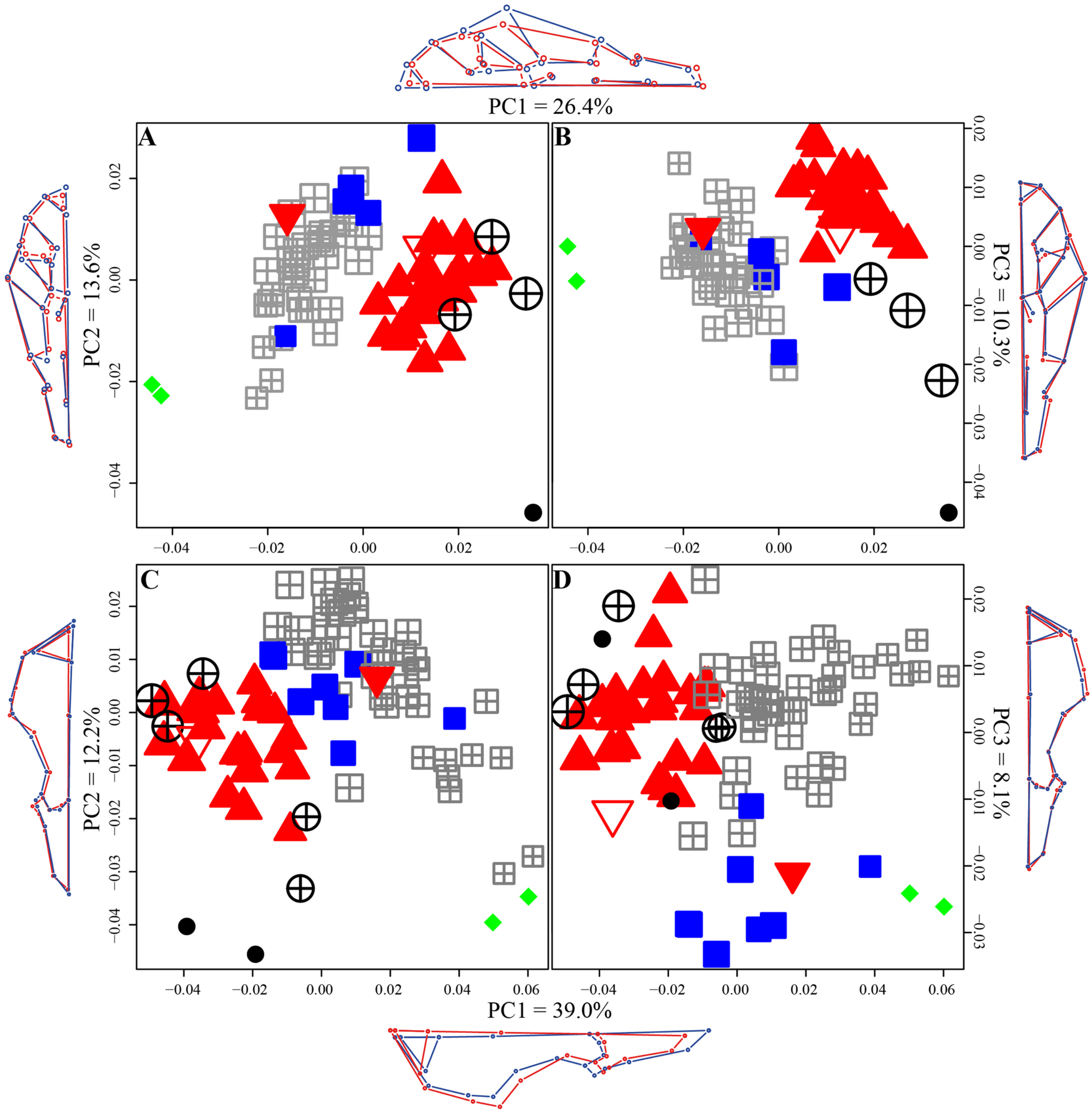

Figure 4. Principal component and associated patterns of morphological transformation for the ventral and dorsal views of the skulls of Moluccan *Rattus* species. Patterns of shape variation along PC1 and PC2 are shown on the sides of the graph, with blue corresponding to minimum values and red to maximum values. Geography and species are represented by different colours and symbols (see Fig. 3). Taliabu and Mangole = red; Seram = black; Halmahera = grey; Morotai = blue; Obi = green. Symbols proportional to centroid size of the skull.

by lambdoid ridges, and usually slightly overhangs the occipital condyles. The squamosal above each otic capsule and just anterior to the lambdoid ridge is intact (not pierced by a subsquamosal foramen).

The incisive foramina are moderately long, narrow or wide, and their posterior margins are level with the anterior margin of the first upper molars in most species. Except for a pair of grooves, the bony palate (palatal bridge) is smooth; its posterior margin projects beyond the third molars to form a shelf. A pair of posterior palatal foramina penetrate the palate at the maxillopalatine suture opposite each third molar. The toothrows diverge slightly posteriorly.

The mesopterygoid fossa is broad and its walls are pierced by two elongate wide or narrow openings (sphenopalatine vacuities). The pterygoid plates adjacent to the mesopterygoid fossa are slightly or moderately excavated and each is pierced by a sphenopterygoid vacuity. The posterolateral and posterior edges of each plate converge posterior to the foramen ovale to form a broad and smoothly rounded ridge that defines the anterolateral border of the medial lacerate foramen separating the pterygoid plate from the bullar capsule. Just medial to this pterygoid ridge is a deep groove for the infraorbital branch of the stapedial artery. The point where the artery leaves the groove and enters the dorsal surface of the pterygoid plate defines the posterior opening of the alisphenoid canal.

Each ectotympanic bulla is slightly inflated and bears a short and broad bony eustachian tube. The mid-sagittal plane of each bullar capsule is inclined at approximately 45 degrees to the longitudinal axis of the skull, and the capsule does not cover the entire surface of the enclosed periotic bone, leaving a posteromedial segment and a narrow flange extending anteriorly between the ectotympanic and basioccipital. The carotid canal is bounded by the periotic and the adjacent ectotympanic. All specimens of each species have a large stapedial foramen penetrating the fissure (the petromastoid fissure) between the bullar capsule and the periotic. A large middle lacerate foramen separates the bullar capsule from the posterior margin of the pterygoid plate.

In lateral view a flange of periotic is exposed along the anterodorsal margin of the bullar capsule. The capsule and periotic are separated from most of the squamosal by a wide postglenoid foramen, which merges with a large ventral middle lacerate foramen. The mastoid portion of the periotic is slightly inflated; its outer wall is complete. The squamosal root of the zygomatic arch sits low on the side of the braincase, but dorsal to the auditory bulla.

Within the orbit, the ethmoid foramen is small and the optic foramen moderately large. The orbitosphenoid, alisphenoid and frontal bones join to form a solid section of the braincase wall (unbroken by a sphenofrontal foramen). The sphenopalatine and dorsal palatine foramina are separate, a pattern similar to that found in other *Rattus* species (Musser, 1982:22).

In the alisphenoid region posterior to the orbit (seen in lateral view), a bony alisphenoid strut is absent, resulting in the coalescence of the foramen ovale accessorius and the masticatory-buccinatory foramina. Exposed to view is the anterior opening of the alisphenoid canal, the open canal itself, and the foramen ovale.

All specimens of *Rattus* discussed here have a carotid plan that is derived for muroid rodents in general, but primitive for members of the subfamily Murinae (character state 2 of Carleton [1980]; pattern 2 described by Voss [1988]; conformation diagram for *Oligoryzomys* of Carleton & Musser [1989]). In this pattern, no sphenofrontal foramen penetrates the bony junction of the orbitosphenoid, alisphenoid and frontal bones; no squamosal-alisphenoid groove scores the inner surface of each wall of the braincase; and no shallow trough extends diagonally across the dorsal (inner) surface of each pterygoid plate; but there is a large stapedial foramen in the petromastoid fissure and a deep groove extending from the middle lacerate foramen to the foramen ovale on the ventral posterolateral surface of each pterygoid plate. This arrangement of foramina and grooves indicates that the stapedial artery branches from the common carotid artery, enters the periotic region through a large stapedial foramen, the infraorbital branch of the stapedial artery exits the periotic region through the middle lacerate foramen, runs in a short groove on the outer surface of the pterygoid plate to disappear into the braincase through the alisphenoid canal, from which it emerges to run through the anterior alar fissure into the orbit. The supraorbital branch of the stapedial is absent. This circulation plan is common in mammals (Musser & Newcomb, 1983; Musser & Heaney, 1992).

Each dentary is either moderately robust or gracile. The delicate coronoid process projects dorsally at or above the level of the elongate condyloid (articular) process; the sigmoid notch is deep and the angular notch (outline of the posterior dentary margin between the articular and angular processes) is deep and broadly concave. Capsular projection of the lower incisor forms a bulge and generally terminates at a level below the coronoid process. Masseteric ridges on the lateral surface of each dentary are moderately developed.

The ungrooved enamel of the upper and lower incisors is orange in all *Rattus* species; the lower incisors are slightly paler. The upper incisors emerge from the rostrum at a right angle or nearly so (orthodont form) in some specimens, or curve slightly caudad (opisthodont configuration) in others (see Thomas [1919] for definitions of these incisor configurations).

Molars of *Rattus* have multiple roots. Five roots anchor each first upper molar: a large anterior root, two smaller lingual roots, a large posterolabial root and a small labial root. The second maxillary molar has four roots of approximately the same size. Two medium-sized anterior roots and a large posterior root hold each third upper molar in place. There are four roots under the first lower molar and three under the second and third molars. The anterior root on the first molar is large and strong, the labial and lingual roots are small, and the posterior root is thick and wide, slightly narrower than the width of the tooth. A similarly wide and thick posterior root and two smaller round anterior roots anchor the second molar. Two anterior roots and a single posterior anchor project from under each third molar.

The molars are brachydont and taper in size within each row: the first is the largest, the third the smallest. The cusp rows incline caudad, so that within each maxillary row the first molar overlaps the second and the second is slightly inclined towards the third; the third molar in each mandibular row is inclined towards the second and this tooth slightly overlaps the first. In most teeth the rows of cusps are moderately close together rather than widely spaced.

Relatively simple occlusal patterns characterize the upper (maxillary) and lower (mandibular) molars. Cusp t3 (the anterolabial cusp) of each first upper molar is fused with the central cusp t2 to such an extent that the two form a single structure (the outlines of each cusp remain in some young specimens but are lost in most others); the anterior row of cusps takes the form of a curved or transverse lamina with a large caudally directed lingual projection representing cusp t1. The cusps in each of the other rows on all upper molars are also broadly confluent, giving the adult occlusal plane a serial pattern of slightly arcuate or chevron-shaped occlusal surfaces. There is no enamel ridge or cusp (cusp t7) on the lingual margin of each upper molar between cusps t4 and t8. Although they are close together, cusps t4 and t8 do not meet along their lingual margins until they are worn down to the cingulum. Cusp t3 is either absent or inconspicuous on the anterolabial margin of each second molar. A posterior cingulum is either absent from the dorsum of the first and second molars or present as a small ridge. The anterior cingular surface of each first maxillary molar is smooth in most specimens but shows a small pimple-like cusp (t1bis) in others. The cusp rows are free and not connected by labial or lingual enamel bridges (stephanodont crests as described by Misonne [1973:55]).

The occlusal topography of each mandibular toothrow consists mainly of coarse curved or chevron-shaped laminae, each representing the complete fusion of two cusps. A large posterior cingulum, elliptical in cross-section, is located posterior to each first and second molar. In front of the first molar there is an anteroconid composed of large anterolabial and anterolingual cusps and an anterocentral cusp (often fused with either an adjacent anterolabial or anterolingual cusp), which have fused to form a large oblong lamina (without discernible cusp boundaries in some specimens, but clearly formed from two cusps in others) that is either slightly or narrower than the lamina behind it. Various combinations of anterior and posterior labial cusps, together with an anterolabial cusp on the second and third molars of some specimens, form minor components of the occlusal surface.

Systematics

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Murinae Illiger, 1811

Rattus Fischer, 1803

Type species *Mus decumanus* Pallas, 1779 = *Rattus norvegicus* (Berkenhout, 1769)

The Seramese *Rattus*

Rattus ceramicus Thomas, 1920

Type material studied. The holotype (NHMUK ZD 1920.7.26.28; Figs 5–10) is an adult male collected at 6000 feet (1830 m) on Gunung Manusela, Seram Island, South Maluku (Fig. 1). The label indicates “trapped in heavy jungle.” Collected by the Pratt brothers in January 1920 and described by Oldfield Thomas in the same year (Thomas, 1920). Two other specimens were collected by the Pratt brothers at the same altitude (NHMUK ZD 1920.7.26.29 and NHMUK ZD 1920.7.26.30). All of these specimens are held by the Natural History Museum, London (NHMUK).

Referred specimens. Another adult male was trapped in 1987 by a Western Australian Museum field crew headed by D. J. Kitchener (WAM M33490; Helgen, 2003).

Taxonomic history. Thomas (1920) originally described *R. ceramicus* as a species of *Stenomys* based on his concept of the genus at that time, although he noted that the new species only superficially resembled *Stenomys* from New Guinea (“this species … is really very different”) based on features of the auditory bullae and palate. In the past, small mountain rats from New Guinea were most commonly placed in this genus (type species *Stenomys verecundus*), which is currently synonymized with *Rattus*. Thomas (1922) later established a monotypic genus, *Nesoromys*, for *ceramicus*, an arrangement maintained by Aplin *et al*. (2003) and Musser & Carleton (2005), but not supported by our results (although there is a broader potential need to redefine the generic name of *Rattus* from the Australo-Papuan region, the Maluku Islands, and also the *Rattus xanthurus* species group from Sulawesi; see ‘Discussion’ below). On the basis of our molecular results and our morphological comparisons, we definitively place the species here within a monophyletic radiation of Australo-Papuan and Moluccan *Rattus* (see Discussion) and recover it as the sister species of *Rattus feliceus*, another Seramese endemic (Fig. 2).

Distribution. *Rattus ceramicus* has only been recorded from Gunung Manusela, but may also occur in other higher elevation areas on Seram. Its recorded altitude range is 1500–1830 m (Helgen, 2003).

Emended diagnosis. *Rattus ceramicus* is a small rat with soft and dull rufous fur covering both the upper and lower parts of the head and body (Fig. 5). This species is characterized by the following features: (1) a dark brown monochromatic tail almost equal to the length of the head and body (TL/HB = 104–107%; Table 2); (2) long hind feet relative to the length of the head and body; (3) weak interorbital and postorbital ridges and only weakly developed temporal ridges (Fig. 6); (4) the bony palate protruding well beyond the upper molar 3 to form an extensive bony shelf, which is the most distinctive feature of this *Rattus* species (Fig. 7); (5) a narrow zygomatic plate and shallow zygomatic notch (Fig. 8); (6) a long and narrow rostrum; (7) viewed laterally, the dorsal outline of the skull forms a convex arc between the nasal tips and the occipital bone; (8) the zygomatic arch is broadly widened parallel to the upper dentary; (9) in ventral view, the squamosal root of the zygomatic arch is anterior to the level of the tympanic bulla; (10) in ventral view, the maxillary root of the zygomatic arch is placed at the level of the first upper molar (M1); (11) the posterior margins of the very short incisive foramina terminate well anterior to M1; (12) the condyloid process of the dentary is elongated, upwardly directed and curved; (13) the angular process does not project beyond the posterior part of the condyloid process and is not well developed; (14) the incisors are opisthodont with a narrow tip blade that is smaller than its longest basal width (an abnormal notch is present on the upper incisor in the specimen vouchered as WAM M33490); (15) a posterior cingulum is present on M1 but is weakly developed (Fig. 9); (16) cusp t3 is present on M2 but absent on the third molar; (17) t1 bis is present on the first maxillary molar; (18) cusp t1 of M1 is either at the same level as or slightly posterior to cusp t3, cusps t1 + t2 + t3 form a U-shaped lamina; (19) anterolabial and posterolabial cusplets are present on lower molar 1 (m1; Fig. 10); (20) an anterolabial cuspid and posterolabial cusplet are present on m2 of the holotype, but a comparable cusplet is not visible on the other NHMUK and WAM specimens; (21) m3 has an anterolabial cuspid but lacks a posterolabial cusplet.

Ecology. Nothing is known about the ecology of this species except that it was collected in primary montane forest at 6000 ft (about 1830 m). It co-occurs with species of *Melomys* (*Melomys aerosus*, *Melomys fraterculus*, *Melomys fulgens*, and *Melomys paveli*) as well as *Rattus feliceus* and the two introduced species of *Rattus* found in Seram mountains—*R. nitidus* and *R. exulans* (Helgen, 2003). Judging by its relatively short tail and elongated hind feet, *R. ceramicus* is probably terrestrial in lifestyle.

Figure 5. Dorsal and ventral views of study skins of the two endemic Seramese *Rattus* species. (*a, c*) *Rattus ceramicus* (NHMUK ZD 1920.7.26.28 holotype); (*b, d*) *Rattus feliceus* (NHMUK ZD 1920.7.26.4, paratype). Scale bars 10 mm.

Rattus feliceus Thomas, 1920

Type material studied. The type specimen (NHMUK ZD 1920.7.26.7) is an adult female collected at 6000 feet (1830 m) on Gunung Manusela, Seram Island, South Maluku (Figs 5–10). This specimen was caught by the Pratt brothers in February 1920 and described by Oldfield Thomas in the same year (Thomas, 1920). Four other specimens were collected by the Pratt brothers between 1200 m and 1830 m (NHMUK ZD 1920.7.26.4–6 and NHMUK ZD 1920.7.26.8). The zoological expedition to Seram that produced the original specimens was undertaken by three of the four sons of the Victorian naturalist A. E. Pratt from late 1919 to early 1920. Oldfield Thomas (1920) remembered Felix Pratt, for whom he named "this fine species." The label states that it was collected "in heavy jungle in precipitous limestone country." All of these specimens are held by the Natural History Museum, London (NHMUK).

Referred specimens. Three adult females and one subadult male were captured by an Australian Museum field team in 1993 between 300 and 400 m (Flannery, 1995; Helgen, 2003). An additional specimen from Gunung Manusela was collected more recently by Museum Zoologicum Bogoriense ornithologists (MZB 22684).

Distribution. *Rattus feliceus* is found from lowland to highland contexts (0–2000 m) at several localities on Seram, and may be widespread on the island.

Emended diagnosis. *Rattus feliceus* is a large-bodied rat with spiny, reddish-brown fur over the upperparts and softer white fur covering the belly; the dorsal fur contrasts

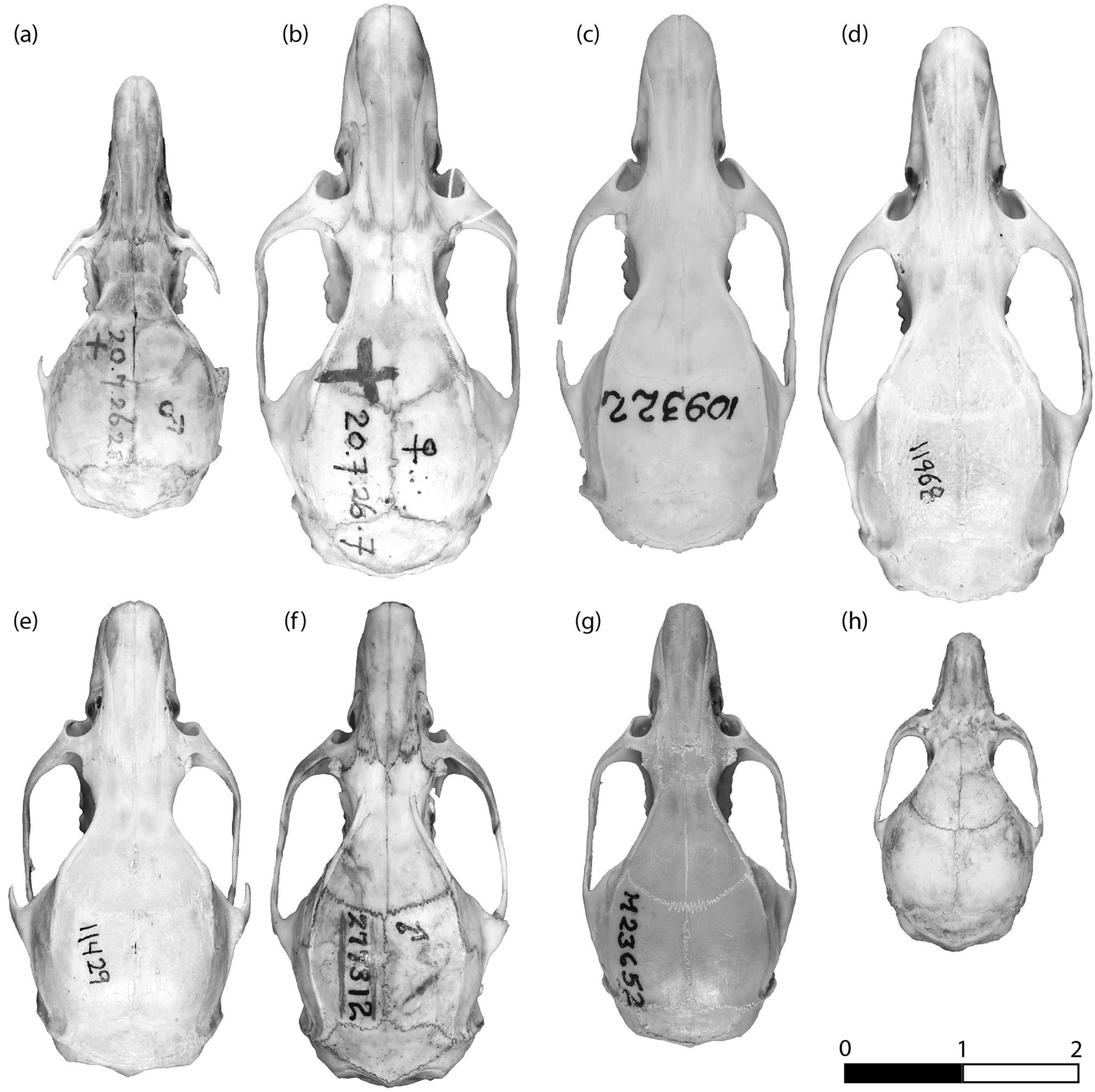

Figure 6. Dorsal views of skulls of (*a*) *Rattus ceramicus* (NHMUK ZD 1920.7.26.28 holotype); (*b*) *R. feliceus* (NHMUK ZD 1920.7.26.7 holotype); (*c*) *R. elaphinus* (AMNH 109322 paratype); (*d*) *R. taliabuensis* sp. nov. (SNSD 11968 holotype); (*e*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*f*) *R. morotaiensis* (USNM 277312 holotype); (*g*) *R. halmaheraensis* sp. nov. (AM M.23652 holotype); (*h*) *R. obiensis* sp. nov. (MZB 38231 holotype). Scale bar 2 cm.

sharply with the white ventral fur (Fig. 5). The mammae formula (given in pairs plus total number) is: 1 pectoral, 1 post-axillary, 0 abdominal and 2 inguinal (1+1+0+2=8). This *Rattus* species is characterized by the following features: (1) a single-coloured pale brown tail shorter than the head-body length (TL/HB = 68–91%; see also Table 2 and Fig. 5), (2) slender and elongated hind feet, but of medium length compared to the head-body length, (3) a moderately long and broad rostrum, (4) prominent temporal, interorbital and post-orbital ridges (Fig. 6), (5) the palatal bridge protruding well beyond M3 to form a moderately large bony shelf (Fig. 7), (6) a wide and deep zygomatic notch and a wide zygomatic plate, (7) viewed laterally, the upper edge of the skull is almost flat between the nasals and the occiput, (8) the eustachian tube is shorter and narrower than in *R. ceramicus*, (9) the angular process of the dentary is broad, (10) the large incisors are opisthodont, (11) the incisor blade is broad, with a size equal to or greater than its longest basal width, (12) the posterior cingulum forms a small bulge on M1 (Fig. 9), (13) cusp t3 is present on both M2 and M3, (14) t1 bis is absent on M1, (15) cusp t1 on M1 is posterior to cusps t2 and t3 and forms a pinched lingual bulge on the M1 lamina, (16) cusp t8 on M1 and M2 is well developed compared to other cusps, (17) there is no anterolabial cusp on m1 (Fig. 10), (18) the posterolabial cusplet is always present on m1, (19) anterolabial cuspid and posterolabial cusplet are present on m2, (20) the presence of posterolabial cusplet is variable on m3 (present in two specimens).

Comparisons between *Rattus ceramicus* and *Rattus feliceus*: Despite a relatively small molecular divergence (4% *Cytb* nucleotide divergence) between *R. ceramicus* and *R. feliceus* (Fig. 2), these two taxa are strikingly different in their external and cranial morphology. At the same time, they share features that clearly distinguish them together from other Moluccan *Rattus* (Figs 2, 5–10). The very distinct external appearance of these two species of Seram rats masks their close relationship. *Rattus feliceus* is a large-bodied rat with a clearly defined dorsal and ventral coat, and is at least twice the mass of the small, dark, single-coloured *R. ceramicus* (Figs 3 and 5; Table 2). In terms of coat texture, *R. feliceus* has a harsh and very spiny coat compared to the soft, short coat of *R. ceramicus*. Tail proportions are also different, as *R. feliceus* has a low TL/HB ratio (68–91%) compared to the almost equal TL/HB ratio of *R. ceramicus*.

Regarding the skull (Figs 6–8), the interorbital, postorbital and temporal ridges are well developed in *R. feliceus* compared to *R. ceramicus*. The dorsal contour of the skull in lateral view is almost flat from the nasals to the highest point of the skull (occiput) in *R. feliceus*, whereas it is slightly convex in *R. ceramicus*. The rostrum of *R. ceramicus* is thinner and longer relative to the size of the skull than the bulky rostrum of *R. feliceus*. The zygomatic plate and arch are narrower and more slender in *R. ceramicus* than in *R. feliceus*. In *R. ceramicus*, the maxillary root of the zygomatic plate is at the level of the first upper molar; this, together with the slender rostrum, is in many ways reminiscent of the structure found in some shrew rats, such as *Archboldomys* (Musser, 1982; Balete *et al*., 2012), or to a lesser extent *Melasmothrix naso* and *Tateomys macrocercus* (Musser, 1982). Most of the maxillary root in *R. feliceus* is located anterior to the first upper molar. The jugular process is also proportionally longer in *R. feliceus*. The posterior palatal foramina reach the middle of M3 in *R. feliceus* but extend posteriorly to M3 in *R. ceramicus*. The incisive foramina of *R. ceramicus* are short and do not reach M1, compared to the long and wide incisive foramina of *R. feliceus*, in which the posterior margins of the incisive foramina reach the anterior edge of M1. The palatal bridge extends well beyond M3 in *R. ceramicus* compared to *R. feliceus*; although other species have a long palatal bridge, that of *R. ceramicus* is relatively longer and extends further posteriorly than in most members of the Rattus Division. The tympanic bullae of *R. ceramicus* are slightly more distended than those of *R. feliceus* relative to the length of the skull. The zygomatic notch is closer to the zygomatic plate in *R. feliceus* than in *R. ceramicus*. The incisors are opisthodont and the enamel is orange, but the incisor blades of *R. ceramicus* are narrower than those of *R. feliceus*. On M1 the cusp t1bis is present in *R. ceramicus* and absent in *R. feliceus* (Fig. 9). Cusp t3, present on M3 of *R. feliceus*, is absent on M3 in *R. ceramicus*. Cusp t1 on M1 differs in its position in relation to t2 and t3; the latter two cusps are more anterior to t1 in *R. feliceus* compared to *R. ceramicus*. The cusps on the upper molars are more divided in *R. feliceus* compared to *R. ceramicus*, giving a more chevronate structure, and each upper molar appears more elongate. The shape of the lower molars (Fig. 10) is similar in both taxa, with some differences in the cusplets–the anterolabial cusplet of m1 is absent in *R. feliceus* and present in *R. ceramicus*, and the posterior cingulum of m1 and m2 is proportionally smaller in *R. feliceus* than in *R. ceramicus*.

Ecology. Little is known about the ecology of *Rattus feliceus*, except that the few existing specimens were collected in forest ranging from coastal forest at sea level to primary montane moss forest up to 1830 m. This species co-occurs with species of *Melomys* (*M. aerosus*, *M. fraterculus*, *M. fulgens*, and *M. paveli*) as well as *R. ceramicus* and at least two introduced species of *Rattus, R. exulans* and *R. nitidus* (Helgen, 2003). *Rattus feliceus* is probably terrestrial in lifestyle (Flannery, 1995), especially judging by its short tail and long hind feet relative to head and body length (Table 2).

The *Rattus* species of the Sula Islands

Rattus elaphinus Sody, 1941

Type material studied. The holotype, an adult female, was collected by J. J. Menden between September and October 1938 on the plains of Taliabu Island (MZB 4087), probably at sea level. The tag indicates the following location: Soela Islands (Sula Archipelago), Taliaboe (Taliabu Island), "plains". Sody (1941) did not comment on his choice of "*elaphinus*" ("deer-like") as the species name, but presumably applied it to describe the fulvous dorsal pelage colour exhibited by this species.

Referred specimens. At least 33 specimens of this species were collected by Menden from Taliabu Island. Tim Flannery subsequently collected four specimens on Mangole Island but did not find the species on nearby Sanana Island (Flannery, 1995).

Diagnosis. *Rattus elaphinus* is a medium-sized rat with a soft coat that is buffy grey on the underparts and reddish brown on the upper parts (Fig. 11). This species is characterized by the following features: (1) a monochromatic dark brown tail subequal to the head-body length (TL/HB = 93–102%; Table 2); (2) hind feet of medium length in relation to the head-body length; (3) interorbital and postorbital ridges well developed, as well as the temporal ridges (Fig. 6); (4) the zygomatic plate is broad, the rostrum is moderately long and wide and appears chunky; (5) the palatal bridge projects beyond M3 as a moderately extended bony shelf (Fig. 7); (6) viewed laterally, the skull is almost flat (slightly convex) between the nasal tip and the occiput (Fig. 8); (7) the posterior palatal foramina are located between M2 and M3 or at the anterior level of M3; (8) the eustachian tube is short; (9) the post-glenoid cavity is not fused with the middle lacrimal foramen in most specimens; (10) the posterior margins of the wide and long incisive foramina reach M1; (11) the incisor enamel is orange and the upper incisors are either opisthodont or orthodont relative to the rostrum; (12) the incisor blade is wide and equal to or greater than its longest basal width; (13) the posterior cingulum is either absent on M1 or rarely forms a slight bulge; (14) cusp t3 is reduced or absent on M2 but absent on M3 in all specimens observed; (15) t1 bis is absent on M1; (16) cusp t1 of M1 is well separated from cusps t2 and t3; (17) the anterocentral cusplet is absent on m1 (Fig. 9); (18) anterolabial and posterolabial cusplets are present on m1 in most specimens (Fig. 10), apart from one individual (MZB 4078) which lacks an anterolabial cusplet; (19) anterolabial cuspid and posterolabial cusplet are present on m2; (20) m3 has an anterolabial cuspid which may disappear with wear in older specimens; (21) the formula for the mammae is 1 pectoral + 1 post-axillary + 0 abdominal + 2 inguinal mammae (1+1+0+2=8).

Comment. No molecular data are yet available for this species. *Rattus elaphinus* is morphologically very close to the *R. leucopus* group (an Australo-Papuan lineage; Musser & Carleton, 2005) and in some ways to *R. hoffmanni* (Musser & Holden, 1991) and is the only Moluccan *Rattus* to be included in a previous morphological systematic revision of *Rattus*, by Musser & Holden (1991), which focused on the systematics of *R hoffmanni*. As *R. hoffmanni* is closely related to *R. argentiventer* (Rowe *et al.*, 2019) as well as to other Asian *Rattus* species belonging to the *R. rattus* and *R. norvegicus* clades, *R. elaphinus* may also be closely related to this clade. Sody's (1941) description of the species is amplified by a detailed description and comparison with *R. hoffmanni* by Musser & Holden (1991:386–388).

Ecology. Little is known about the ecology of *R. elaphinus*. All individuals have been caught near sea level (Flannery, 1995). This species is probably terrestrial in lifestyle, judging from the relative lengths of the tail and hind feet. The Taliabu species *R. taliabuensis* sp. nov. and *R. feileri* sp. nov. co-occur with *R. elaphinus*.

Rattus feileri sp. nov.

urn:lsid:zoobank.org:act:BEB15FE6-3CA4-439E-9688-BE8A07C59E75

Figs 6e, 7e, 8e, 9e, 10e, 11a,d, 12b, 13g, 14g, 18a

Holotype. The holotype (in Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde, SNSD 11429) is a young adult (scrotal) male collected by J. J. Menden on 30 September 1938 (original number 68) on "Insel Taliaboe Molukken" (Taliabu Island, Maluku). Method of collection and exact locality are not known. The skin is very well preserved. The skull is intact except for the zygomatic arches which are detached from their squamosal roots. Known only from the holotype.

Type locality. Taliabu Island (Fig. 1), Maluku, Indonesia.

Etymology. We name this species in honour of German zoologist Alfred Feiler, who worked at the Staatlichees Naturhistorische Sammlunggen in Dresden until his retirement. Feiler kindly arranged the loan of Taliabu Island specimens to G. G. Musser, assisted K. M. Helgen on several visits to the museum in Dresden, and helped with our research in many other ways. We commemorate his significant contributions to knowledge of the mammal fauna of the Indo-Pacific region, and to Wallacea and Maluku in particular.

Distribution. Known only from the type locality, Taliabu Island (Fig. 1), Maluku, Indonesia.

Diagnosis. *Rattus feileri* is of medium size, with a spiny coat overall, which is reddish grey on the upperparts and pale ochraceous, buff or whitish on the undersides, with a rusty wash on parts of the chin, forelegs and chest (Fig. 11). The tail is long in relation to the length of the head and body (TL/HB = 134%; Table 2), with a terminal tuft or "pencil" (Fig. 12). This species is also characterized by the following features: (1) a dark brown tail much longer than the length of the head and body; (2) moderately long and wide hind feet relative to the length of the head and body (Table 2); (3) upper incisors orthodont, with orange enamel faces; (4) wide incisor blade, width at tips greater than longest basal width (Fig. 7); (5) short and wide rostrum with shallow zygomatic notch (Fig. 6); (6) viewed laterally, the top of the skull is convex between the nasal tips and the occiput (Fig. 8); (7) posterior palatal foramina level with the posterior portion of M2; (8) posterior margin of palatal bridge does not extend beyond the posterior margins of M3, which is unusual in the species of *Rattus* examined here; (9) wide and moderately long eustachian tube; (10) the post-glenoid vacuity is not fused with the middle lacrimal foramen; (11) the incisive foramina are long and narrow with their posterior margins aligned with the anterior surface of M1; (12) M2 is bulky and slightly wider than M1 and M3 (Fig. 9); (13) posterocone is absent on M1; (14) cusp t3 is present on M2 and M3, and is wider on M3; (15) t1 bis is absent on M1; (16) cusp t1 on M1 is slightly posterior to cusps t2 and t3 and forms a well separated cusp; (17) anterolabial and anterolingual cuspids as well as an anterocentral cusplet are present and fused to form the anteroconid on m1, likely due to dental wear (Fig. 10); (18) an anterolabial cuspid and posterolabial cusplet are present on m2; (19) m3 shows a ridge-like anterolabial cuspid but lacks the posterolabial cusplet. The mammae formula is unknown, the only available specimen being male.

Description and comparison with Taliabu *Rattus* and *R. morotaiensis, R. halmaheraensis* and *R. obiensis*. *Rattus feileri* is of medium body size with a distinctive long tufted tail (Table 2 and Figs 11–12) and moderately long hind feet, and is similar in proportions to *Rattus halmaheraensis* sp. nov. and *Rattus obiensis* sp. nov. Apart from its superficial resemblance to these two species in external proportions, *Rattus feileri* has no morphological counterpart elsewhere and cannot be confused with any known species of Indo-Pacific *Rattus*. Its unusually long tail has a rare feature found only in this *Rattus* lineage and to a lesser extent in the *Rattus morotaiensis* group: a rufous, tufted tail (Fig. 12). Other murine species, such as *Chiropodomys karlkoopmani*, have similarly developed tufted tails (Musser, 1979), but a pencil tail has never been reported in any other *Rattus* species. *Rattus feileri* is also characterized by distinctive brown, square or hexagonal tail scales. For most of its length, the tail is covered with fine reddish-brown hairs the length of a single scale; near the tip, the hairs are less abundant but longer, forming a tuft that extends 10 mm beyond the tip of the tail. There are approximately 9–11 scale rows per centimetre measured near the base of the tail, each scale bearing 3 hairs. The dorsal coat bears a mixture of (1) spines with white bases and rufous or dark rufous tips, (2) soft guard hairs, (3) charcoal grey undercoat that is almost woolly, and (4) long and stiff guard hairs that are dense with white or buff bases and rufous tips (Fig. 11). The dorsal fur is generally spiny and greyish-reddish chestnut with a few ivory thin spines. The spines of *R. feileri* are shorter than the stiff guard hairs which are thin and tubular, shorter on the shoulders (1.0–1.7 mm) and longer on the rump (3.0–3.5 mm). The rump hairs are longer than other areas of the dorsal coat such as the head and shoulders. Like *R. taliabuensis* and some spiny rats (e.g., *Halmaheramys*), *R. feileri* has longer guard hairs and longer spines on the rump. The guard hairs and spines do not completely cover the undercoat, giving a layered appearance.

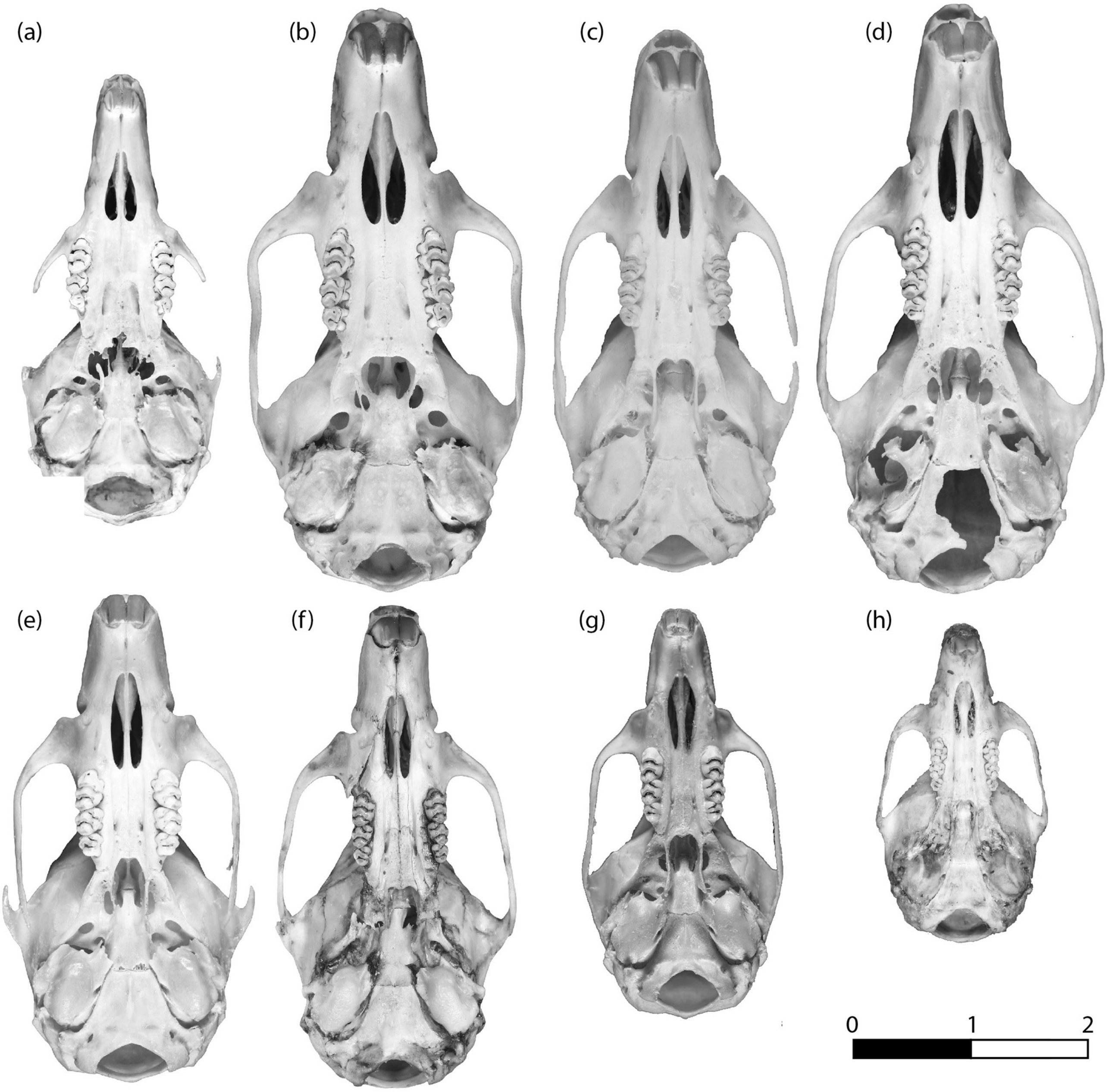

Figure 7. Ventral views of skulls of (*a*) *Rattus ceramicus* (NHMUK ZD 1920.7.26.28 holotype); (*b*) *R. feliceus* (NHMUK ZD 1920.7.26.7 holotype); (*c*) *R. elaphinus* (AMNH 109322 paratype); (*d*) *R. taliabuensis* sp. nov. (SNSD 11968 holotype); (*e*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*f*) *R. morotaiensis* (USNM 277312 holotype); (*g*) *R. halmaheraensis* sp. nov. (AM M.23652 holotype); (*h*) *R. obiensis* sp. nov. (MZB 38231 holotype). Scale bar 2 cm.

There appears to be a lateral line separating the dorsal and ventral coats. The ventral coat is softer and less dense than the dorsal coat and is predominantly buff or pale ochre with thinner spines and a greyish white woolly undercoat, except on the chin, throat and chest. Here the coat darkens to a chestnut colour, probably the result of staining. Some of the ventral spines have brown tips and are more sparsely distributed from the pectoral region caudad to the pelvic region. Compared to the *Rattus morotaiensis* group, *R. feileri* has a less spiny coat, a more rufous dorsal coat and a denser undercoat. The skin of the forelegs is brownish dorsally and ventrally, covered with tiny pale hexagonal scales. The fur on the forefeet is greyish-white with buff or rusty patches. Coloration of the dorsal and ventral sides of the foreleg are well defined. Considering the forefoot, the first digit is reduced, leaving only a small first interdigital pad projecting medially. The other four digits are long and appear to be of equal length. All four have digital pads and the scales on the digits are annular. The forefeet have three almost equal interdigital palmar pads and two large thenar and hypothenar pads, similar to the *R. morotaiensis* group. The fingers are elongated compared to *R. taliabuensis*, with large terminal digital pads and long curved claws with silvery hairs on their anterior edges. The claws also bear some silvery hairs that are nearly as long as the claw lengths. On the hindfeet the first digit is reduced and appears approximately half the length of the other four, which are subequal in length. All the digits have digital pads, and as on the hands the scales on

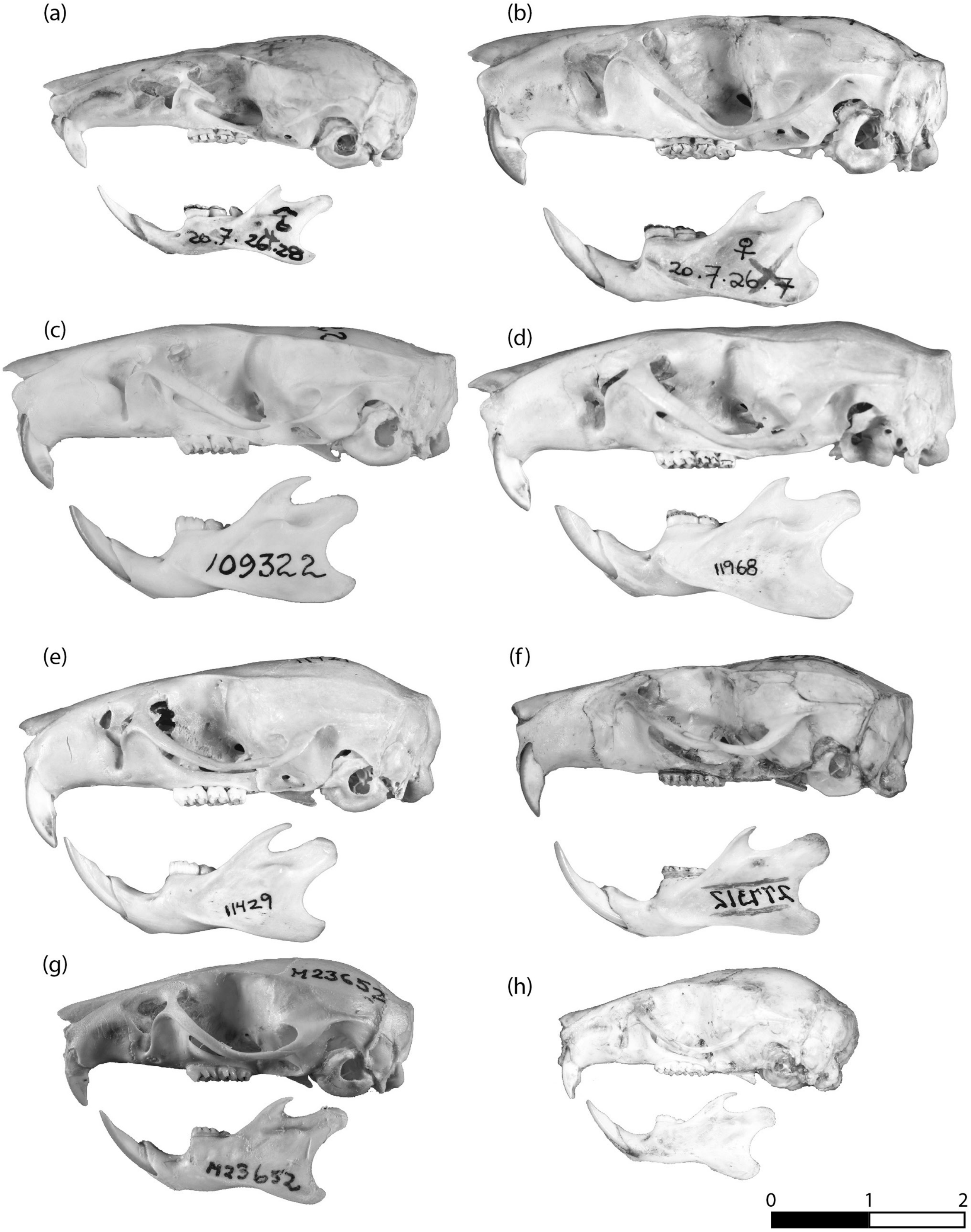

Figure 8. Lateral views of skulls of (*a*) *Rattus ceramicus* (NHMUK ZD 1920.7.26.28 holotype); (*b*) *R. feliceus* (NHMUK ZD 1920.7.26.7 holotype); (*c*) *R. elaphinus* (AMNH 109322 paratype); (*d*) *R. taliabuensis* sp. nov. (SNSD 11968 holotype); (*e*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*f*) *R. morotaiensis* (USNM 277312 holotype); (*g*) *R. halmaheraensis* sp. nov. (AM M.23652 holotype); (*h*) *R. obiensis* sp. nov. (MZB 38231 holotype). Scale bar 2 cm.

the digits are annular. The first and fourth interdigital pads are larger than the second and third, the metatarsal pads are elongated. The head is characterized by moderately long bicoloured ears clothed with creamy or brownish fur near the notch (11 mm) and dark brown fur at the apex (4 mm). A distinctive trait that aids in identification of *R. feileri* is the presence of dark eye-rings encircled by dark brown hairs that are well demarcated from the paler facial fur. The mystacial whiskers are long (55–70 mm maximum length) and rufous-brown throughout their length or tipped in silver. The three superciliary and genal whiskers are also moderately long and caudal to the eyes. There is a tuft of blond ulnar carpal vibrissae above each wrist.

The coat colour and skull proportions of *R. feileri* appear similar to the *R. morotaiensis* group, but the skull bears several discrete features not present in other Moluccan rats. Dorsally, the rostrum is short and broad compared to *R. morotaiensis* and *R. halmaheraensis* sp. nov. (Fig. 6 and Fig. 18). The rostrum appears to be enlarged posteriorly with a proportionally wider nasal area. The zygomatic plate does not extend significantly anteriorly as in the *R. morotaiensis* group. The postorbital region is only slightly ridged, similar to *R. halmaheraensis* sp. nov. Another clear distinction from the *R. morotaiensis* group is a zygomatic arch that does not curve as strongly posteriorly as in *R. elaphinus*. Compared to *R. elaphinus*, the rostrum of *R. feileri* is very short and the braincase is wider. In lateral view, the braincase of *R. feileri* is curved, with the height of the braincase dropping significantly from the top of the parietal bones to the tip of the nasal bones. The zygomatic plate of the holotype does not extend significantly anteriorly, and the squamosal root of the zygomatic arch inserts high above the auditory bulla. The zygomatic arch does not extend ventrally and does not reach the upper molar row in lateral view. The tympanic bulla is not inflated. The skull of *R. feileri* appears more bulky in ventral view than the skull in species of the *R. morotaiensis* group (Fig. 7, Fig. 18). In ventral view, the incisor blades are wide compared to their basal length, as in *R. elaphinus* and *R. taliabuensis* (Fig. 7). The incisive foramina are long and extend towards M1. One of the most distinctive features distinguishing *R. feileri* from the *R. morotaiensis* group is the wide and bulky upper molars (M2 is wide compared to M1 and M3) and a palatal bridge that does not extend beyond M3. The molars are generally much wider and more massive than those of the *R. morotaiensis* group. The tympanic bullae are also proportionally larger in *R. feileri* than in *R. morotaiensis* species. The jaw of *R. feileri* is similar to that of the *R. morotaiensis* group, with a narrow incisor alveolus and a short angular process that does not extend beyond the articular process. The jaw of *R. feileri* is more gracile compared to larger rats such as *R. taliabuensis* and *R. feliceus*.

As discussed above, the dentition of *R. feileri* is easily distinguished from all Taliabu *Rattus* and species within the *R. morotaiensis* group by its wider and more robust molars. The teeth of the *R. xanthurus* species group from Sulawesi are very similar in shape to *R. feileri* and are also wide and robust (Figs 13–14); however, cusp t3 on the M1 of *R. xanthurus* group species is larger and has a well-defined boundary in the first lamina as compared to all Moluccan *Rattus* (Fig. 13). In *R. feileri*, M2 is wider than M1 and M3 and square in shape (Fig. 9), and both M2 and M3 have a cusp t3 on the holotype. Cusp t3 on the third upper molar is well developed and wider than on M2, a feature also found in the *R. xanthurus* species group. On M1, the first lamina has a well-separated cusp t1 posterior to cusps t2 and t3 and the posterocone is absent. The lower molars of *R. feileri* are also relatively wide (Fig. 10) and likewise bear resemblance to species in the *R. xanthurus* species group. Anterolabial and anterolingual cuspids, as well as an anterocentral cusplet, are present and are fused together to form the anteroconid on m1, likely due to dental wear. An anterolabial cuspid and posterolabial cusplet are present on m1 and m2; m3 has only a ridge-like anterolabial cusplet.

Ecology. Little is known about the ecology of this species. Judging from its morphological features it is probably arboreal or at least scansorial. The presence of a long, tufted tail and a short, chunky rostrum are usually associated with arboreal habits in murines. Given ongoing habitat disturbance on Taliabu due to logging, agriculture, and forest fires (Rheindt, 2010), this species may be threatened or even possibly extinct, though much more survey work is required to more fully understand the extant mammal fauna of Taliabu. *Rattus feileri* probably co-occurs with *Rattus taliabuensis* and *Rattus elaphinus*.

Rattus taliabuensis sp. nov.

urn:lsid:zoobank.org:act:05A95DE3-1F93-4C3C-A581-81AB5C971FA1

Figs 6d, 7d, 8d, 9d, 10d, 11c,f

Holotype: The holotype is an adult (scrotal) male collected by the commercial collector J. J. Menden on 27 September 1938 on "Insel Taliaboe Molukken" (Taliabu Island, Maluku) and labelled SNSD 119968 (in Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde). Method of collection and exact locality are not known. The skin is in good condition, with the tail slightly split across its length due to skin preparation. The skull is intact apart from a broken basioccipital and tympanic bulla. The holotype is the only known specimen.

Type locality. Sula Islands, Taliabu Island. The label indicates a 300 m altitude for the type locality.

Etymology. *Rattus taliabuensis* is named after its geographical provenance, from Taliabu in the Sula Archipelago, Maluku, off eastern Sulawesi.

Distribution. Known only from the type locality, Taliabu (Fig. 1), Maluku, Indonesia.

Diagnosis. *Rattus taliabuensis* is a large-bodied rat with a spiny coat that is dark reddish-brown on the upperparts (brown with reddish-brown guard hairs on the back) and lighter reddish-brown on the underparts (Fig. 11). This rat has a short tail compared to its head and body length (TL/HB = 70%; see also Table 2), with large tail scales. This species is distinguished from all other species of *Rattus* by the following set of characters: (1) a dark tail, shorter than its head-body length (Table 2); (2) short hind feet relative to head-body size; (3) the incisor enamel is orange and the upper incisors are opisthodont in conformation; (4) the incisor blade is moderately narrow and its size is less than or equal to its longest basal width; (5) the zygomatic plate is wide and the rostrum is long and narrow; (6) laterally, the

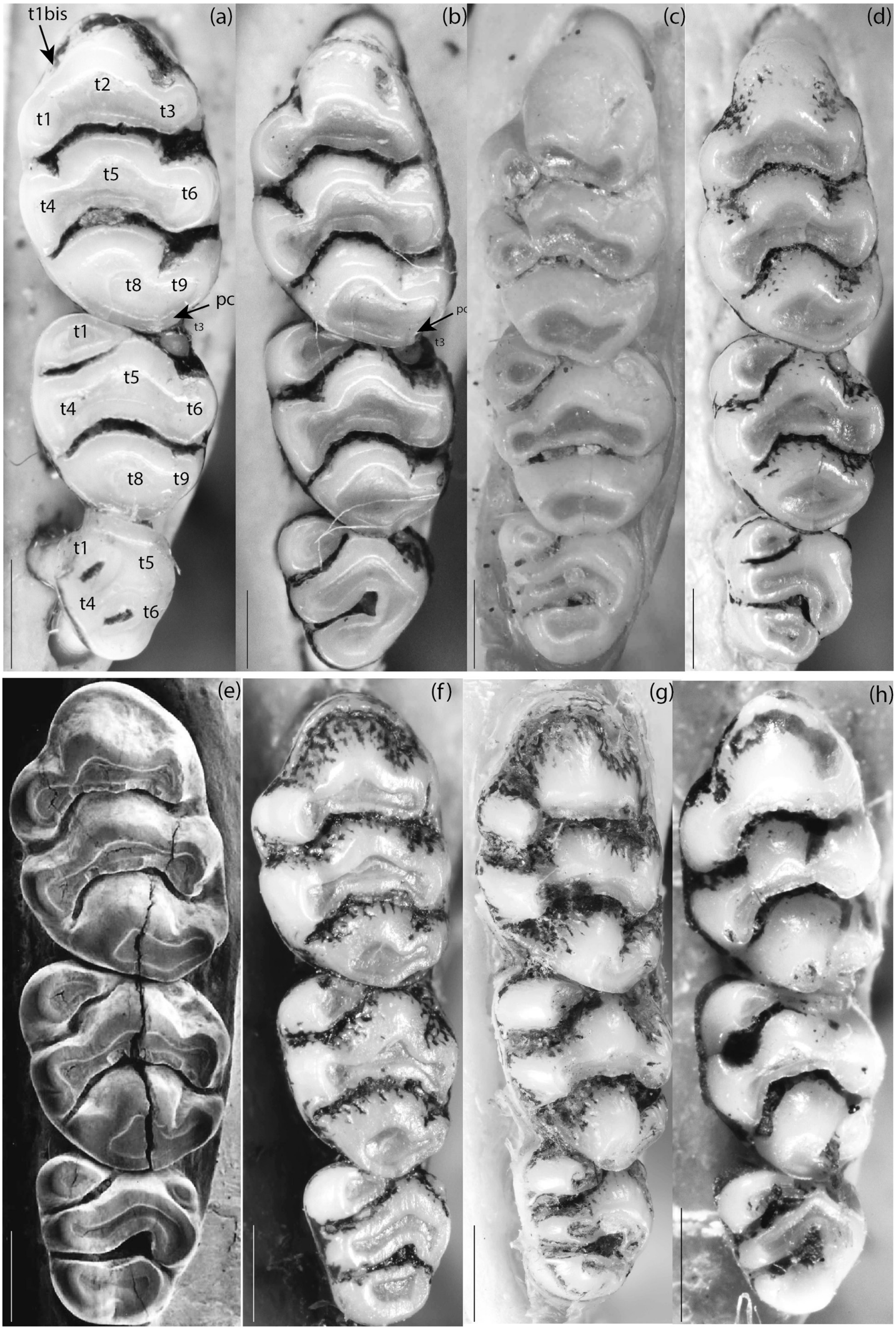

Figure 9. Occlusal views of maxillary molar rows of (*a*) *Rattus ceramicus* from Seram (NHMUK ZD 1920.7.26.28 holotype); (*b*) *R. feliceus* from Seram (NHMUK ZD 1920.7.26.7 holotype); (*c*) *R. elaphinus* (MZB 4082); (*d*) *R. taliabuensis* sp. nov. (SNSD 11968 holotype); (*e*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*f*) *R. morotaiensis* (USNM 277312 holotype); (*g*) *R. halmaheraensis* sp. nov. (MZB 33270); (*h*) *R. obiensis* sp. nov. (MZB 38231 holotype). Cusp names are indicated on the upper left molar images. Scale bar 1 mm.

Figure 10. Occlusal views of lower molar rows from (*a*) *Rattus ceramicus* from Seram (NHMUK ZD 1920.7.26.28 holotype); (*b*) *R. feliceus* from Seram (NHMUK ZD 1920.7.26.7 holotype); (*c*) *R. elaphinus* (MZB 4082); (*d*) *R. taliabuensis* sp. nov. (SNSD 11968 holotype); (*e*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*f*) *R. morotaiensis* (USNM 277312 holotype); (*g*) *R. halmaheraensis* sp. nov. (MZB 33270); (*h*) *R. obiensis* sp. nov. (MZB 38231 holotype). Cuspid features are labelled as follows: a-ling = anterolingual; a-cen = anterocentral; a-lab = anterolabial; md = metaconid, pd = protoconid, alc = anterolabial cusplet; plc = posterolabial cusplet (white arrow on m3); pli = posterolingual cusplet. Scale bar 1 mm.

skull is almost flat between the nasal tips and the occiput; (7) the posterior palatine foramina are at the level of the anterior part of M3; (8) the palatal bridge extends beyond M3 to form a broad bony shelf, as in most of the other *Rattus* species considered here; (9) the eustachian tube is large (long and wide, Fig. 7); (10) the post-glenoid cavity is not fused with the middle lacerate foramen; (11) the posterior margins of the long and wide incisive foramina reach the levels of the first upper molars; (12) the posterior cingulum is absent on M1 and M2 (Fig. 9); (13) cusp t3 is present on M2 but not on M3; (14) t1 bis is absent on M1; (15) cusp t1 of the first upper molar is at the same level as cusps t2 and t3; (16) there is no anterocentral cusplet on m1 (Fig. 10); (17) anterolabial and posterolabial cusplets are present m1; (18) anterolabial cuspid and posterolabial cusplet are present on m2; (19) only an antero-labial cusplet is present on m3. The mammae formula is unknown, the only known specimen being an adult male.

Description and comparison with *Rattus feliceus* and *Rattus elaphinus*: *Rattus taliabuensis* is a large, dark rufous rat with a short tail measuring 70% of the length of the head and body (Table 2 and Fig. 11). The fur covering the upper parts is rufous, with longer guard hairs on the rump. The coat is very spiny, with some long spiny guard hairs prominent on the rump (20–30 mm) and shorter ones on the head, neck, and shoulders (6–20 mm). There are long reddish guard hairs with dark tips, which are more sparsely distributed in the antero-dorsal region. The front of the body is paler and more rufous than the back, which is darker. The belly is lighter with a few medium sized, hard spines that vary from cream rufous, orange rufous to dark rufous. There is a darker area at the base of the scrotum and between the shoulders. Despite some similar external proportions between *R. feliceus* and *R. taliabuensis*, their colour pattern is very different, with *R. feliceus* having both a distinctive white belly and a darker colouration on the upperparts. The overall orange-red belly colouration of *R. taliabuensis* is quite distinct from all Maluku rats. Like several other species of Indo-Pacific *Rattus*, *R. taliabuensis* is covered with very spiny hairs, although the spines are not as thick as those of *R. feliceus* and *R. morotaiensis*. These spines have a thin base and are white in colour with dark brown or orange tips. The guard hairs between these spines have a grey base with an orange or dark brown tip. Similar to the morphology of *Halmaheramys bokimekot* and *H. wallacei* (Fabre *et al*., 2018: 192, fig. 2C), this species has some long guard hairs that extend onto the rump fur. In terms of external proportions, *R. taliabuensis* is characterized by a shorter tail (70% of head body length) and a shorter hind foot length than any other Moluccan species (Table 2 and Fig. 11). Its short tail is very characteristic due to the presence of large squarish scales (6–7 scale rows per centimetre measured near the base of the tail), all of which contain very short hairs half the length of a tail scale. These square-shaped tail scales are very rare in murids from the region and are only found in *Halmaheramys bokimekot* and *H. wallacei*, albeit with spiny hairs instead. The forefeet of *R. taliabuensis* exhibit the normal *Rattus* morphology, with three interdigital pads and thenar and hypothenar pads. The morphology of the forefeet is also distinctive with two large thenar and hypothenar pads and a central interdigital pad larger than both lateral and medial pads. The dorsal part of the hand is almost bare, with very small scales covered with tiny rufous hairs. The toes are strong and short, with short and narrow claws. The claws on the forefeet are small and almost devoid of fine hair. The chunky, short toes on the forefeet contrast with the thinner and longer toes of *R. elaphinus* from Taliabu. The hind feet of *R. taliabuensis* are broad with a moderately long thenar pad and a small hypothenar pad. The pale dorsal part of the hind foot contrasts well with its darker ventral side. There are more silvery hairs covering the dorsal part of the hind feet, as well as a small tuft of silvery hairs on the edge of the claws. This rat has very long reddish mystacial vibrissae (50–75 mm) extending beyond the posterior part of the ears. A few superciliary (30–45 mm) and 1–2 genal (25–30 mm) whiskers are also present, and these are moderately long compared to the mystacial whiskers. The small ears are dark brown and covered with tiny silvery hairs.

Dorsally, the skull of *R. taliabuensis* is longer than that of *R. elaphinus*, with a proportionally longer rostrum (Fig. 6). The postorbital ridge is well developed. However, compared to *R. elaphinus* and *R. feliceus*, the postorbital ridge is reduced from the middle of the parietal. The zygomatic notch is similar to *R. feliceus* and reduced compared to *R. elaphinus*. On the lateral side, the zygomatic plate is broad, with a zygomatic arch that hangs well above the level of the molar row, as in other Taliabu and Moluccan *Rattus*. The top of the skull is flat as in *R. feliceus* and *R. elaphinus*. As in *R. feliceus*, the tympanic bulla of *R. taliabuensis* is not swollen (Fig. 8), and the middle lacerate foramen is well separated from the front of the tympanic bulla and connected to the post-glenoid foramen. The incisive foramen is shorter in *R. taliabuensis* than in *R. feliceus*. The palate of *R. taliabuensis* does not extend as far back from M3 as in *R. feliceus*. The 2 most distinctive features of *R. taliabuensis* compared to *R. feliceus* and *R. elaphinus* are its wide and long eustachian tube and its reduced auditory bullae. The upper incisors are orange and opisthodont as in *R. feliceus*. The mandible of *R. taliabuensis* is also very similar to that of *R. feliceus*. Its angular process is broad and stocky, with a large anterior deep masseter ridge. The coronoid is broad and poorly developed (possibly broken due to poor cleaning), but otherwise similar to *R. feliceus*.

The molars of *R. taliabuensis* are narrower than those of *R. feileri*. Compared to *R. elaphinus*, they are slightly larger and morphologically similar (Fig. 7). There is a clear difference between the upper molars of *R. taliabuensis* and *R. elaphinus*. In fact, cusps t1 and t4 are less separated from their corresponding cusps t2+t3 and t5+t6, respectively (Fig. 9). These cusps t1 and t4 appear to be very small and well separated from their lamina in *R. elaphinus*, reminiscent of the molar morphology of *R. hoffmanni* (Musser & Holden, 1991), which is not the case in *R. taliabuensis*. Regarding the lower molars (Fig. 10), the morphology of *R. taliabuensis* includes a classical shape with a wide lamina, both anterolabial and posterolabial cusps are present and large on m1 and m2. In *R. elaphinus* they are present but smaller in proportion. The anterolabial cusplet of m3 is wider than in all observed specimens of *R. elaphinus*. If the global morphology of the skull shape of *R. taliabuensis* is close to that of *R. feliceus*, the shape of their teeth is also similar (see Figs 9–10), with the anterolabial cusplet being significantly larger in *R. taliabuensis*.

Ecology. Little is known about the ecology of *Rattus taliabuensis*. Morphological features suggest that it is probably terrestrial in lifestyle. In rats, a short tail, large body size and broad feet are usually associated with terrestrial habits. Given ongoing habitat disturbance on Taliabu due to logging, agriculture, and forest fires (Rheindt, 2010), this species may be threatened or even possibly extinct, though much more survey work is required to more fully understand the extant mammal fauna of Taliabu. It probably co-occurs with *Rattus feileri* and *Rattus elaphinus*.

The *Rattus morotaiensis* group

Rattus morotaiensis Kellogg, 1945

Type material studied. The holotype (USNM 277312) is an adult male collected on Morotai (= Morty) Island on 25 October 1944 by J. F. Cassel and R. M. Roecker and described by Kellogg (1945). Six other specimens were also collected from the same locality (USNM 277309–277311; 277313–277315).

Type locality. The type locality is Morotai Island, North Maluku, Indonesia.

Referred specimens. One specimen was collected in 1991 by Indonesian mammalogist Boeadi (AM M.26618) on Morotai Island. We also examined modern (AM M.7083–7086) and subfossil specimens of *Rattus morotaiensis* discussed by Aplin *et al*. (2023).

Distribution. *Rattus morotaiensis* is thus far known only on Morotai Island. All specimens have so far been collected at low elevations.

Emended diagnosis. *Rattus morotaiensis* is a medium to large rat with a spiny coat that is dark reddish brown (Table 2 and Fig. 15). This species of *Rattus* is characterized by the following features: (1) a dark brown tail longer than its head and body length (TL/HB = 109–126%, Fig. 3), sparsely haired and slightly tufted at the tip; (2) long hind feet relative to head and body length for this presumably scansorial or arboreal rat species (Table 2); (3) the postorbital ridge is well developed and marked, and the temporal ridge is well developed (Fig. 6); (4) the palatal bridge moderately extended behind M3 (Fig. 7); (5) the zygomatic notch is moderately wide and the rostrum is short and narrow; (6) laterally, the skull is almost flat between the nasal and occipital (or slightly curved between the interparietal and frontal; Fig. 8); (7) in lateral view the zygomatic arch well upon the level of the upper molar row; (8) in ventral view, the zygomatic root of the zygomatic arch does not reach or just overlaps the level of M1; (9) posteriorly, the incisive foramina are short and just reach or do not reach the front of M1; (10) the usual mammae formula is 1 pectoral + 1 post-axillary + 0 abdominal + 3 inguinal (1+1+0+3=10), but one specimen has eight mammae (one of the paratypes from Morotai lacks a pair of pectorals, but see description in Kellogg, 1945); (11) the angular process does not extend behind the posterior part of the condylar process and is not very developed; (12) the incisor blade is narrow and its size is less than its longest basal width; (13) the posterocone is present on M1 (Figs 9 and 13); (14) cusp t3 is present on M2 and usually on M3; (15) cusp t1 of M1 is located just behind the level of cusps t2 and t3; (16) there are large and prominent peg-like anterolabial and anterolingual cuspids on m1 (Figs 10 and 14); (17) anterolabial and anterolingual cuspids on m1 are of almost equal size; (18) anterolabial and posterolabial cusplets are present on m1 in most specimens, the anterolabial cusplet always being smaller than the anterolabial cuspid on m1; (19) a wide cingular margin is present on m2; (20) an anterolabial cuspid is always present on m2 and m3; (21) a posterolabial cusplet is always present on m2 and absent on m3; (22) strongly crenulated enamel is present on all molars.

A detailed description of *Rattus morotaiensis* was also provided by Kellogg (1945), and a detailed comparison between *R. morotaiensis* and the two *Rattus* species from Halmahera and Obi can be found in the descriptions below.

Rattus halmaheraensis sp. nov.

urn:lsid:zoobank.org:act:89C27A8B-B0CA-4CD7-92AF-84EDA15944EA

Figs 6g, 7g, 8g, 9g, 10g, 12a, 13a–c,
14a–c, 15b,e, 16a,b, 19

Holotype. The holotype (in the Australian Museum, Sydney, AM M.23652) is a young adult male collected on the island of Halmahera on 1 May 1991 by Tim Flannery near Goal, Sahu Timur, West Halmahera Regency (North Maluku Province, Indonesia). The skin, skull, and jaws are intact and in good condition. **Paratypes**. Three specimens from Halmahera collected in 1991 by an Australian Museum field crew headed by T. Flannery (AM M.26614, female, body in fluid; AM M.26615, male, skin, and skull; AM M.26965, female, skin, and skull).

Type locality. The type locality, in the northwest of the island of Halmahera Island (North Maluku Province, Indonesia), close to Goal locality (1.2115°N 127.56007°E). This trapping site was situated along the edge of primary forest.

Referred specimens. Specimens previously attributed to *Rattus morotaiensis* from the island of Bacan (Flannery, 1995) are here referred to *R. halmaheraensis*, including AM M.23653 (male, skin and skull), AM M.23720 (female, body in fluid with skull extracted), AM M.26616 (male, body in fluid), AM M.26617 (female, body in fluid), and AM M.27011 (male, skin and skull). A previously overlooked specimen in the Australian Museum, from Ternate (AM M.23655, female, skin and skull, from Ayr Tege Tege, Ternate, collected 2 January 1991 by T. Flannery), is also referred to *R. halmaheraensis*. A team from MZB recently collected a large series of *R. halmaheraensis* on Halmahera (Fig. 1 and Appendix 1). Six specimens from the island of Moti (MZB 33573–7) are more tentatively referred here to *R.* sp. cf. *halmaheraensis* but may represent an additional undescribed species (see phylogenetic results, Table 1 and Fig. 2).

Etymology. We name this species after the island of Halmahera, where the type locality is situated.

Distribution. *Rattus halmaheraensis* is widespread on Halmahera (Fig. 1), occurring at altitudes from sea level to 1000 m. Populations morphologically similar to *R. halmaheraensis* have been documented from the adjacent

Figure 11. Dorsal and ventral views of study skins of (*a, d*) *Rattus feileri* sp. nov. (SNSD 11429 holotype); (*b, e*) R. *elaphinus* (AMNH 109322 paratype); and (*c, f*) *R. taliabuensis* sp. nov. (SNSD 11968 holotype). Scale bar 10 mm.

islands of Bacan and Ternate, and are tentatively referred to here as *R. halmaheraensis*, but these have not yet been included in our molecular comparisons. Another allied population on Moti is known from a few specimens that are genetically (Fig. 2) and morphologically distinct from Halmaheran samples of *R. halmaheraensis*, indicating the need for further taxonomic study (Anang Achmadi, personal communication).

Diagnosis. *Rattus halmaheraensis* is medium-sized rat, smaller than *R. morotaiensis*, with a spiny coat that is dark reddish-brown (Fig. 15). This species is characterized by: (1) a dark brown tail longer than head and body length (TL/HB = 110–136%; Table 2), sparsely haired and slightly tufted at the tip (Fig. 12); (2) a distinctive spiny coat speckled with large flat spiny guard hairs; (3) a long hind foot relative to the length of the head and body; (4) the bony palate extends a moderate distance behind M3 to form a narrow shelf; (5) the postorbital and temporal ridges are moderately developed; (6) the rostrum is narrow and its ventral side is characterized by a depression of the premaxillary bone, visible in both ventral and lateral views; (7) the zygomatic plate is moderately wide; (8) in lateral profile, the skull is arched between the nasal and occipital; (9) in ventral view, the squamosal root of the zygomatic arch is positioned at the level of the tympanic bulla; (10) in ventral view, the maxillary root of the zygomatic arch is positioned anterior to, or at, the first upper molar; (11) the incisive foramina are long and reach the anterior edge of M1 (Fig. 7); (12) the mammae formula is 1 pectoral + 1 post-axillary + 0 abdominal + 3 inguinal (1+1+0+3=10); (13) the angular process does not extend beyond the posterior part of the articular condyle; (14) the incisor blade is very narrow, less than or equal to its longest basal width; (15) the posterior cingulum is weakly developed or absent on M1 (Figs 9 and 13); (16) cusp t3 is usually present on the second upper molar (in 85% of available specimens); (17) cusp t1 of M1 is located just behind the level of cusps t2 and t3 and is well separated from the lamina in young specimens; (18) there are large peg-like anterolabial and anterolingual cuspids, subequal in size, on m1 (Fig. 10); (19) anterolabial and posterolabial cusplets are always present on m1; (20) the anterolabial cusplet on m1 is as large as the anterolabial cuspid and often accompanied by a second, tiny cusplet (alc2, Fig. 14b); (21) a posterolingual cusplet is present in several specimens (pli, Fig. 14a); (22) anterolabial cuspid and posterolabial cusplets are always present on m2 and m3 (23) the posterolabial cusplets on m3 produce a distinct labial notch (Fig. 14a–c, white arrows); (24) a wide cingular margin is present on m2; (25) crenulated enamel is present on all molars. Our molecular phylogenetic results, as well as those published by Thomson *et al.* (2018), indicate that this species is related to *R. morotaiensis* and *R. obiensis* sp. nov., but is well differentiated genetically as well as morphologically.

Figure 12. Terminal tips of tails illustrating scales and tail hairs: (*a*) *R. halmaheraensis* sp. nov. (AMNH 267681); (*b*) *R. feileri* sp. nov. (SNSD 11429 holotype); and (*c*) *R. elaphinus* (AMNH 109322 paratype).

Description. *Rattus halmaheraensis* is medium-sized, with spiny fur, dorsally grizzled olive-brown mottled with reddish patches, and a long tail, 110–136% of head and body length (Table 2 and Fig. 15). It is smaller in body and cranial size than *R. morotaiensis*. Body mass can reach approximately 250 grams. On the dorsum, the wide (0.02 mm) and long spines (10 to 16 mm long, compared to more than 20 mm long on the rump in *R. morotaiensis*) are pale ivory or olive-grey from base to tip, and dark brown or blackish for the distal third. There are long, soft guard hairs between these spines, which are usually bicoloured, grey proximally and reddish distally. These guard hairs are usually only slightly longer than the spines, but some can reach as long as 40 mm on the rump of the animal. The spines are channelled and convex on the underside, forming a pointed and inverted groove. The dorsum of juveniles may be slightly spiny, but they usually have a softer coat with some thin inflated spines, and the youngest individuals (e.g., MZB 33551) have moulting grey hairs. Adults and juveniles usually have a whitish belly, throat, and undersides of the legs and chin, often with some orange or rust colouring on the throat. White spines and guard hairs are usually shorter on the belly and on the undersides of the legs. Juvenile coats are usually softer with thinner white hairs, but always whitish on the belly and hind legs. The colour of the upperparts varies in the large series of specimens from Halmahera at the MZB, with young animals being darker, and older animals being paler and also having a broad brownish tinge on the throat. Mystacial, superciliary and submental, genal and interramal vibrissae adorn the head. Most of the mystacial vibrissae are dark brown or blackish with an unpigmented distal end that varies in length. The ears are of medium size (9–11% of the head body length) with a dark brown or brownish tip and a buff or pale grey base. From the base to the tip, a few very short and thin buffy or silvery hairs cover the outer ear. The dorsal surfaces of the front and hind feet, including the proximal part of the digits, are covered with very short buff or brown hairs. The distal ends of the digits on the front and hind feet are covered with short silvery hairs. The nails are cream-coloured, each covered with silvery hairs that are more abundant on the hind feet. The palmar and plantar surfaces are pinkish or whitish-brown, unpigmented and hairless. The manus has two large and prominent metacarpal pads and three smaller interdigital pads. Both the interdigital and metacarpal pads are connected. Digital pads are also well developed on the digits of the fore and hind feet. On the hind feet, four interdigital pads are moderately developed. The two central interdigital pads are in close contact and both are connected to large lateral interdigital pads. The hypothenar is broad, as is the thenar. The thenar pads are long and have a broad comma shape with a distal wider base. Ulnar vibrissae are visible, mostly unpigmented but somewhat darker in three specimens. The tail is dark brown, with large square tail scales, with 8–9 scales per centimetre (juvenile tails have 9–11 scales per centimetre), and three hairs per scale, each slightly longer than a scale. A small tuft of dark hairs is present at the tip of the tail, but this is not as strongly developed as in *R. feileri* (Fig. 12). Females usually have 10 functional teats with 1 pectoral, 1 post-axillary and 3 inguinal pairs.

The skull of *R. halmaheraensis* is smaller than in *R. morotaiensis* (Figs 6–8). It has a short and narrow rostrum with a weakly developed lacrimal groove. The frontal and postorbital ridges are present in adults but not in juveniles (Fig. 16 and Fig. 19); these ridges are less pronounced overall, and less developed in immature specimens, than in *R. morotaiensis* (Figs 6, 18, 19). In lateral profile the top of the skull curves from nasal to occipital, a distinctive feature compared to *R. morotaiensis*. In *R. halmaheraensis* the braincase is smaller with a more rounded shape and an antero-posteriorly reduced interparietal bone than in *R. morotaiensis*. A distinctive feature of *R. halmaheraensis* is its very narrow rostrum, with a diagnostic premaxillary constriction, most visible from the ventral side (Fig. 7). In ventral view, the incisive foramina of *R. halmaheraensis* are longer than in *R. morotaiensis*, slightly overlapping the anterior surface of the first upper molars (Fig. 7). The palatal bridge in *R. halmaheraensis* does not extend as far behind the third molars as in *R. morotaiensis*. In *R. halmaheraensis*, the maxillary root of the zygomatic arch reaches the first upper molar, and the squamosal root of the zygomatic arch reaches the level of the tympanic bulla. The upper incisors of *R. halmaheraensis* are more gracile and less opisthodont than in *R. morotaiensis*.

The dentition of *R. halmaheraensis* is very distinctive. The upper and lower molar rows are proportionally smaller relative to the skull size compared to *R. morotaiensis* (Figs 7, 13–14). The strongly crenulated enamel, molar cusp patterns, and shape of the laminae are similar in size to *R. morotaiensis*, though the antero-posterior decrease from M1 to M3 is more pronounced in *R. halmaheraensis* (Figs 13–14). Cusp t3 is usually present on M2 (85% of specimens) and M3 (75% of specimens). The most distinctive upper molar features of *R. halmaheraensis* are (1) a smaller cusp t1 on M1, placed more ventrolaterally to the t2+t3 lamina compared to *R. morotaiensis*, and (2) cusps t2 and t3 of M1, which are fused into a distinctive, straight lamina compared to the more tuberculate lamina of *R. morotaiensis* (Fig. 13). The anterolabial cuspid and posterolabial cusplet are always present on m1 and m2 and also on m3. Unlike *R. morotaiensis*, this posterolabial cusplet forms a distinct notch on the hypoconid of m3 (Fig. 14; white arrows). The most distinctive feature of the m1 of *R. halmaheraensis* is an anterolabial cusplet which is as large as the anterolabial cuspid and often followed by a second tiny cusplet (alc2, Fig. 14b). An unusual posterolingual cusplet is also present in several specimens (pli, Fig. 14a). All specimens show strongly crenulated enamel ridging, which is unique to *R. halmaheraensis* and *R. morotaiensis* within *Rattus*.

Rattus obiensis sp. nov.

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Figs 6h, 7h, 8h, 9h, 10h, 13d,e, 14d,e,
15c,f, 16c, 20

Holotype. The holotype (in the Museum Zoologicum Bogoriense, Cibinong MZB 38231) is a juvenile female (Fig. 20) (study skin, cleaned skull, postcranial skeleton, and tissue sample in ethanol) collected by P.-H. Fabre on 27 November 2013 with a live rat-trap baited with coconut and peanut butter. The dentition is fully erupted, the sutures on the skull are not fully closed, and the woolly coat is in immature pelage. **Paratype**. A paratype (MZB 38232) was also collected by P.-H. Fabre on 28 November 2013. It is a juvenile female (study skin, cleaned skull, postcranial skeleton, and tissue sample in ethanol).

Type locality. The type locality, in the southwest of the island of Obi (North Maluku Province, Indonesia), is on Gunung Sere above the villages of Tapaya and Wayaloar. The holotype was collected along a ridge at 970 m asl, near a campsite at 1.624°S 127.709°E, 870 m asl. The trapping site sits in disturbed secondary forest that was logged less than 20–25 years ago, as explained by the local community (Pak Sabar, personal communication).

Etymology. This species is named after the island of Obi, where the type locality is situated.

Distribution. *Rattus obiensis* is endemic to Obi Island, Maluku, Indonesia and has only been recorded at the type locality. The species may be more abundant at higher altitudes, as we did not catch it during 8 nights with 200 rat traps at a lower altitude camp (40–70 m) in the northern part of Obi Island; it was also not encountered by Tim Flannery during mammal surveys at low elevations in Obi and Bisa in January 1990 (Flannery, 1995).

Diagnosis. As we only have two immature specimens, we focus our diagnosis on a selected set of external and cranio-mandibular characters stable across both adults and juveniles of *Rattus*. These consist especially of occlusal features of the molars. The molars of our specimens are fully erupted and very distinctive compared to other Moluccan *Rattus*. Even though we only have immature specimens, it is clear that, when grown, this new species would be a smaller animal than *R. morotaiensis* and *R. halmaheraensis*, the other members of the *Rattus morotaiensis* group.

Rattus obiensis is a small rat with broad spiny hairs, characterized by the following features: (1) a long dark tail, which is longer than the head and body length (TL/HB = 128–130%; see also Table 2; Fig. 15 and Fig. 20); (2) long hind feet in proportion to the head and body length; (3) the palatal bridge extends slightly beyond M3 (Fig. 16); (4) a broad zygomatic arch that curves posteriorly outwards (Fig. 4); (5) the zygomatic plate is reduced and the rostrum is short and narrow; (6) in ventral view the squamosal root of the zygomatic arch does not overlap the level of the tympanic bulla; (7) in ventral view the zygomatic root of the zygomatic arch slightly overlaps at the level of the first upper molar; (8) the eustachian tube is slightly developed; (9) the short incisive foramina reach the first upper molar posteriorly; (10) the upper incisors are orthodont in configuration, with orange enamel faces, and have a distinct notch; (11) the incisor blade is narrow, less than or equal to its longest basal width; (12) a well developed posterior cingulum is present on M1 (Fig. 13); (13) cusp t3 is present on M2 (and variably present on M3); (14) on M1, cusps t1 and t4 are situated well posterior to the first (cusps t2 and t3) and second laminae (cusps t5 and t6), respectively; (15) large, peg-shaped anterolabial and anterolingual cuspids, subequal in size, are present on m1 (Fig. 14); (16) a poorly developed anterolabial cusplet is present on m1; (17) an anterolabial cuspid is present on m2 and m3; (18) posterolabial cusplets are present on all lower molars; (19) the posterolabial cusplet on m3 is distinct and produces a labial notch (Fig. 14d–e; white arrows); (20) the posterior cingulum is present and well developed on m1 and m2; (21) crenulated enamel is present but relatively poorly developed. The mammae formula is as yet unknown. Our morphological results indicate that this species is closely related to *R. morotaiensis* and especially *R. halmaheraensis* but is well differentiated genetically.

Description and comparison with immature *Rattus halmaheraensis*. Within the genus *Rattus*, *R. obiensis* is a distinctive lineage in its molecular phylogenetic divergence (Table 1 and Fig. 2), as well as in terms of body proportions and cranio-mandibular and dental characters. We captured two immature animals during our fieldwork on Obi Island but were unable to obtain any adults. Given the difficulty of accessing these islands and the significant human activity, we describe this new species here on the basis of these two specimens. Among semi-arboreal *Rattus* species, *R. obiensis* has the longest tail, which is 128–130% of head-body length (Table 2). The tail is covered with short squarish scales that are much smaller than those found on *R. halmaheraensis* of similar age. Because they are immature, the fur of these specimens is greyish with a woolly undercoat, but is beginning to show some adult features, including flat spiny hairs and some longer brownish guard hairs. On the dorsum the hairs are soft, buff and grey. The guard hairs are bicoloured, with bases that are whitish grey and tips that are golden brown, buff, or greyish brown as in *R. halmaheraensis* of the same age. Some of the guard hairs are thickened and ivory coloured. The dorsal fur is darkest, becoming paler along the mid-line of the body, where the dorsum meets the venter, and here the guard hairs are whitish brown or yellowish brown. The cheeks are greyish. The belly is whitish grey, and one of the two specimens has a white pectoral patch. On the mid-belly, yellowish or golden brown hairs mix with the grey hairs. The undersides of the legs are whitish grey. Compared to immature specimens of *R. halmaheraensis*, *R. obiensis* is much smaller, has a paler coat, and has a longer tail with more hairs at the tip (though not so developed as the pencillate tail tip of *R. feileri*; Fig. 12). In addition, its coat is woollier, and its belly is covered with grey fur, a characteristic not observed even in very young individuals of *R. halmaheraensis*. Young *R. halmaheraensis* usually have less woolly and darker dorsal fur, with a paler white belly.

The skull of *R. obiensis* has a short and narrow rostrum with a narrow lacrimal region (Fig. 16). *Rattus obiensis* has a similar dorsal cranial shape in lateral view compared to *R. halmaheraensis* but is significantly smaller in size compared to juveniles or subadults of that species. Compared to *R. halmaheraensis* juveniles, it has a proportionally larger braincase, a narrower orbit, and a narrower interparietal region that is closely attached to the margin of the nuchal crest. The upper incisors are orthodont and both upper incisors have a prominent notch, seen in both specimens. The upper incisors are very narrow compared to *R. halmaheraensis* of similar age. In lateral view, the zygomatic arch sits at the level of the upper molar row and its squamosal root lies well in front of the post-glenoid process. The incisive foramina are proportionally larger than in immature specimens of *R. halmaheraensis*. The upper molars are proportionally smaller than in *R. halmaheraensis*. The tympanic bullae and braincase are proportionally similar to those of *R. halmaheraensis*, but *R. obiensis* has a distinctly larger and longer eustachian tube. The mandible of *R. obiensis* is wider and higher, with a narrower but longer angular process than in *R. halmaheraensis* of similar age.

The upper molars are very small in *R. obiensis* and have a distinctive laminar pattern compared to all other Moluccan and Indo-Pacific *Rattus* (Figs 13–14). The laminae on the upper molars are oblique, with cusp t1 situated well behind cusps t2 + t3 on the first lamina, and cusp t4 situated well behind cusps t5 + t6 on the second lamina. Thus, the third, posterior lamina (cusps t8 and t9) appears anteriorly surrounded by the second lamina (cusps t4, t5 and t6). A similar pattern is observed on M2. This configuration is distinctive compared to all Maluku, Sulawesi, and Australo-Papuan *Rattus* (Musser & Holden, 1991; Taylor & Horner, 1973; Taylor *et al*., 1982). Compared to juveniles of *R. halmaheraensis*, *R. obiensis* has narrower laminae. In contrast to the condition in *R. morotaiensis* and *R. halmaheraensis*, *R. obiensis* has less developed enamel crenulation, similar to the extent of crenulation in some other *Rattus* species (e.g., *R. leucopus*). On M1, the posterior cingulum is well developed, and cusps t8 and t9 are proportionally reduced, compared to *R. halmaheraensis*. Cusp t3 is present on M2 in both specimens, but variable on M3 in the two available specimens (Fig. 13d–e). The lower molars are very small, with a cusp pattern very similar to *R. halmaheraensis* in

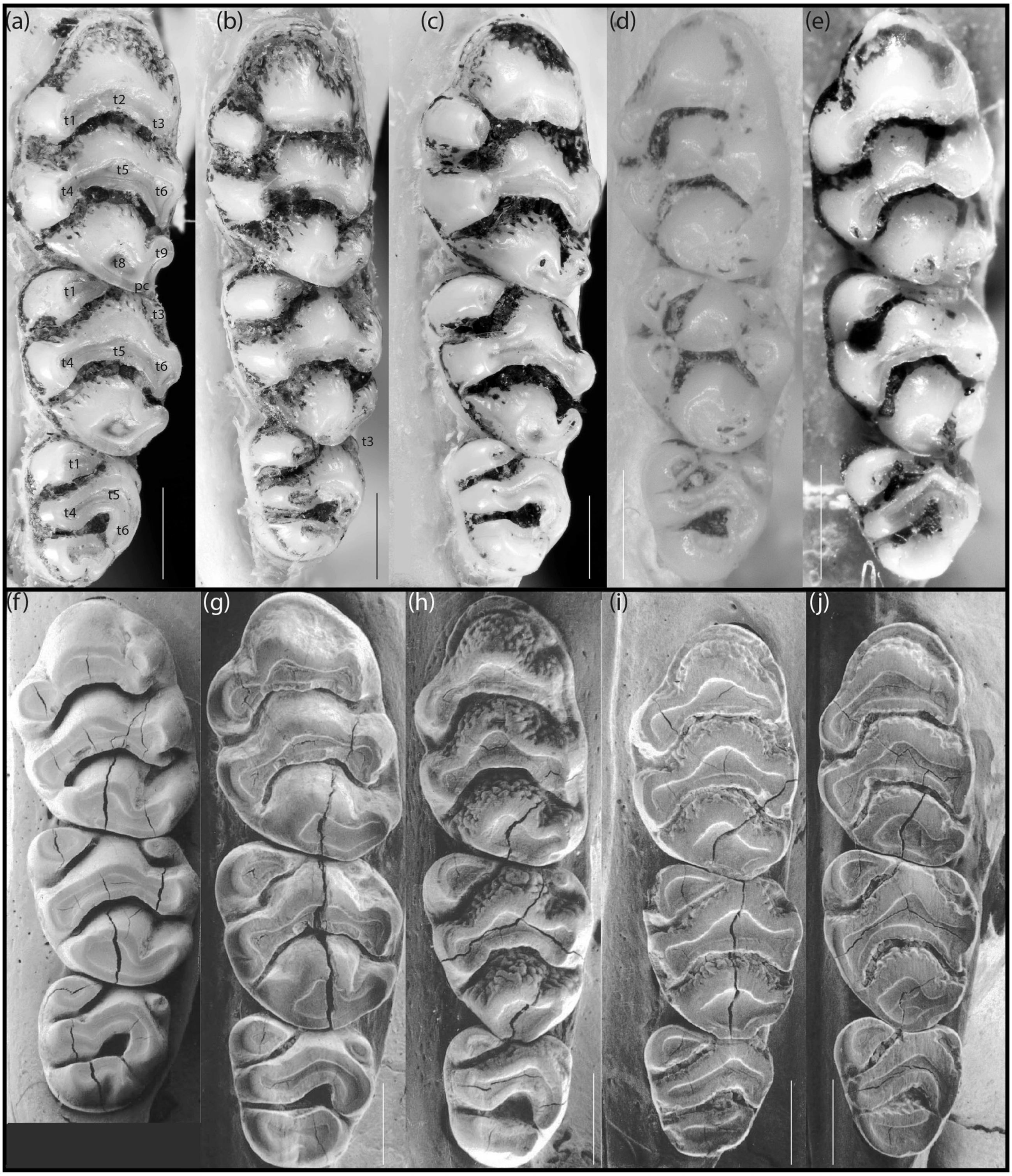

Figure 13. Occlusal views of maxillary molar rows from (*a–c*) *Rattus halmaheraensis* sp. nov. (MZB 33234, MZB 33270, MZB 33548); (*d, e*) *R. obiensis* sp. nov. (MZB 38232, MZB 38231 holotype); (*f*) *R. xanthurus* from Sulawesi (AMNH 223225, no scale available); (*g*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*h–j*) *R. morotaiensis* (USNM 277309, USNM 277312 holotype, USNM 277310). Cusp names are indicated on the upper left molar pictures labeled (a) and (b). Scale bar 1 mm.

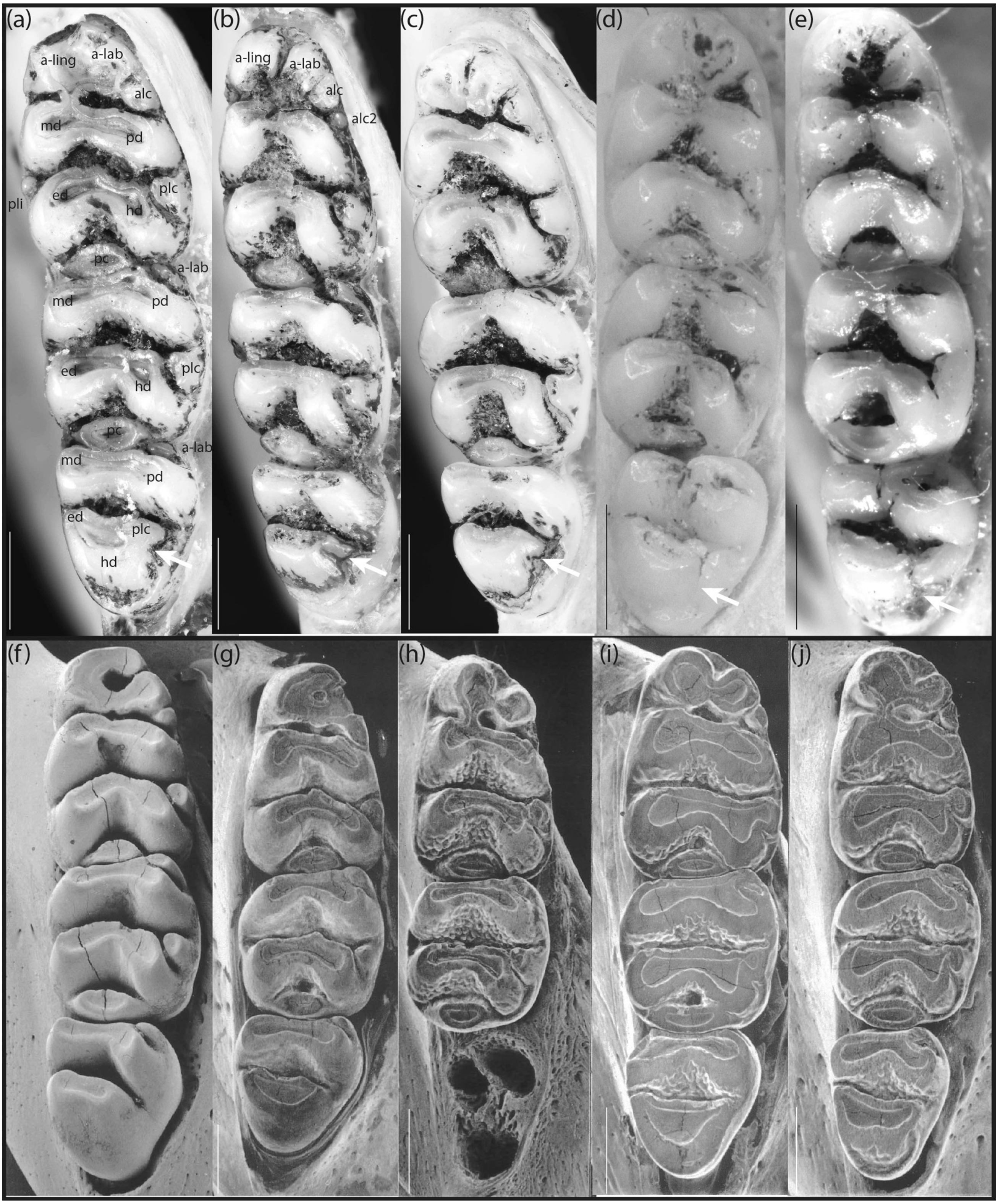

Figure 14. Occlusal views of mandibular molar rows from (*a–c*) *Rattus halmaheraensis* sp. nov. (MZB 33234, MZB 33270, MZB 33548); (*d, e*) *R. obiensis* sp. nov. (*d* MZB 38232, *e* MZB 38231 holotype); (*f*) *R. xanthurus* from Sulawesi (AMNH 223225, no scale available); (*g*) *R. feileri* sp. nov. (SNSD 11429 holotype); (*h–j*) *R. morotaiensis* (USNM 277309, USNM 277312 holotype, USNM 277310). Cuspid features are labelled as follows: a-ling = anterolingual; a-cen = anterocentral; a-lab = anterolabial; md = metaconid, pd = protoconid, alc = anterolabial cusplet; plc = posterolabial cusplet (white arrow on m3); pli = posterolingual cusplet. Scale bar 1 mm.

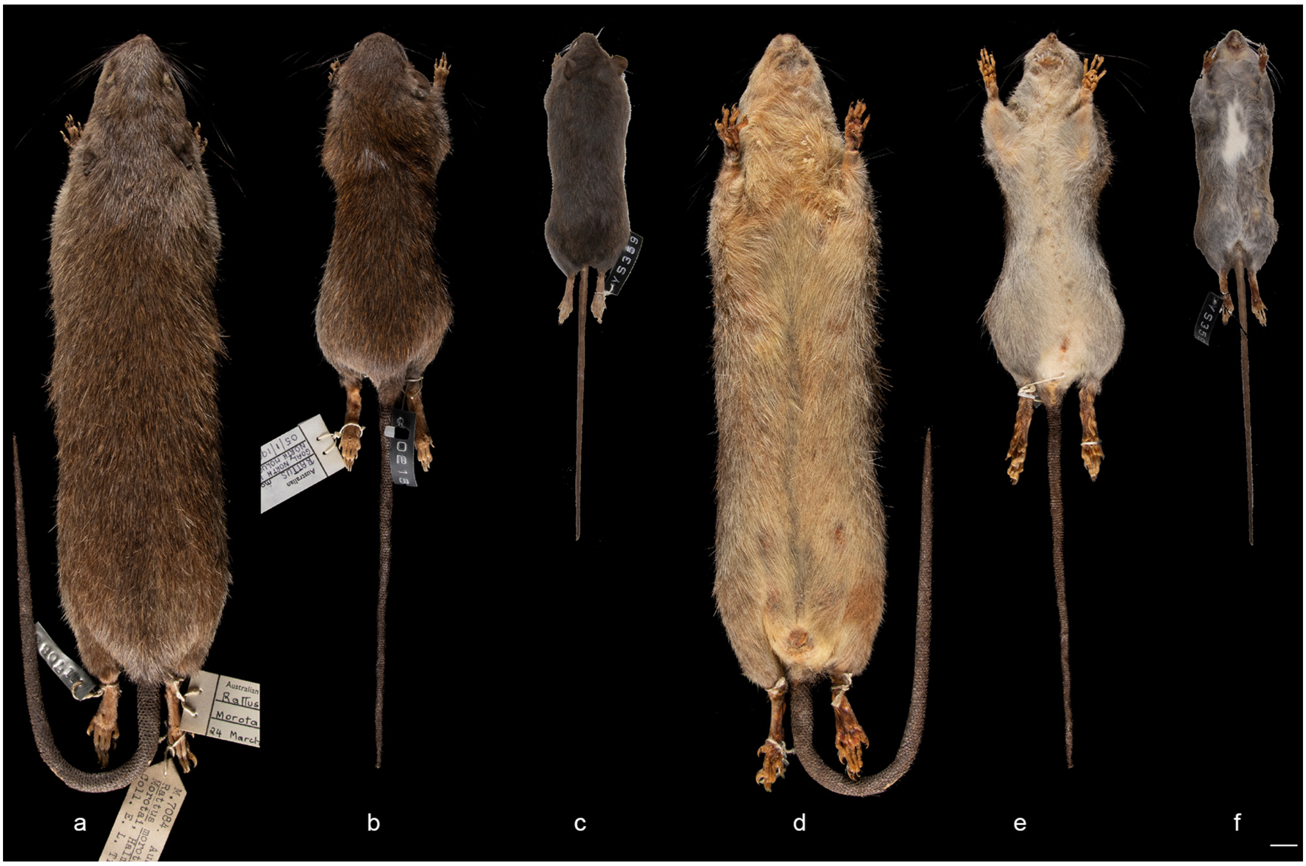

Figure 15. Dorsal and ventral views of study skins of (*a, d*) *Rattus morotaiensis* (AM M.7084); (*b, e*) *R. halmaheraensis* sp. nov. (AM M.23652 holotype); and (*c, f*) *R. obiensis* sp. nov. (MZB 38231, holotype). Scale bars 10 mm.

several key aspects. First, m1 has large peg-like anterolabial and posterolabial cuspids. Second, m2 has an anterolabial cuspid and posterolabial cusplets. Third, m3 has a well differentiated posterolabial cusplet, a diagnostic feature of both *R. obiensis* and *R. halmaheraensis* compared to *R. morotaiensis* and other *Rattus* from the region. Anterolabial cuspids on m3, present in *R. morotaiensis* but only in a minority of specimens of *R. halmaheraensis*, are present in both specimens of *R. obiensis*.

Discussion

Moluccan *Rattus* in taxonomic, biogeographic, and ecomorphological context

The murine genus *Rattus* is one of the most speciose mammalian genera as currently defined taxonomically, with a natural distribution encompassing mainland Asia and extending through the archipelagos of Southeast Asia, through Wallacea to the Sahulian continental components of New Guinea, Australia, and Tasmania, and onward to the oceanic islands of the Bismarck and Admiralty archipelagos of Northern Melanesia (Musser & Carleton, 2005). Some species in the genus have been widely introduced anthropogenically beyond their native distributions (especially *R. norvegicus*, the *R. rattus* species complex, and *R. exulans*, but also including *R. argentiventer*, *R. nitidus*, and *R. praetor*), giving the genus a nearly global current distribution, even reaching many of the world's most remote islands. Because they are so widespread and occur in commensal relationships with human populations, they have had massive impacts on humanity–in both historical and modern contexts–as agricultural pests, vectors of zoonotic disease, and as model organisms fundamental to studies of biomedicine. Thomson *et al.* (2018) thus aptly labelled them "the vertebrates with the most influence on human welfare." As a result, clearer understanding the full scope of the evolutionary genomics and morphological variation in species of *Rattus* remains an active goal across many disciplines within evolutionary biology, in part to illuminate their evolutionary history, including deep and more recent patterns of speciation and dispersal, and to identify potential underlying factors in their successful occurrence across a great variety of ecological contexts (Aplin *et al*., 2003).

To date, the Maluku Islands have been one of the least studied regions within the natural distribution of the genus for the systematics and biogeography of *Rattus*, such that major patterns in their diversity and evolutionary history have been obscure until now. In this paper we have provided a more comprehensive review of Moluccan *Rattus* systematics, reporting newly documented species, and more clearly identifying phylogenetic relationships both among species in the region, and in broader context within the evolution of *Rattus* and related genera within the tribe Rattini. We have documented the phylogenetic position of the nominal genus *Nesoromys*, often recognized as a monotypic genus for the Seramese endemic species *R. ceramicus*, as phylogenetically nested among other *Rattus*, and thus subsume *Nesoromys* into the taxonomic synonymy of *Rattus*, at least for the

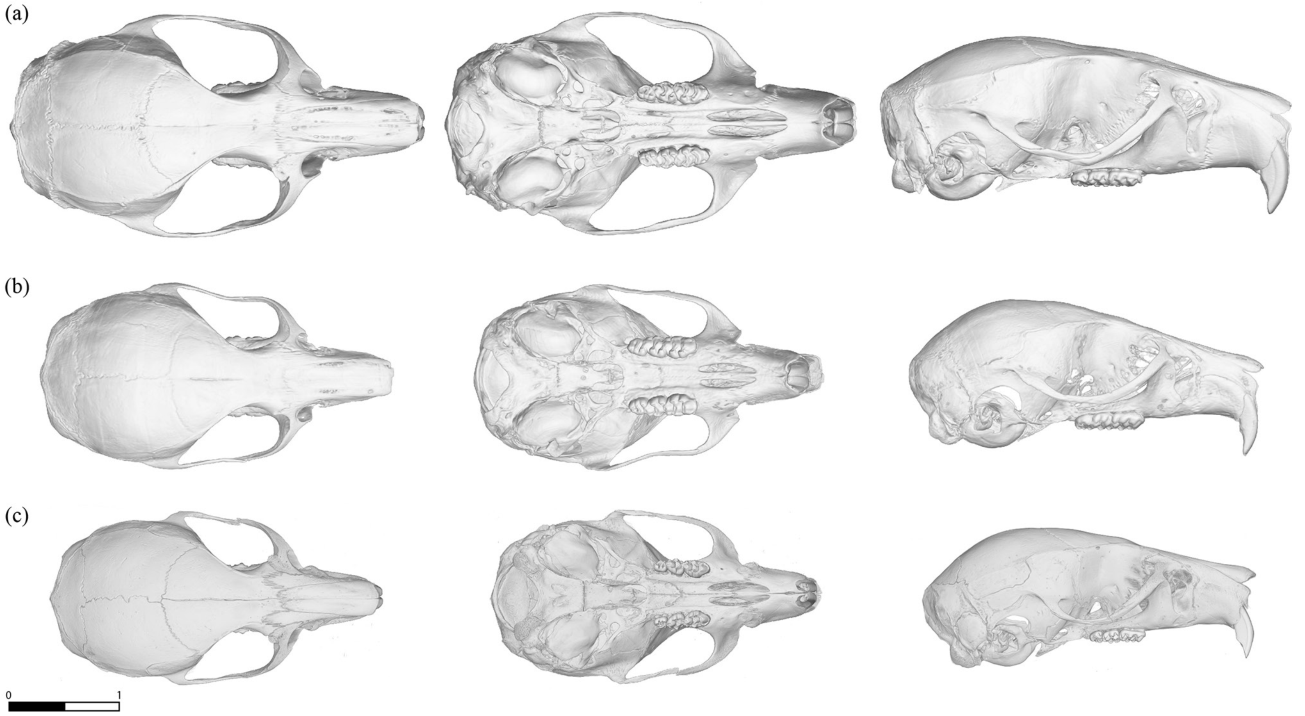

Figure 16. Dorsal, ventral, and lateral views of the skull of (*a*) a young adult *Rattus halmaheraensis* sp. nov. (MZB 33229); (*b*) an immature *R. halmaheraensis* sp. nov. (MZB 33551); (*c*) an immature *R. obiensis* sp. nov. (MZB 38231, holotype).

present. This continues a now longstanding research effort, led especially by Musser throughout his career as a murine taxonomist, to clarify the membership and boundaries of *Rattus* sensu stricto in both phylogenetic and morphological terms. Over time, this has mostly led to many generic-level lineages within the Rattini, often previously included in *Rattus*, being placed outside the phylogenetic scope of the genus, including, for example, *Sundamys*, *Kadarsanomys*, *Tarsomys*, *Limnomys*, and others (Musser, 1981; Musser & Newcomb, 1983; Musser & Heaney, 1992; Musser & Carleton, 2005).

More work remains to define *Rattus* taxonomically, as its current phylogenetic scope is paraphyletic with respect to other currently recognized genera, and it continues to incorporate various deep lineages that may warrant generic-level recognition (e.g., Fig. 2). Various possibilities mark potential paths forward in taxonomic delineation of *Rattus*. Because the type species of *Rattus* is *R. norvegicus*, one possibility might be to restrict the definition of the genus to *R. norvegicus* and its closest relatives, like *R. nitidus*, and perhaps other closely-related species of Asian origin (e.g., Fig. 2). Restricted concepts of *Rattus*, such as this one, would require different generic names to be used for various other lineages currently subsumed in *Rattus* (Rowe *et al*., 2011, 2019, Fabre *et al*., 2013, 2018, Robins *et al*., 2014, Rowsey *et al*., 2022). This includes the monophyletic group of species that incorporates all native *Rattus* from the Australo-Papuan region, plus most Moluccan species, and members of the *xanthurus* species group from Sulawesi (Steppan & Schenk, 2017; Thomson *et al*., 2018), the earliest generic name for which is *Stenomys* Thomas, 1910. Alternately, the phylogenetic definition of *Rattus* could be expanded to include many closely-related lineages, such as *Abditomys*, *Baletemys*, *Tarsomys*, *Limnomys*, *Kadarsanomys*, and likely *Tryphomys*, such that the genus encompasses a broader scope of "core" Rattini lineages. This might even make the genus easier to diagnose morphologically, as current working definitions, like that proposed by Musser & Newcomb (1983), involve various characters that are suboptimal or confusing, including various plesiomorphic and variable traits.

In any case, our work in this paper highlights for the first time the distinctness of various Moluccan species currently assigned to *Rattus* in the broader context of closely related murines. Given that *Rattus* spread from the Asian continent into the Indo-Pacific islands (Rowe *et al*., 2019), areas to the east of the Huxley and Wallace Lines–the Philippines and the various subregions of Wallacea (Sulawesi, the Moluccas, and Nusa Tenggara) are important in understanding arrival of *Rattus* and other Rattini into the Australo-Papuan region from the Asian continent (Fabre *et al*., 2013, 2018; Rowe *et al*., 2019). Wallacean islands represent a particularly important potential dispersal pathway in the history of *Rattus* spread and diversification (Rowe *et al*., 2011), and we now know that the Moluccas in particular are home to important evolutionary radiations with the genus, with unique ecomorphological features.

For example, the framework developed here helps to illuminate that North Moluccan *Rattus* (*R. morotaiensis*, *R. halmaheraensis*, and *R. obiensis*) are morphologically a very distinctive cluster, especially in their molar morphology. Their molars are characterized by a well-developed posterior cingulum on m1 and m2, as well as anterolabial and anterolingual cuspids on each m1 that are almost equal in size and each shaped like a peg, characteristics that are never found in other *Rattus*. The cusps are also rather low compared to other *Rattus*; they also have more complex surfaces due to well-developed cingula around the anterior margins of M1 and m1, and elsewhere along the margins of the molars. Further, the distinctive posterolabial cusplet on m3 is found only in *R. obiensis* and *R. halmaheraensis* and is a rare feature in murids that is not found in other *Rattus* species. Finally, the strong crenulation over the unworn parts of the molars in *R. morotaiensis* and *R. halmaheraensis* is a feature not seen often in other murids and is unique within *Rattus*; these structures roughen the surfaces of the teeth everywhere except on the worn occlusal parts. These morphological features probably indicate an affinity between these three species, and with an expanded molecular dataset, these three species may be shown more clearly to form a clade (cf. Fig. 2).

Our molecular phylogenetic analyses (Fig. 2) also reveal that several Moluccan *Rattus* lineages may occupy basal and divergent positions within the Australo-Papuan *Rattus* clade (see also Helgen, 2003; Rowe *et al*., 2011; Fabre *et al*., 2013, 2018). Most of the earliest divergences in this lineage involve progressive divergences of Moluccan endemic species from Taliabu and subsequent splits involving Seramese (*R. ceramicus* and *R. feliceus*) and North Moluccan species (*R. morotaiensis*, *R. halmaheraensis*, and *R. obiensis*). However, these relationships remain incompletely resolved and will require a larger gene dataset to be delineated in more detail and with greater confidence; the two new *Rattus* species from Taliabu Island seem to represent divergent lineages and their phylogenetic position will likely shift when datasets including more nuclear genes are available. Based on our morphological analyses, *R. feileri* exhibits various morphological features similar to the *xanthurus* species group. On the other hand, the phylogenetic position of the Seram *Rattus* and the *Rattus morotaiensis* groups demonstrates membership in a moderately supported clade that also includes the *R. xanthurus* species group of Sulawesi and the Australo-Papuan *Rattus* clade, which has been recovered in other studies (Rowe *et al*., 2019; Roycroft *et al*., 2022).

The one Moluccan endemic species we were not able to place in our molecular phylogeny is *Rattus elaphinus*, because we were not successful in extracting sequence data from museum specimens so far. Given its morphological attributes (Musser & Holden, 1991; Musser & Carleton, 2005), we suggest that *R. elaphinus* is either a member of the Australo-Papuan clade or a member of a clade that includes *R. hoffmanni* and *R. argentiventer* (cf. Fig. 2). This suggests that the *Rattus* assemblage on Taliabu results from more than one, and possibly several, independent colonization events involving different lineages within the genus. Apart from *R. elaphinus*, the two newly described species from Taliabu, *R. feileri* and *R. taliabuensis*, appear to represent molecularly and morphologically divergent lineages that might be the results of multiple dispersal events. However, these types of scenarios and hypotheses will need to be evaluated with a larger genetic dataset before clarity can emerge.

Important biogeographic patterns are starting to emerge elsewhere for Moluccan Rattini, as well. In the North Moluccas, on the island clusters of Morotai, Halmahera-Bacan, and Obi-Bisa, it is now clear that two distinct Rattini lineages have spread and diversified in parallel across these islands, namely the four described species of *Halmaheramys* (Fabre *et al*., 2013, 2018; Aplin *et al*., 2023), and the three described species of the *Rattus morotaiensis* group (Fabre *et al*., 2013; Rowe *et al*., 2019). Another surprising result concerns the sister relationship recovered between *Rattus ceramicus* and *Rattus feliceus*. Previously classified in two different genera (*Nesoromys* and *Rattus*; Thomas, 1922; Musser & Carleton, 2005), these very distinct species (Figs 2–4) are in fact very closely related (Table 1) and may well be the result of rare *in situ* speciation along the altitudinal gradients in Seram, probably facilitated by altitudinal ecological speciation, a pattern only rarely found on islands (Heaney *et al*., 2018), apart from very large islands. This provides the first indication (perhaps also indicated by two related *Halmaheramys* on Morotai–Aplin *et al*., 2023), that some Moluccan islands may be large enough, and have murine evolutionary histories deep enough, to support intra-island diversification. Of course, future taxonomic discoveries and the development of larger molecular genetic datasets may shift and more expansively illuminate these initial glimpses into these patterns.

Maluku is a very complex set of islands and archipelagos with various distinct and contrasting geological histories and geomorphologies (Hall *et al*., 1991; Hall, 2002, 2013; Watkinson *et al*., 2011; Nugraha & Hall, 2018). Among the larger islands, Halmahera and Obi may be among the geologically oldest parts of the archipelago (Hall, 2002, 2013), but several other large islands, such as Seram and Buru, may also be quite old, and their origins probably all predate the origin of murines in Asia (older than 10–14 million years; Kimura *et al*., 2016; Pagès *et al*., 2016). Our phylogenetic results clearly support multiple colonization events across islands and archipelagos for Moluccan *Rattus* and related Rattini, with some clustered communities at least on Seram and the North Moluccas. The Sunda Shelf, Sulawesi, and the Philippines may have provided source pools for these various Moluccan colonizations, and one or more dispersal waves from the western Indo-Pacific region may be at the origin of Australo-Papuan *Rattus* diversification. Again, more comprehensive molecular and morphological comparisons will be required in order to propose a clearer biogeographical framework and more clearly illuminate ecomorphological patterns in these radiations. For example, clustered phylogenetic patterns identified so far can help us to understand the origins of common ecomorphological aspects of Moluccan rat communities–for example, long-tailed rats and large short-tailed rats often co-occurring on various large Moluccan islands (Fig. 1). Four long-tailed rats with a short rostrum and a probable scansorial or arboreal lifestyle (*R. morotaiensis, R. halmaheraensis*, *R. obiensis,* and *R. feileri*) are now documented in the region. On Seram, however, these long-tailed *Rattus* are absent, possibly because of the rich *Melomys* fauna on the island (4 species: Fabre *et al*., 2017), which also have a long tail and a semi-arboreal lifestyle. On the other hand, large short-tailed spiny-furred rats are known in murine communities by *Rattus* species from Taliabu (*R. taliabuensis*) and Seram (*R. feliceus*), and by *Halmaheramys* species, which probably play a very similar ecological role, from Halmahera (*H. bokimekot*), Morotai (*H. funderus* and *H. bellwoodi*), and Obi and Bisa (*Halmaheramys wallacei*) (Fabre *et al*., 2013, 2018; Aplin *et al*., 2023). Environmental filtering may have operated to shape patterns on these islands, where rat communities are much less diverse taxonomically and ecomorphologically compared to those on very large islands such as Luzon, Sulawesi, or New Guinea, which harbor rich murine radiations (e.g., Heaney *et al*., 2013, 2016).

Conservation biology of Moluccan murines

Original habitats in the Moluccas are currently under considerable threat from logging and other deforestation, and the impacts of extractive industries, especially gold and nickel mining. These impacts have led to considerable removal of primary forest cover, a threatening process for many endemic species across the Moluccas (e.g., Monk *et al*., 1997; Davidson *et al*., 1995; Rheindt, 2010; Rheindt & Hutchinson, 2013; Rheindt *et al*., 2020; Voigt *et al*., 2021). However, for most of the murine species discussed in this paper, our understanding of conservation threats and impacts remains minimal, and based mainly on glimpses generated from recent fieldwork in the region.

One interesting glimpse into relevant environmental issues comes from our recent fieldwork on Obi. Obi is currently most threatened by nickel mining, and this activity has already affected the landscape, with few primary forest habitats remaining. The rodent fauna of Obi is quite rich, and there may be additional murid species yet to be discovered on this island, especially in the mountains (which we suspect to be the case across many Moluccan islands). Commensal species appear to be less abundant in Obi compared to the other islands in the Moluccas. During a month of fieldwork on Obi we collected many specimens of native murines, including *M. obiensis* (20 specimens), *Hydromys chrysogaster* (4 specimens), *Halmaheramys wallacei* (3 specimens), *Rattus obiensis* (2 specimens) and a new species of *Uromys* (1 specimen). Most of these were captured in the highlands (900–1000 m), but we also collected some *Melomys* in the lowlands. Most of the habitat on Obi consisted of second growth that had been logged 20–25 years ago (local community, pers. comm.) and was heavily disturbed by both hunters and local people's activities. Notably, a hiatus in human archaeological evidence on Obi may indicate a reduced human presence lasting several millennia during Obi's deep past (Shipton *et al*., 2020), and Flannery (1995) also mentioned evidence the island has not always been populated. Relatively reduced human impacts during Obi's history may explain why Obi may have more native and fewer commensal rats compared to other Moluccan islands, which were more exposed to intensive trade and anthropogenic disturbance (Kealy *et al*., 2017). However, archaeological data are scarce across Maluku (Aplin *et al*., 2023), and a large variety of factors may have influenced the endemic fauna and the differential dynamics of species invasion in Obi and elsewhere.

Another glimpse of possible environmental impacts in the Moluccas comes from our work in Buru. Confusingly, surveys on the large island of Buru have never yielded evidence of any native rodent species, in contrast to the murine faunas now known especially from Seram, Obi, Halmahera, Morotai, and Taliabu. Nevertheless, we suspect that endemic murines are most likely present on an island so large, high, geologically ancient, and centrally positioned within Maluku as Buru. During two months of fieldwork on Buru (March 2011 and January 2014), sampling two primary forests at 1600 m on Kapalat Mada (northwest Buru) and on Gunung Adat at 2000 m (central Buru), our team only managed to collect the commensal rat *Rattus exulans* (150 specimens) and the commensal shrew *Suncus murinus* (30 specimens). Buru has one of the highest mountains in the region (Kapalat Mada, 2428 m). Here *Rattus exulans* was captured in large numbers, especially between 1600–1800 m on Kapalat Mada, and we collected them both on the ground and in trees. *Rattus exulans* are present and abundant in both secondary and primary forests on Buru, and may compete with endemics that might be present at very low densities. On most other Moluccan islands, however, including Obi, Halmahera, and Seram, recent trapping efforts have recorded commensal species only near villages and in agricultural areas, including *R. exulans*, *R. tiomanicus*, *R. nitidus,* and *R. rattus*. Further ecological surveys on Buru and other Moluccan islands might further illuminate possible impacts of introduced species like *R. exulans*, and other species, on Wallacean native rodent faunas.

As highlighted by the papers in this volume, and in other recent vertebrate taxonomic discoveries reported from the region (e.g., Rheindt *et al*., 2020), additional and immediate biological surveys are urgently needed to document and describe biodiversity across the archipelagos of Maluku, especially in the face of many ongoing anthropogenic impacts on Wallacean habitats and species. We suspect that many additional species of living rodents remain as yet undocumented across these islands, and some of the species being documented as new today, such as *R. feileri* or *R. taliabuensis*, have not been documented by biologists in many decades. Palaeontological and archaeological studies in the region, especially in Nusa Tenggara and North Maluku, highlight that many extinctions of endemic murines have recently taken place in Wallacean islands (Musser, 1981; Aplin & Helgen, 2010; Veatch *et al*., 2019, 2023; Aplin *et al*., 2023; Louys *et al*., 2023), highlighting the urgency and importance of both biodiversity knowledge and conservation action in addressing the potential for further and ongoing extinctions.

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Appendix 1. Gazetteer and specimen list of the Moluccan *Rattus* specimens examined or collected by the authors. The numbers preceding each locality are keys to the map in Fig. 1.

The Seramese *Rattus*

Rattus ceramicus Thomas, 1920

(1) Pulau Seram, Gunung Manusela (2.9798°S 129.6105°E): NHMUK ZD 1920.7.26.28–1920.7.26.30, WAM M33490.

Rattus feliceus Thomas, 1920

(1) Pulau Seram, Gunung Manusela (2.9798°S 129.6105°E): NHMUK ZD 1920.7.26.4–1920.7.26.7 and MZB 22684.

(2) Pulau Seram, Piliana village (3.20501°S 129.57604E): AM M.30807–M.30808.

The *Rattus* species of the Sula Islands

Rattus elaphinus Sody, 1941

(3) Pulau Taliabu (1.8268°S 124.7741°E): AMNH 109318–109335 and MZB 4076–4086.

(4) Pulau Mangole, Capalulu village (1.9°S 125.9°E): AM M.26609–26610, AM M.26463–26464.

Rattus feileri sp. nov.

(3) Pulau Taliabu (1.8268°S 124.7741°E): SNSD 11429.

Rattus taliabuensis sp. nov.

(3) Pulau Taliabu (1.8268°S 124.7741°E): SNSD 11968.

The *Rattus morotaiensis* group

Rattus morotaiensis Kellogg, 1945

(5) Pulau Morotai, Timber Camp (2.4505°N 128.3666°E): AM M.26618.

(6) Pulau Morotai, North of Wama (2.042°N 128.319°E): AM M.7083–7086, USNM 277309–277315.

Rattus halmaheraensis sp. nov.

(7) Pulau Halmahera, Kau District, Kai (1.1745°N 127.8859°E): AMNH 267681.

(8) Pulau Halmahera, Goal (1.2115°N 127.56007°E): AM M.23652.

(9) Pulau Halmahera, Tanah Putih (0.9937°N 127.5812°E): AM M.26965, AM M.26614–26615.

(10) Pulau Halmahera, Tofu Blewen (0.803°N 128.023°E): MZB 23241, MZB 33229, MZB 33231–33236, MZB 33238–33240, MZB 33247.

(11) Pulau Halmahera, Boki Mekot (0.612°N 128.047°E): MZB 23242, MZB 33248–33249, MZB 33252–33256, MZB 33259.

(12) Pulau Halmahera, Kaorahai II (0.669°N 127.973°E): MZB 33498, MZB 33500–33503.

(13) Pulau Halmahera, Ake Sake (0.487°N 127.988°E): MZB 33542, MZB 33544, MZB 33547–33550.

(14) Pulau Ternate (0.80911°N 127.338°E): AM M.23655.

(15) Pulau Moti (0.45717°N 127.41461°E): MZB 33573–33577.

(16) Pulau Bacan, Kampong Tomori (0.666°S 127.48342°E): AM M.27011, AM M.26616.

(17) Pulau Bacan, 6 km east of Labuha (0.6561°S 127.550°E): AM M.23720, AM M.23653.

Rattus obiensis sp. nov.

(18) Pulau Obi, Gunung Sere (1.624°S 127.709°E): MZB 38231–38232.

Appendix 2. Supplementary figures and tables.

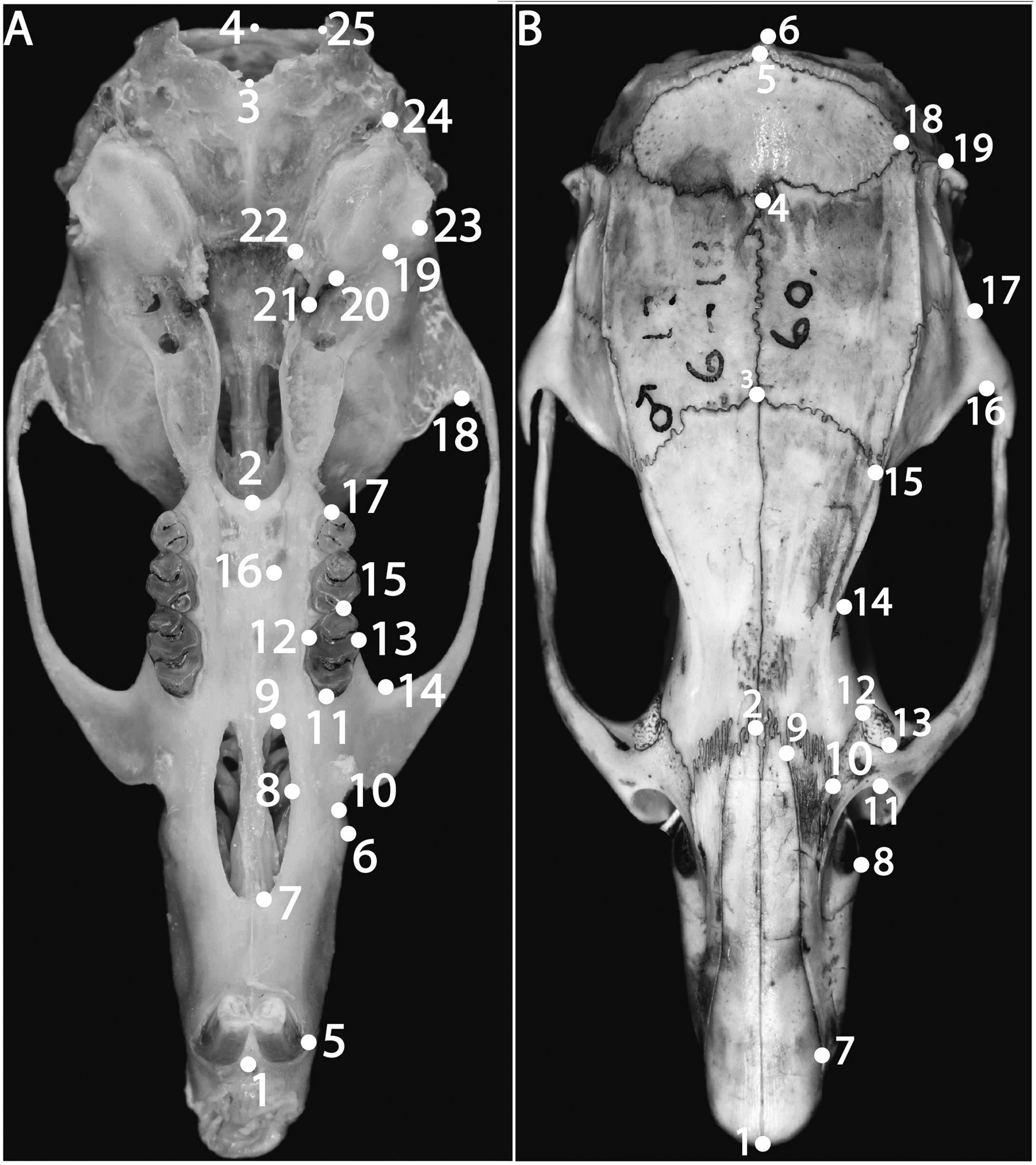

Figure 17. **(A)** Landmark locations on palatal side: (1) premaxillary bone between anterior margin of upper incisors, (2) posterior margin of the palatal bone, (3) anterior margin of the foramen magnum, (4) posterior margin of the foramen magnum, (5) lateral margin of the right incisor, (6) lateral margin of the lacrimal notch, (7) anterior margin of the incisive foramina, (8) lateral margin of the incisive foramina, (9) posterior margin of the incisive foramina, (10) maxillary insertion of the zygomatic root, (11) anterior margin of the first upper molar, (12) lingual margin of M1 at the level of the second lamina, (13) labial margin of M1 at the level of the second lamina, (14) anterior margin of the orbit, (15) posterior margin of M1, (16) posterior margin of the posterior palatine foramina, (17) postero–lateral margin of M3, (18) posterior margin of the temporal fossa, (19) suture between squamosal and sphenoid, (20) junction between tympanic bulla and eustachian tube, (21) lateral tip of the eustachian tube, (22) junction between basioccipital and basisphenoid, (23) most internal point of the external auditory meatus, (24) contact between tympanic bulla and jugular process, (25) lateral margin of the foramen magnum. **(B)** Landmark locations on dorsal side: (1) nasal bones mid-distal margin, (2) nasal bones mid-proximal margin, (3) frontal bones mid-proximal margin, (4) parietal bones between their mid-proximal margin, (5) interparietal bone mid-proximal margin, (6) occipital bone most distal mid-point, (7) most lateral margin of the nasal bone, (8) most lateral margin of the lacrimal capsule, (9) point between nasal, premaxillary and frontal sutures, (10) point between maxillary, premaxillary and frontal sutures, (11) most anterior margin of the infra-orbital fossa, (12) proximal edge of the lacrimal bone, (13) distal edge of the lacrimal bone, (14) frontal constriction, (15) parietal and fronto-squamosal antero-dorsal suture, (16) posterior margin of the temporal fossa, (17) posterior margin of the squamosal close to the jaw joint, (18) most lateral point of the interparietal bone linking occipital squamosal and parietal bones, (19) posterior edge of the nuchal crest near the mastoid region.

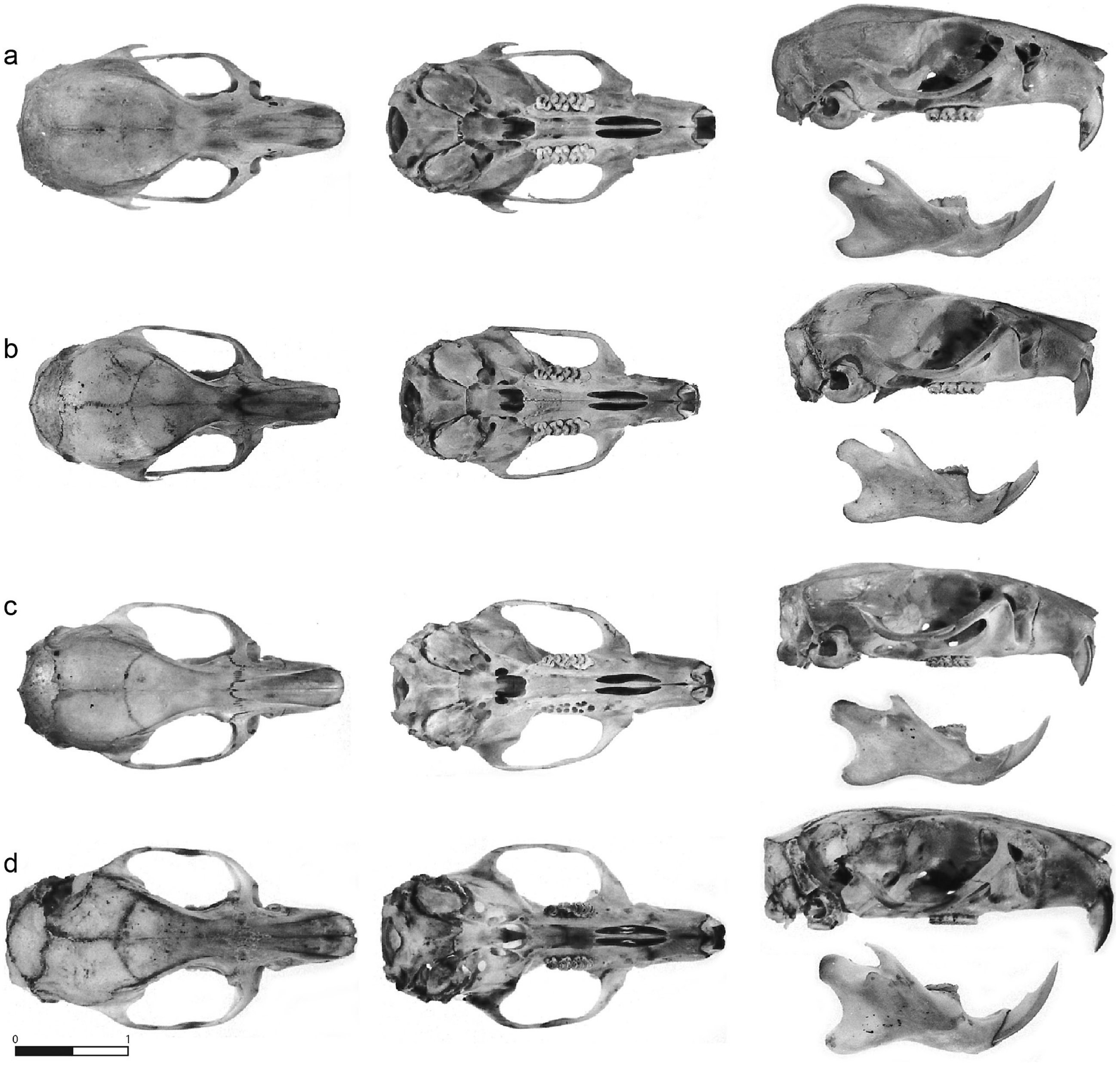

Figure 18. Dorsal, palatal, and lateral view of the skull from (*a*) *Rattus feileri* sp. nov. (SMF 11429, holotype); (*b*) an immature *R. morotaiensis* (USNM 277314); (*c*) an adult of *R. morotaiensis* (USNM 277309); and (*d*) an old adult of *R. morotaiensis* (USNM 277313).

Figure 19. Dorsal and palatal views of *Rattus halmaheraensis* for adult (MZB 33234, 33235), subadult (MZB 33270, 33548), and juvenile (MZB 33551) specimens.

Figure 20. External appearance (*a*) of the holotype of *Rattus obiensis* sp. nov. shortly after capture. Both fore and hind feet are pictured (*b*–*c* and *d*–*e*, respectively).

Table 6. List of Asian and Australo-Papuan Rattini specimens included in this study and GenBank accession numbers of the sequences. "*this study*" signifies newly generated sequences; *—sequences obtained thanks to Emily Roycroft and Kevin C. Rowe, available at https://data.bioplatforms.com/; **—sequences obtained thanks to Vicki Thomson and not deposited in GenBank; na—not available.

Specimen	Voucher	Voucher institution	*Cytb*	BRCA1	GHR	IRBP	RAG1
Abditomys latidens	USNM 357244	United States National Museum	*this study*	na	na	na	na
Baletemys kampalili	FMNH 194804	Field Museum of Natural History	OM502714	na	OM502622	OM502591	OM502575
Bandicota bengalensis	T065	na	AM408336	na	AM910945	AM408331	na
Bandicota indica	ABTC 64912	South Australian Museum	KY753950	na	na	HM217713	na
Bandicota savilei	R1191	na	HM217385	na	na	HM217665	na
Diplothrix legata	HS 1163	na	AB033696	EU349670	EU349799	AB033706	EU349885
Kadarsanomys sodyi	MZB 34728	Museum Zoologicum Bogoriense	MG189671	*this study*	MG189687	MG189697	*this study*
Limnomys bryophilus	FMNH 148182	Field Museum of Natural History	OM502705	na	OM502616	OM502586	OM502570
Limnomys sibuanus	FMNH 206281	Field Museum of Natural History	OM502706	na	OM502617	OM502587	OM502571
Nesokia indica	Nind580	na	AF160605	—	—	—	—
Palawanomys furvus	FMNH 196056	Field Museum of Natural History	OM502717	na	OM502626	na	na
Rattus andamanensis	AMNH 272324	American Museum of Natural History	KY754124	na	na	HM217641	MF097929
Rattus argentiventer	MSB 93171	Museum of Southwest Biology	KY754125	na	na	HM217602	MF097930
Rattus baluensis	EBD 30360M	Estación Biológica de Doñana	NC_035621	na	na	na	na
Rattus burrus	USNM 111810	United States National Museum	Thomson *et al*., 2018**	na	na	na	na
Rattus ceramicus	NHMUK ZD 1920.7.26.28	Natural History Museum (London)	*this study*	na	na	na	na
Rattus colletti	ABTC51642	South Australian Museum	na	HQ334408	na	HQ334596	HQ334665
Rattus detentus	PNGMAG274363	Australian Museum	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*
Rattus everetti	FMNH 142350	Field Museum of Natural History	DQ191485	na	na	DQ191513	na
Rattus exulans	NK 80010	na	NK 80010	na	DQ019074	KC953446	DQ023455
Rattus facetus	MVZ 225821	Museum of Vertebrate Zoology	MN273046	MN272962	MN272984	MN273005	MN273026
Rattus feileri	SNSD 11429	SNSD Dresden[b]	*this study*	na	na	na	na
Rattus feliceus	NHMUK ZD 1920.7.26.7	Natural History Museum (London)	*this study*	*this study*	*this study*	*this study*	*this study*
Rattus fuscipes	GI02R01/ABTC8644	South Australian Museum	na	HQ334429	na	HQ334620	HQ334683
Rattus giluwensis	ABTC87301	South Australian Museum	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*	Roycroft *et al*., 2022*
Rattus hainaldi	WAM M35570	Western Australian Museum	Thomson *et al*., 2018**	na	na	na	na
Rattus halmaheraensis	ASA M85	Museum Zoologicum Bogoriense	MN273047	MN272963	MN272985	MN273006	Roycroft *et al*., 2022*
Rattus halmaheraensis	MZB 33500	Museum Zoologicum Bogoriense	*this study*	na	*this study*	*this study*	na
Rattus halmaheraensis	MZB 33501	Museum Zoologicum Bogoriense	*this study*	na	*this study*	*this study*	na
Rattus halmaheraensis	MZB 33469	Museum Zoologicum Bogoriense	*this study*	*this study*	*this study*	*this study*	na
Rattus hoffmanni	MVZ 225813	Museum of Vertebrate Zoology	KC878168	MK920935	KC878200	KC878238	MK920936
Rattus hoogerwerfi	ANSP 20319	Drexel University[c]	MN126561	na	na	na	na
Rattus jobiensis	NHMUK ZD 46.633	Natural History Museum (London)	*this study*	*this study*	*this study*	*this study*	*this study*
Rattus kandianus	ABTC 08529	South Australian Museum	JN675603	na	na	na	na
Rattus korinchi	RMNH 23151	Naturalis Museum	NC_049042	na	na	na	na
Rattus leucopus	ABTC42806 /KU 160770	SAM and KUM[d]	na	HQ334396	EU349825	HQ334582	HQ334652
Rattus losea	ABTC 118627	South Australian Museum	HM031715	na	na	na	na

Table 6. *Continued ...*

Table 6. *Continued.*

Specimen	Voucher	Voucher institution	*Cytb*	BRCA1	GHR	IRBP	RAG1
Rattus lugens	USNM 121534	United States National Museum	Thomson *et al.*, 2018**	na	na	na	na
Rattus lutreolus	ABTC 51720	South Australian Museum	GU570671	na	na	HQ334603	HQ334669
Rattus macleari	OUMNH 18844	OUMNH[f]	PRJEB50610	PRJEB50610	PRJEB50610	PRJEB50610	PRJEB50610
Rattus marmosurus	HS2570	na	Thomson *et al.*, 2018**	na	na	na	na
Rattus mindorensis	FMNH 222185	Field Museum of Natural History	OM502739	na	OM502645	na	na
Rattus montanus	PDZ 41	na	KY986747	na	na	na	MN160099
Rattus morotaiensis	USNM 277315	United States National Museum	Thomson *et al.*, 2018**	na	na	na	na
Rattus niobe	AM M.17664	Australian Museum	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus nitidus	L0192	na	HM217479	na	na	HM217711	na
Rattus norvegicus	Rnor_6.0 AR106[a]	NCBI	EU349782	EU349671	NC_005101	NC_005115	AY294938
Rattus novaeguineae	AM M.19055	Australian Museum	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus obiensis	MZB 38231	Museum Zoologicum Bogoriense	*this study*	*this study*	*this study*	*this study*	*this study*
Rattus obiensis	MZB 38232	Museum Zoologicum Bogoriense	*this study*	*this study*	*this study*	*this study*	*this study*
Rattus praetor	ABTC 47252	South Australian Museum	na	HQ334403	na	HQ334591	HQ334660
Rattus pyctoris	NHMUK ZD 23.9.1.56	Natural History Museum (London)	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus richardsoni	AM M.30618	Australian Museum	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus sakeratensis	R4724	na	JX534060	na	na	na	na
Rattus satarae	T-0828	University of Montpellier Tissue Collection	HM217739	na	na	HM217749	na
Rattus sordidus	ABTC 51664	South Australian Museum	na	HQ334411	na	HQ334599	na
Rattus sp. from Sibuyan	FMNH 135719	Field Museum of Natural History	OM502742	na	OM502647	OM502598	OM502581
Rattus steini	AM M.17691	Australian Museum	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus taliabuensis	SNSD 11968	SNSD Dresden[b]	*this study*	na	na	na	na
Rattus tanezumi	ABTC 08576	South Australian Museum	FR775851	na	na	na	na
Rattus tiomanicus	NMV Z25161	Museums Victoria	na	na	MN272987	na	MN273028
Rattus tunneyi culmorum	RAT132	Centre for Animal Conservation Genetics	na	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus vandeuseni	AM M.30812	Australian Museum	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus verecundus	NHMUK ZD	Natural History Museum (London)	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus verecundus	AM M.17628	Australian Museum	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*	Roycroft *et al.*, 2022*
Rattus villosissimus	ABTC 00549	South Australian Museum	EU349729	EU349673	EU349826	HQ334576	EU349915
Rattus xanthurus	NMV Z54170	Museums Victoria	MK920960	MK920956	MK920957	MK920958	MK920959
Rattus everetti	FMNH 146722	Field Museum of Natural History	OM502721	na	OM502636	OM502595	OM502578
Rattus rattus	Rrattus_CSIRO_v1	CSIRO[e]	GCF_011064425	GCF_011064425	GCF_011064425	GCF_011064425	GCF_011064425
Tarsomys apoensis	FMNH 148178	Field Museum of Natural History	OM502763	na	GQ405395	DQ191516	na
Tarsomys echinatus	FMNH 206296	Field Museum of Natural History	OM502764	na	OM502665	na	na
Tarsomys sp.	FMNH 208755	Field Museum of Natural History	WAK13171	na	WAK13100	na	na

[a] Rnor_6.0 reference Annotation Release 106.

[b] SNSD—Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde.

[c] The Academy of Natural Sciences of Drexel University.

[d] South Australian Museum / Kansas University Museum.

[e] The Commonwealth Scientific and Industrial Research Organisation.

[f] Oxford University Museum of Natural History.

Table 7. ANOVA on geometric size of log shape ratio (*a*), ventral skull (*b*), and dorsal skull (c) datasets are provided with species and sex as tested effects. P = *P*-value (* P < 0.05; ** P < 0.01; *** P < 0.001); df = degrees of freedom; F = F statistic provided by R. Colon ":" indicates tested interactions between variables.

	(a) LSR				(b) Ventral skull				(c) Dorsal skull			
Factors	SS	df	F	P	SS	df	F	P	SS	df	F	P
species	1345.21	7	9.5416	< 0.0001***	15.2356	7	16.2971	< 0.0001***	12.2601	7	10.7431	< 0.0001***
sex	65.07	1	3.2307	0.07706	0.5389	1	4.0352	0.04931	0.1565	1	0.9602	0.3305
species:sex	6.34	3	0.1049	0.95692	0.271	3	0.6764	0.57009	0.2507	3	0.5126	0.6749
residuals	1268.85	63			7.6125	57			11.4121	70		

Table 8. MANOVA on the non null PCs of log-shape ratios, ventral skull, and dorsal skull datasets. *P*-value: * P < 0.05, ** P < 0.01, *** P < 0.001; *df*: degrees of freedom; Pillai statistic provided by R; colon ":" indicates tested interactions between variables; *num., den.,* and *pc*: abbreviations for numerator, denominator, and Principal Component(s).

	3pc						36pc						35pc					
	(a) LSR						(b) Ventral skull						(c) Dorsal skull					
Factors	df	Pillai	approx.F	num.df	den.df	*P*	df	Pillai	approx.F	num.df	den.df	*P*	df	Pillai	approx.F	num.df	den.df	*P*
size	1	0.76724	59.334	3	54	< 0.0001***	1	0.9878	17.3337	42	9	< 0.0001***	1	0.9652	21.4001	35	27	< 0.0001***
species	7	1.75729	11.313	21	168	< 0.0001***	7	6.3016	3.2225	294	105	< 0.0001***	7	5.3367	3.0251	245	231	< 0.0001***
sex	1	0.17875	3.918	3	54	0.01328*	1	0.865	1.3726	42	9	0.3197	1	0.669	1.5592	35	27	0.1181
species:size	4	0.0429	0.203	12	168	0.99819	3	2.3314	0.9132	126	33	0.6495	4	2.3065	1.1674	140	120	0.1918
species:sex	1	0.01334	0.243	3	54	0.8657	1	0.8041	0.8798	42	9	0.6405	1	0.6395	1.3685	35	27	0.2016
size:sex	3	0.07012	0.447	9	168	0.90773	3	2.5175	1.3665	126	33	0.1501	3	1.5888	0.9329	105	87	0.6348
species:size:sex	1	0.0427	0.803	3	54	0.4977	2	1.6799	1.2493	84	20	0.2939	3	1.6592	1.0253	105	87	0.4542
residuals	56						50						61					

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Two New Species of *Halmaheramys* (Murinae: Rattini) from Archaeological Deposits on Morotai Island, North Moluccas, Indonesia

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Abstract. Two new species of murine rodents (*Halmaheramys funderus* sp. nov. and *H. bellwoodi* sp. nov.) are described from remains in an archaeological site on Morotai Island in North Maluku (Maluku Utara) Province of Indonesia. Both species are approximately the same size, (about the size of a Norway or brown rat, *Rattus norvegicus*) but they differ from each other in the degree of elongation of the snout and in molar size relative to osseous structures. These morphological contrasts are suggestive of dietary differences. Both species survived into the Holocene, and because the modern mammal fauna of Morotai is very little studied, it is possible that these species may still be extant on the island. Recognition of these taxa helps to demonstrate the distinctive nature of the Morotai murine fauna, which has unique species of *Rattus* and *Halmaheramys* compared to Halmahera-Bacan on one hand, and to Obi-Bisa on the other. The subfossil record (and modern fauna) of Morotai also lacks other Australo-Papuan genera that characterize other North Moluccan islands, such as *Hydromys* and *Uromys* (known from Obi) and *Melomys* (known from Halmahera and Obi-Bisa).

Abstrak (Bahasa Indonesia). Dua spesies baru tikus kelompok murinae (*Halmaheramys funderus* sp. nov. and *H. bellwoodi* sp. nov.) dideskripsi dari peninggalan di situs arkeologi di Pulau Morotai, Provinsi Maluku Utara, Indonesia. Kedua spesies tersebut kurang lebih memiliki ukuran yang sama, (seukuran dengan Tikus Norwegia atau Tikus Coklat, *Rattus norvegicus*), namun keduanya memiliki perbedaan pada tingkat pemanjangan moncong dan ukuran gigi geraham dibandingkan dengan struktur tulang.

Keywords: biogeography, *Rattus*, rodents, taxonomy, Wallacea
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Perbedaan morfologi ini menunjukkan perbedaan pola makan. Kedua spesies bertahan hidup sampai pada zaman Holosen, dan dikarenakan fauna mamalia modern di Morotai masih jarang dipelajari, ada kemungkinan spesies-spesies tersebut masih ada di pulau ini. Pengenalan terhadap taksa ini membantu dalam menunjukkan sifat alami yang berbeda dari fauna tikus murinae Morotai, yang mempunyai spesies unik *Rattus* dan *Halmaheramys* dibandingkan dengan Halmahera-Bacan di satu sisi, dan Obi-Bisa di sisi lain. Catatan subfosil (dan fauna modern) Morotai juga tidak terdapat genera Australo-Papua lain yang mencirikan pulau-pulau lain di Maluku Utara, seperti *Hydromys* dan *Uromys* (diketahui dari Obi) dan *Melomys* (diketahui dari Halmahera dan Obi-Bisa).

Introduction

The contemporary vertebrate fauna of the northern Moluccan islands (North Maluku Province of Indonesia; Fig. 1) includes several native murine rodents, some of which are endemic to these islands. These rodent faunas have remained very poorly known until recent years. The current report focuses on the rodents of the island of Morotai, the northernmost of the largest islands in the North Moluccas. Morotai lies immediately north of Halmahera and is separated from the latter island by a relatively narrow strait (15 km across) but quite deep water, perhaps up to 585 m (Bellwood *et al*., 2019). Current understanding of this considerable depth between these islands, and their differential tectonic histories (e.g., Hall *et al*., 1988; Hall, 2013) means that it is unlikely that a land bridge has connected these islands (Bellwood *et al*., 2019). Much remains to be learned about the biodiversity of all islands in the region, but Morotai is probably the least biologically explored of the major islands of the north Moluccas, which also include Halmahera, Bacan, and Obi (Fig. 1).

For most of the twentieth century, comparatively better information on Moluccan rodent faunas came from further south—from the island of Seram, which was first surveyed in some depth for rodents in 1920 (Thomas, 1920; Flannery, 1995; Helgen, 2003). Seram has the richest known murine fauna, with a total of six endemic species—four species of *Melomys* and two species of *Rattus* (Helgen, 2003; Fabre *et al*., 2017a, 2018, 2023; Turvey *et al*., 2023). The rodent assemblages present on the island groups of the Northern Moluccas have only more recently come into focal view. The major islands of the northern cluster—Morotai, Halmahera, Bacan, and Obi, and their smaller satellite islands, are now known to host 5 endemic rodents classified in the Rattini (the genus *Rattus* and its close relatives: Pages *et al*., 2010), all described since the Second World War and most described in the past decade. These are *Rattus morotaiensis* Kellogg, 1945, from Morotai; *Rattus halmaheraensis* Fabre *et al*., 2023, from Halmahera, Bacan, Ternate, and Moti; *Rattus obiensis* Fabre *et al*., 2023 from Obi; *Halmaheramys bokimekot* Fabre *et al*., 2013, from Halmahera; and *Halmaheramys wallacei* Fabre *et al*., 2018, from Obi and Bisa. Additional species of rodents classified in the Hydromyini, which have their centre of diversification in New Guinea and Australia, are known from some North Moluccan islands, but not yet from Morotai: the genus *Melomys* is known from Halmahera (*Melomys* sp. cf. *burtoni*—Fabre *et al*., 2017a) and Obi and Bisa (*Melomys obiensis* Thomas, 1911—Flannery, 1995), and *Hydromys chrysogaster* and an undescribed species of *Uromys* also occur on Obi (Flannery, 1995; Fabre *et al*., 2023).

Until now, the only native rodent recorded from Morotai is the living species *Rattus morotaiensis*, first documented by Kellogg (1945), which Fabre *et al*. (2023) have shown to be endemic to Morotai. However, an additional key resource for understanding Morotai's rodent diversity is a collection of murine remains deriving from archaeological excavation in 1991 of several sites on the island by archaeologist Professor Peter Bellwood and collaborators, particularly the Holocene site known as Daeo Cave no. 2 on the south coast of the island (Bellwood *et al*., 1993, 1998, 2019; Flannery e*t al*., 1998; Hull *et al*., 2019). Subfossil rodent material from Daeo Cave no. 2 was first studied by Flannery *et al*. (1998), who indicated that additional rodent diversity might have been present in the Quaternary fauna of Morotai. Flannery *et al*. (1998) noted the presence of three rodent taxa in this assemblage, one of which was identified as *Rattus morotaiensis*; the other taxa were referred to as "*Rattus* sp. 1" and "*Rattus* sp. 2." We have now re-examined this material and identify a total of four rodent species represented in this sample: the Morotai endemic species *Rattus morotaiensis* (a member of the Australo-Papuan *Rattus* + Sulawesi *Rattus xanthurus* clade; Fabre *et al*., 2013; Rowe *et al*., 2019); a commensal species, belonging to the *Rattus rattus* Species Complex (*sensu* Aplin *et al*., 2003, 2011); and two new species of the Northern Moluccan endemic genus *Halmaheramys. Halmaheramys* is a genus only recently characterized taxonomically, known by two previously described species, *H. bokimekot* of Halmahera, and *H. wallacei* of Obi and Bisa (Fabre *et al*., 2013*,* 2018). Here we describe the two new species of *Halmaheramys* from Morotai based on remains from Daeo Cave no. 2.

Materials and methods

The Morotai subfossil specimens are registered in the palaeontological collection of the Australian Museum, Sydney, as indicated by an AM F prefix. Modern voucher specimens cited in comparisons are from the mammal collections of the Australian Museum, Sydney (AM M), the Australian National Wildlife Collection, Canberra (ANWC), the Museum Zoologicum Bogoriense, Cibinong, Indonesia (MZB), and the South Australian Museum (SAM M). All measurements are expressed in millimetres (mm). The archaeological context of the remains was described by Bellwood *et al.* (1993, 1998, 2019) and Flannery *et al.* (1998). All of the material is of terminal Pleistocene to Holocene age, the bulk probably dating to within the last 6000 years or so (Bellwood, 2019; Hull *et al*., 2019). Molar cusp names and other anatomical terminology are used according to the conventions established especially by Guy Musser in numerous publications (e.g., Musser, 1981, 1991; Musser & Newcomb, 1983; Aplin & Helgen, 2010).

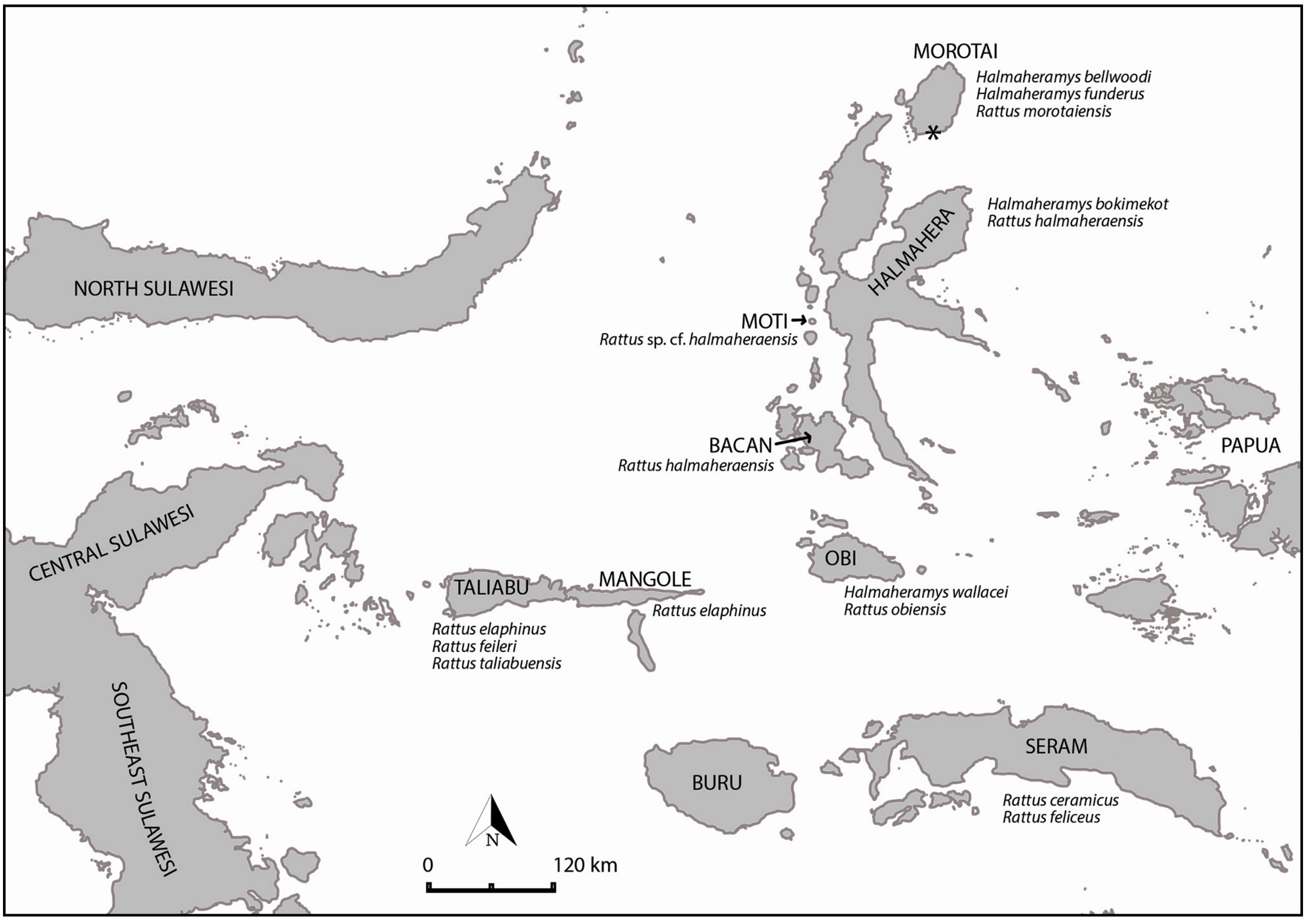

Figure 1. Map showing the location of the major islands and localities mentioned in the text, with Rattini species described from Moluccan islands to date. The star shows the location on Morotai of Daeo Cave no. 2, the archaeological site discussed in the paper, and the type locality for *Halmaheramys funderus* and *H. bellwoodi*.

We analyzed the mandibles of *Halmaheramys* specimens using two dimensional geometric morphometrics (2DGM). Lateral view photographs of the mandible were taken for 10 specimens comprising the four species of *Halmaheramys*. Following Fabre *et al*. (2017b), 10 landmarks were placed on each mandible image (Fig. 2) and 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. Due to the small sample size, we did not perform any statistical tests.

Results

We distinguish four murine species in the Daeo Cave no. 2 assemblage: two species of *Halmaheramys, Rattus morotaiensis* (Figs 3–5)*,* and a member of the *Rattus rattus* Species Complex (Fig. 6). These allocations are documented as follows.

Attribution of two new species to *Halmaheramys* Fabre, Pagès, Musser, Fitriana, Semiadi & Helgen 2013

Species of *Halmaheramys* differ from other murine rodents in having the following combination of features: a five rooted M^1; elongate and narrow upper molars with labial and lingual cusps broadly fused to the central cusp series; third (upper and lower) molars much smaller than second molars; M^{1-2} lacking cusp t7 and posterior cingulum; short anteroconid on M_1; accessory labial cuspids on M_{1-3} fused or only weakly differentiated from primary labial cusps; and broad incisive foramina that terminate forward of M^1. They differ specifically from *Rattus* in having narrower, more laminate upper molars; more laminate lower molars without chevronate or mammelonate cusps/cuspids; a less elongate anteroconid and less distinct accessory labial cusplets on M_{1-3}.

Both new species described here share the following dental features with other *Halmaheramys*: (1) extreme reduction or loss of the anterolabial cusps of the second and third lower molars; and (2) close union of the anteroconid of the first lower molar against the front of the anterior lamina, with virtual obliteration of the anterolabial and anterolingual flexids. The following dental and cranial features of *Halmaheramys* are further confirmed in *H. funderus* (no

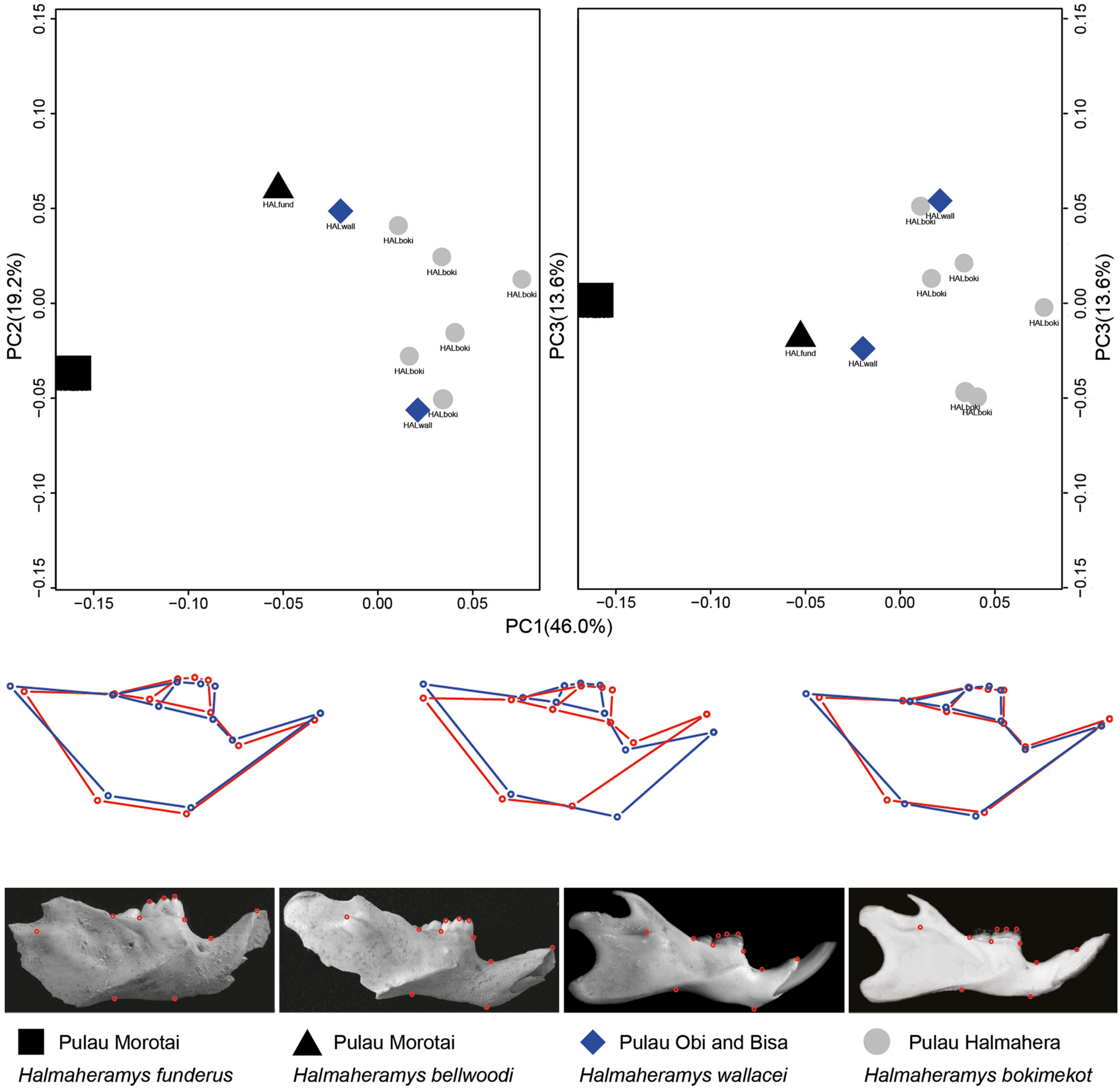

Figure 2. Two dimensional geometric morphometric comparisons of the mandibles of the four species of *Halmaheramys*. The first Principal Component (PC1) is plotted against the second (PC2) and third (PC3). Variance explained by each component is illustrated in parentheses for each component.

upper dental and cranial elements being yet firmly known from *H. bellwoodi*, but see the image in Hull *et al*., [2019: 145], which seems to show a maxilla of *H. bellwoodi* exhibiting these features): (3) fusion of the principal cusps of the upper molars into arcuate laminae; (4) significant size reduction of the third molars; (5) possession of short incisive foramina that do not penetrate between the upper molar rows (unlike most species of *Rattus* but shared with the *Rattus morotaiensis* and related species that occur in the Northern Moluccas; Fabre *et al*., 2023); and (6) reduction of the palatal grooves that fade out before meeting the incisive foramina, unlike most of the *Rattus* species from the Indo-Pacific region.

Both new species of *Halmaheramys* are larger-toothed than *R. morotaiensis* and members of the *Rattus rattus* Species Complex (Table 1). They differ from each other in molar dimensions and details of molar morphology, and more dramatically, in the dimensions of the lower jaw relative to the molars. Like Flannery *et al*. (1998), we have no hesitation in distinguishing two new species in the sample. However, our allocation of specimens differs somewhat from this earlier treatment (see below).

Rattus morotaiensis Kellogg, 1945

The distinctive extant murine *Rattus morotaiensis* was originally described by Kellogg (1945) from a series of specimens collected on the island of Morotai. More recently, specimens of native *Rattus* from the North Moluccan islands of Halmahera and Bacan have been referred to this species (Flannery, 1995a; Hasegawa & Syaffrudin, 1995b) and a similar species has more recently been collected from Obi

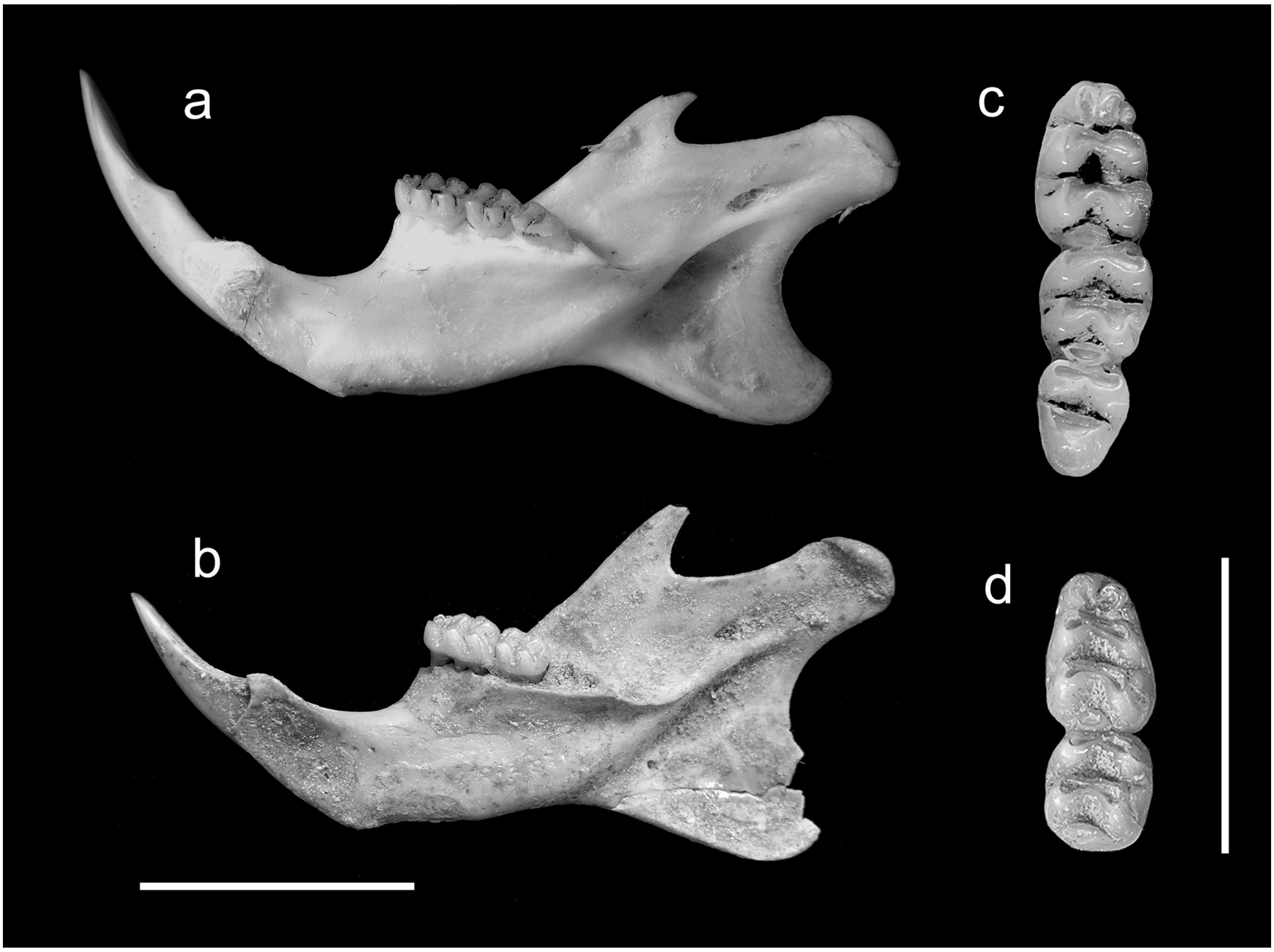

Figure 3. Subfossil specimen of *Rattus morotaiensis* from Morotai (AM F101473) compared with a modern specimen of the closely related *R. halmaheraensis* from Bacan (AM M.23653); (*a*) lingual side of right dentary AM M.23653; (*b*) lingual side of right dentary AM F101473; (*c*) occlusal view of right $M_{1–3}$ of AM M.23653; (*d*) occlusal view of right $M_{1–2}$ of AM F101473. Horizontal scale bar represents 10 mm; vertical bar represents 5 mm.

(Fabre *et al*., 2023). However, specimens from islands other than Morotai have now been shown by Fabre *et al*. (2023) to represent two distinct species, *Rattus halmaheraensis* (recorded from Halmahera, Bacan, Ternate, and Moti) and *Rattus obiensis* (recorded from Obi). Three partial dentaries and one isolated upper incisor from Daeo Cave no. 2 are referred to *R. morotaiensis* (Figs 3–5; Table 1). Measurements of these and several modern specimens of *R. morotaiensis* are shown in Table 1. The subfossil specimens are an excellent match in both size and morphology for modern voucher specimens.

Rattus morotaiensis is a distinctive taxon with broad, low-crowned molars and crenulated enamel (Figs 3–5). It differs in many ways that can be observed in subfossil remains from those of similar-sized commensal *Rattus* such as *R. rattus* and *R. nitidus*. In the upper dentition of *R. morotaiensis*, the posterocone is present on M^1 and cusp t1 of the M^1 is placed just below the level of cusps t2 and t3, and M^2 exhibits wide cingular margins and a cusp t3. The first lower molar is particularly distinctive, with a short anterior lamina that consists of subequal anterolabial and anterolingual cusps separated by a deep anterior groove. The middle and posterior laminae are weakly folded. There are large and distinctive peg-like anterolabial and anterolingual cusplets on m_1 and m_2, anterolabial and posterolabial cusplets on m_1 and m_2, and an anterolabial cusplet on m_3. The dentary is unusual in having an elongate and broad condylar process that projects behind the angular process.

Rattus rattus species complex

Two partial dentaries (Fig. 6) are identified as a member of the "*Rattus rattus* Species Complex" (see Aplin *et al*. [2003, 2011] for a discussion of taxonomic issues in this group). Both specimens were recovered from with the upper 20 cm of the Daeo Cave no. 2 deposit. They appear less mineralized than the other subfossil remains and may represent a more recent addition to the archaeological deposit. It is not possible at present to identity the subfossil taxon any more precisely, pending clarification of species boundaries within the *Rattus rattus* Species Complex (Aplin *et al*., 2003, 2011). In recent decades, many authors have referred to populations previously identified as "*Rattus rattus*" in the southeast Asian region as a separate species, *Rattus tanezumi*, following Musser and Carleton (2005). However, the true taxonomic situation is much more complex, involving

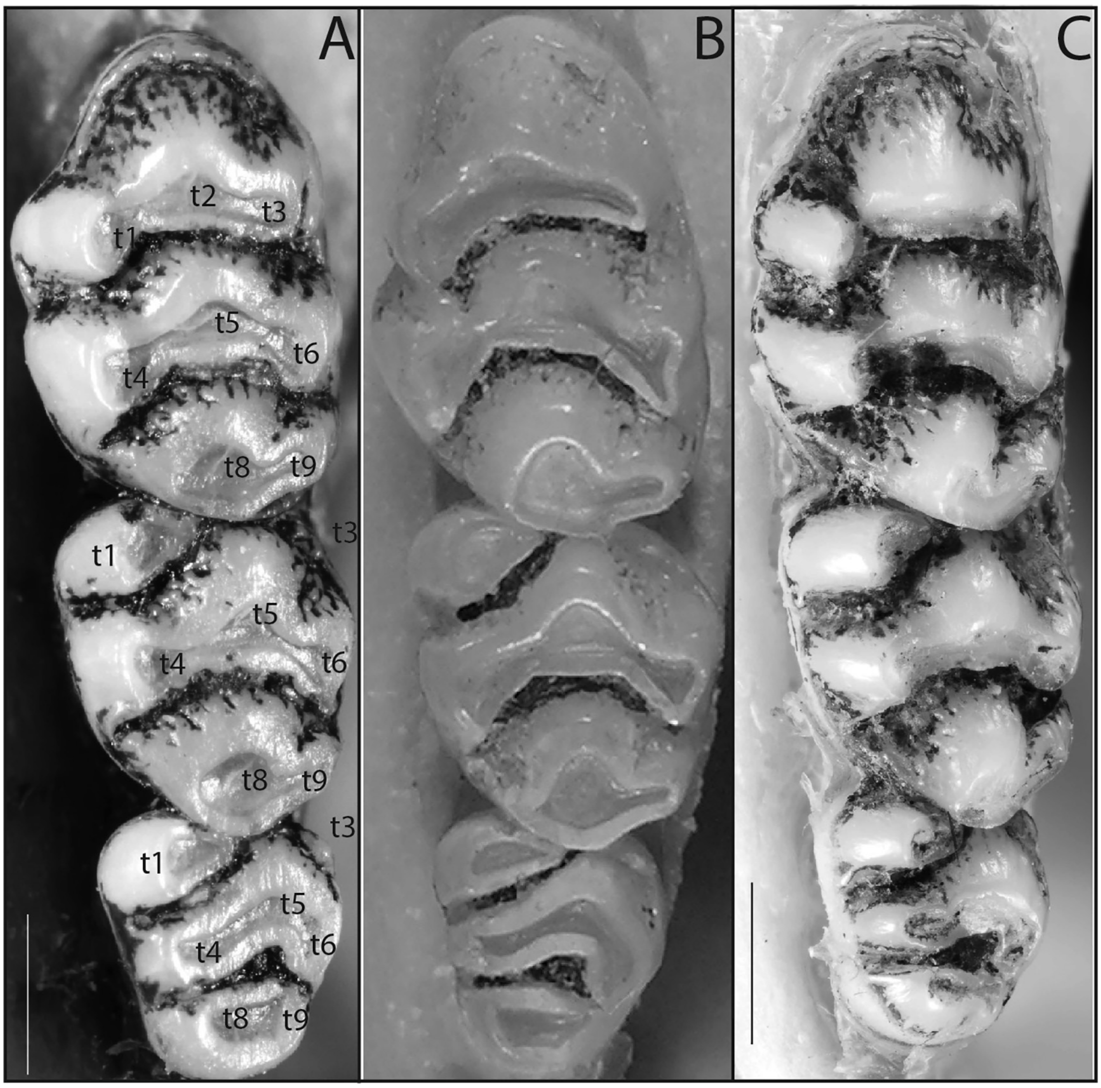

Figure 4. Upper molar rows of Moluccan *Rattus morotaiensis* species-group members (*A*) Modern *R. morotaiensis* from Morotai (USNM 277312, holotype); (*B*) Modern *R. halmaheraensis* from Bacan (AM M.23653); (*C*) Modern *R. halmaheraensis* from Halmahera (MZB 33270). All pictures to scale (cf. measurements provided in Table 1).

various evolutionary lineages, with differential human-mediated dispersal histories, that are closely related to *Rattus rattus* in the strict sense (e.g., Aplin *et al*., 2011; Louys *et al*., 2020). The widespread commensal *Rattus tiomanicus*, usually considered to be restricted to the continental shelf of Sundaland (e.g., Musser & Newcomb, 1985; Corbet & Hill, 1992; Musser & Carleton, 2005) is also a member of the *Rattus rattus* Species Complex (Aplin *et al*., 2011) and has recently been identified living in Wallacea, on the island of Halmahera (Fabre *et al*., 2023). This points to a need to more firmly resolve the taxonomy of all commensal medium-sized *Rattus* populations, both modern and Holocene, that have been referred to *Rattus rattus*, *Rattus tanezumi*, and *Rattus tiomanicus* in recent publications. In any case, the subfossil specimens under discussion would traditionally be identifiable as "*Rattus rattus*" (and more recently as "*R. tanezumi"*) and pending further clarifying work, we refer to these specimens from Daeo Cave no. 2 as "*Rattus* sp. cf. *rattus*."

These subfossil specimens referred to "*Rattus* sp. cf. *rattus*" are immediately distinguished from *R. morotaiensis* by their smaller and higher-crowed molars (Table 1; Fig. 6),

Figure 5. Lower molar rows of modern and subfossil Moluccan *Rattus morotaiensis* species-group members. (*A*) Modern *R. morotaiensis* from Morotai (USNM 277312, holotype); (*B*) subfossil *R. morotaiensis* from Morotai (AM F101465); (*C*) modern *R. halmaheraensis* from Halmahera (MZB 33270); (*D*) modern *R. halmaheraensis* from Bacan (AM M.23653). All pictures to scale (cf. measurements provided in Table 1).

less crenulated enamel, more elongate and unevenly bilobed anterior lamina on M_1, shallower lower incisor and various details of dentary morphology including the lower placement of the mandibular foramen. They differ from *R. nitidus,* another commensal species in the region, in the form of the angular process of the dentary, which is narrower and projects further posteriorly in *R. nitidus*. *Rattus nitidus* is native to mainland Southeast and East Asia but occurs as a consequence of human introduction in several parts of island Southeast Asia including, relative to Morotai, the island of Seram to the south, Sulawesi to the west, and the Vogelkop Peninsula of New Guinea to the east, as well as from Luzon in the Philippines and Palau in Micronesia (Musser & Newcomb, 1985; Helgen, 2003). The timing and pattern of spread of *R. nitidus,* which usually occurs as an introduced species in montane contexts, has received less attention than the dispersal of other murine commensals in the region and remains a fascinating area of study for archaeologists, geneticists, and mammalogists in the future, as it may illuminate important aspects of human history across the archipelagos of the Asia-Pacific.

Figure 6. Subfossil specimen of *Rattus* sp. cf. *R. rattus* from Morotai (AM F101467); lingual side of left dentary. Scale bar represents 10 mm.

Table 1. Dental measurements of subfossil (AM F) and selected modern (AM M) murine specimens from Morotai Island (plus one comparative specimen of *Rattus halmaheraensis* from Bacan). Specimen AM F101459 is a maxillary toothrow; all others are mandibular.

Specimen	M1–3	M1–3	M1	M2	M3	I_1
	Cr L	Alv L	L × W	L × W	L × W	W × D
Rattus morotaiensis						
AM F101465	6.4	6.8	2.7 × 1.8	2.1 × 1.8	2.0 × 1.5	1.3 × 2.8
AM F101473	—	6.4	2.6 × 1.9	2.1 × 1.9	—	1.1 × 2.4
AM F101474	—	6.7	—	—	1.6 × 1.7	1.1 × 1.6
AM M.7085	6.7	6.4	2.7 × 1.9	1.9 × 2.0	1.8 × 1.9	1.6 × 2.7
AM M.26618	6.3	6.4	2.7 × 1.8	2.2 × 1.8	2.0 × 1.5	0.7 × 1.6
Rattus halmaheraensis						
AM M.23653	6.5	6.8	2.7 × 1.9	2.0 × 1.9	2.1 × 1.5	1.1 × 2.3
Rattus* sp. cf. *rattus						
AM F101467	—	7.3	3.1 × 2.1	2.3 × 2.2	—	1.4 × 2.1
AM F101468	—	6.8	—	2.2 × 2.1	1.9 × 1.7	—
Halmaheramys funderus						
AM F101459	8.8	9.1	4.6 × 2.6	2.8 × 2.5	1.8 × 1.8	—
AM F101457	8.4	8.4	3.3 × 2.2	2.6 × 2.6	2.1 × 2.2	1.1 × —
AM F101464	—	8.6	— × 2.2	—	—	—
AM F101463	8.2	8.4	3.4 × 2.3	2.5 × 2.5	2.1 × 1.9	—
Halmaheramys bellwoodi						
AM F101455	8.9	9.6	3.8 × 2.4	3.0 × 2.5	2.2 × 2.3	1.7 × —
AM F101456	—	9.6	3.8 × 2.4	2.9 × 2.6	—	1.5 × —
AM F101461	—	9.5	—	—	2.5 × 2.3	—
AM F101458	—	—	4.1 × 2.6	—	—	1.7 × 2.6
AM F101462	—	—	—	—	2.5 × 2.2	—
AM F101454	—	—	—	—	2.4 × 2.3	—
AM F101470	—	—	—	3.1 × 2.5	-	—
AM F101471	9.5	—	—	—	2.5 × 2.3	—
AM F101472	—	—	—	—	—	1.5 × 2.4
AM F162028	9.3	9.3	3.7 × 2.4	2.9 × 2.7	2.3 × 2.1	—

Systematics

Order Rodentia Bowdich, 1821

Family Muridae Illiger, 1811

Subfamily Muridae Illiger, 1811

Halmaheramys Fabre, Pagès, Musser, Fitriana, Semiadi & Helgen, 2013

Halmaheramys funderus sp. nov.

urn:lsid:zoobank.org:act:91C4586B-FC9F-4CDF-8239-02B75871E45A

Figs 7–8, 9D, Tables 1–2

Holotype: AM F101459, a fragmentary left maxilla with M^{1-3} in a moderate state of wear and preserving portions of the palatal side of the maxillary bone.

Paratypes: Among murine rodents, the upper molar row is almost always slightly longer than the associated lower molar row. The following lower jaws are associated with the holotype on the basis of cheektooth size and overall morphology: AM F101457, a fragmentary right dentary with M_{1-3} in a moderate state of wear and the basal portion of I_1 in the alveolus; AM F101463, a fragmentary right dentary with M_{1-3} in a moderate state of wear; AM F101464, a fragmentary right dentary with M_1 in an advanced state of wear.

Type locality and age: Known only from the archaeological deposit in Cave no. 2 behind Daeo village, southern side of Morotai Island, North Maluku (Maluku Utara) Province, Indonesia. The bulk of the remains are believed to date from terminal Pleistocene to mid-Holocene times (Flannery *et al*., 1998).

Diagnosis: *Halmaheramys funderus* is smaller than *H. bellwoodi* sp. nov. of Morotai, and is further distinguished from that species by the presence of a bilobed anterior lamina on M_1, more extreme reduction of anterolabial cusps on M_{2-3} as well as by its less proodont lower incisor and less elongate mandibular diastema, leading to more steeply inclined lower incisor (together signifying a shorter rostrum).

Halmaheramys funderus of Morotai (M^{1-3} crown length 8.8 mm) is distinguished from *H. bokimekot* of Halmahera by its much larger size (M^{1-3} crown length 6.4–6.8 mm in *H. bokimekot*, n = 6), and from *H. wallacei* of Obi and Bisa by its somewhat larger size (M^{1-3} crown length 7.8–8.4 mm in *H. wallacei*, n = 4). It further differs from both species in that all of its molar lophs are more laminar, more inclined antero-posteriorly, with less distinct cusps. The anterior loph of M^1 in particular is highly laminar relative to the extant species, the t3 being shifted well anteriorly and poorly defined. The labial cusp t4 both on M^1 and M^2 is antero-posteriorly developed with a distinct anterior inflection not seen in the two extant

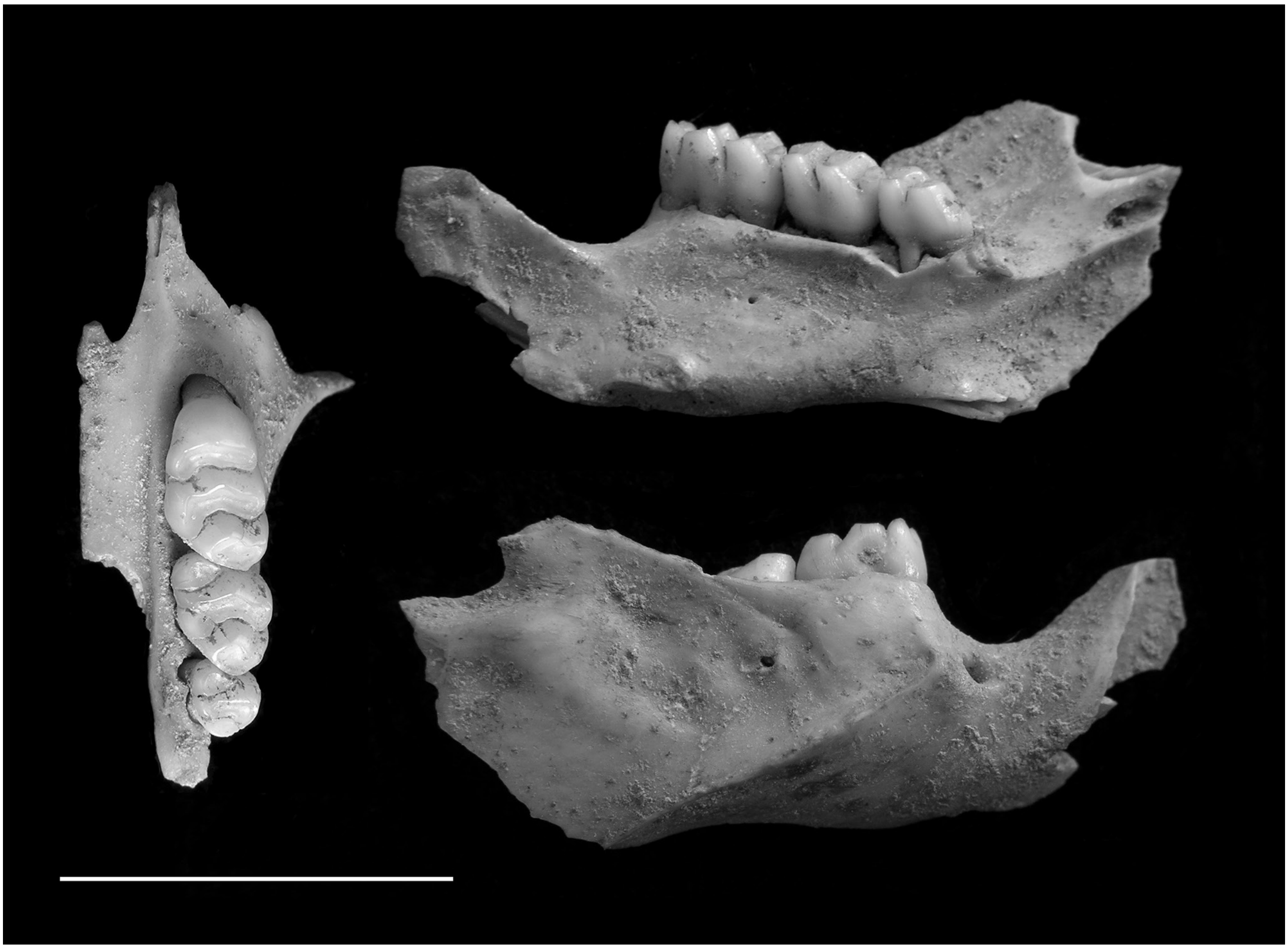

Figure 7. Subfossil specimens of *Halmaheramys funderus* sp. nov.; (*a*) ventral side of holotype left maxilla AM F101459; (*b*) lingual side of right dentary AM F101457; (*c*) labial side of right dentary AM F101457. Scale bar represents 10 mm.

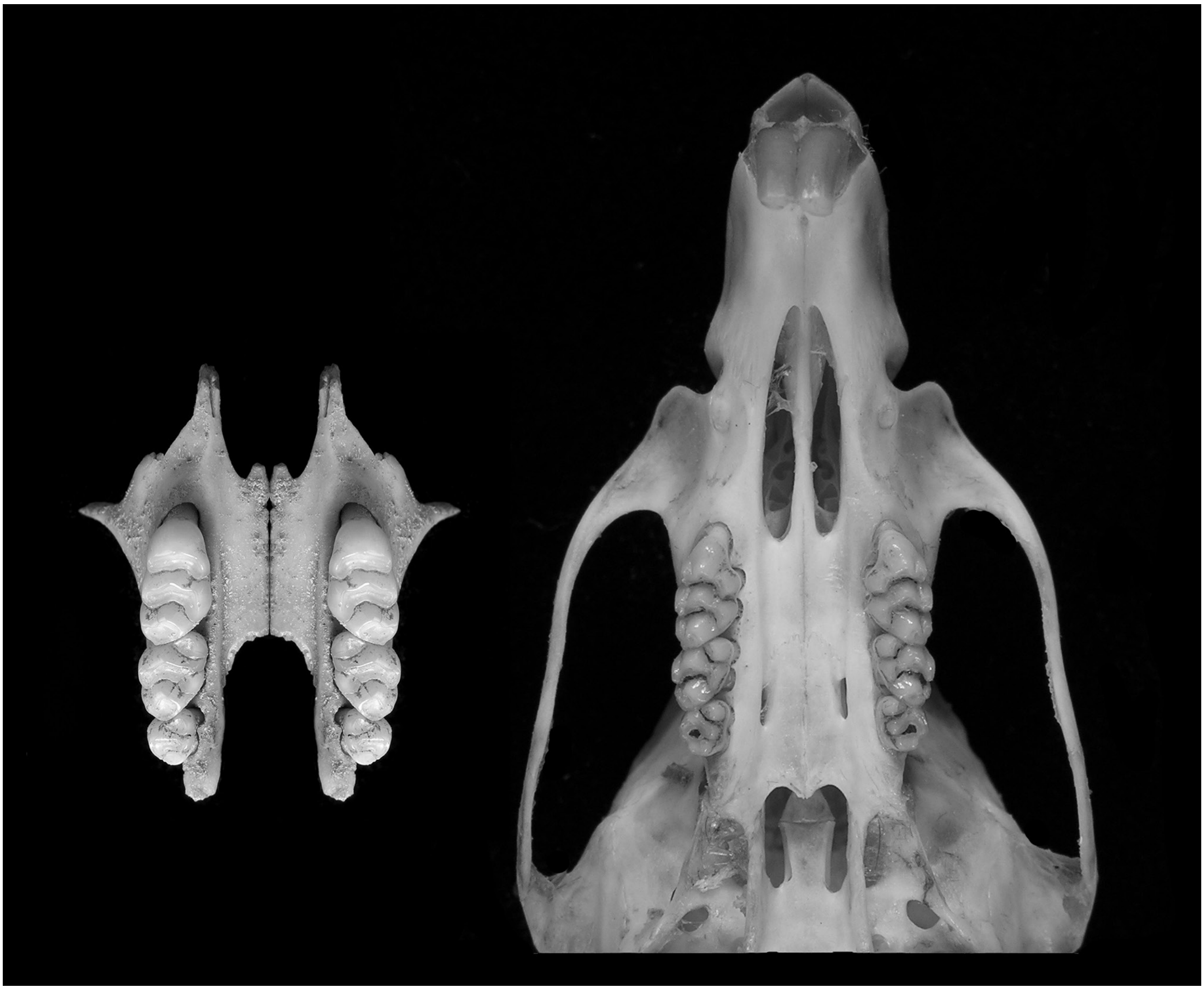

Figure 8. Palate of *Halmaheramys funderus* sp. nov. Reconstructed palatal region of *Halmaheramys funderus* (based on left maxilla and its mirror image), compared with the same region in a specimen of *Rattus rattus* (ANWC CM2768). The two specimens are scaled such that maxillary length (measured from premaxillary suture to palatine suture) is equal.

species of *Halmaheramys*. Compared to *H. wallacei* and *H. bokimekot,* the lower molars lack posterolabial cusplets, and the posterior cingular is smaller on M_1 and M_2.

Etymology: The species name is Latin for "to fuse", in reference to the fusion of molar cusps into transverse laminae in the molars.

Description. The maxilla is known only for the holotype (Figs 7–9). This specimen retains part of its palatal side as well as all three molars at an early to moderate stage of occlusal wear. Although the anterior portion of the palatal lamina has also suffered damage, a small section of the premaxillary suture is preserved alongside the postero-lateral margin of the incisive foramen. This is positioned 4.4 mm forward of the anterior root of M^1. The midline and palatine sutures are also partially preserved; the latter runs very close alongside the lingual roots of the posterior molars and swings medially to join the midline suture level with the posterior end of M^1. The posterior end of the fragment preserves a small portion of the palatine suture, situated 1.5 mm behind the rear of M^3.

The maxilla of *H. funderus* is relatively gracile in construction. The alveolar portion of the maxilla is shallow, especially above the posterior molars, and the transition from the labial surface to the orbital surface is gently rounded rather than sharply angular as it is in species of *Rattus* and many other murines (see below for detailed comparisons).

The palatal lamina is thin and only slightly thickened along the midline suture. The palatine sulcus (that carries blood vessels and nerves between the posterior palatal and incisive foramina) is broad and well-defined posteriorly but it shallows and fades anteriorly, and is indistinct forward of cusp t1 of M^1. The incisive foramen penetrates 4.1 mm behind the premaxillary suture; its lateral margin is arcuate and it terminates in a broad V-shaped broad point, 1.1 mm forward of the anterior root of M^1. The position of the posterior palatal foramen is indeterminate.

Although the malar process of the maxilla is damaged, it is clear that the zygomatic plate was relatively narrow and gracile in form. The postero-medial border of the zygomatic plate is weakly developed; its anterior edge starts antero-lateral of the forward root of M^1 and its posterior edge ends midway along the border of the incisive foramina.

The position of the maxillo-palatine suture relative to the molar row gives some indication of the degree of elongation of the palatal bridge. As indicated above, this suture lies 1.5

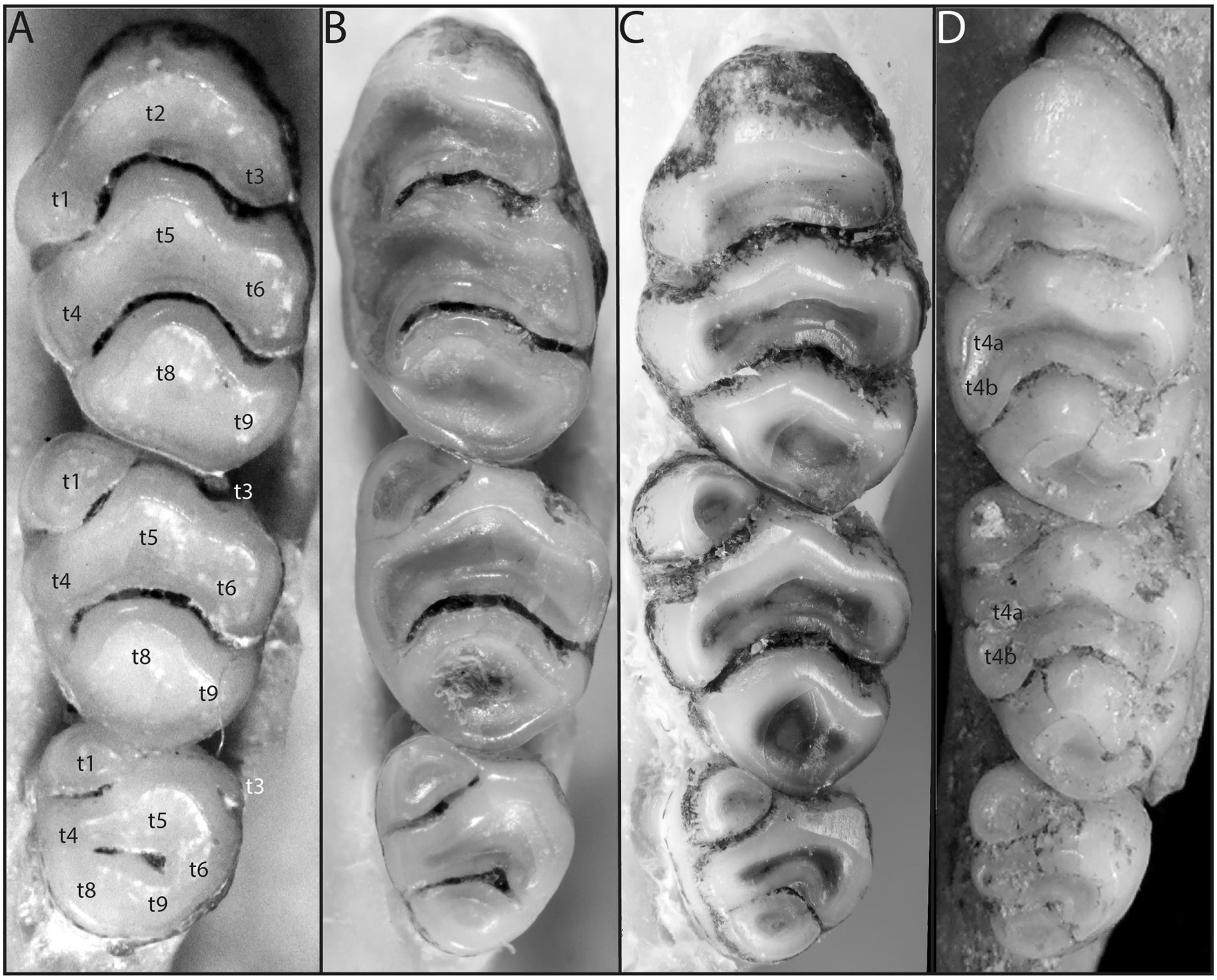

Figure 9. Upper molars of *Halmaheramys*. Occlusal views of the right maxillary upper molar rows of (*A, B*) *Halmaheramys wallacei,* (*A*) AM M.24389, Bisa, and (*B*) MZB 38227, Obi; (*C*) *Halmaheramys bokimekot* (MZB 33266, Halmahera); and (*D*) *Halmaheramys funderus* sp. nov. (AM F101459, Morotai, holotype). All pictures scaled to same size (cf. measurements in Table 2).

mm behind the molar row in *H. funderus*. In a specimen of *R. halmaheraensis* (AM M.23653) of approximately equal size it is located 1.9 mm behind the molar row.

A good impression of palatal dimensions and morphology in *H. funderus* is obtained by reflecting an image of the holotype along the midline suture (Fig. 8). This reveals a relatively narrow palate dominated by proportionally large molars set in weakly divergent rows. The incisive foramina are wide and bowed, and probably measured around 3.6 mm in combined width. The palatal width measured at the midloph of M^1 is 4.1 mm to the lingual side of the molars, 9.3 mm to the labial side of the molars. The relatively large molars of *H. funderus* are evident in comparison with the palate of a more typically proportioned rat such as *Rattus rattus* (Fig. 8).

The holotype retains all three molars in a state of slight to moderate wear (Table 1; Fig. 9). The first molar is considerably longer but only slightly wider than the second molar; the second molar is considerably longer but is considerably wider than the third. All molars show a moderate degree of longitudinal overlap.

The M^1 has five roots, one positioned anteriorly and two on each side of the tooth. The anterior root, supporting cusps t2 and t3, exceeds all others in bulk. The posterolabial root, supporting cusps t8 and t9, is next largest. The centrolabial, centrolingual, and posterolingual roots are subequal in size and support cusps t6, t1, and t4, respectively. The posterolabial root is positioned slightly behind the level of the posterolingual root.

The M^1 crown is relatively elongate and narrow, and is lamellate rather than cuspidate in form. The enamel is smooth where contact with food bolus has abraded the surface but coarsely punctate in more protected areas (Fig. 9). The cusp pattern is simple and follows the general murine pattern, with three primary cusps in each of the anterior and central laminae and two in the narrower, posterior lamina.

The anterior lamina is broadly arcuate with each of the labial (t3) and lingual (t1) cusps strongly united with the central cusp (t2). However, its occlusal surface is distinctly asymmetric, giving the impression that cusp t1 is positioned closer to cusp t2 than is cusp t3. Cusps t1 and t3 are positioned at a similar level relative to the front of the tooth; both cusps are rounded posteriorly, without accessory ridging.

The second lamina is slightly more cuspidate due to the presence on the anterior surface of the lamina of broad grooves between the central cusp (t5) and each of a labial cusp

Table 2. Dental measurements (means, ranges, and samples sizes) of the species of *Halmaheramys*. $M^{1–3}$cl = crown length of upper molar row; $M_{1–3}$l = alveolar length of lower molar row; M^1w = breadth of anteriormost upper molar; M_1w = breadth of anteriormost lower molar; M_2w = breadth of middle lower molar; M_3w = breadth of posterior lower molar.

Element	Taxon			
	H. bokimekot Halmahera	*H. wallacei* Obi and Bisa	*H. bellwoodi* Morotai	*H. funderus* Morotai
$M^{1–3}$cl	6.60	8.20	—	8.80
	6.36–6.77	7.8–8.4	—	8.80
	n = 6	n = 4	—	n = 1
$M_{1–3}$l	6.39	8.00	9.44	8.47
	6.26–6.54	7.10–8.40	9.20–9.60	8.40–8.60
	n = 6	n = 4	n = 5	n = 3
M^1w	2.00	2.30	—	2.60
	1.89–2.04	2.10–2.40	—	2.60
	n = 6	n = 4	—	n = 1
M_1w	1.79	2.09	2.45	2.23
	1.76–1.82	2.03–2.12	2.40–2.60	2.20–2.30
	n = 6	n = 4	n = 4	n = 3
M_2w	1.92	2.31	2.58	2.53
	1.86–2.01	2.17–2.40	2.50–2.60	2.5–2.6
	n = 6	n = 4	n = 4	n = 3
M_3w	1.48	1.90	2.25	1.97
	1.40–1.56	1.69–2.00	2.10–2.30	1.80–2.20
	n = 6	n = 4	n = 6	n = 3

(t6) and a lingual cusp (t4). Cusps t4 and t6 are both slightly posterior to t5. Cusp t6 is subequal in size to t5 and rounded in occlusal shape. Cusp t4 is more elongate and angular in form due to a posterior extension, a distinctive feature. A slight indentation of the lingual margin of this structure suggests the presence of a partially discrete cusp (t4b) situated posterior to cusp t4 (see accounts of M^2, below).

The third lamina consists of a rounded central cusp (t8) and a smaller, rounded labial cusp (t9). These cusps are broadly united but clearly defined by a broad groove on the anterior surface of the lamina. Cusp t8 is slightly larger than cusp t5. Cusp t9 is smaller than cusp t6 but subequal to cusps t1 and t3. A weak enamel ridge ascends the lingual surface of cusp t8; it meets the posterior tip of cusp t4. A slight flexure of the posterior margin of the tooth between cusps t8 and t9 suggests a remnant of a posterior cingulum. The posterior surface of the tooth is indeed weakly grooved in this position.

The pattern of wear on M^1 and M^2 is stepped, wherein the occlusal surfaces of the laminae are angled relative to the overall occlusal plane of the molars.

The M^2 is shorter and slightly narrower than the M^1. It is supported by four separate roots, two on each side of the crown. The M^2 is shield-shaped in outline, tapering posteriorly; it is slightly longer than wide. The cusp pattern follows the typical murine pattern, cusps t1 and t3 representing isolated elements of the anterior lamina, followed by complete second and third laminae that mirror the construction seen in M^1. Cusp t1 of M^2 is a well-defined, sub-rounded cusp that lies on a common occlusal plane with cusp t8 of M^1; its anterior surface projects well forward of the anterior surface of cusp t5. In contrast, cusp t3 is a small structure that is closely adpressed to the anterolabial face of t5; it lies above the occlusal plane of the tooth. The central lamina on M^2 is broadly arcuate and almost symmetrical in structure. Cusp t5 is rounded but separated from the flanking cusps by broad grooves. Cusp t6 is similar in size to the equivalent cusp on M^1 but is more angular due to the presence of a weak posterior ridge. The lingual end of the anterior lamina is complex in form consisting of a small anterior cusp (t4a), that is broadly united to cusp t5, and a larger posterior cusp (t4b) that is adpressed against cusp t4 but separated from it by a deep lingual fissure and retains a complete enamel rim at occlusal level (Fig. 9). It is unclear if this structure reflects an unusual ridging, or is a discrete cusp, which would generally be identified as t7 by its position. However, it is clearly not the same as the structure labelled t7 in various other Asian murines such as species of *Chiropodomys* and *Lenothrix* (in these taxa cusp t7 is associated with the posterior lamina; Misonne, 1969; Musser, 1979; Musser & Newcomb, 1983); for purposes of discussion, we will refer to this unusual structure in *H. funderus* as an "accessory lingual cusp".

The posterior lamina on M^2 is dominated by a cusp t8 that is narrower but slightly longer than its serial homologue on M^1. Cusp t9 is well-defined but considerably smaller than on M^1. The anterolingual ridge on t8 is weakly developed.

The M^3 is considerably shorter and narrower than the M^2. Three roots are present, two anteriorly and one supporting the posterior lamina of the tooth. Cusp t1 on M^3 is very similar in size, shape and relations to this cusp on M^1. Cusp t3 on M^3 is represented by a tiny tubercle above the occlusal surface. The central lamina on M^3 is an irregular structure tentatively made up of a relatively small central cusp t5, a narrow cusp t4 that extends lingually from t5, and a hook-like posterolabial extension from t5 that presumably represents t6. The posterior lamina of M^3 consists of a single rounded cusp that is sharply divided from cusp t4 but linked to the putative cusp t6 by a high enamel ridge that encloses a small posterolabial fosette.

The three dentaries represent different individuals with cheektooth wear ranging from moderate to advanced stages. All are damaged but collectively lack only the tip of the coronoid process, and details of the condylar and angular processes (Fig. 7). The horizontal ramus is small and lightly built relative to the size of teeth but shows developed muscular features involving deep masseter layers. Indeed, the masseteric crest is well developed, relatively straight and starting behind the mental foramen. The anterior section of the crest, below M_1, is less prominent than the more posterior section below the rear molars and ascending ramus. The mental foramen is in the usual position, below and forward of M_1. The lower incisor is absent or broken on all specimens. However, the orientation of the alveolus suggests a relatively steeply angled incisor and correspondingly short diastema. The symphyseal region is relatively slender, reflecting the overall gracility of the dentary. The ascending ramus rises to the level of the M_2 anterior lamina; it has a straight anterior margin that forms an angle of 140° with the plane of the cheekteeth. Although the tip of the coronoid process is missing, the coronoid clearly rose above the level of the condylar notch (retained on one specimen). The incisor tubercle is situated below the coronoid process and condylar notch. The lower incisor is represented by a basal fragment embedded in AM F101457. This shows a tooth that is approximately 1.1 mm in width and slightly higher than wide. The enamel is orange, ungrooved and covers the ventral surface and the lower one-third of the labial surface of the tooth.

Two dentaries retain all three lower molars in a moderate state of wear (Table 1, Fig. 7). The third specimen retains M_1 in a more advanced state of wear. The $M_{1–3}$ crown lengths are 8.2 and 8.4 mm, and $M_{1–3}$ alveolar length ranges from 8.4–8.6 mm. M_1 is longer and slightly narrower than M_2. M_3 is shorter and narrower than M_2. All molars are laminate and relatively brachyodont, with forwardly inclined laminae. As for the upper molars, the enamel is finely punctate apart from on thegotic facets. The pattern of wear on M_1 and M_2 is stepped, matching that observed in the upper molars.

The M_1 retains the usual murine arrangement of cusps, with an anterior group of cusps (collectively, the anteroconid), four primary cusps arranged in two more or less transverse laminae, and a distinct posterior cingulum. The tooth is relatively broad and chunky; it is broadest across the posterior lamina, narrowing to the front. All cusps are weakly bulbous towards the crown base. The pattern of roots below M_1 follows the pattern observed in *Rattus* and related genera, with one large circular root situated beneath the anterior cluster of cusps; two small circular roots are positioned on either side and near the rear of the second lamina; and one large, oval-shaped root is located below the posterior lamina. The central roots lie closer to the posterior than the anterior root. The anteroconid of M_1 is a short, broad structure that consists of two rounded cusps, positioned side by side and separated by a deep anterior groove. The anterolingual cuspid is slightly larger in occlusal area than the anterolabial cuspid (greater size disparity in AM F101463 than in AM F101457). The anteroconid is tightly adpressed against the second lamina such that the anterolabial and anterolingual flexids each penetrate less than one-quarter of the way across the tooth. The anterior lamina of M_1 is considerably broader than the anteroconid, which is a common characteristic of all *Halmaheramys* species. It is dumbbell shaped in occlusal outline, with concave anterior and posterior occlusal margins. The labial protoconid and lingual metaconid are sub-rectangular in occlusal outline and broadly united. The approximate boundary between the two cuspids is evident only from the concave posterior surface of the lamina; this suggests a slightly greater occlusal area for the protoconid over the metaconid. As in most *Halmaheramys* specimens, there is no trace of an accessory labial cusplet associated with either the anterior or middle laminae (but see AM M.24389). The posterior lamina of M_1 is slightly broader than the anterior lamina. It repeats the basic structure of the anterior lamina but with a straighter anterior occlusal margin. The labial and lingual cuspids (the hypoconid and entoconid, respectively) are subequal in occlusal area. There is no trace of a posterolabial cusplet associated with the posterior lamina. The posterior cingulum is a broad, oval shaped cusp. It is positioned low and centrally at the rear of the tooth and, unlike the primary cusps, is vertical rather than forward sloping. The occlusal surface of the posterior cingulum lies in the same occlusal plane as the anterior lamina of M_2.

The M_2 is square in basal outline and noticeably wider than the posterior lamina of M_1. The crown is more bulbous than M_1, particularly so on the labial side of the tooth. Five roots support the crown, two beneath the anterolabial corner of the tooth, and one beneath each of the three other corners. The divided anterolabial root is an unusual feature among murines. The arrangement of primary cusps on the M_2 is similar to that observed on the two laminae of M_1. The anterior lamina is notable for its breadth, being the widest element in the entire toothrow. The posterior lamina is substantially narrower and is surpassed in width by both the anterior and posterior laminae of M_1. Both laminae on M_2 have broadly concave posterior surfaces. The posterior cingulum of M_2 replicates the structure on M_1. Small but distinct anterolabial cusps are present on both examples of M_2. On the less-worn M_2 of AM F101457 this structure is represented by a tiny tubercle, attached to the anterior face and lying below the occlusal surface of the protoconid. On AM F101463 a small but distinct cusp is present in the same position. In this specimen it possesses a separate, functional dentine basin. However, further wear would soon see this basin merge into the anterolabial end of the anterior lamina. There is no trace of a posterolabial cusplet associated with the posterior lamina.

The M_3 is substantially shorter and narrower than M_2. The crown is lower than either anterior tooth. The anterior lamina on M_3 is more strongly folded than on the preceding tooth, reflecting a slight posterior expansion of the protoconid. The posterior lamina is a simple D-shaped structure, flattened anteriorly and concave posteriorly. A small anterolabial cusp is present on AM F101463, situated just below the occlusal surface. This cusp is absent on AM F101457. There is no trace of a posterolabial cusplet associated with the posterior lamina.

Halmaheramys bellwoodi sp. nov.

urn:lsid:zoobank.org:act:394DE26D-8BA9-4088-9849-13DBA0BFF45D

Figs 10–11, Tables 1–2

Holotype: AM F101456, a fragmentary left dentary with $M_{1–3}$ in a moderate state of wear and the basal portion of I_1 in the alveolus.

Paratypes: AM F101454, a fragmentary right dentary with M_3 in a moderate state of wear; AM F101455, a fragmentary left dentary with $M_{1–2}$ in a moderate state of wear and the basal portion of I_1 in the alveolus; AM F101458, a fragmentary left dentary with I_1 and M_1 in an advanced state of wear; AM F101461, a fragmentary right dentary with M_3 in a moderate state of wear and the basal portion of I_1 in the alveolus; AM F101462, a fragmentary left dentary with M_3 in a moderate state of wear; AM F101470, a fragmentary left dentary with M_2 in a moderate state of wear; AM F101471, a right dentary with M_3; AM F101472, an incisor; AM F162028, left dentary with $M_{1–3}$ in moderate state of wear.

Additional attributed specimens: An additional maxilla and mandible from the type locality figured by Hull *et al*. (2019: 145), attributed to "*Rattus morotaiensis*", would appear to represent this species. We presume these specimens are stored at the Australian National University in Canberra.

Type locality and age: Known only from the archaeological deposit in Cave no. 2 behind the village of Daeo, on the southern side of Morotai Island, North Maluku (Maluku

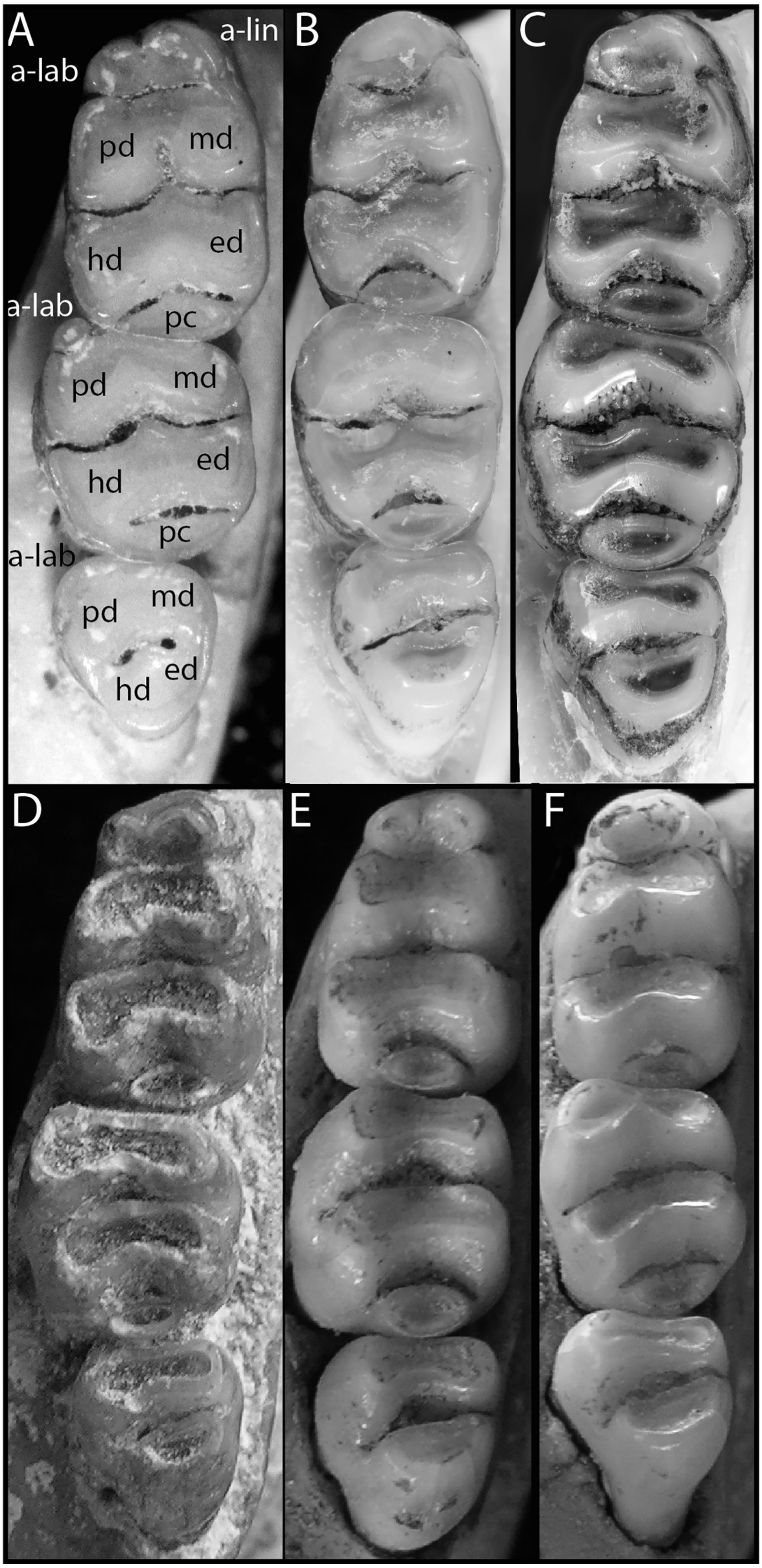

Figure 10. Lower molar comparisons of *Halmaheramys*. Occlusal views of the right lower molar rows of (*A, B*) *H. wallacei,* (*A*) AM M.24389, Bisa, and (*B*) MZB 38227, Obi; (*C*) *H. bokimekot* (MZB 33266, Halmahera); (*D–E*) *H. funderus* (AM F101463, AM F101457); and (*F*) *H. bellwoodi* sp. nov. (AM F101456, mirrored).

Figure 11. Subfossil specimens of *Halmaheramys bellwoodi* sp. nov.; (*a*) lingual side of holotype left dentary AM F101456; (*b*) labial side of holotype left dentary AM F101456; (*c*) lingual side of left dentary AM F101458; (*d*) lingual side of right dentary AM F101461 (image reversed). Scale bar represents 10 mm.

Utara) Province, Indonesia. The bulk of the remains are believed to date from terminal Pleistocene to mid-Holocene times (Flannery *et al*., 1998; Hull *et al*., 2019). Hull *et al*. (2019) noted that "these sole cranial elements of rodent in the [Daeo Cave no. 2] assemblage are from Squares E4–E5 at 10–15 cm, and hence postdate the C14 date of 6463–6194 cal. BP (ANU 9452)."

Diagnosis: *Halmaheramys bellwoodi* is larger than other *Halmaheramys* species, with a M_{1-3} alveolar length of 8.9 mm, versus a mean of 8.3 mm in *H. funderus* (8.2–8.4, n = 2), 8.0 mm in *H. wallacei* (7.1–8.3, n = 4), and 6.4 mm in *H. bokimekot* (see Table 2). Compared with *H. bokimekot* and *H. wallacei*, the molar lophids are more laminar, with less distinct cuspids. It is further distinguished from *H. funderus* by the presence of unicuspid anterior lamina on M_1, weakly indicated labial cusplets on M_{1-3}, and a more elongate mandibular diastema leading to a less steeply inclined lower incisor, signifying a longer rostrum.

Etymology: This species is named for Professor Peter R. Bellwood of the Australian National University, Canberra, in recognition of his seminal efforts in the study of Moluccan prehistory.

Description: The dentary is represented by eight specimens that collectively illustrate the entire mandibular morphology save for the tip of the coronoid process (Fig. 11). The most complete specimen is AM F101455 and the following description is based on this specimen unless indicated otherwise. The horizontal ramus is moderately large and robust relative to the size of teeth and shows strongly developed muscular features. The masseteric crest is well defined, relatively straight and terminates 1.5–2 mm behind the mental foramen. The anterior section of the crest, below M_1, is less prominent than the more posterior section below the rear molars and ascending ramus. The mental foramen is in the usual position, below and forward of M_1. The lower incisor is complete and in position in AM F101458 and AM F101470. It is oriented at a shallow angle and terminates level with the occlusal plane and 18.8 mm forward of the M_1. The symphyseal region is moderately robust, reflecting the overall condition of the dentary. The ascending ramus arises level with the midpoint of M_2; it has a straight anterior margin that forms an angle of 135° with the plane of the cheekteeth. Although the tip of the coronoid process is missing, this process clearly rose above the level of the condylar notch. The incisor proximal tubercle is situated below the coronoid process and condylar notch; it is a prominent structure and encloses a deep posterior zygomaticomandibularis fossa. The postalveolar foramen lies 5.3 mm behind the rear of M_3 and just above the occlusal plane of the cheekteeth. The articular condyle is unusually elongate compared with "typical" murines of similar jaw size (e.g., *R. norvegicus*) and lies relatively close behind the mandibular foramen. The angular process, complete on AM F101461, is unusually broad and bears a conspicuous masseteric scar on its latero-ventral surface for the insertion of the posterior deep masseter muscle. The inner surface of the angular process bears a broadly concave medial pterygoid fossa that lacks conspicuous internal scarring. The mandibular foramen is located in the usual position, near the front of the internal pterygoid fossa. Complete lower incisors are retained in AM F101458 and AM F101470, with basal fragments embedded in several other dentaries. The complete incisors measure 2.4–2.6 mm in depth and 1.5–1.7 mm in width, and have radii of curvature of 17.0–18.5 mm. The tip of both complete incisors is accuminate rather than chisel-shaped as in most murines, and the occlusal surface is remarkably elongate, measuring 8.7–8.8 mm in length. The enamel is orange, ungrooved, and covers the ventral surface and the lower one-half of the labial surface of the tooth.

At least two examples are available for each of the lower molars, with varying stages of wear represented (Table 1). The M_{1-3} crown length is 8.9 mm, and M_{1-3} alveolar length ranges from 9.2–9.6 mm. M_1 is longer and subequal in width to M_2. M_3 is shorter and narrower than M_2. Basic molar configurations mirror those described for *H. funderus*. The following account focuses on key points of difference between the two species. The M_1 is retained in three specimens. These differ from the M_1 of *H. funderus* in having anterior and posterior laminae of equal width, slightly less bulbous metaconids and entoconids, a more deeply folded anterior lamina, and an anteroconid formed of a single, oval-shaped cusp rather than the paired cusps seen in *H. funderus*. A small anterolabial cusplet is present on the anterior surface of the protoconid of AM F101456 and AM F101458; this structure is represented by a cingular crest on AM F101455. Posterolabial cusplets are indicated on all specimens by grooves on the anterolabial surface of the hypoconids. The root pattern of M_1 differs from that *H. funderus* in showing a broadening of the anterior root and its partial fusion with that positioned below the protoconid; the tip of the latter root remains separate (Fig. 10). Three specimens retain the M_2. Where both M_1 and M_2 are present, the latter tooth is equal in width to the posterior lamina of M_1, rather than broader than M_1 as in *H. funderus*. The crown is less bulbous than the M_2 of *H. funderus* and has a more deeply folded anterior lamina. There is no trace of an anterolabial cusp on any specimen. However, one specimen (AM F101456, the holotype) has a posterolabial cusplet defined by a weak groove on the outer surface of the hypoconid. Five specimens retain the M_3. This tooth is substantially shorter than M_2 but only slightly narrower. Compared with the condition in *H. funderus*, the anterior lamina of M_3 is less deeply folded. A small anterolabial cusp is present on AM F101461 but absent on all other specimens.

Discussion

Comparisons within *Halmaheramys*

Geometric morphometric results. Mandibular shape morphology of the two Morotai *Halmaheramys* species were quantitatively compared to other previously described species from the oceanic islands of Halmahera and Obi using 2DGM and visualized by a PCA (Fig. 2). The first principal component (PC1) explains 46% of the variance and is mainly influenced by size, with larger jaws loading negatively (*H. funderus*) and smaller jaws loading positively (*H. bokimekot*). *Halmaheramys funderus* differs from all other *Halmaheramys* species by its proportionally smaller lower molars and larger incisor root compared to jaw size, as well as its opisthodont lower incisor. The jaw shape of other three *Halmaheramys* species are more similar, with more positive loadings on PC1, loading from the largest to the smallest species (*H. bellwoodi*, *H. wallacei*, and *H. bokimekot*, respectively). PC2 and PC3, which explain 19.2% and 13.6% of the variance respectively, do not show clear distinctions between species, probably due to our small sample size of landmarks and specimens.

Distinctions between the Morotai taxa. The two Morotai species differ only slightly in tooth size and molar morphology and there can be little doubt that they are closely related. Whether they are sister species that have potentially diverged within the island, as appears to be the case for two other Moluccan murines, *Rattus feliceus* and *R. ceramicus* of Seram, as recently demonstrated by Fabre *et al*. (2023), awaits more detailed analysis, including future genetic comparisons. Nevertheless, the observed differences in molar proportions, M_1 anteroconid morphology and labial cusplet development are comparable in kind and degree to interspecific differences within other murine genera. More significant contrasts are observed in the morphology and proportions of the dentary. In *H. funderus* the cheekteeth are large relative to the dimensions of the dentary and the lower incisor is steeply inclined, indicating a short rostrum and diastema. In contrast, *H. bellwoodi* has relatively smaller cheekteeth for the size of the dentary, coupled with an exceptionally low angled incisor that creates an elongate diastema. Other differences in jaw morphology, including the varying development of the incisor tubercle and differential development of the masseteric crest, presumably reflect associated modifications in jaw architecture and masticatory adaptations between the two species.

Without more complete fossil material, it is difficult to identify the ecological significance of the morphological differences between these two *Halmaheramys* subfossil species. However, the morphological configuration of *H. bellwoodi*—combining an elongate lower jaw diastema, low angled lower incisor and relatively small molars for the size of the jaw—is reminiscent of some species of the Sulawesian genus *Bunomys* (e.g., *B. chrysocomus*) and some New Guinean species of *Rattus* (e.g., *R. verecundus*), and seen in more extreme expression in New Guinean species of *Leptomys* and *Paraleptomys* (Taylor *et al*., 1982; Musser, 1991, 2014; Musser *et al.,* 2008), for example. All of these taxa are terrestrial animalivores, feeding on snails, earthworms and insects, and perhaps in some cases, small vertebrates, and their morphological adaptations are plausibly related to the demands of this lifestyle (Musser & Heaney, 1992; Helgen & Helgen, 2009; Musser & Durden, 2014; Musser, 2014; Rowe *et al*., 2016; Veatch *et al*., 2023). In contrast, the short lower jaw diastema and larger molars of *H. funderus* are more reminiscent of taxa with a herbivorous diet, and in particular, of species known to feed primarily on fruits or large seeds that require heavy gnawing activity to penetrate tough skin or nut casing followed by heavy mastication to process fibrous flesh or pith (e.g., Samuels, 2009). At present, and with the materials at hand, it is premature to speculate further on the ecological adaptations. In future, stable isotope analysis of bones might be employed to revisit these questions of dietary adaptation and general ecology from a more solid analytical foundation.

Biogeography

Morotai (= Morty) is the northernmost of what is sometimes characterized as the Halmahera Group of islands, which in addition to Morotai includes the large, four-armed island of Halmahera (= Gilolo) and the smaller satellite islands of Bacan (= Batjan), Ternate, Tidore, Kayoa, and Mota, among several others. Halmahera and Bacan are separated by a relatively shallow-water channel, and during periods of lowered sea level during the Late Pleistocene these islands were united at times as a single, larger landmass. In contrast, Halmahera and Morotai, as noted above, are separated by much deeper water and have more independent recent histories as a result (Hall *et al*., 1988, 1991; Hall, 2002, 2013; Bellwood, 2019).

Together, the islands of the Halmahera support a highly unique, well-isolated biota, and are generally united together as a single biogeographic province within the Wallacean region (Monk *et al*., 1997; Stattersfield *et al.,* 1998; Wikramanayake *et al.,* 2002). The various small oceanic islands situated off western Halmahera (such as Ternate, Tidore, and Kayoa) are of geologically recent, volcanic origin (Monk *et al*., 1997), and seem to have faunas derived from Halmahera-Bacan. The more southerly island of Obi and its satellites (including the islands of Bisa and Obilatu) share many restricted-range bird species with the Halmahera Group and are often included within this biogeographic province (e.g., Stattersfield *et al.,* 1998; Wikramanayake *et al.,* 2002). However, our ongoing studies of Moluccan mammals reveal that the mammal faunas of the Halmahera and Obi island groups are biogeographically similar but somewhat divergent, and that Morotai is also distinctive within the northern Moluccas. For example, recent taxonomic work, including that documented here, shows the distinctiveness of the assemblage of Rattini from Obi-Bisa (*Halmaheramys wallacei* and *Rattus obiensis*) from Halmahera-Bacan on the one hand (*Halmaheramys bokimekot* and *Rattus halmaheraensis*) and Morotai on the other (*Halmaheramys funderus*, *Halmaheramys bellwoodi*, and *Rattus morotaiensis*), with significant rodent endemism in each cluster (Fabre *et al*., 2013, 2018, 2023). The subfossil record (and modern fauna) of Morotai also lacks other Australo-Papuan genera that characterize other North Moluccan islands, such as *Hydromys* and *Uromys* (known from Obi) and *Melomys* (known from Halmahera and Obi-Bisa) (Fabre *et al*., 2017a, 2018, 2023).

To date, faunistic surveys of the Halmahera Group have recorded a moderately diverse suite of nonvolant mammals that includes the cuscus *Phalanger ornatus,* the marsupial glider *Petaurus breviceps,* the shrew *Suncus murinus,* the macaque *Macaca nigra,* the civets *Paradoxurus hermaphroditus* and *Viverra tangalunga,* the murines *Rattus morotaiensis* and related species (Fabre *et al*., 2023)*, Rattus exulans,* and *Rattus* sp. cf. *rattus*, a pig *Sus* sp. cf. *S. celebensis,* and the rusa deer *Rusa timorensis* (Table 3). In marked contrast, cave deposits of Holocene age on Halmahera (*ca*. 5200–3400 BP) contain a more limited mammal fauna that includes only the wallaby *Dorcopsis* sp. cf. *D. muelleri,* an unnamed endemic bandicoot (probably *Echymipera* sp.), *Phalanger ornatus,* postcranial remains of a relatively small rat (probably *R. halmaheraensis*), and, in later layers, *Sus* (Flannery *et al.,* 1995). Late Pleistocene to Holocene archaeological deposits on Morotai (*ca*. 14,000 to 5,500 BP) have yielded only *Phalanger ornatus, Rattus morotaiensis, Halmaheramys bellwoodi, H. funderus,* and, in later layers, a representative of the *Rattus rattus* Species Complex (Flannery *et al.,* 1998; Table 3).

It thus appears that the pre-human nonvolant mammal fauna of the Halmahera Group comprised but three marsupials (*Dorcopsis* sp. cf. *D. muelleri*, *Phalanger ornatus* and a peroryctid bandicoot) and species of *Rattus, Halmaheramys*, and *Melomys*. All other nonvolant mammals in the modern fauna of the Halmahera Group (species of

Table 3. Late Quaternary and modern nonvolant mammal records in the Halmahera Group, North Moluccas. Archaeological deposits from three islands have been studied to date: Halmahera (H), Morotai (M), and Kayoa (K); the modern fauna of sixislands have been surveyed to date: Ternate (Te), Halmahera (H), Bacan (B), Morotai (M), Tidore (Ti), and Moti (Mo), in decreasing level of exhaustiveness. Species endemic to the North Moluccas are shown in bold. Sources: Corbet & Hill (1992); Koopman & Gordon (1992); Flannery (1995); Flannery *et al*. (1995, 1998); Monk *et al*. (1997); Helgen (2002); Fabre *et al*. (2013, 2017a, 2018, 2023).

Taxa	Late Quaternary (14,000–3,000 BP)	Modern (last 150 years)
Echymipera sp.	H	—
Dorcopsis sp. cf. *muelleri*	H	—
Phalanger ornatus	H, M, K	H, B, M, Te, Ti
Petaurus breviceps	—	H, B, Te
Suncus murinus	—	H, B, Te
Macaca nigra	—	H[a], B
***Halmaheramys bellwoodi* sp. nov.**	M	—
Halmaheramys funderus	M	—
Melomys sp. cf. *burtoni*	—	H
Rattus exulans	—	H, B, M, Te
Rattus morotaiensis	M	M
Rattus halmaheraensis	H	H, B, Te, Mo
Rattus sp. cf. *rattus*	M[b]	H, B, Te
Rattus tiomanicus	—	H[c]
Paradoxurus hermaphroditus	—	H, B
Viverra tangalunga	—	H, B
Sus celebensis	H[d]	H, B, M, Te
Rusa timorensis	—	H, B, M, Te

[a] Recorded as a captive animal only from Halmahera, so perhaps restricted to Bacan within the Moluccas (Koopman & Gordon, 1992).

[b] From deposits 5530 ± 70 BP and younger (Flannery *et al.,* 1998).

[c] Recorded as a commensal species from Halmahera by Fabre *et al.* (2023).

[d] From deposits 1870 ± 80 BP, and possibly as early as 5120–3410 BP, but absent from the Morotai Holocene record (Flannery *et al.,* 1995, 1998).

Petaurus, *Suncus*, *Macaca*, *Paradoxurus*, *Viverra*, *Rusa,* and *Sus*, as well as *Rattus exulans* and *Rattus* sp. cf. *R. rattus*) have been widely translocated by humans elsewhere in the Malay Archipelago (Glover, 1986; Flannery, 1995) and likewise appear to have reached the North Moluccas through human agency during the Holocene. Flannery *et al.* (1998) suggested that the *Dorcopsis* recorded from Halmahera was also introduced some time prior to 10,000 BP, perhaps from the West Papuan land-bridge island of Misool. However, to us the absence of an earlier faunal record from the area, together with the presence of several endemic north Moluccan marsupial lineages (*Phalanger ornatus*, and a bandicoot), leaves open the possibility that *Dorcopsis* was a native element in the fauna. Whatever the case, with the possible exception of *Dorcopsis*, all nonvolant mammals recorded in the Halmahera Group during the early to middle Holocene are endemic at the species level. This striking endemism results from the trenchant geographic isolation of the archipelago and highlights the faunal distinctiveness of Halmahera and its satellites relative to all other regions within Melanesia and Wallacea, including New Guinea, Sulawesi, and other areas in between, including the islands of Seram and Buru. Rodent endemism in the North Moluccas is especially notable—*Halmaheramys* is the only generic level mammal lineage known only from the Moluccas, and the *Rattus morotaiensis* species group (*R. morotaiensis*, *R. halmaheraensis*, and *R. obiensis*) is distinctive among *Rattus* (Musser & Carleton, 2005; Fabre *et al*., 2023).

Today, the island of Morotai is covered in broadleaf evergreen and semi-evergreen rainforest. Wet evergreen forest occurs across the majority of the island, but a large tract of semi-evergreen forest is found in the island's drier southwest (Monk *et al.,* 1997). The modern vegetation of the Daeo Cave area (and much of the southern and eastern coasts of Morotai) consists of lowland evergreen forest on limestone. Late Quaternary habitats in the immediate area were probably similar to those of the present, as apart from *Halmaheramys* the fauna in the Daeo Holocene deposit includes *Phalanger ornatus, Rattus morotaiensis,* and *Pteropus caniceps* (Flannery *et al.,* 1998)—species characteristic of lowland evergreen rainforest elsewhere in Morotai, Halmahera, and Bacan today.

Though both species of *Halmaheramys* from Morotai are currently known only from subfossil remains, it should not be assumed that they are extinct. The remains of both species are scattered through the Daeo Cave deposit (Flannery *et al.,* 1998), with no indication that either became extinct prior to the late Holocene. More pertinently still, the modern rodent fauna of Morotai remains particularly poorly inventoried, and rodent collecting efforts in the Halmahera Group as a whole have focused on a limited number of habitats. To date, only three cursory efforts have been aimed at rodent-collecting in Morotai: a brief survey by personnel of the United States National Museum in October 1944, which yielded *Rattus exulans* and *Rattus morotaiensis* (Kellogg, 1945); a brief visit by E. le G. Troughton of the Australian Museum in 1945, who collected small series of *R. morotaiensis* and *R. exulans;* and a three-day visit in November 1991 by one of us (Boeadi), who collected a single subadult specimen of *Rattus morotaiensis* in a corn garden situated in forest adjacent to a logging camp. Historical and recent efforts to document wild-living nonvolant mammals both on Morotai and on the other islands in the Halmahera Group have focused almost entirely on modified habitats such as traditional gardens, plantations, secondary forest, and forest in the near-vicinity of settled areas (e.g., Koopman & Gordon, 1992; Flannery, 1995; Hasagawa & Syaffrudin, 1995a, 1995b), and these efforts have concentrated mostly on lowland habitats (< 200–300 m), rather than lower or upper montane forests.

Deforestation and mining (especially nickel mining) are the most pressing conservation threats to restricted-range species in the North Moluccas (Stattersfield *et al.,* 1998; Brooks *et al.,* 1999; Poulsen & Lambert, 2000; Wikramanayake *et al.,* 2002). Human occupation in the region extends back to 35,000 BP (Bellwood *et al.,* 1998), and throughout this time people undoubtedly cleared some forested areas in Morotai for gardens and settlements, especially in coastal areas. However, over the past century forest clearance has accelerating sharply beyond these traditional impacts. Monk *et al.* (1997) noted that enforced cultivation and commercial logging, including clear-felling (Ellen, 1997), have reduced Morotai's rainforest cover since the 1920s, and that large tracts of lowland rainforest were cultivated with papaya (*Carica papaya*) during the Second World War. In tandem, the human population on Morotai has grown explosively over the last century and continues to grow at a very high rate (Monk *et al.,* 1997). If *Halmaheramys bellwoodi* and *H. funderus* are still extant and rely on relatively undisturbed rainforest, these ongoing human impacts may explain why these species have not yet been encountered by researchers working in coastal or settled areas since rodent collecting efforts began in Morotai in 1944.

At present there are no gazetted protected areas on Morotai or elsewhere in the North Moluccas, although Wayabula in north-central Morotai (830 km^2) is an important proposed protected area (Stattersfield *et al.,* 1998). Much of the interior of Morotai, including Wayabula, is incorporated in an expansive but relatively low montane massif (to 1250 m above sea level) which still supports primary forest, despite increasing logging activity (Monk *et al.,* 1997). As far as we are aware, these inland forests remain unknown mammalogically, and constitute the best place to search for living populations of *Halmaheramys*. Nonvolant mammal assemblages from primary evergreen forests in the mountainous interiors of the higher adjacent islands of Halmahera (mountains to 1630 m) and Bacan (to 2100 m) also remain entirely or largely unsampled, and these are areas which should also be targeted in the search for extant populations of endemic north Moluccan mammals, including, for example, both *Halmaheramys* and the unnamed bandicoot recorded only from subfossil deposits on Halmahera. Obviously, such surveys remain important regional priorities both for systematic mammalogy and for conservation biology.

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Appendix. Comparative material: gazetteer and specimens examined for extant *Halmaheramys*.

Halmaheramys bokimekot

Halmahera Island, Boki Mekot (0.612°S 128.05°E, altitude 900 m): MZB 33261–33266.

Halmaheramys wallacei

Bisa Island, Air Durian (1.23°S 127.58°E, altitude 0 m): AM M.24389.

Obi Island, Gunung Sere (1.62°S 127.71°E, altitude 870 m): MZB 38225, MZB 38226.

Obi Island, Cabang Sumbali (1.38°S 127.66°E, altitude 40 m): MZB 38227.

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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 toothrow 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

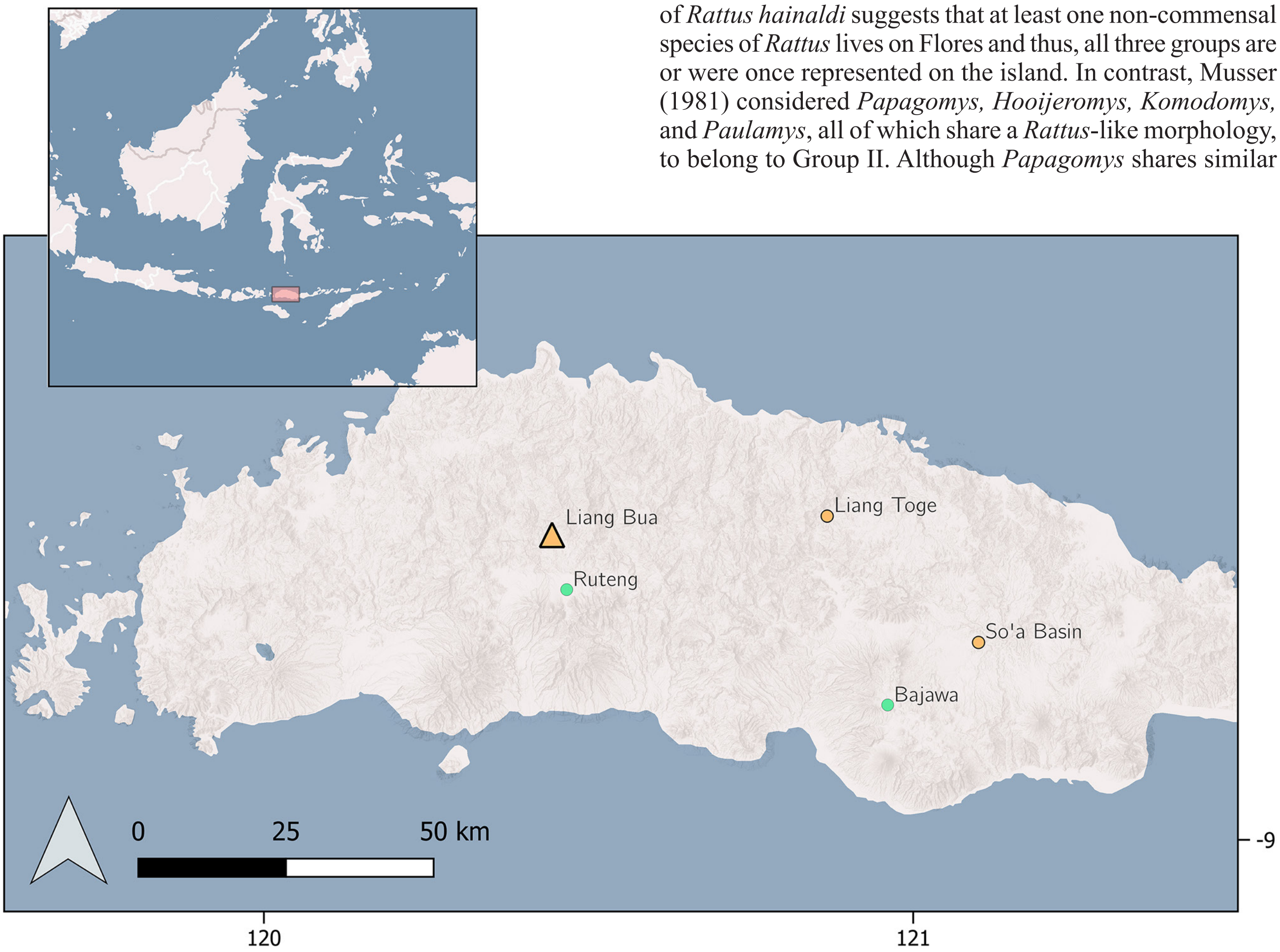

Figure 1. Map of Flores within the Indonesian archipelago showing the location of archaeological sites (yellow) in the western and central parts of the island mentioned in text. The nearest large towns are shown in green.

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]
Papagomys armandvillei	1200–2500[c]	giant	yes	leaves, fruits, insects	terrestrial, burrowing	closed, semi closed
Papagomys theodorverhoeveni	600–1600[d]	huge	uncertain	fruits, insects	terrestrial	closed, semi closed
Spelaeomys florensis	600–1600[d]	huge	uncertain	leaves, flowers, buds	arboreal	closed
Hooijeromys nusatenggara	300–600[d]	large	uncertain	unknown	terrestrial	open, semi open
Komodomys rintjanus	100–200[e]	medium	yes	unknown	terrestrial	open, semi open
Paulamys naso	100–200[f]	medium	yes	fungi, insects, snails, earthworms, fruits	terrestrial, burrowing	closed, mossy
Rattus hainaldi	40–100[i]	small	yes	unknown	terrestrial, nesting	commensal
Rattus exulans[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

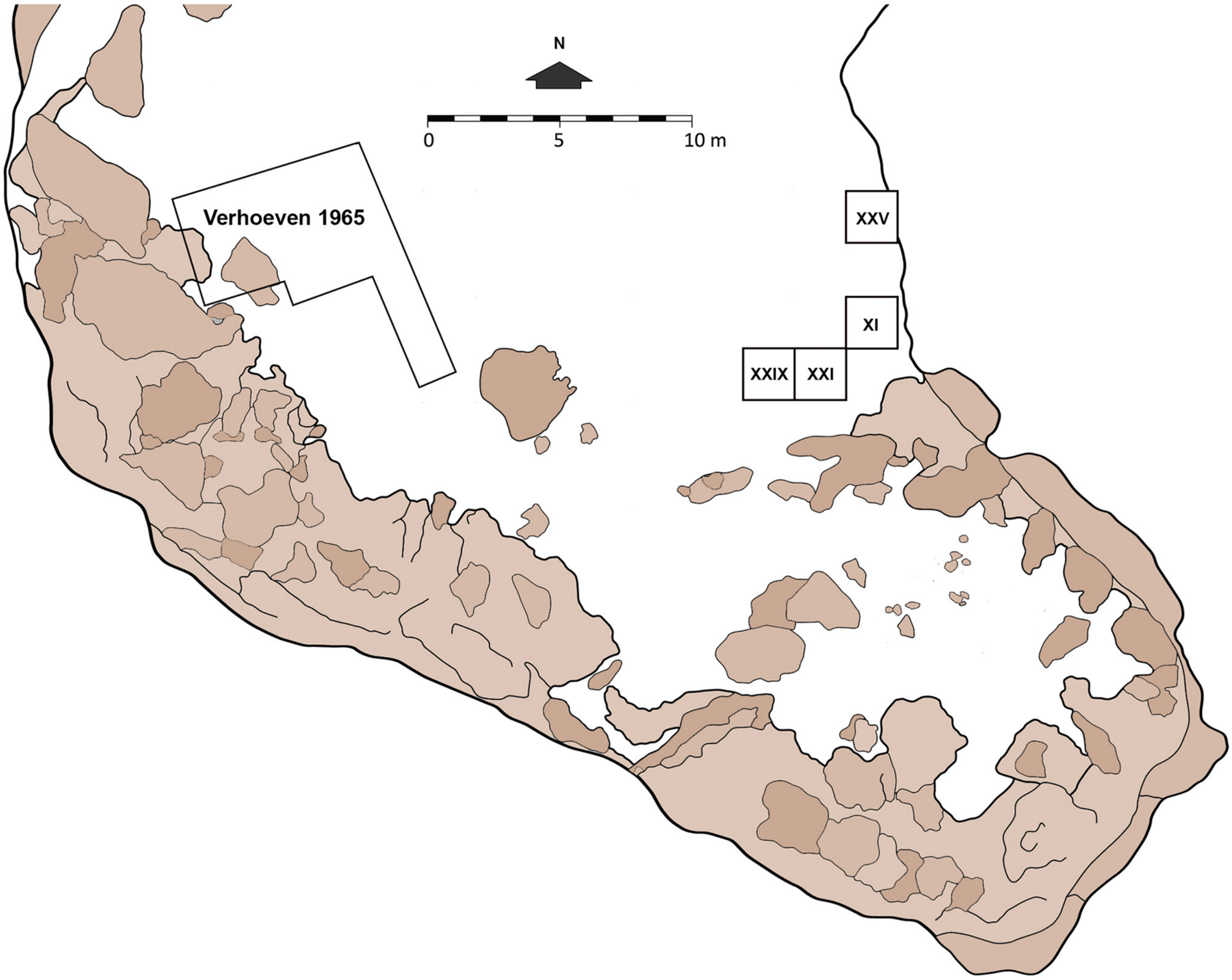

Figure 2. Plan of Liang Bua showing the locations where specimens of *Lawomys rokusi* have been recovered. Roman numerals denote specific 2 × 2 m excavation areas and the larger polygon at left shows the area excavated by Theodor Verhoeven in 1965.

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.

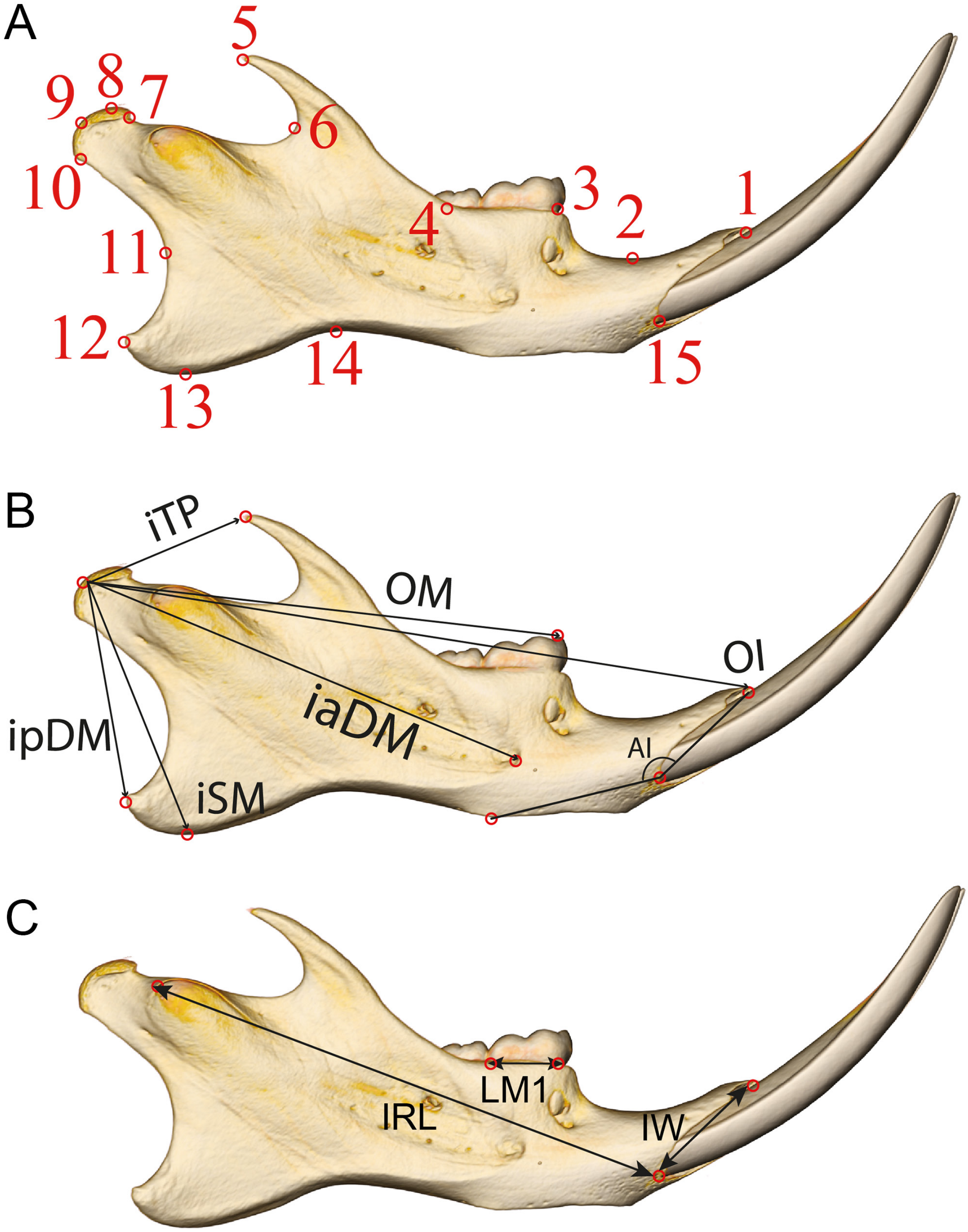

Figure 3. (*A*) Landmarks used in the 2D GMM analysis (see Fig. 8). (*B*) Distances used in the in-lever (i) and out-lever (O) analysis (see Fig. 10). (*C*) Dental measurements including length of the first molar (LM1), incisor width at the alveolus (IW), and internal incisor length (IRL) (see Figs 10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

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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 (⅓ to ½ 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.

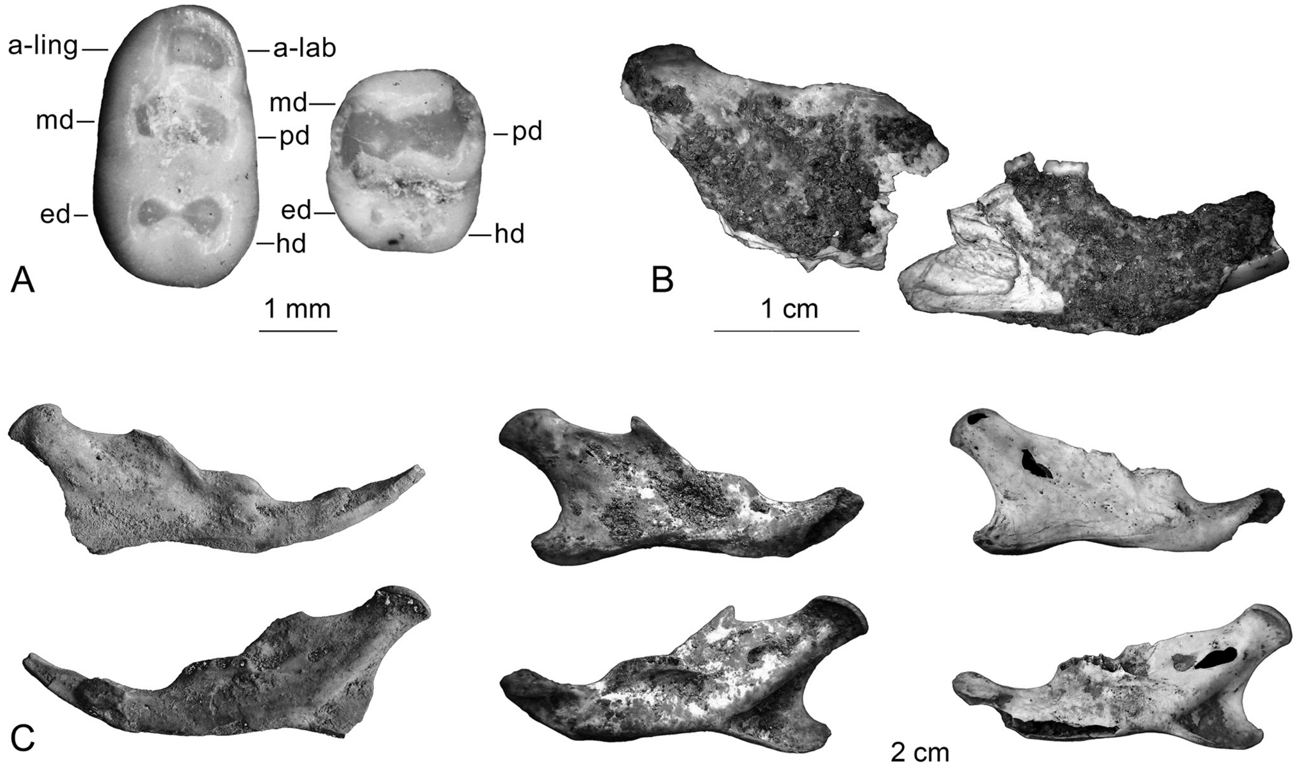

Figure 4. (*A*) *Lawomys rokusi* holotype first (at left) and second (at right) right molar occlusal surfaces (*a-ling,* anterolingual cusp; *a-lab,* anterolabial cusp; *md,* metaconid; *pd,* protoconid; *ed,* entoconid; *hd,* hypoconid). (*B*) *Lawomys rokusi* holotype right mandible showing the posterior 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.

urn:lsid:zoobank.org:act:E19E2F3A-BE7C-495F-B056-64DECF70D468

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.

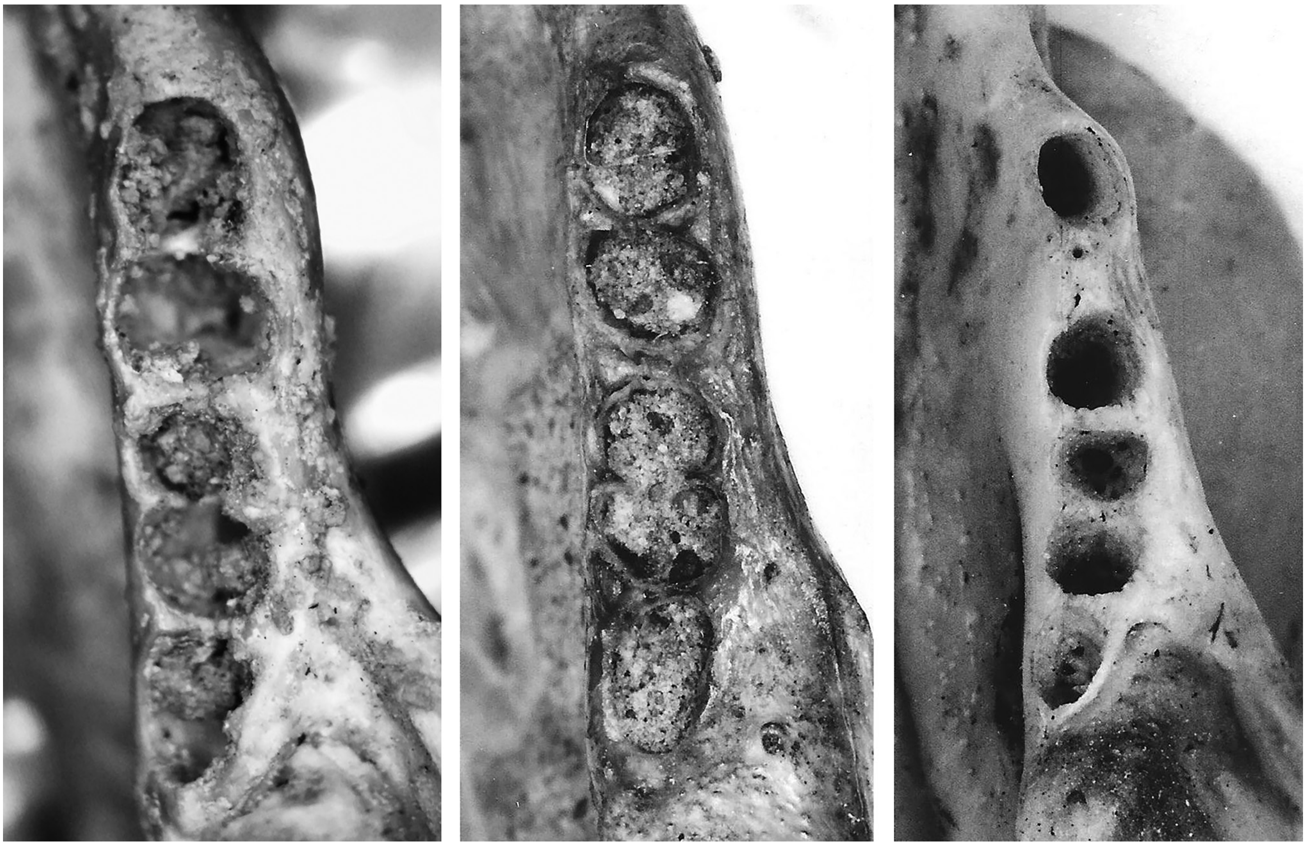

Figure 5. Alveoli of right lower toothrows of two specimens of *Lawomys rokusi* (left, LB-MUR-6484; middle, LB 36) compared with a specimen of *Chrotomys mindorensis* (right, AMNH 12972). Specimens scaled to same size.

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 Budianto 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

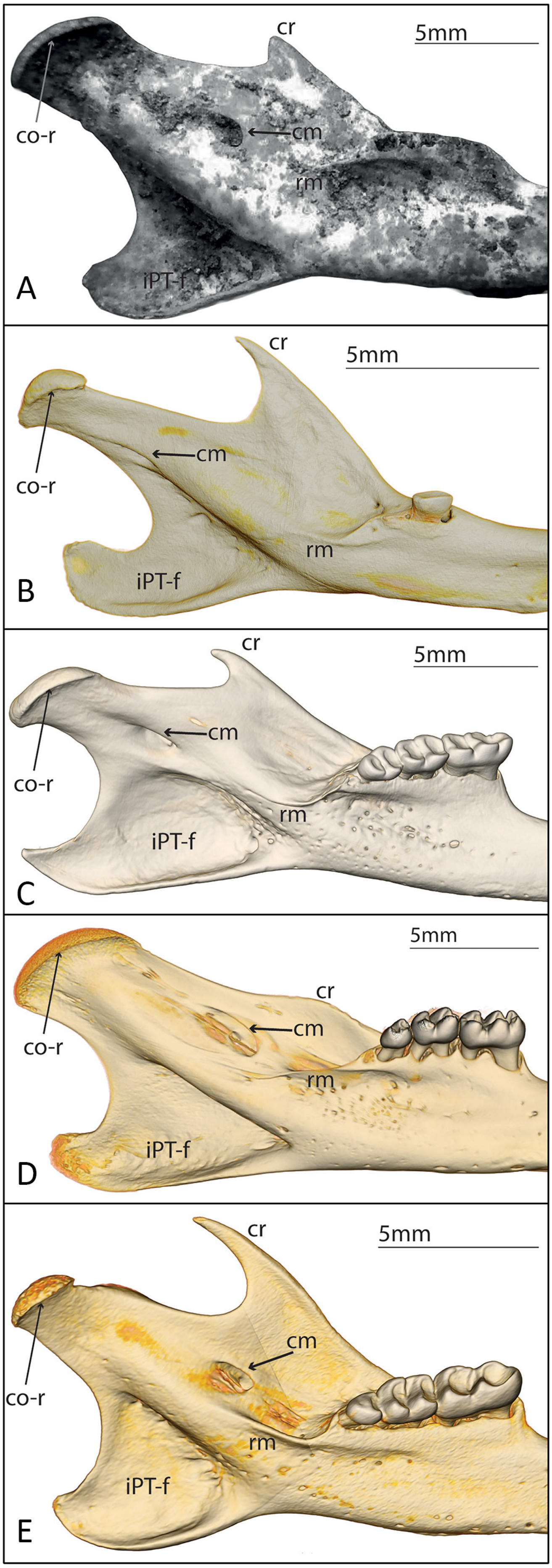

Figure 7. Morphological comparison of the medial side of the mandible showing the location of features mentioned in text (*cr,* coronoid process; *cm,* mandibular foramen; *iPT-f,* internal pterygoid fossa, *co-r,* condyloid ridge; *rm,* retromolar fossa ridge) between (*A*) *Lawomys rokusi* LB-MUR-6484, (*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.

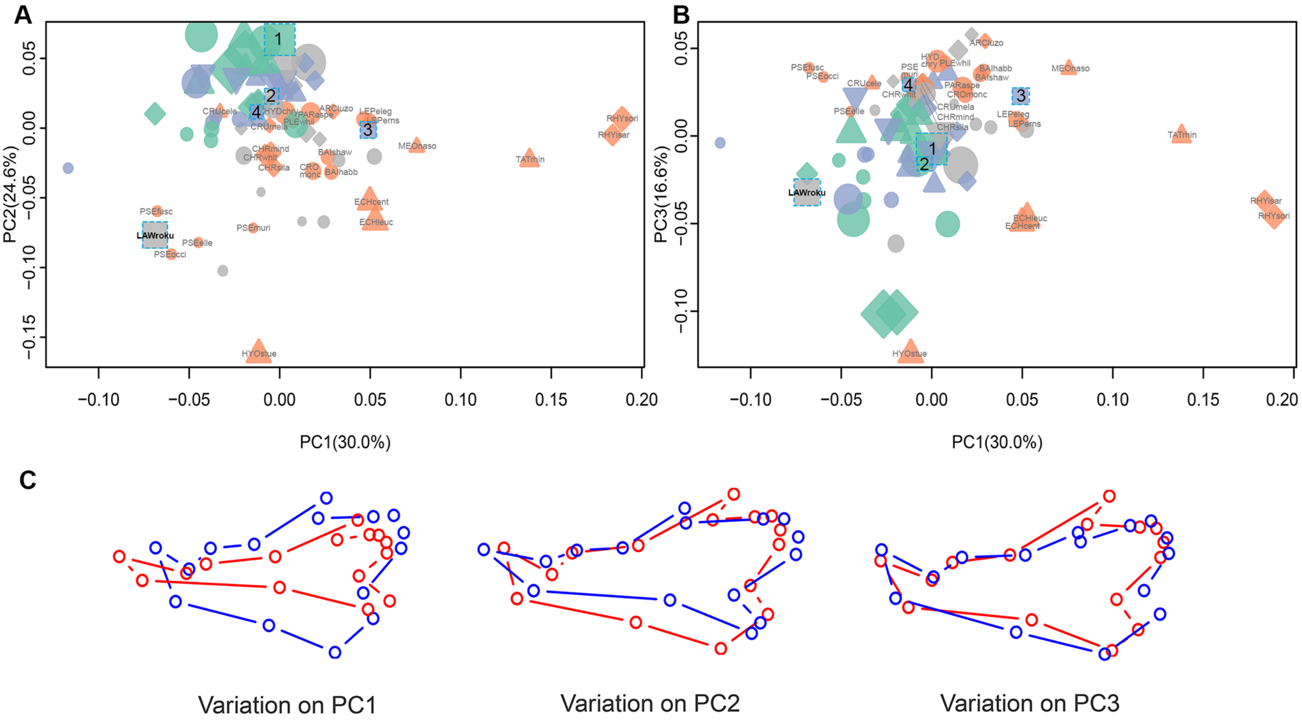

Figure 8. (*A–B*) Principal components analysis of 2DGMM comparing murid jaw shape and (*C*) shape profiles for principal component 1–3 showing the mandibular configuration on the extreme positive (red) and negative (blue) ends. Genus and species names are abbreviated (e.g., ECHcent) for carnivorous 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 rokusi* 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).

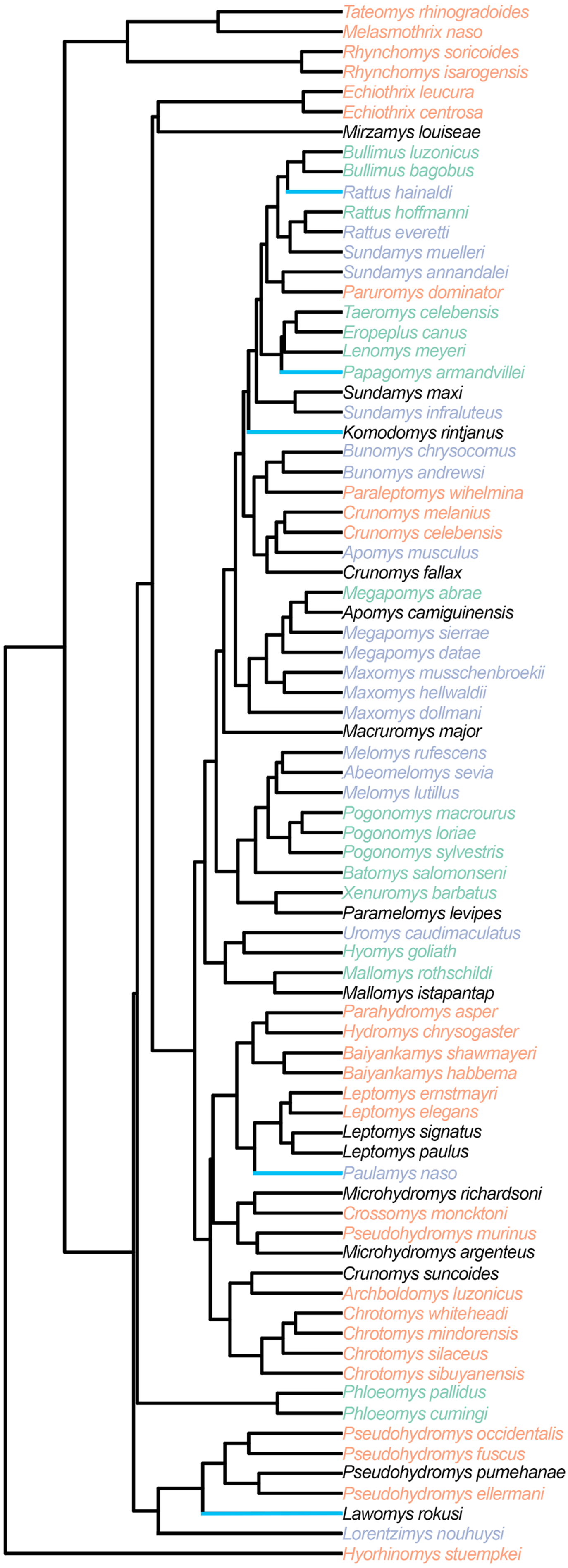

Figure 9. A cluster analysis using Procrustes distances showing the nearest neighbour based on 2DGM results. Colours denote diet; peach = carnivorous, green = herbivorous, blue = omnivorous. Branches highlighted in blue indicate species endemic to Flores. The clustering indicates phenetic similarity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

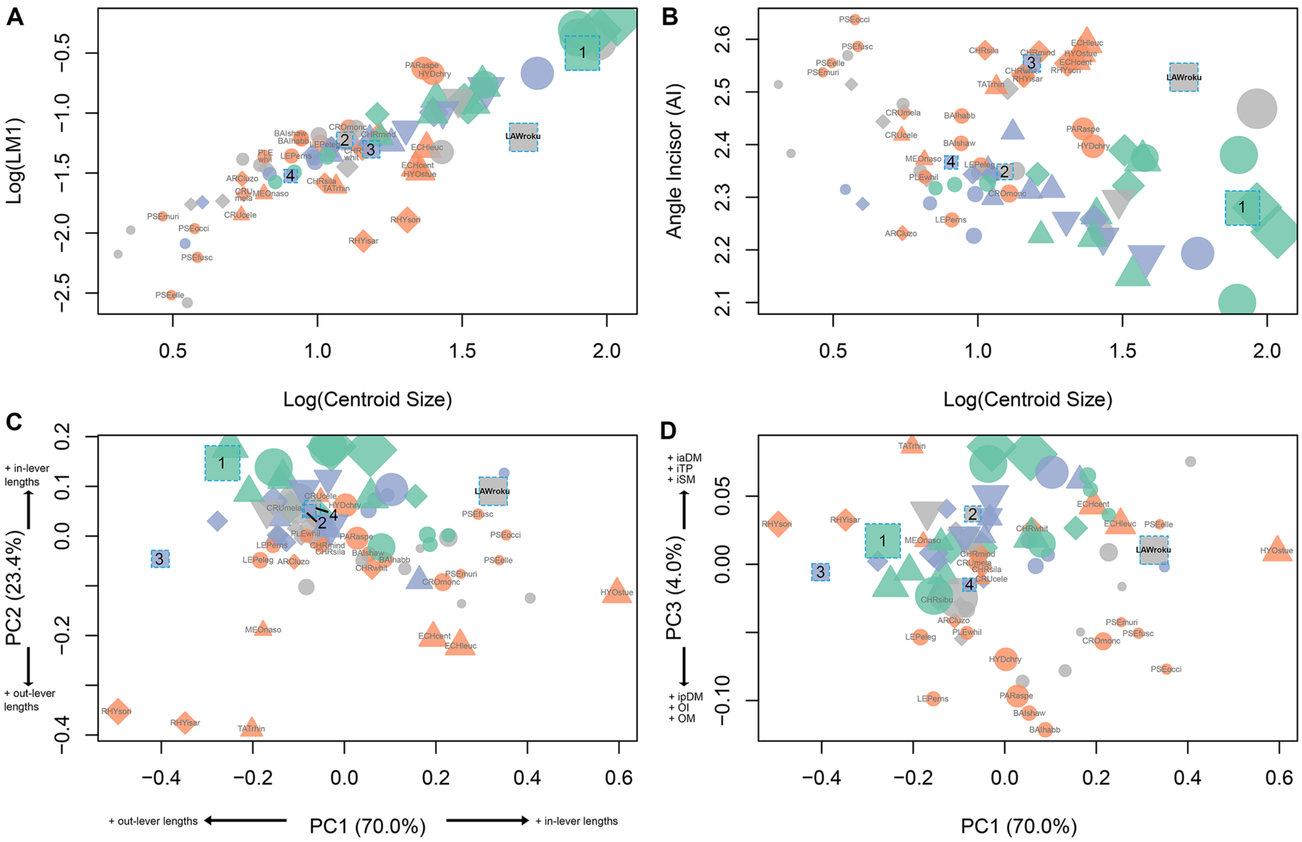

Figure 10. (*A*) The logged value of the jaw centroid size against the logged value of the lower first molar length (LM1) and (*B*) an angle measuring incisor orientation (AI). (*C–D*) Principal components analysis of the in-lever and out-lever distances. Description of variable loadings are provided 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*.

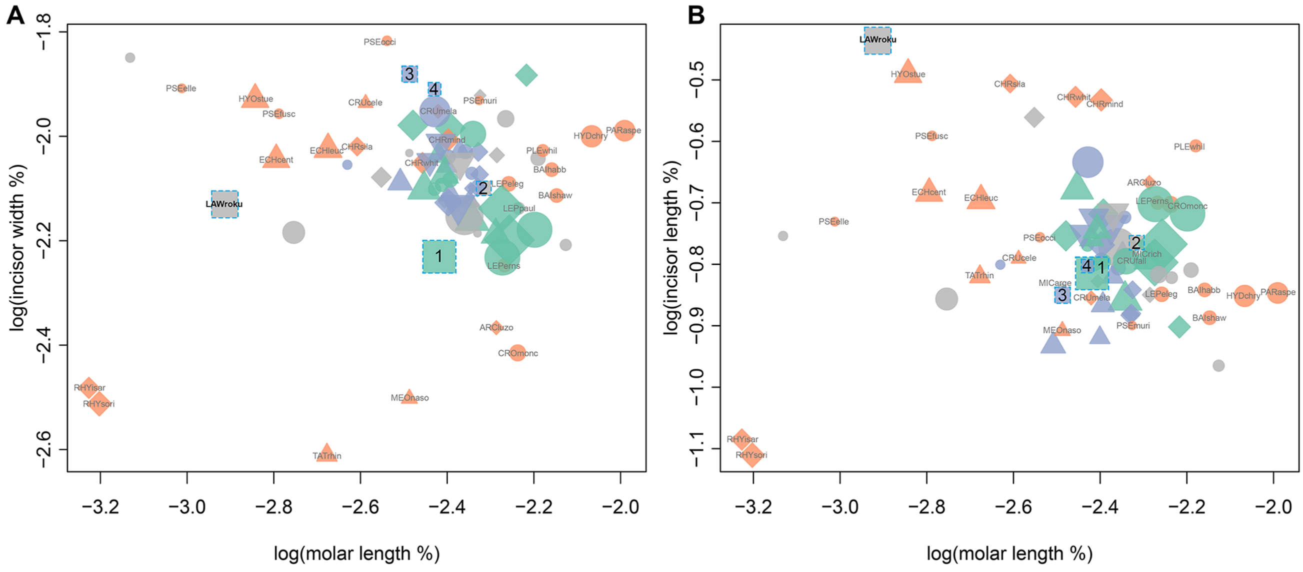

Figure 11. The relationship between molar length relative to centroid size (logged) against (*A*) incisor width relative to centroid size (logged) and (*B*) incisor length relative to centroid size (logged). Genus and species names are abbreviated (e.g., ECHcent) for carnivorous murids only. The relative 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 &

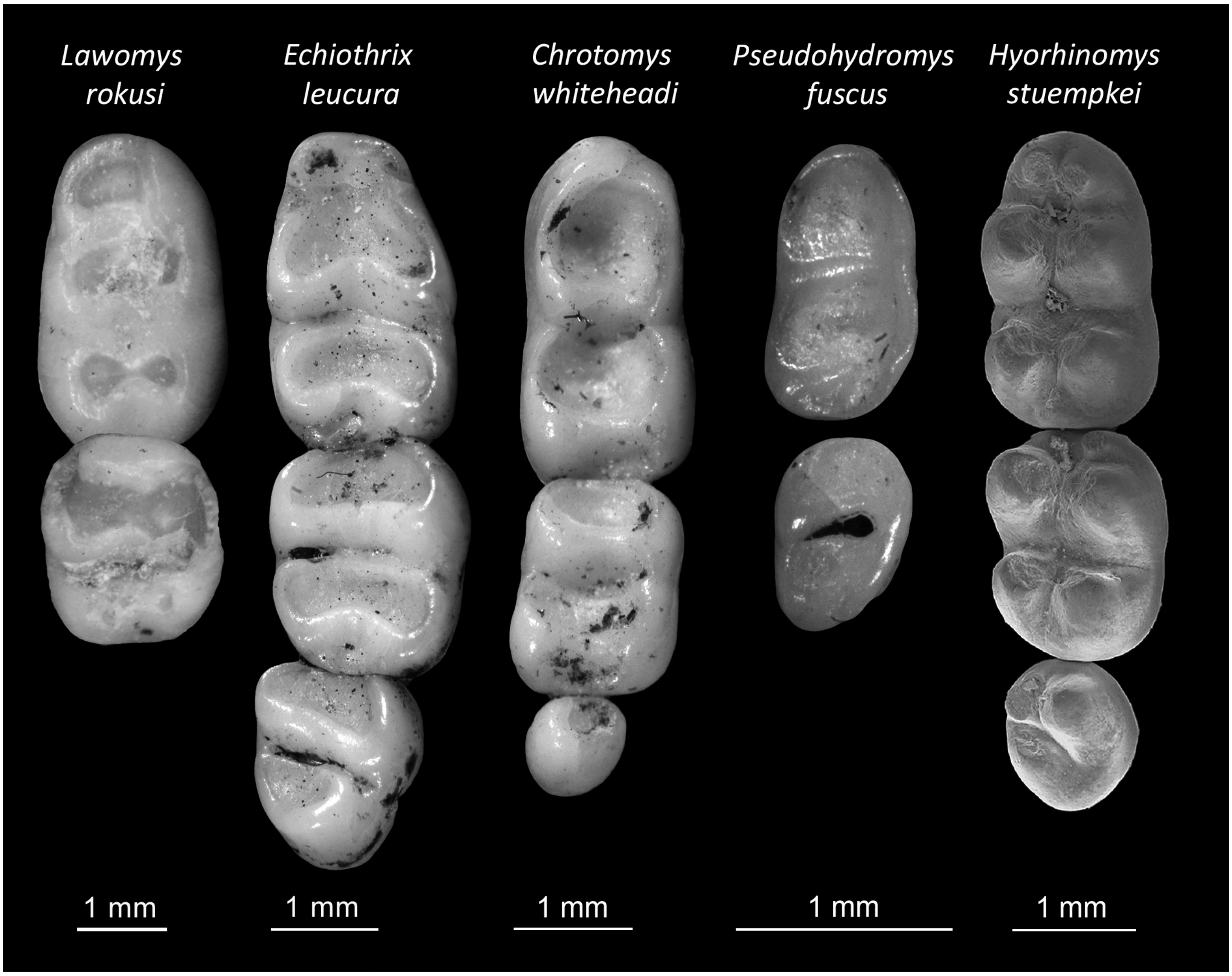

Figure 12. Comparison of the lower right toothrow between *Lawomys rokusi* (LB-MUR-6488), *Echiothrix leucura* (NHMUK ZD 797.1.2.45; mirrored), *Chrotomys whiteheadi* (NHMUK ZD 95.8.2.20; mirrored), *Pseudohydromys fuscus* (NHMUK ZD 53.301), and *Hyorhinomys stuempkei* (LSUMZ 37060, SEM image modified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

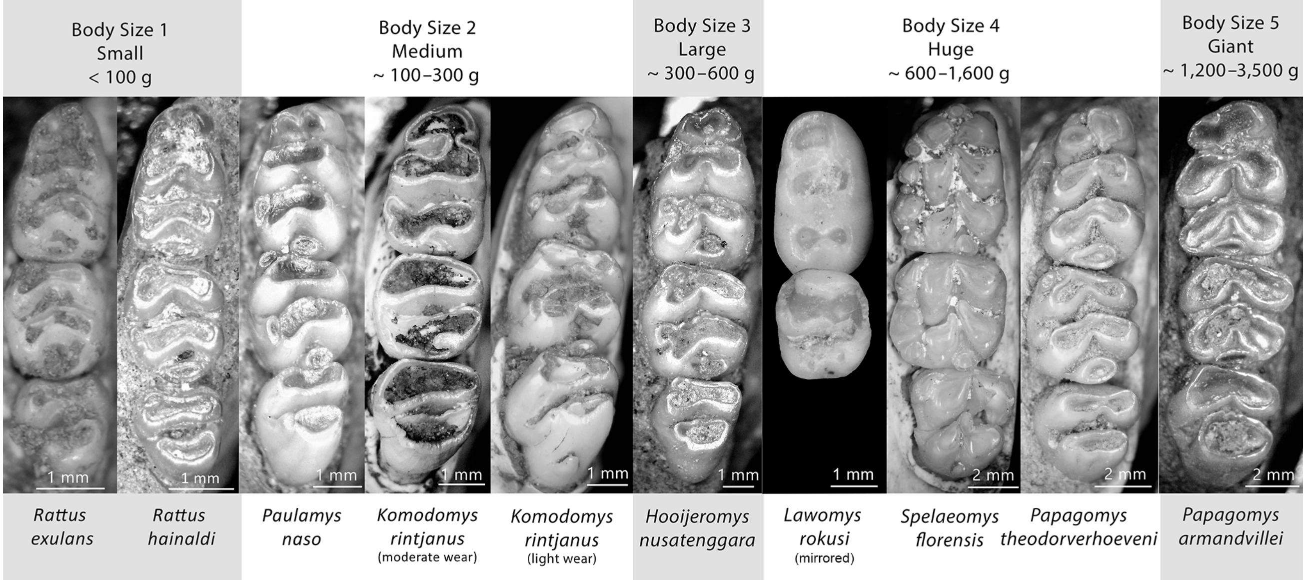

Figure 13. Left lower toothrows of Flores murines from Liang Bua scaled to approximately the same size to show occlusal patterns. Delineations of murine body size ranges are also shown.

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	
Papagomys armandvillei	1146	1037	1508	2866	3450	1037–3450	1495–2285[b]
Lawomys rokusi	623	564	771	1245	1594	563–1594	—
Komodomys rintjanus	97	88	100	98	152	88–152	—
Paulamys naso[a]	128	116	136	144	216	116–215	122[a]
Rattus hainaldi	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

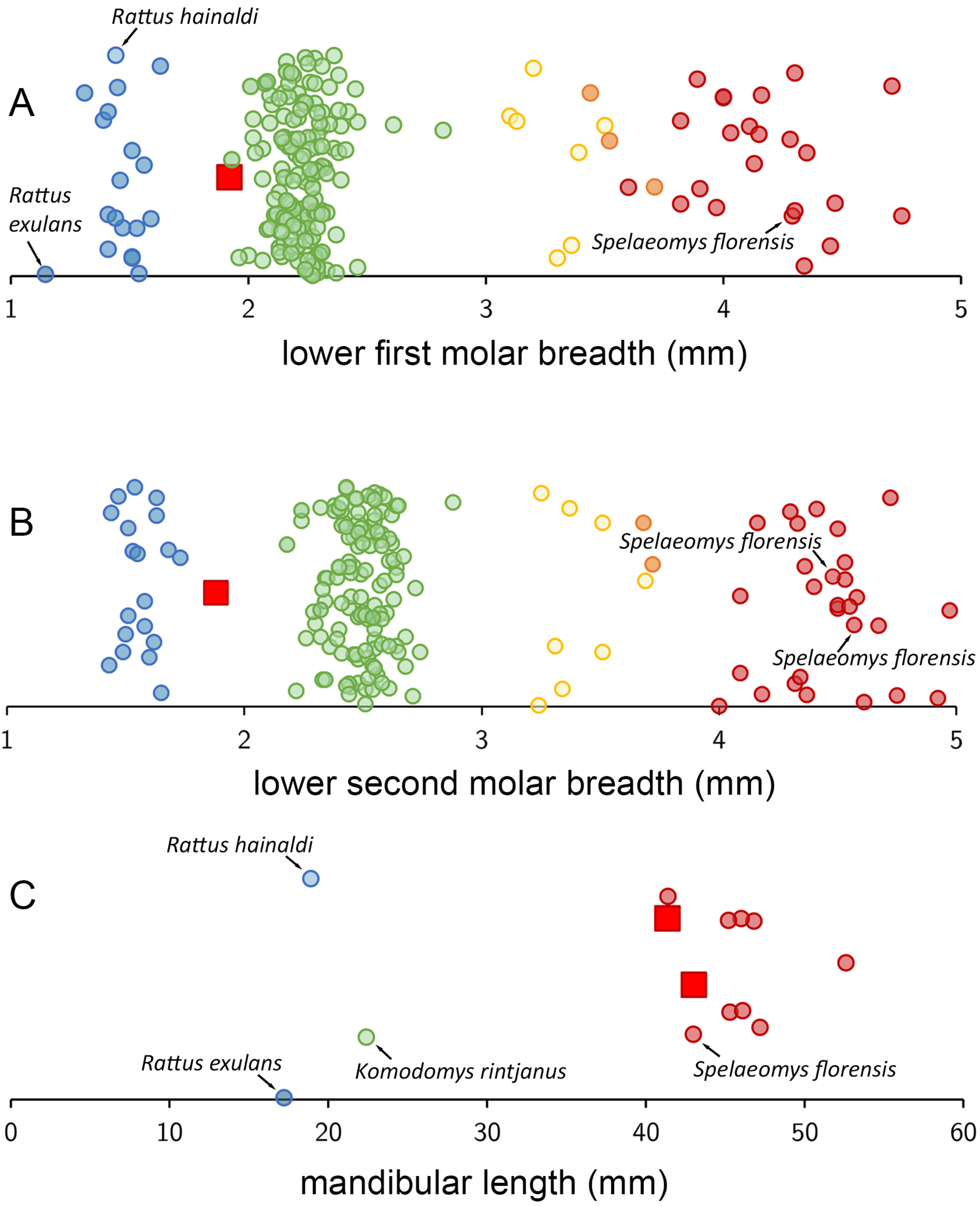

Figure 14. A comparison of molar and mandibular measurements between *Lawomys rokusi* (red square) and Flores taxa. Measurements include breadth of the lower first molar (*A*), lower second molar (*B*), and maximum length of the mandible (*C*). Samples of Flores taxa include archaeological and museum 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; *Komodomys 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.

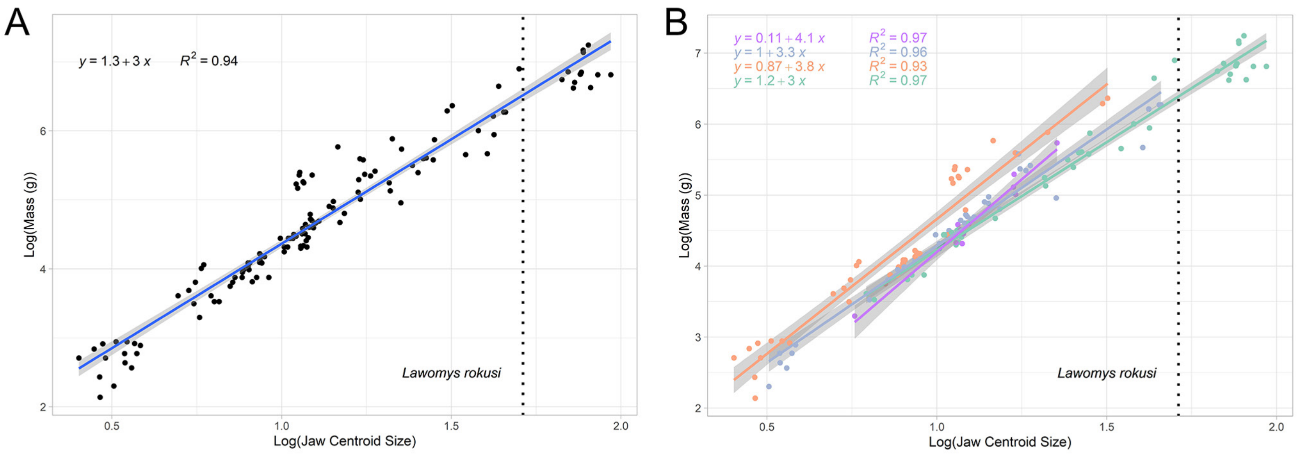

Figure 15. (*A*) Linear regression model showing the relationship between the natural log of jaw centroid size and known body masses (g) of murine taxa from the Indo-Pacific region (SI Table 3). The shaded region represents the 95% confidence interval. The dotted line represents the logged jaw centroid 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*, *Spelaeomys 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 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.

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.

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).
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Late Quaternary Mammal Introduction and Extinction Records from Archaeological Cave Deposits in Timor-Leste

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ABSTRACT. Humans have influenced island biotas in the last few millennia through widespread forest clearances and the introduction of commensals and pest species, causing the extinction of island endemics around the world. This is particularly evident in Timor, where more than 40,000 years of human habitation produced few if any extinctions until the last few thousand years when Timor lost most of its endemic murids. We present new records and dates for endemic rodents and introduced fauna from archaeological cave deposits in Timor-Leste that captures this human-mediated transition. We discuss the chronology of faunal introductions and losses at these sites, and compare the Timor records to other records in surrounding islands. We find no directly dated evidence for significant overlap between the introduction of exotics and extinction of murid endemics at ecological timescales, although determining true extinction and introduction ages will require direct dating and modelling of taxon occurrences, which may bring extinction and introduction closer together in time. Nevertheless, we suggest that, based on current data, the almost complete loss of Timor's endemic forests were the primary driving force in rodent extinctions.

ABSTRAK [Bahasa Indonesia]. Manusia telah memengaruhi keragaman biota pulau dalam beberapa milenia terakhir melalui pembabatan hutan yang luas dan introduksi spesies komensal dan hama, yang menyebabkan kepunahan hewan endemik pada beberapa pulau di seluruh dunia. Hal ini terutama terlihat di Timor, di mana lebih dari 40.000 tahun umur hunian manusia yang hanya menyebabkan sedikit atau hampir tidak ada kepunahan, sampai beberapa ribu tahun terakhir ketika Timor kehilangan sebagian besar tikus endemiknya. Kami menyajikan data dan penanggalan baru terkait tikus endemik dan fauna yang diintroduksi ke dalam pulau berdasarkan pada temuan dari gua arkeologi di Timor-Leste yang merekam perubahan yang disebabkan oleh manusia. Kami membahas kronologi introduksi fauna dan dampak negatif di lokasi-lokasi ini, dan membandingkan data di Timor dengan data lain di pulau-pulau sekitarnya. Kami

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tidak menemukan bukti penanggalan yang dapat dicocokkan korelasinya antara waktu pengenalan fauna eksotis dan kepunahan tikus endemik dalam skala waktu ekologis, walaupun menentukan usia kepunahan dan introduksi fauna yang sesungguhnya akan memerlukan penanggalan secara langsung dan pemodelan kemunculan taksonomi, yang mungkin dapat menunjukkan waktu kepunahan dan introduksi lebih dekat. Meskipun demikian, berdasarkan data yang ada saat ini, kami berpendapat bahwa hampir hilangnya hutan endemik di Timor merupakan faktor utama dalam kepunahan tikus.

Rezumu [Tetum language]. Emar fó ona influénsia ba biota insulár sira iha miléniu hirak liubá, liuhusi tesi ai no hamate floresta (ai-laran) iha fatin barak no liuhusi hatama espésie komensál sira no kuit (praga), hodi provoka estinsaun ba espésie endémika insulár iha mundu tomak. Prosesu ida ne'e ita bele haree liuliu iha Timor, iha ne'ebé, durante tinan rihun 40 resin ho prezensa emar nian, estinsaun sira la iha, ka iha uitoan de'it, maibé iha tinan rihun balun ikus ne'e, Timor lakon maioria husi ninia murídeu (balada maktohik ka roedór) endémiku sira. Ami aprezenta rejistu no data foun sira kona-ba roedór endémiku sira no kona-ba fauna ne'ebé hatama ona. Dadus sira ne'e ami rekolle iha depózitu arkeolójiku sira iha fatuk-kuak Timor-Leste nian, ne'ebé hatudu tranzisaun ida ne'e, ne'ebé akontese tanba prezensa emar nian. Ami diskute kronolojia kona-ba introdusaun (hatama) no perda (lakon) sira fauna nian iha fatin sira ne'e, no ami kompara rejistu sira husi Timor ho rejistu husi illa sira ne'ebé besik. Ami la hetan prova sira ho data ne'ebé bele hatudu duni sobrepozisaun (akontese iha tempu hanesan) maka'as entre introdusaun (hatama) espésie ezótika sira no estinsaun (lakon nafatin) husi murídeu endémiku sira iha eskala tempu ekolójika nian sira, maske definisaun ho loloos kona-ba idade estinsaun no introdusaun presiza datasaun (atribui data) direta no modelasaun konaba okorrénsia (mosu) *táxones* (grupu ka divizaun iha sistema biolójiku) nian, no definisaun ida ne'e bele hatudu katak estinsaun no introdusaun akontese iha tempu besik. Maske nune'e, ami sujere katak, bazeia ba dadus ne'ebé oras ne'e daudaun iha, lakon kuaze totál husi floresta (ai-laran) endémika Timor nian maka razaun prinsipál ba estinsaun roedór sira nian.

Introduction

Humans have had a disproportional impact on island biotas over the last few millennia (Ceballos & Ehrlich, 2018; Louys *et al*., 2021; Nogué *et al*., 2021), and the widespread introduction of commensals and pest species have been implicated in the extinction of island endemics around the world (Wood *et al*., 2017; Castilla-Beltrán *et al*., 2021). However, based on current archaeological and palaeontological records, humans and other hominins may have had more limited impacts on island ecosystems prior to the widespread adoption of agriculture, maritime trade, and domestication (Leppard, 2014; Rozzi *et al*., 2023; Louys *et al*., 2021; Wood *et al*., 2017), but this record is not well resolved for earlier periods of the Pleistocene. On the island of Timor, more than 40,000 years of human habitation produced very few extinctions (Hawkins *et al*., 2017; Louys *et al*., 2021); although an example of the latter includes a crane (*Grus* sp.) that likely became extinct in the Late Pleistocene (Meijer *et al*., 2019). It was only in the last few thousand years that Timor lost a disproportionate amount of its endemic biota (Aplin & Helgen, 2010).

Prehistoric excavations on Timor documenting some of these losses began in rockshelters near Nikiniki, southwest Timor (Fig. 1), by Alfred Bühler in 1935 (Sarasin, 1936) (no local names of the rockshelters are provided and they are referred to as "Abri" [rockshelter] I, II, and III). Bühler uncovered pottery fragments and domestic animals that were likely Holocene in age, as well as giant rat fragments from Abri II which were subsequently described by Schaub (1937) as the extinct species *Coryphomys buehleri.* In 1938, Willems of the Oudheidkundige recovered relatively recent archaeological material from Ulnam Cave on the slopes of Gunung Mutis located NW of Nikiniki (Oudheidkunig Verslag, 1939: 12). Two additional caves, Liang Leluat II and Liang Djenilu, excavated by Verhoeven in 1954, produced more Holocene material, including blades, scrapers, and worked points (Verhoeven, 1959).

Older deposits on Timor were first identified at Lene Hara cave in the eastern part of the island by the Portuguese anthropologist Antonio de Almeida in 1963. The site contained an 80 cm deep cultural assemblage with marine shells and stone artefacts found throughout the sequence, but with pottery fragments restricted to the surface (Fig. 1). A brief report on the stone artefacts described them as typologically "pre-Neolithic" (Almeida & Zybszweski, 1968). However, the site was never dated, and none of the fauna was properly described. In 1966, Glover visited the site and photographed Almeida's trench, which was still open (Glover, 1969). Glover made a small cutting on the edge of the trench, which confirmed Almeida's observation that pottery was absent below the surface (Glover, 1969).

Glover conducted additional excavations between 1966–1967 at Uai Bobo 1 and 2, Lie Siri, and Bui Ceri Uato in eastern Timor and found large amounts of prehistoric terrestrial faunal remains that, together, provided a baseline cultural sequence for the island (Glover, 1986) (Fig. 1). Glover (1986: appendix 2) presented new giant murids from his excavations, with initial identification of murid cranial remains made by Dan Witter, with further work and tabulation undertaken by Jack Mahoney, as described in Glover's (1986) Appendix 2. Mammalogist Guy Musser of the American Museum of Natural History subsequently agreed to take over the study of the fossil rodents, and he later passed on the material to Kristofer Helgen, who studied the collection with mammalogist and zooarchaeologist Kenneth P. Aplin (KPA). In addition to *Coryphomys,* three undescribed genera of giant rats were recognized in Glover's monograph. Pending formal description, these were designated "Large murid, genus A" (Glover, 1986: plate 49), "Large murid, genus B" (Glover, 1986: plate 50), and "Large murid, genus C" (Glover, 1986: plate 51). These are hereafter referred to as Genus A, B, and C, respectively. Genus C is absent from Bui Ceri Uato but otherwise all three genera are present in all of Glover's sites.

Following the annexation of Timor-Leste by Indonesia

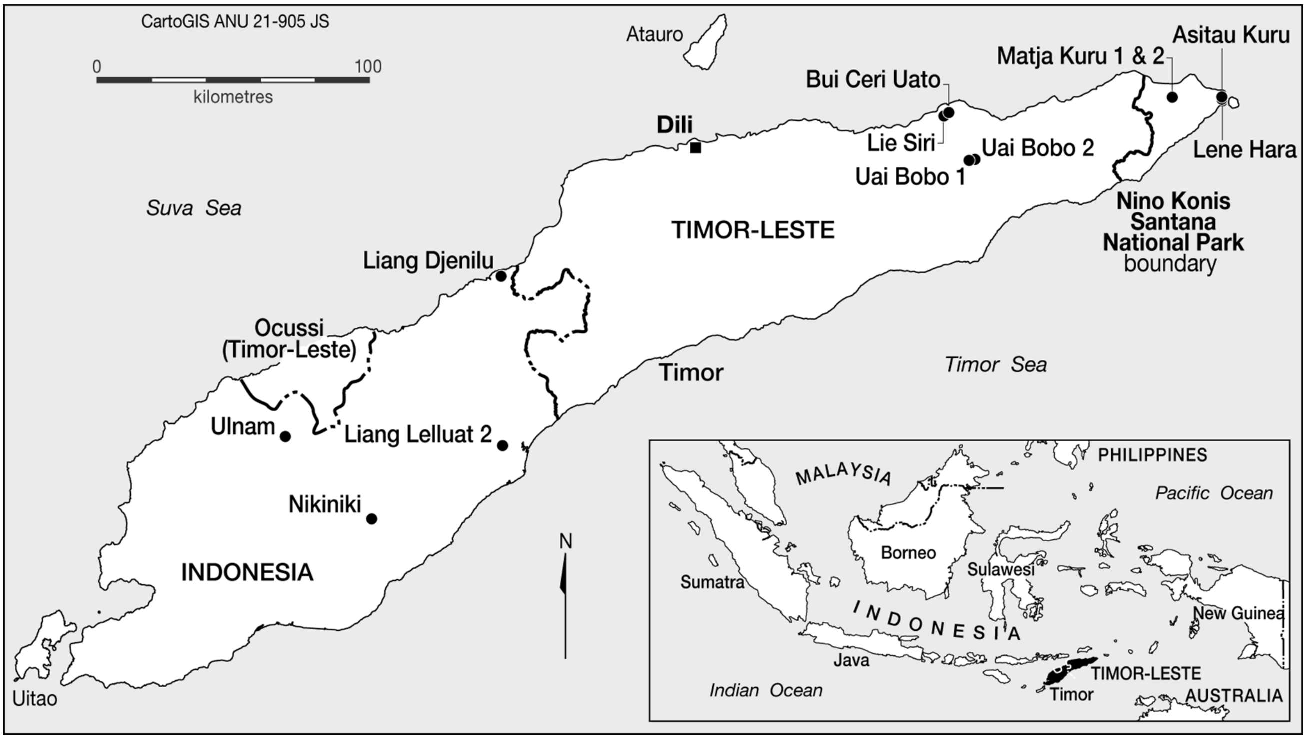

Figure 1. Map of Timor island showing the location of all the sites discussed in the text. Produced by CartoGIS Services, The Australian National University.

in 1975, archaeological research paused until The East Timor Archaeological Project (ETAP) was initiated in 2000 (O'Connor *et al*., 2002). The ETAP initiated new surveys to locate other prospective caves and middens in eastern Timor-Leste and opened a test excavation at Lene Hara (O'Connor *et al*., 2002). Renewed excavation at Lene Hara focused on a 1 × 1 m test pit situated adjacent to Almeida's trench near the southern entrance (Square A). This test pit at Lene Hara and the first excavations at Matja Kuru caves 1 and 2 and Jerimalai rockshelter (now known as Asitau Kuru) under ETAP revealed human occupation dating back at least 40,000 years, associated with a diverse marine and terrestrial zooarchaeological record (O'Connor, 2007; O'Connor *et al*., 2002; O'Connor *et al*., 2010; O'Connor & Aplin, 2007; Samper Carro *et al*., 2023; Shipton *et al*., 2019; Veth *et al*., 2005).

Ken Aplin played a significant role in analysing faunal material from Timor, including material from the caves described above (O'Connor & Aplin, 2007). For example, a thorough revision of *Coryphomys* based on faunal material from Matja Kuru caves 1 and 2 and Asitau Kuru, as well as specimens previously excavated by Glover (1986) from the sites mentioned above, revealed a new species of giant murine, *Coryphomys musseri* (Aplin & Helgen, 2010). Descriptions of additional giant rat genera and species first identified in Glover (1986) have been ongoing, with descriptions of Glover's Genus A, B, and C and their constituent species currently in preparation.

In addition to these findings, KPA also analysed a sample of the terrestrial faunal components of Lene Hara, Matja Kuru 1 and 2, and Asitau Kuru, tabulating numbers of identified specimens of mostly terrestrial fauna for each excavated unit (EU) of select excavation squares dating from the Late Pleistocene to the recent. These records span several important faunal events such as the introduction of domestics and commensals to the island, as well as the extinction of the giant rat fauna. Before a description of these results could be published, KPA passed away in 2019. Here, we present KPA's records (except for Matja Kuru 2), new date estimates for giant rat faunal material, and new chronological models for Glover's and ETAP sites. We use these to examine and describe late Quaternary introductions and extinctions on Timor and compare them to other faunal records in surrounding islands.

Methods

Geochronology

Three approaches to determining the first and last appearance dates (FAD and LAD, respectively) for faunal accumulations and geochronological events at Asitau Kuru, Bui Ceri Uato, Lena Hara, Lie Siri, Matja Kuru 1, Uai Bobo 1, and Uai Bobo 2 were applied. First, specimens representing either extinct or introduced taxa were directly dated using radiocarbon 14 (^{14}C) where possible (Zazzo & Saliège, 2011). Second, excavated units (EU) in which remains were found were dated using ^{14}C on marine shell and charcoal fragments, as well as optical luminescence (OSL) dating techniques on sediment samples (SI Tables) (Huntley *et al*., 1985). Where datable material has not been reported from the first or last occurrences in EUs, the EU age was estimated by bracketing the maximum and minimum ages from the EUs above and below the EU of interest for the excavation square in which it was found. All dates and/or lab codes considered in the bracketing are indicated in the *Supplementary Information* (SI) material. All direct ages are reported as unmodelled calibrated ages, while associated and bracketing ages are reported as modelled ages, following calibration. All radiocarbon ages discussed and listed here are calibrated ages unless otherwise indicated. For direct and associated ages based on the dating of a single sample, the median age of that sample was used for a single point estimate. Bracketing ages were based on the earliest extent of the lower date 95.4% probability range and the latest extent of the upper date range. For example, Matja Kuru 1 Square AA produced a date range of 4639–4135 cal BP and 5200–4514 cal BP at 95.4% probability for spits 3 and 5, respectively. Spit 4 is therefore bracketed between 5200 and 4135 cal BP (see Table 1 and SI).

The calibration of dates and the various modelled ages were obtained through the OxCal v4.4 online platform (Bronk Ramsey, 2009a). All dates obtained from terrestrial carbons (i.e., charcoal or bone) were calibrated with a mixed U(0,50) curve, combining the IntCal20 (Reimer *et al*., 2020) and SHCal20 (Hogg *et al*., 2020) curves, as recommended for dates from the Inter-Tropical Convergence Zone (Hogg *et al*., 2020; Marsh *et al*., 2018). All marine shell sample dates were calibrated with the Marine20 curve (Heaton *et al*., 2020). A chronostratigraphic model for each site analysed in this study was constructed using the multi-phase Bayesian modelling applications in OxCal v4.4. This produces a series of chronostratigraphic phases which we use to interpret the site formation history. For charcoal dates in these models, we applied the Charcoal Plus t-type Outlier Model with a prior outlier probability of 10%, which is specifically designed to account for the inbuilt age of charcoal (old wood effect), while also allowing for some stratigraphic movement in an archaeological context (Bronk Ramsey, 2009b; Dee & Bronk Ramsey, 2014). The General t-type Outlier Model with a prior outlier probability of 5% was used for all other dates (i.e., bone and shell), following commonly used modelling procedures for general archaeological dates (Bronk Ramsey, 2009b; Wood *et al*., 2016).

Each chronostratigraphic model, in addition to using all available dates, maximizes the addition of relative stratigraphic information (e.g., superpositioning, stratigraphic layers, vertical distance between samples). For Bui Ceri Uato, Lie Siri, and Uai Bobo 1 & 2, there was sufficient, comparable data to run depositional models which could interpolate "missing" ages across the stratigraphy based on age-depth correlation. In these depositional models we assume a Poisson (random) accumulation of sediment (Bronk Ramsey, 2008), calculated from the available age data by averaging the model over many values of k (Bronk Ramsey & Lee, 2013). The unit of depth used was in centimetres (cm) with a model interpolation rate set to a single date per ~5 cm for sites with reliable depth measurements (Lie Siri and Uai Bobo 2). For sites lacking reliable depths, such as Bui Ceri Uato and Uai Bobo 1, volume (m^3) was used instead with interpolation set to one date per ~5 cm^3.

For Asitau Kuru, Lene Hara, and Matja Kuru 1, neither depths nor volumes were readily available and/or informative to the model. For example, excavations at Lene Hara have produced a set of dates from different excavations distributed widely across the site which can be correlated to separate phases of occupation thanks to extensive efforts to interpret the site's stratigraphy and sedimentary history (see SI and references therein). Due to the site's complex depositional history (e.g., Squares A and B record phases of occupation which pre-date the entirety of the Square F sequence), individual depths associated with the different dates across the entire site do not lend themselves to a depositional model. For such sites we simply ran chronostratigraphic multi-phase models without the age-depth interpolation. Details on model specifics and results for each site is available in the *Supplementary Information* (SI).

For each extinct or introduced species considered, their last appearance ages for each site in which they are found are shown as a horizontal bar graph. A comparison of LADs and FADs was produced using the youngest and oldest representative sample, respectively, across all sites considered herein.

Faunal analysis

All ETAP sites were excavated in units (EU) ranging from 2 to 10 cm in depth, varying across sites, depending on squares and stratigraphic features. All excavated material was then sieved using fine-meshed sieves (≤ 2 mm). Bone samples were treated in weak acetic acid to dissolve adhered carbonate and sediment in instances where specimens were obscured. All archaeological samples were sorted by broad group (i.e., reptiles, birds, fish) and mammalian elements were separated by cranial versus post-cranial remains, or samples were left as "unidentified" bone. Mammal bones were further sorted according to rodents, bats, marsupials, larger mammals (e.g., introduced taxa), and humans where possible. All diagnostic elements were identified to generic- or species-level. Rodents were identified using maxillary and mandibular fragments as well as individual teeth. When species identification was not possible, rodent elements were assigned to a size category based on visual assessment by KPA. The identification of murid material from the ETAP sites was made based on reference material available and illustrated in Glover (1986). Counts of large murid NISPs supplemented the ETAP records from Glover's sites and were taken directly from his monograph (Glover, 1986: p. 79, 119, 156, 191). Reference to other fauna recovered by Glover is made in the discussion where appropriate.

Different taxonomic treatments of species and sites reflects KPA's evolving interests and understanding of the faunal diversity of Timor over time. As such, it is not clear if the lists are complete for non-rodent taxa. For example, the first sites that KPA examined (Lene Hara and Matja Kuru 1) do not list humans, reptiles, bats, or sharks but did record pottery, shrews, dogs, civets, deer, and macaques. Due to this inconsistency, fish, turtle, and other marine remains are not reported here (although they are known for some sites, e.g., Matja Kuru 1 and Lene Hara). All sites discussed here list the following genera: *Melomys, Komodomys, Rattus, Coryphomys, Phalanger, Sus*, as well as Glover's giant rat Genera A, B, and C. For Lene Hara and Matja Kuru 1, small and medium *Komodomys*-like specimens were initially separated; for this study, these distinctions are grouped together under the category *"Komodomys"*; this includes "*K.*" *timorensis*, reflecting KPA's unpublished revision of *Rattus timorensis*, which re-classifies this species in the genus *Komodomys* (see also Thomson *et al*., 2018), and a larger-bodied *Komodomys.* We treat *"K." timorensis* as an extant taxon, although its taxonomic and conservation status remain to be clarified. We treat the larger-bodied *Komodomys* as a separate, extinct species; however, confirmation of this status awaits full taxonomic analysis and description.

These records more accurately represent a presence rather than presence/absence as we cannot be certain that all material

Table 1. FADs and LADs of select taxa considered in this study, ages presented as cal BP. Full details of the calibration and age modelling of the samples are provided in the *Supplementary Information*.

Square	Taxon	Excavation unit	Date name	Date type	Modelling	Max	Median	Min
Matja Kuru 1 Square A								
MK1 A	Giant rat indet	Spit 1	End Phase 2	Associated	Modelled	1399	1175	508
MK1 A	Giant rat indet	4	Wk-25443	Direct	Unmodelled	1525	1453	1376
MK1 A	*Coryphomys*	2	Wk-25443 and End Phase 2	Bracket	Modelled	1531	—	508
MK1 A	Genus B	2	Wk-25443 and End Phase 2	Bracket	Modelled	1531	—	508
MK1 A	Genus C	4	Wk-25443	Associated	Modelled	1531	1453	1365
MK1 A	Genus A	12	NZA-17007	Associated	Modelled	3715	3539	3370
MK1 A	Large *Komodomys*	1	End Phase 2	Associated	Modelled	1399	1175	508
MK1 A	Small *Melomys*	7	Wk-25638	Associated	Modelled	3826	3661	3565
MK1 A	Large *Melomys*	8	S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	*Phalanger*	31	Wk-31509	Direct	Unmodelled	2916	2821	2763
MK1 A	*Paradoxurus*	13	Wk-31508	Direct	Unmodelled	2919	2817	2756
MK1 A	*Phalanger*	13	NZA-17007 and ANU-11632	Bracket	Modelled	3849	—	3370
MK1 A	*Paradoxurus*	13	NZA-17007 and ANU-11632	Bracket	Modelled	3849	—	3370
MK1 A	*Sus*	12	NZA-17007	Associated	Modelled	3715	3539	3370
MK1 A	*Rattus rattus*	11	NZA-17007 and S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	*Rattus exulans*	11	NZA-17007 and S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	*Canis*	11	NZA-17007 and S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
MK1 A	*Macaca*	8	S-ANU-55223, Wk-25635, NZA-16135	Bracket	Modelled	5310	—	1306
Matja Kuru 1 Square AA								
MK1 AA	Genus B	1	ANU-11834 and End Phase 2	Bracket	Modelled	4639	—	508
MK1 AA	Large *Komodomys*	1	ANU-11834 and End Phase 2	Bracket	Modelled	4639	—	508
MK1 AA	*Coryphomys*	6	ANU-11622 and ANU-11621	Bracket	Modelled	6053	—	4514
MK1 AA	Large *Melomys*	6	ANU-11622 and ANU-11621	Bracket	Modelled	6053	—	4514
MK1 AA	Genus A	7	ANU-11621	Associated	Modelled	6053	5841	5633
MK1 AA	Genus C	9	ANU-11620	Associated	Modelled	5330	5136	4880
MK1 AA	Small *Melomys*	4	ANU-11622 and ANU-11834	Bracket	Modelled	5200	—	4135
MK1 AA	*Rattus rattus*	12	ANU-11618 and ANU-11619	Bracket	Modelled	5609	—	4420
MK1 AA	*Paradoxurus*	10	ANU-11619 and ANU-11620	Bracket	Modelled	5330	—	4420
MK1 AA	*Phalanger*	8	ANU-11620 and ANU-11621	Bracket	Modelled	6053	—	4880
MK1 AA	*Macaca*	6	ANU-11621 and ANU-11622	Bracket	Modelled	6053	—	4514
MK1 AA	*Sus*	6	ANU-11621 and ANU-11622	Bracket	Modelled	6053	—	4514
MK1 AA	*Canis*	4	ANU-11622 and ANU-11834	Bracket	Modelled	5200	—	4135
Lene Hara Square A								
LH A	Giant rat indet.	4	ANU-11400 and OZF-213	Bracket	Modelled	3535	—	323
LH A	Genus A	9	OZF-213 and End Phase 6	Bracket	Modelled	3535	—	1582
LH A	*Phalanger*	3	Start Phase 7 and ANU-11400	Bracket	Modelled	1885	—	323
LH A	*Sus*	3	Start Phase 7 and ANU-11400	Bracket	Modelled	1885	—	323
LH A	*Canis*	5	OZF-212 and End Phase 6	Bracket	Modelled	4556	—	1582
Lene Hara Square D								
LH D	*Paradoxurus*	18	ANU-12059	Associated	Modelled	3815	3568	3356
LH D	*Rattus exulans*	18	ANU-12059	Associated	Modelled	3815	3568	3356
LH D	Large *Melomys*	5	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	*Rattus rattus*	13	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	*Phalanger*	11	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	*Sus*	11	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
LH D	Cervid	4	ANU-12059 and end Phase 7	Bracket	Modelled	3815	—	16
Lene Hara Square F								
LH F	Genus A	17	ANU-12042 and Transition Phase 5/6	Bracket	Modelled	4567	—	3498
LH F	Giant rat indet.	12	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	Large *Komodomys*	11	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	Large *Melomys*	7	Start Phase 7 and ANU-12140	Bracket	Modelled	1885	—	283
LH F	*Phalanger*	34	Wk-31507	Direct	Unmodelled	2490	2397	2341
LH F	*Phalanger*	14	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	*Canis*	15	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	*Rattus exulans*	15	ANU-12041, ANU-12029 and ANU-12136	Bracket	Modelled	3850	—	2552
LH F	*Sus*	6	Start Phase 7 and ANU-12140	Bracket	Modelled	1885	—	283
LH F	*Rattus rattus*	7	Start Phase 7 and ANU-12140	Bracket	Modelled	1885	—	283

Table 1. *Continued ...*

Table 1. *Continued*.

Square	Taxon	Excavation unit	Date name	Date type	Modelling	Max	Median	Min
Asitau Kuru Square B								
AK B	*Coryphomys*	19	Wk-18158 and Wk-18157	Bracket	Modelled	6092	—	4959
AK B	Genus A	3	Wk-19230 and Wk-19228	Bracket	Modelled	4838	—	13
AK B	Large *Melomys*	3	Wk-19230 and Wk-19228	Bracket	Modelled	4838	—	13
AK B	Large *Komodomys*	5	Wk-19230 and End Phase 3	Bracket	Modelled	4838	—	1258
AK B	Small *Melomys*	26	Wk-18159 and Wk-17832	Bracket	Modelled	6419	—	5590
AK B	*Sus*	3	Wk-19230 and Wk-19228	Bracket	Modelled	4838	—	13
AK B	*Phalanger*	7	Wk-19230 and End Phase 3	Bracket	Modelled	4838	—	1258
AK B	*Rattus exulans*	17	Wk-18158 and Wk-18157	Bracket	Modelled	6092	—	4959
Lie Siri								
Lie Siri	Giant rat indet.	Horizon VIb	ANU-172, ANU-173	Associated	Modelled	3957	—	2417
Lie Siri	Genus A	Horizon Vc	Horizon Vc	Associated	Modelled	7717	7253	6627
Lie Siri	*Coryphomys*	Horizon Va	Horizon Va	Associated	Modelled	7976	7707	7452
Lie Siri	Genus B	Horizon III	Horizon III	Associated	Modelled	8338	8027	7702
Lie Siri	Genus C	Horizon III	Horizon III	Associated	Modelled	8338	8027	7702
Bui Ceri Uato								
Bui Ceri Uato	Giant rat indet.	Horizon VIII	ANU-11741	Associated	Modelled	7184	6888	6592
Bui Ceri Uato	Genus A	Horizon IV	ANU-11878	Associated	Modelled	11691	11105	10686
Bui Ceri Uato	*Coryphomys*	Horizon II	ANU-11877	Associated	Modelled	12980	12734	12505
Bui Ceri Uato	Genus B	Horizon II	ANU-11877	Associated	Modelled	12980	12734	12505
Uai Bobo 1								
Uai Bobo 1	Genus B	Horizon V	Horizon V	Associated	Modelled	1290	765	351
Uai Bobo 1	*Coryphomys*	Horizon IV	Horizon IVa and Horizon IVb	Associated	Modelled	2000	—	1157
Uai Bobo 1	Genus A	Horizon IV	Horizon IVa and Horizon IVb	Associated	Modelled	2000	—	1157
Uai Bobo 1	Genus C	Horizon IV	Horizon IVa and Horizon IVb	Associated	Modelled	2000	—	1157
Uai Bobo 2								
Uai Bobo 2	Genus C	Horizon X	Wk-25439	Associated	Modelled	1697	1573	1521
Uai Bobo 2	*Coryphomys*	Horizon IX	ANU-239, Wk-25631, Wk-25630	Associated	Modelled	4235	—	1560
Uai Bobo 2	Genus A	Horizon IX	ANU-239, Wk-25631, Wk-25630	Associated	Modelled	4235	—	1560
Uai Bobo 2	Genus B	Horizon IX	ANU-239, Wk-25631, Wk-25630	Associated	Modelled	4235	—	1560

was identified prior to KPA's passing. As such, reports list the minimum number of identified specimens (mNISP) rather than standard NISP counts. While the nature of the data precludes direct quantitative inter-site comparisons because we may not be comparing like-with-like, they do allow for qualitative comparisons between excavation units, squares, and sites. For Lene Hara Square A, the data was supplemented by a more detailed, previously unpublished description of the remains by KPA, which has been updated where necessary. Unfortunately, no similar descriptors by KPA of the other sites he examined is known to us.

Results

All calibrations, modelled ages, and age-depth models for the sites are presented in the SI and illustrated in Figs 2–8. A summary of the LADs and FADs are presented in Table 1 and summarized in Figs 9–11. Below, we discuss the last appearances of extinct taxa and the first appearances of the introduced taxa. There are numerous gaps in taxon presence throughout each excavation square sequence (SI). We do not consider these as genuine absences but rather, given the highly limited spatial scale sampled by each excavation combined with known taphonomic and depositional biases throughout the cave sequences (O'Connor *et al*., 2017; Louys *et al*., 2017; Samper Carro *et al*., 2023), we treat the presence of each extinct taxon as continuous on the island until at least their last dated record. Extant species are treated as continuous through to today. Readers are directed to the SI for the full range of occurrences and associated dates.

Matja Kuru 1 Square A (Fig. 2)

The Matja Kuru 1 chronostratigraphic model revealed only one depositional phase present in Square A from approximately 7479–1175 cal BP (median ages, see SI). The distribution of dates within the square is not homogenous, with numerous instances of reversals and/or mixing. For example, marine shell, giant rat bone, and buttonquail (*Turnix* sp.) bone, all sourced from spit 8, produced median dates of 5133 (NZA-16135), 4040 (Wk-25635), and 1358 (S-ANU-55223) cal BP, respectively. Unidentified giant rat material is found from spit 1 down (i.e., the end of Phase 2 modelled at *ca*. 1175 cal BP) with the youngest direct dates between 1525 and 1376 cal BP (Wk-25443, 95.4% probability range) from spit 4. At the generic level, *Coryphomys* and Genus B are both recorded from spit 2 and Genus C from spit 4 down. Genus A is last reported from spit 12 from which a marine shell provides an associated date between 3715 and 3370 cal BP (NZA-17007, 95.4% probability range). Large *Komodomys* is found from spit 1 down (i.e., up until *ca*. 1175 cal BP, end of Phase 2). Small *Melomys* is last recovered in spit 7. This spit preserves material which has produced a modelled date of 3661 cal BP (Wk-25638, median), while the Large *Melomys* is recovered from spit 8 (which has produced

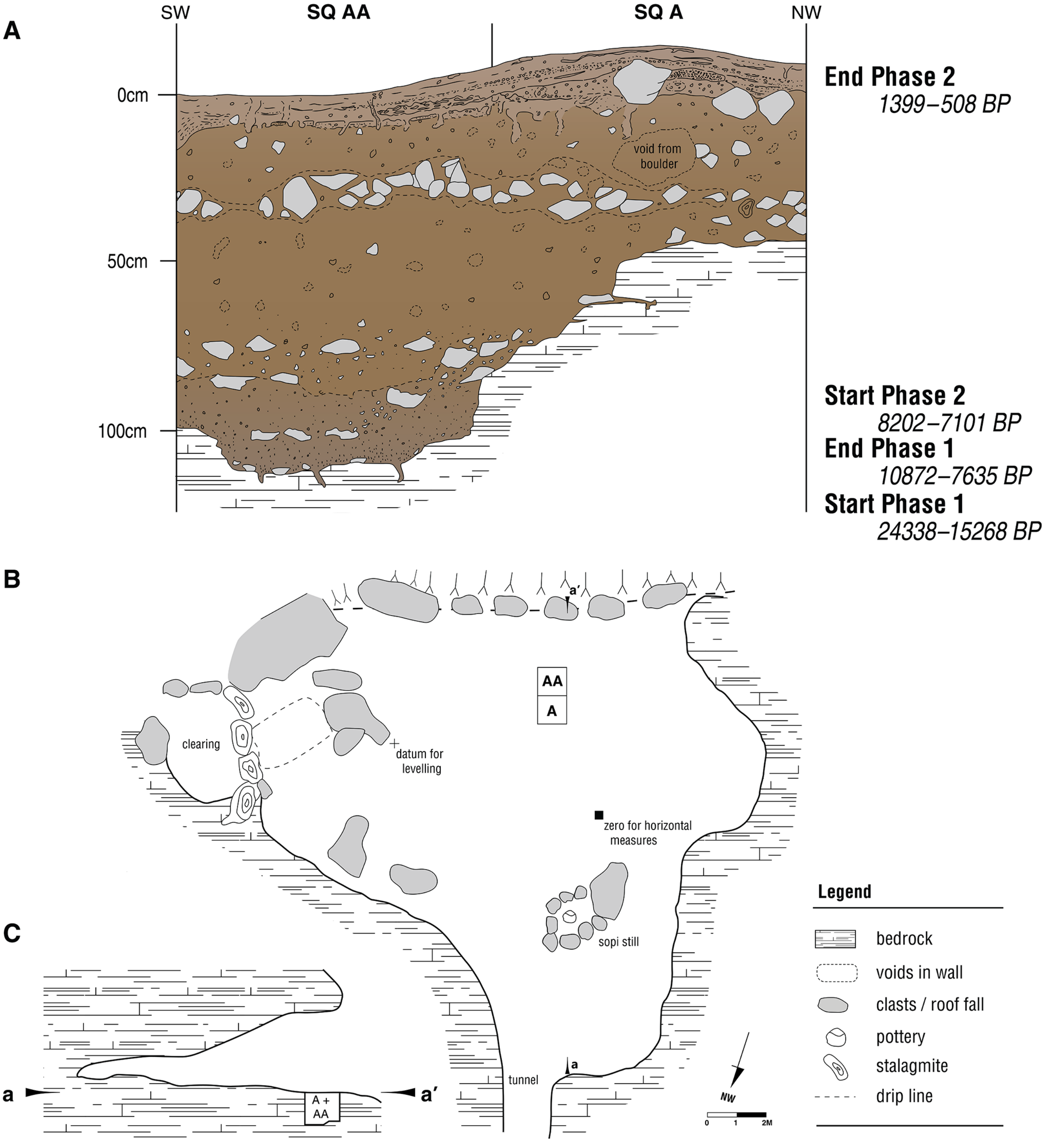

Figure 2. Matja Kuru 1. (*A*) stratigraphic section of Squares A and AA showing the start and end of each chronostratigraphic phase (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details); (*B*) cave site in plan view; (*C*) cave site in section view.

a median date: 4039 cal BP, Wk-25635). Shrews (*Crocidura* spp.) are first reported from spit 11.

In terms of introduced species, cuscus (*Phalanger orientalis*) and civet (*Paradoxurus hermaphroditus*) are first recorded from spit 13, which is bracketed by modelled ages of 3849 and 3370 cal BP (Table 1). There is also a direct date from a *Phalanger* specimen from spit 31, at 2821 cal BP (Wk-31509, median) which indicates it originated from higher in the stratigraphic sequence, and a civet fragment from spit 13 at 2817 cal BP (Wk-31508, median). Pigs (*Sus* sp.) are first recorded from spit 12 which has a median age of 3539 cal BP (NZA-17007), followed by *R. exulans* (Pacific rat), *R. rattus* (Black rat), and dog (*Canis familiaris*) from spit 11, an undated spit but likely roughly coeval with spit 12 based on stratigraphy. Lastly, a single macaque specimen (*Macaca fascicularis*) is recorded from spit 8, which remains ambiguously dated to sometime in the mid to late Holocene.

Matja Kuru 1 Square AA (Fig. 2)

Two depositional phases were identified in Square AA: Phase 1, a terminal Pleistocene sequence modelled as starting around 17,508 cal BP and ending around 9,501 cal BP (median, spits 21–30; see SI); and Phase 2, a Holocene sequence modelled roughly between 7479 cal BP and 1175 cal BP, and also present in Square A (Fig. 2). Genus B and large *Komodomys* are found up into spit 1. Dates obtained from the uppermost stratigraphy derive from spit 3 with an age estimate between 4639 cal BP (ANU-11834; maximum extent of the 95.4% probability range) and 508 cal BP (the end of Phase 2; minimum). *Coryphomys* and the Large *Melomys* are found in varying abundances until spit 6, which is estimated between 6053 cal BP (ANU-11621; maximum, spit 7) and 4514 cal BP (ANU-11622; minimum, spit 5). Genus A is found in varying abundances beginning in spit 25 until spit 7, from which an associated marine shell has produced a median date of 5841 cal BP (ANU-11621). Genus C is sparsely found beginning in spits 20 and 19, as well as spits 13 and 9, from which an associated marine shell has produced a LAD median date of 5136 cal BP (ANU-11620). Finally, the Small *Melomys* is found starting in spit 26, as well as in spits 24-21, 18, 16, 15, 9, and finally, spit 4, which is bracketed by dates of 5200 and 4135 cal BP (Table 1). Shrews (*Crocidura* spp.) are reported from Phase 1 in the terminal Pleistocene.

For introduced species, *R. rattus* is first reported from spit 12 with an estimated age between 5,609 and 4,420 cal BP, but becomes more abundant in spits 8 and 6–4 (Table 1). No specimens identified as *R. exulans* were reported from this square. Civets are reported from spits 10, 8, 5, and 1 and *Phalanger* is found beginning in spits 8 to 5, both of which are bracketed by reversed dates at *ca*. 5000 cal BP. Macaque and pig both first appear in spit 6 between 6053 and 4514 cal BP (Table 1). Finally, a single dog fragment is reported from spit 4 and bracketed between 5200 and 4135 cal BP (Table 1).

Notably, there are significant differences (Kruskal-Wallis test; $H = 15.03$, $p < 0.001$) in the proportion of large *Komodomys* to "*Komodomys" timorensis* in Phase 2 (average 75% of all *Komodomys* across spits) relative to Phase 1 (average 33% of all *Komodomys* across spits).

Lene Hara Square A (Fig. 3F)

In addition to the minimum NISPs, additional previously unpublished observations by KPA from this square are provided below. The stratigraphy of this square shows evidence of disturbance, as discussed in detail in O'Connor *et al*. (2010), and evident from our age modelling for this site (see SI). As KPA's references to the original stratigraphy are no longer valid, the notes have been provided below with updates based on our current understanding of the stratigraphy and the age of this square.

> *The vertebrate fauna comprises marine turtle and fish, freshwater turtle, large and small murid rodents, bats, phalanger, snakes (boids* [i.e., pythons, now classified as Pythonidae] *and colubroids), large and small lizards (including monitors,* Varanus *sp.), and the domestic pig and dog. An 'unidentified' category consists predominantly of large chunks of finely cancellous bone that almost certainly represents fragments of marine turtle limb bones and carapace. One human incisor was recovered from spit 17. A small quantity of marine crab exoskeleton was also recovered in spit 7 and above.*
>
> *Marine turtle occurs at all levels. The importance of this group is most likely better estimated by examining the 'unidentified' category in terms of bone weight—it makes up 80–90% of bone by weight from the lower levels, but from 32–62% in the more recent levels. The marine turtle is too fragmentary for identification to species but based on size and texture it most likely represents one or more species of* Chelonia *or* Natator. *Crab remains were found only in Spit 7 and above. Fish are present throughout the sequence but are nowhere abundant. Bones of terrestrial reptiles were recovered at all levels. Most of the snake remains represent moderately large pythons (two large-bodied species of the genus* Python *still occur on Timor) but some smaller vertebrae represent colubroid (venomous) snakes. A moderately large* Varanus *is represented in spits 6–8 only. Although this material clearly does not represent* V. komodoensis*, it is from a much larger bodied taxon than the only terrestrial monitor found on Timor today (*V. timorensis*). It may represent* V. salvator*, a large coastal dwelling monitor that occurs throughout eastern Indonesia. A freshwater chelid turtle is represented in Spit 1 by a carapace fragment.*
>
> *A few bones of giant rats were recovered. Lene Hara Square A produced only postcranial fragments of these animals, one in each of Spits 4, 8, 9, 15, and 17. A fragmentary femur in Spit 9 is enormous and most likely represents Genus A, the largest of the Timor giant murids.*
>
> *None of the Lene Hara remains represent* R. exulans*, which is distinguishable from the native species by its small size and distinctive dental morphology. Two cranial fragments with teeth from Spits 3 and 10 represent an un-named endemic species that is distantly related to* Rattus *and was about the size of a European Black rat* [these do not appear to be listed in the minimum number of identified specimens but may refer to "*Komodomys*" *timorensis* or large *Komodomys*].
>
> *Several species of insectivorous bat are represented, and one larger bat that is represented only by post-cranial elements. The smaller bats and rodents might represent prey remains of a non-human predator such as a cave-roosting owl.*
>
> *A phalanger is represented by a tibial fragment in Spit 3. Small fragments of pig and dog teeth were found in the upper levels of Test Pit A. Pig is identified from two small fragments of incisors in Spit 3 but a few of the larger, unidentified bone fragments from the upper spits might also represent this species. Dog is represented by a fragmentary right P4 from Spit 5. The P4 is a close match in size with modern Australian dingo specimens from northern Australia.* —Ken Aplin.

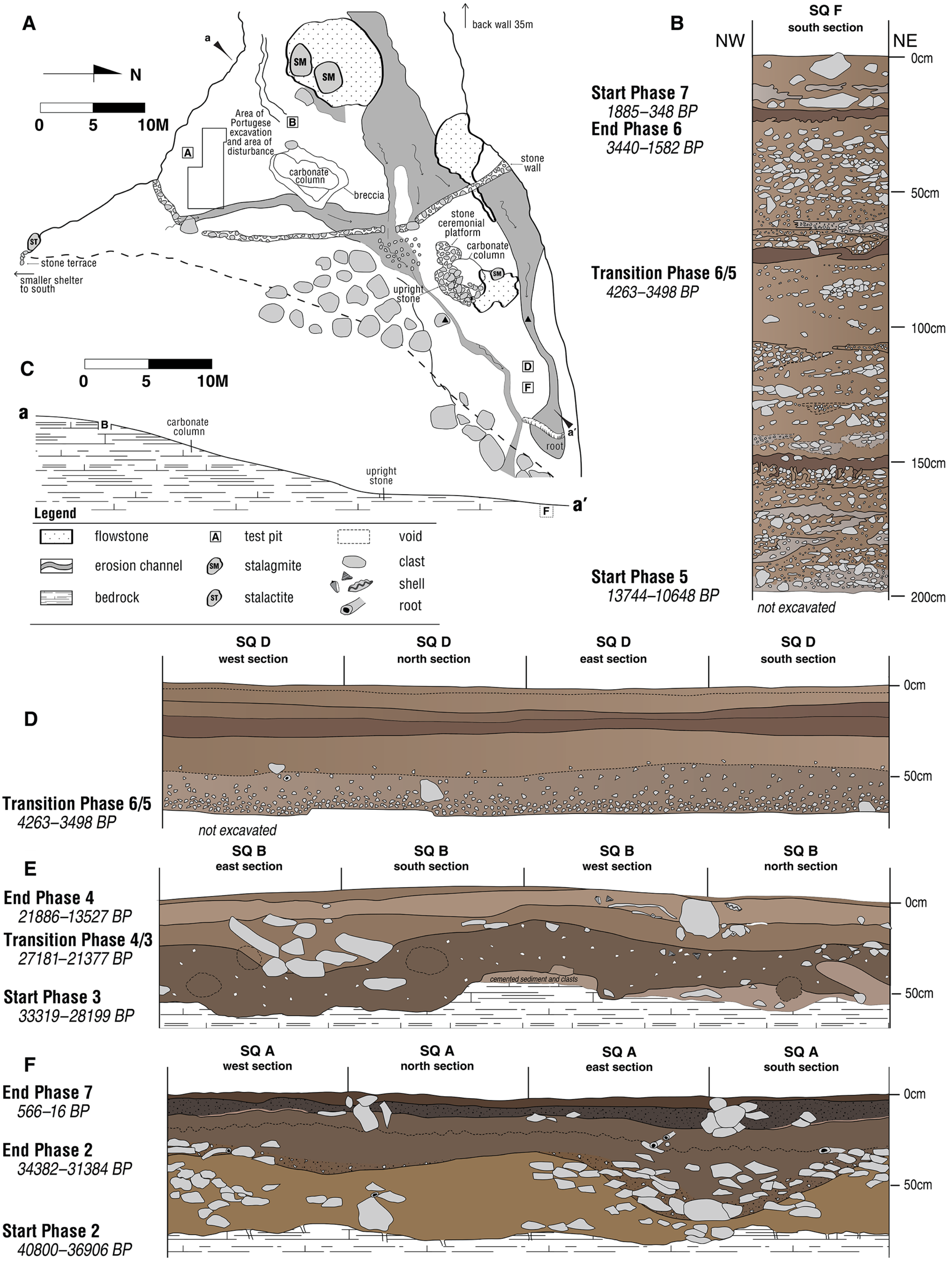

Figure 3. Lene Hara. (*A*) cave site in plan view; (*B*) stratigraphic section of Square F showing the start to end of chronostratigraphic phases 5 to 6 and start of 7; (*C*) transect through the site showing changes in elevation; (*D*) stratigraphic section of Square D showing transition chronostratigraphic phase 6/5; (*E*) stratigraphic section of Square B showing start to end of chronostratigraphic phases 3 and 4; (*F*) stratigraphic section of Square A showing start to end of chronostratigraphic phase 2 and end of phase 7 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details).

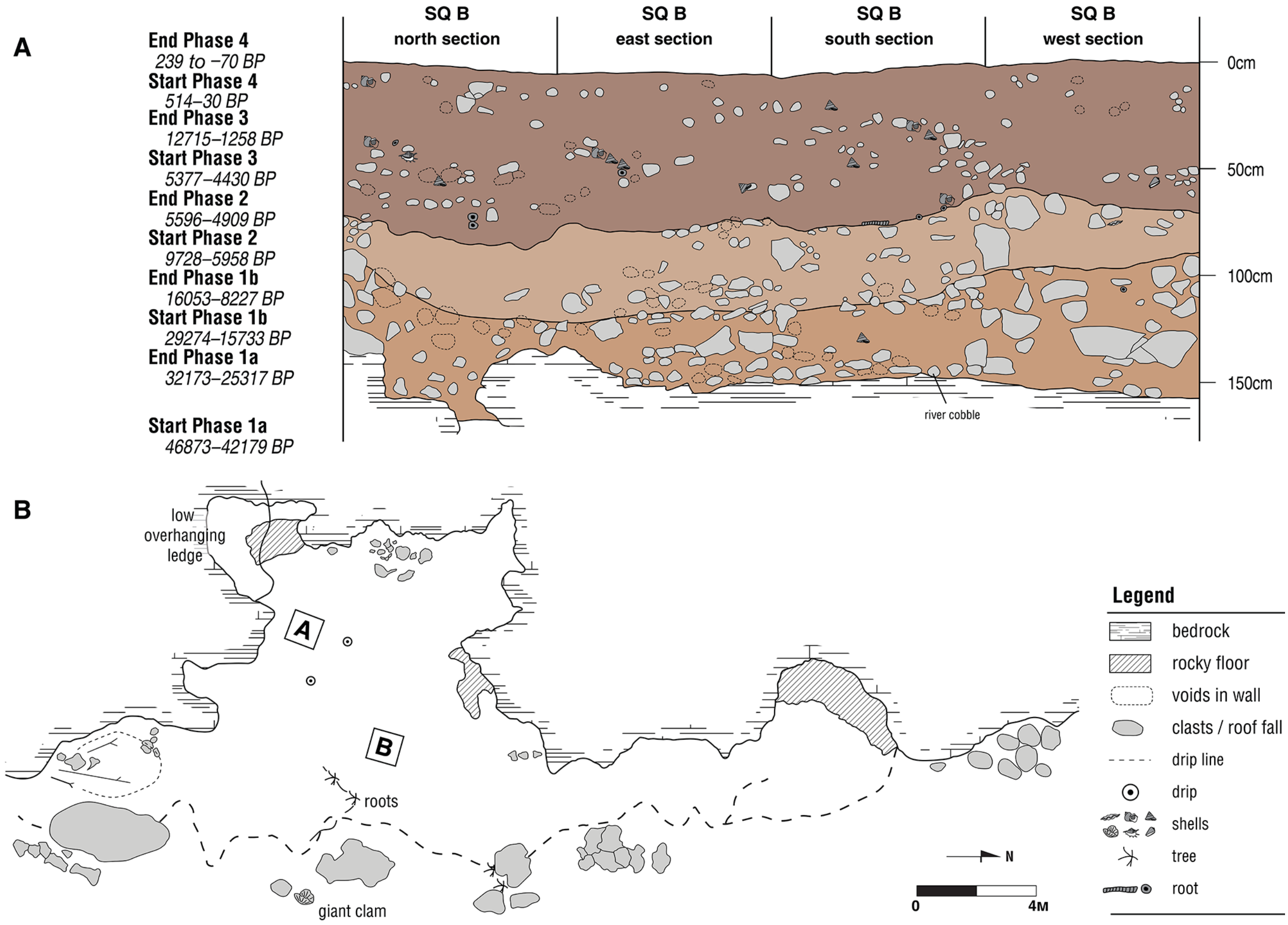

Figure 4. Asitau Kuru. (*A*) stratigraphic section of Square B showing the start and end of each chronostratigraphic phase (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details); (*B*) cave site in plan view.

These descriptions largely correspond to the minimum NISP, although a few points require further explanation. First, the dog remains from spit 17 likely represent disturbed material displaced from the upper spits, as marine shell associated with spit 18 is dated to 34,613 cal BP (ANU-11401), older than any domestic dog remains globally (Ovodov *et al*., 2011). Second, if the unnamed rodent identified in these notes is in fact the large *Komodomys,* there is a transcription error (the notes indicate remains from spits 3 and 10, the NISPs list these as spits 5 and 10). Third, the first appearance of phalanger and pig likely date to sometime between 1885 and 323 cal BP (Start Phase 7 and ANU-11400, respectively—see SI), and are roughly coincident (within the context of this square) with the last appearance of giant rats and the large *Komodomys*.

Lene Hara Square B (Fig. 3E)

This square has only produced Pleistocene dates, with faunal material recorded in KPA's notes for spits 6–17. As such, it does not preserve the last appearance of any extinct rodent nor the first appearance of most commensals. However, there is a record of *R. rattus* from spit 7, material of which is likely older than 21,361 BP (ANU-12141). This is not likely to be an *in situ* recovery, but probably represents recently introduced surficial material. The square also preserves Genus B, "*Komodomys" timorensis*, and Large and Small *Melomys*.

Lene Hara Square D (Fig. 3D)

Minimum NISPs are available for spits 1–18, dated material is available for spits 18 and 20. All of the faunal material from this square was deposited in Phase 6 (between 3834 and 2316 cal BP) or Phase 7 (between 740 and 339 cal BP) (see SI for full model). No *Komodomys* material is recorded from this square. Large *Melomys* is recovered up until spit 5. The deepest records of introduced species are for civet and Pacific rat, from spit 18 which has also produced marine shell dated to 3568 cal BP (ANU-12059). Black rat is recovered from spit 13, phalanger and pig from spit 11, and deer from spit 4. Shrew is recovered from spit 10.

Lene Hara Square F (Fig. 3B)

Square F is a well stratified excavation with three major phases recognized from the dated material. Phase 5 comprises spits 45–18 and spans approximately 11,479–3834 cal BP, Phase 6 consists of spits 17–8 and dates to approximately 3834–2316 cal BP, and Phase 7, spits 7–1, spans approximately 740–339 cal BP (SI).

Only Genus A and unidentified giant rat are recorded in Square F. The youngest record of Genus A is from spit 17 in Phase 6, between 4567 and 3498 cal BP (Table 1). Unidentified giant rat material is found up until spit 12, likely between 3850 and 2552 cal BP (Table 1). Large *Komodomys*

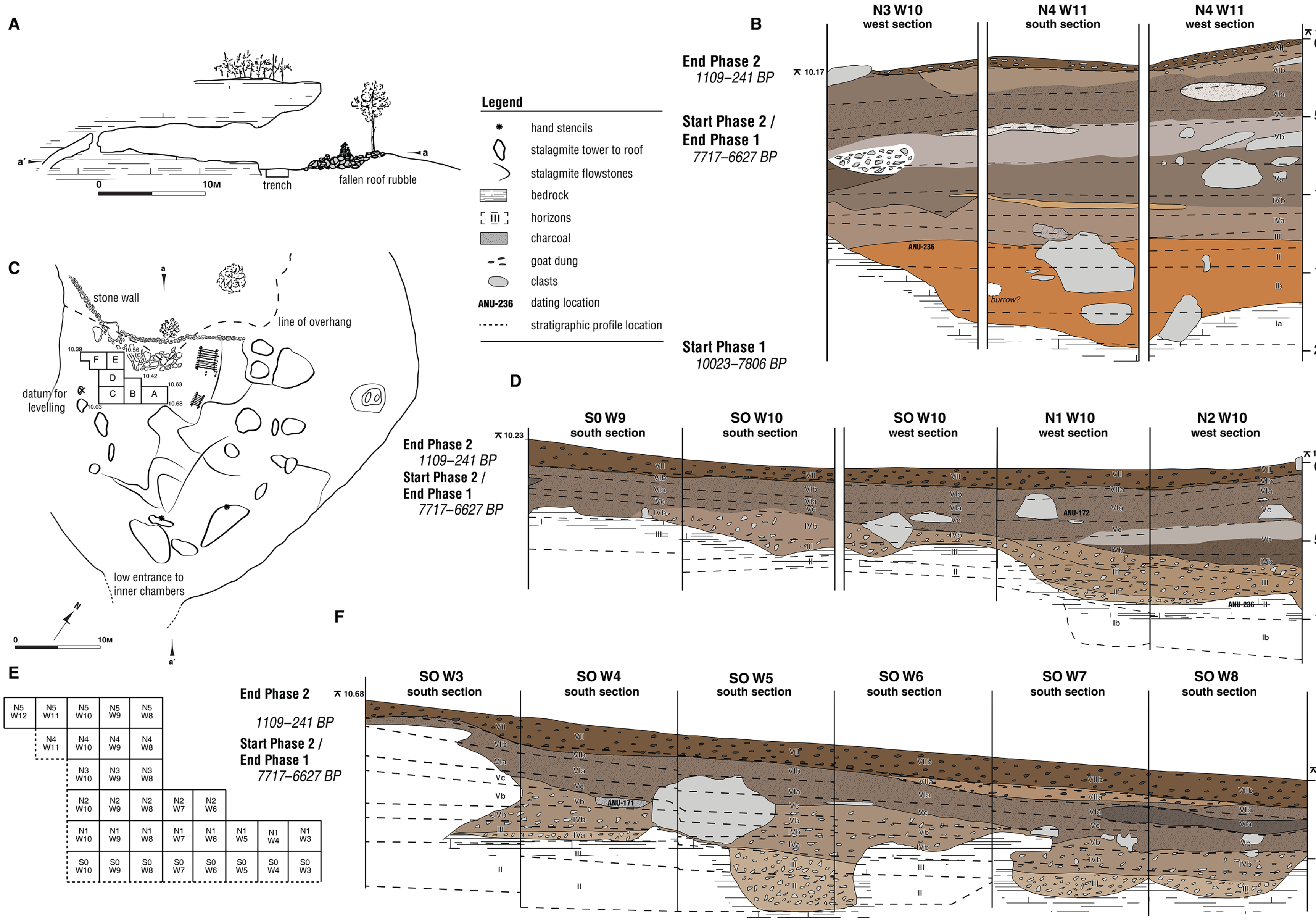

Figure 5. Lie Siri. (*A*) cave site in section view; (*B*) stratigraphic section of Area F showing start and end of phases 1 and 2; (*C*) cave site in plan view; (*D*) stratigraphic section of south section of Areas A–C showing end of phases 1 and 2 and start of phase 2; (*E*) detail of excavation squares; (*F*) stratigraphic section of south section of Areas A–C showing end of phases 1 and 2 and start of phase 2, continued (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).

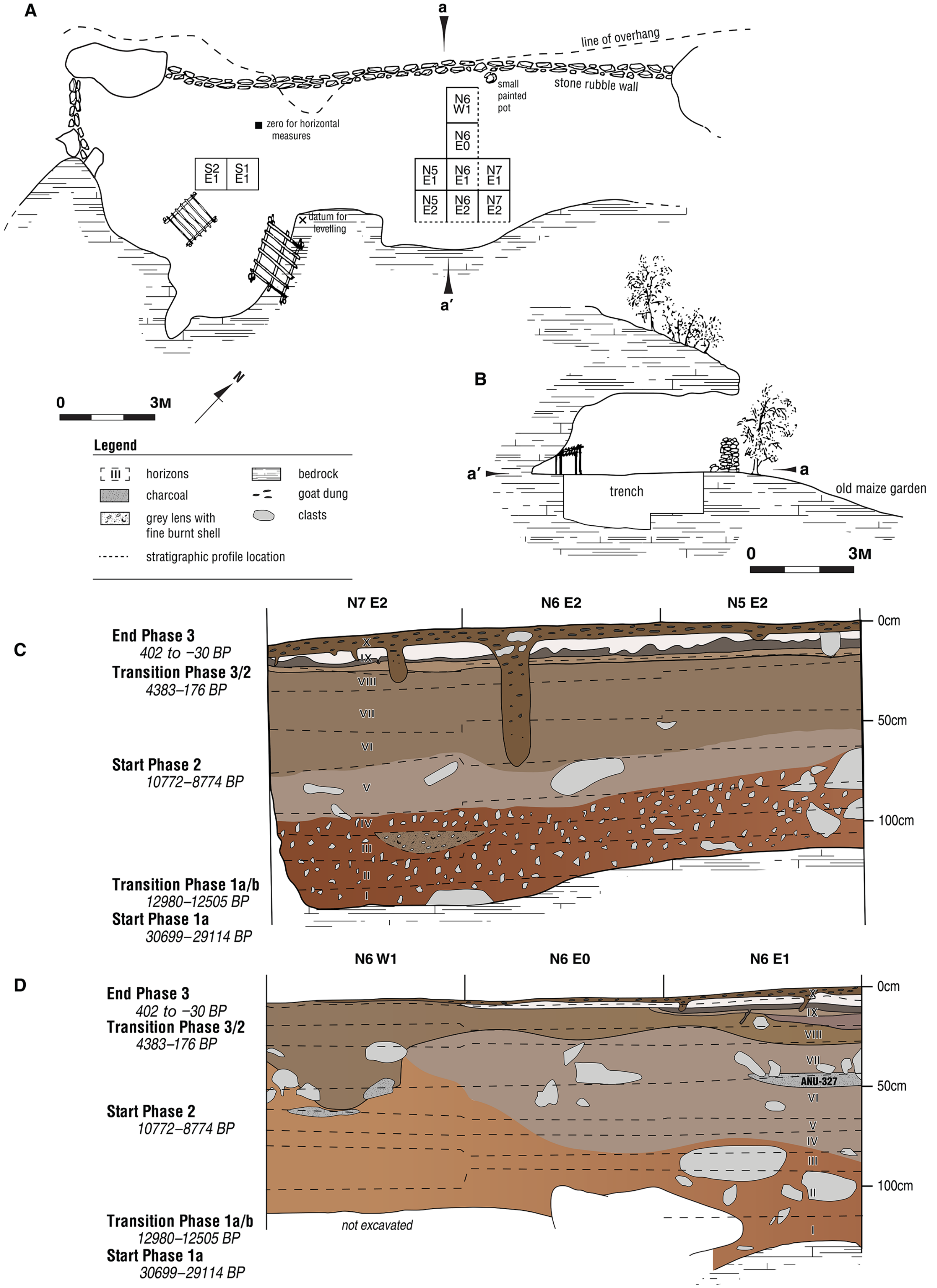

Figure 6. Bui Ceri Uato. (*A*) cave site in plan view; (*B*) cave site in section view; (*C*) stratigraphic section of south section of Squares N7E2, N6E2, N5E2 showing phases 1a to 3; (*D*) stratigraphic section of east section of Squares N6W1, N6E0, N6E1 showing phases 1a to 3 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).

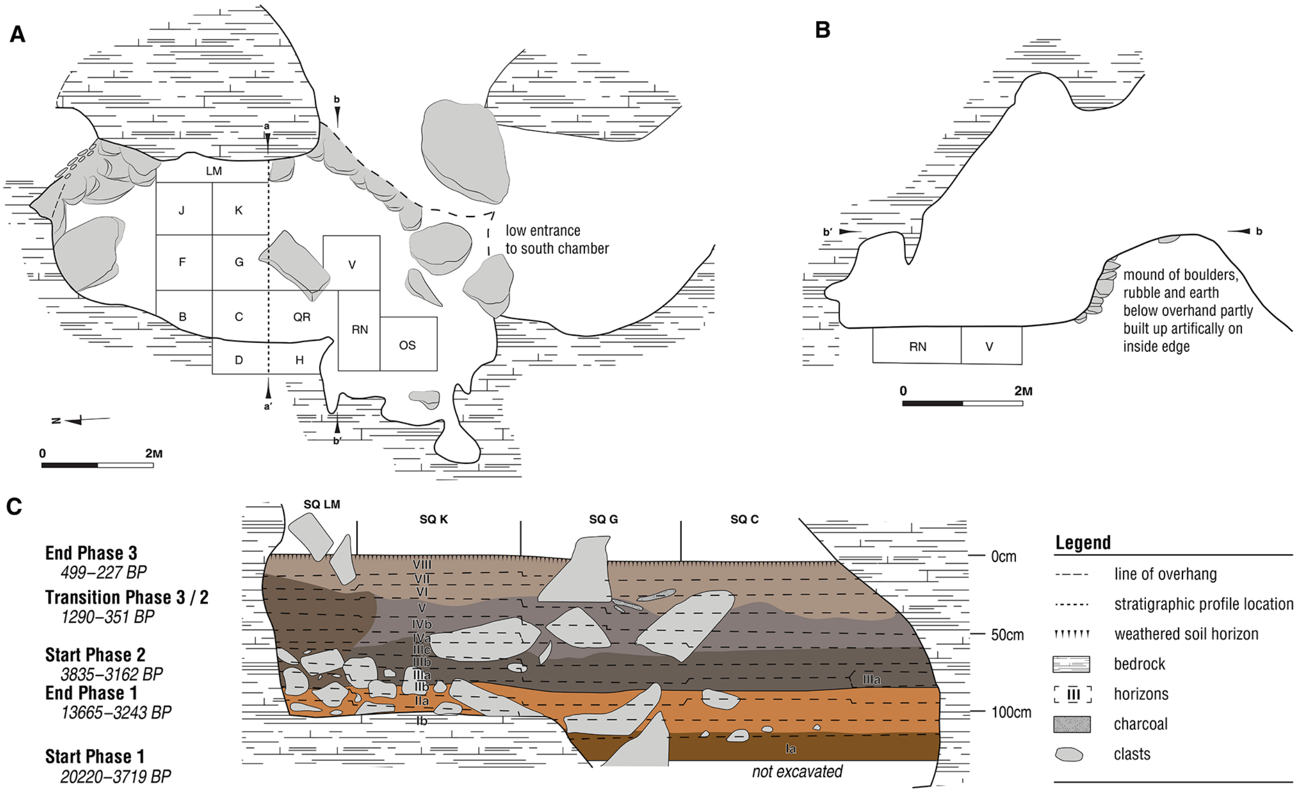

Figure 7. Uai Bobo 1. (*A*) cave site in plan view; (*B*) cave site in section view; (*C*) stratigraphic section of Squares LM, K, G, C showing phases 1 to 3 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).

is reported to a similar age, up to spit 11; "*Komodomys*" *timorensis* however is only recorded up to spit 22 in Phase 5. There is no Small *Melomys* but the Large *Melomys* is reported from spit 7, near the bottom of Phase 7 and thus between 1885 and 283 cal BP (Table 1). *Crocidura* is found to spit 6 and thus Phase 7.

The lowest occurrence of introduced species is likely the cuscus specimen from spit 34 in Phase 5; however, direct dates on this specimen indicate it is derived from younger sediments as it dates to 2397 cal BP (Wk-31507). Pacific and Black rat specimens from this spit are similarly considered introduced from younger deposits. Cuscus also occurs in spit 14, which may be older (possibly between 3850 and 2552 cal BP). A similar age range can be attributed to dog and Pacific rat material recorded in spit 15. Pig is first recorded in spit 6, i.e., between 1885 and 283 cal BP (Table 1). Finally, the Black rat is first recorded from spit 7, with a similar age range as the aforementioned date.

Asitau Kuru Square B (Fig. 4)

While the fauna from this site is sorted according to spits, the dates have been documented relative to depth and stratigraphic layer. Nevertheless, correlations between occurrences and dates can be made based on the depths recorded for spits. There are four phases recorded in this square. Phase 1 likely starts approximately 44,052 cal BP and continues until 14,223 cal BP. There is a hiatus, with Phase 2 starting about 6548 cal BP and continuing until 5301 cal BP. Phase 3 begins *ca*. 4803 cal BP through to 2308 cal BP. Finally, Phase 4 records the very recent past, 250 cal BP until present (*ca*. 53 cal BP) (SI).

The only giant rat records are of *Coryphomys* and Genus A. *Coryphomys* is recovered up to spit 19, which is approximately 45 cm depth, which is likely between 6092 and 4959 cal BP (Table 1). Genus A is recovered from spit 3 with an associated date of 122 cal BP. However, an outlier charcoal date from spit 4 dating to 5080 cal BP (Wk-19229) indicates disturbance in the Phase 4 stratigraphy, reflected in our suggested broad bracketing ages of 4838 cal BP (Wk-19230, spit 9) to 13 cal BP (Wk-19228, spit 3). Two additional taxa, *Komodomys timorensis* and the Large *Melomys*, also make their final appearance in spit 3. The large *Komodomys* is found up to spit 5 (Phase 3), and for similar reasons above is considered to date between 4838–1258 cal BP. Finally, the Small *Melomys* is recorded only in spit 26 which is around 58 cm below the surface; associated marine shells from these depths have been dated to between 6419 and 5590 cal BP (Table 1).

For introduced species, pig is only found in spit 3, so its age is bracketed as above. Cuscus is found as low as spit 7 (Phase 3), approximately 12–13 cm depth, and estimated at between 4838 and 1258 cal BP (Table 1). *Rattus exulans* is recorded from only spit 17, approximately 39 cm depth. Dated material from around this depth shows inverted, but roughly coeval ages, modelled at between 6092 and 4959 cal BP (Table 1).

Lie Siri (Fig. 5)

The stratigraphically highest unidentified giant rat material at this site is found in Glover's horizon VIb, which our modelling suggests is as young as 3957–2417 cal BP (Table

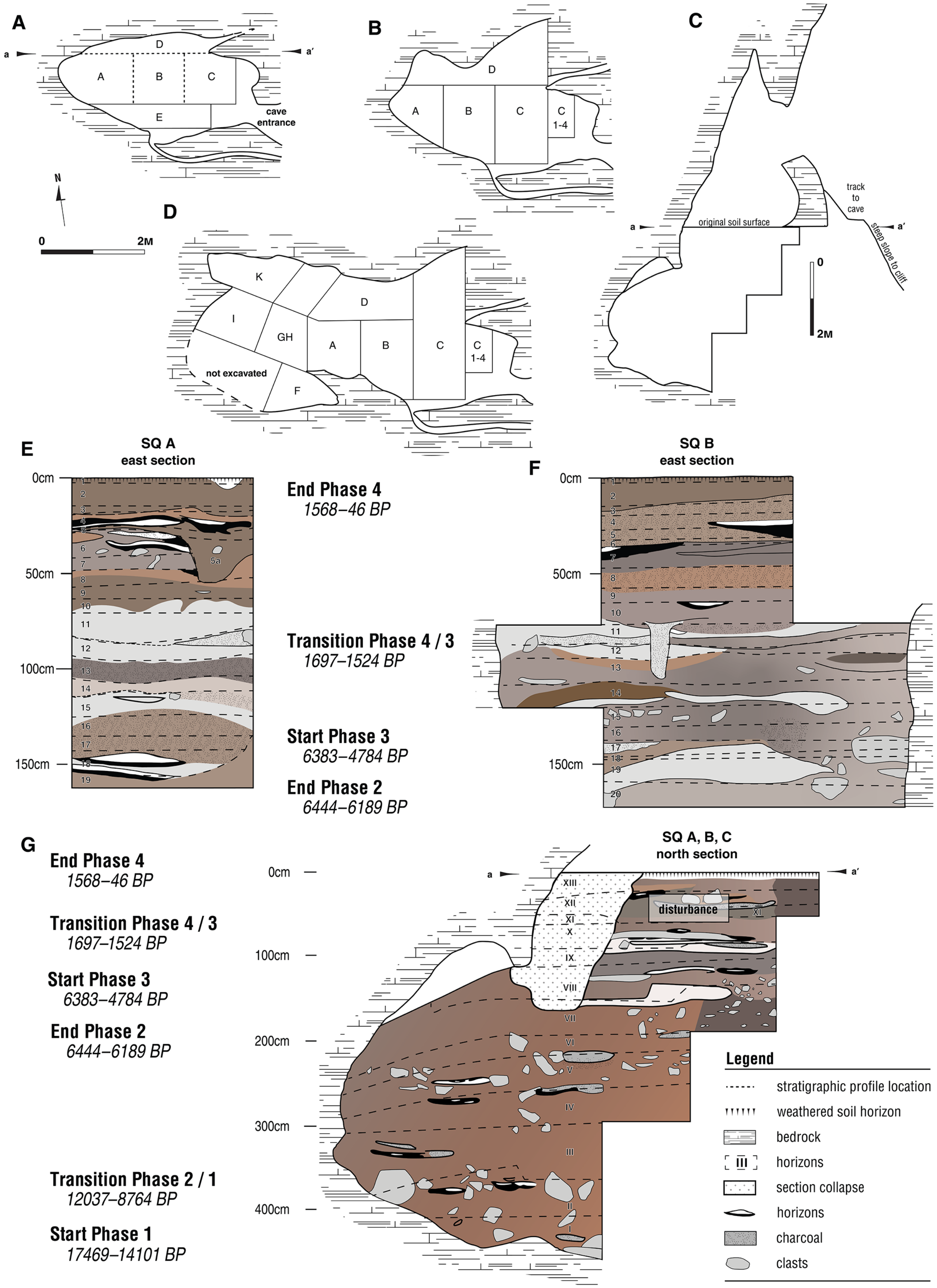

Figure 8. Uai Bobo 2. (*A*) cave site in plan view at surface; (*B*) cave site in plan view at 1.7m below surface; (*C*) cave site in section view; (*D*) cave site in plan view at 4.2m depth; (*E, F*) stratigraphic section of east section at Squares A and B showing end of phase 2 to end of phase 4; (*G*) stratigraphic section of north section at Squares A, B and C showing end of phases 1 to 4 (all phases represent modelled ages calculated from calibrated radiocarbon dates; see SI for details). Redrawn after Glover (1986).

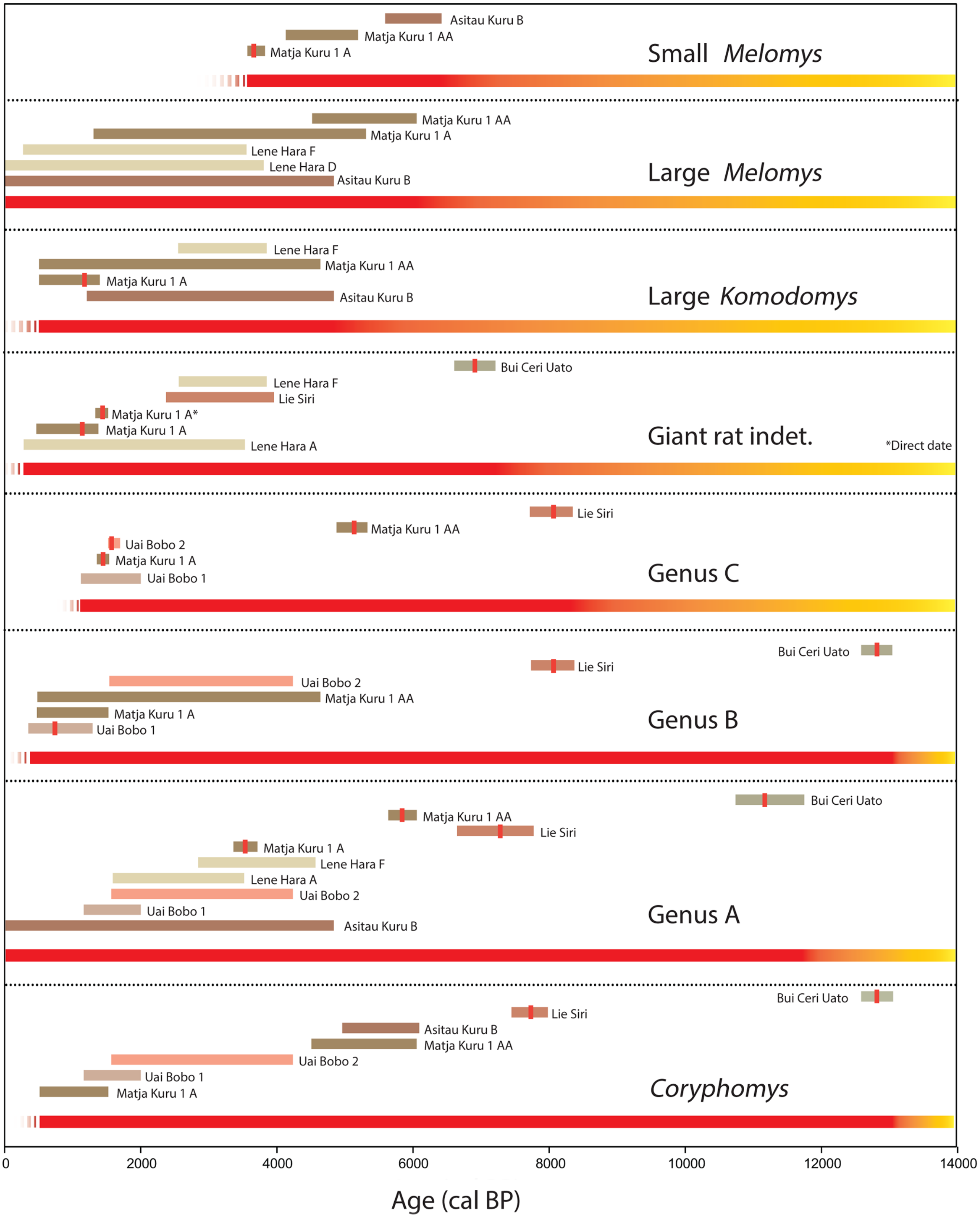

Figure 9. Last appearance dates (LADs) of select extinct fauna from the excavations considered in this study. Median ages are represented by dark vertical lines for each excavation square or site, age ranges (bracket or associated) by lighter bands. All ages in cal BP, full details in the Supplementary Information. It is assumed that all endemic species were present on Timor before their latest appearance (indicated here in graded yellow). Signor-Lipps effect indicated by dashed lines following LADs for each taxon—these are indicative only and have not been quantified.

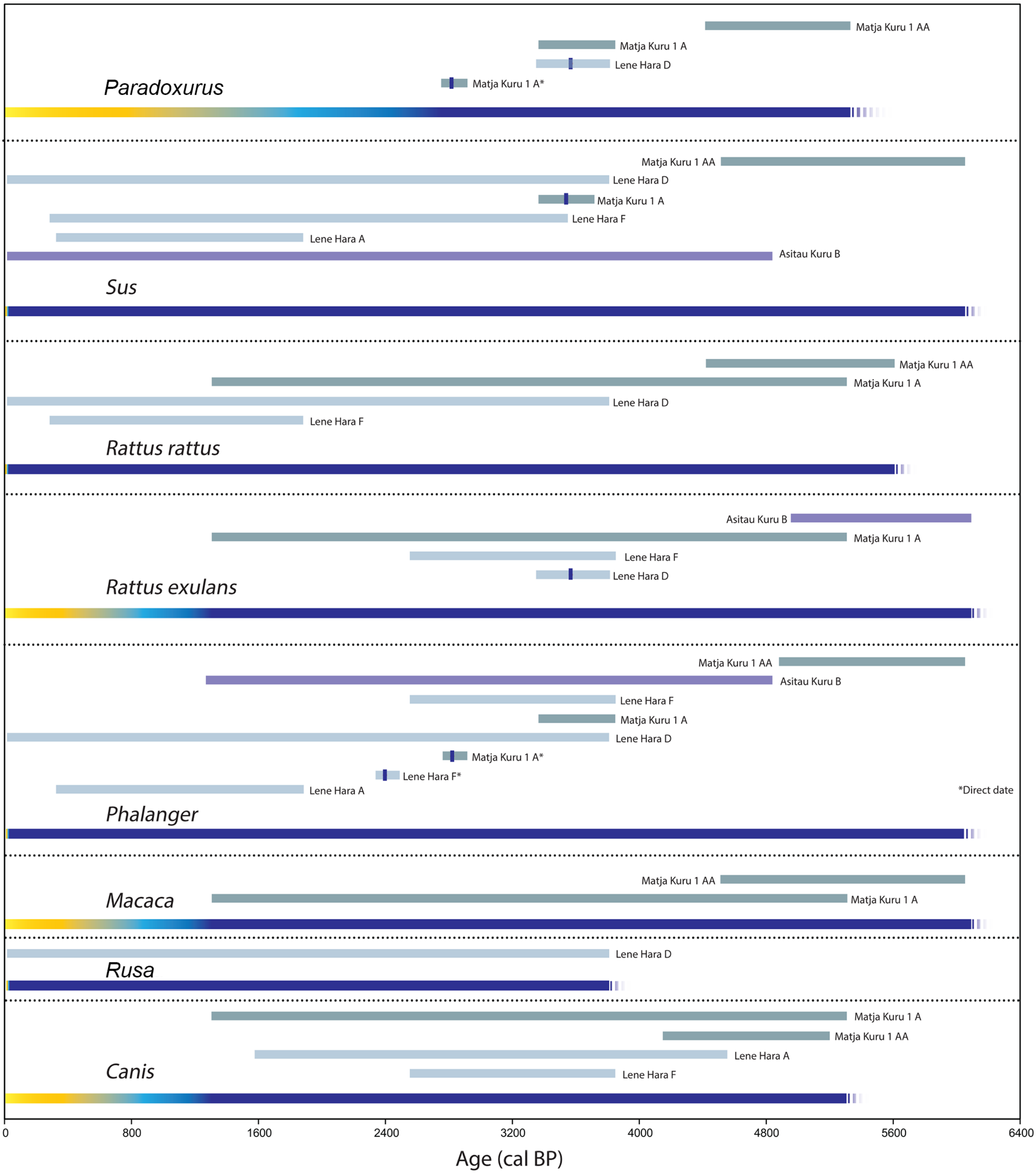

Figure 10. First appearance dates (FADs) of select fauna from the excavations considered in this study. Median ages are represented by dark vertical lines for each excavation square or site, age ranges (bracket or associated) by lighter bands. All ages in cal BP, full details in the Supplementary Information. It is assumed that all introduced species are present on Timor until today (indicated here in graded yellow). Signor-Lipps effect indicated by dashed lines following FADs for each taxon—these are indicative only and have not been quantified.

1). Genus A is found in horizon Vc, which has an age-depth interpolated date of 7717–6627 cal BP (Table 1). *Coryphomys* is found in horizon Va, dated to approximately 7707 cal BP (Table 1). Genus B and Genus C are found at horizon III and below, i.e., between 8338 and 7703 cal BP (Table 1).

Bui Ceri Uato (Fig. 6)

The stratigraphically highest unidentified giant rat material is found in Glover's horizon VIII at this site, which our modelling suggests is *ca*. 6888 cal BP (ANU-11741). Genus A is found in horizon IV, which is between 11,691 and 10,686 cal BP (ANU-11878). *Coryphomys* and Genus B are found in horizon II, dated to approximately 12,980 and 12,505 cal BP (ANU-11877). No Genus C material is recorded from this site.

Uai Bobo 1 (Fig. 7)

The stratigraphically highest giant rat material is Genus B from this site, found in Glover's horizon V. This has age-depth modelled dates of between 1290 and 351 cal BP (Table 1). *Coryphomys,* Genus A and Genus C are all found in horizon IV, which is likely between 2000 and 1157 BP (Table 1).

Uai Bobo 2 (Fig. 8)

The stratigraphically highest giant rat material is Genus C from this site, found in Glover's horizon X, with a direct date between 1695–1522 cal BP (Wk-25439). *Coryphomys,* Genus A and Genus B are all likely recorded in horizon IX, which is modelled between 4235 and 1560 cal BP (Table 1). Two direct dates from giant rats were obtained from this horizon IX material, one on a very large murid (?Genus A) dated to 1275–1076 cal BP (Wk-25630), and another on a large murid dated to 3630–3457 cal BP (Wk-25631).

Discussion

Our study provides a preliminary assessment of the chronological record of extinctions and faunal introductions across several archaeological cave sites in Timor-Leste. These records, although imperfect, provide an important consideration of the sequence of major ecological events on the island. We report only ten direct dates from the taxa considered: a single cuscus specimen from Lene Hara, six dates from Matja Kuru 1 (a cuscus, a buttonquail, a civet, and three unidentified large to giant murids), and three unidentified large to giant murids from Uai Bobo 2. A further ten radiocarbon analyses on bone failed (SI). Given that all other chronologies are by association, we were not able to conduct any quantitative analyses of the Signor-Lipps effect (Signor & Lipps, 1982) on these distributions. As such, our LADs and FADs will represent under and overestimates of extinction and introduction datums, respectively. Nevertheless, they are a good starting point to discuss timings and mechanisms of extinctions on the island.

All murid extinctions likely occurred in the last 2000 years, except perhaps the Small *Melomys,* the last record of which at Matja Kuru 1 is dated to approximately 3661 cal BP (Wk-25638; Table 1). In three instances, extinctions may have occurred within the seventeenth to twentieth centuries, based on the record of Asitau Kuru Square B, Spit 3. An upper age bracket for material from this spit is provided by radiocarbon sample Wk-19228, with associated age of 271–13 cal BP (Table 1), considerably younger than any other extinct giant rat material. However, of note are two additional, much lower charcoal samples, from spits 14 and 33, also dating to around this time (SI), and it is possible that all these charcoal dates are intrusive. The next closest dated material, marine shell from spit 9, provides an associated date of 4541 cal BP (Wk-19230; Table 1). This date seems more congruent with the other records from the cave deposits, and we consider these dates more likely to represent the true age of these remains. Support for this interpretation comes from the excavations at the hilltop village settlements of Ira Ara, Macapainara and Vasino at the eastern end of Timor-Leste, as well as the Leki Wakik village site near Laleia in north central Timor-Leste. These sites were occupied between the fifteenth

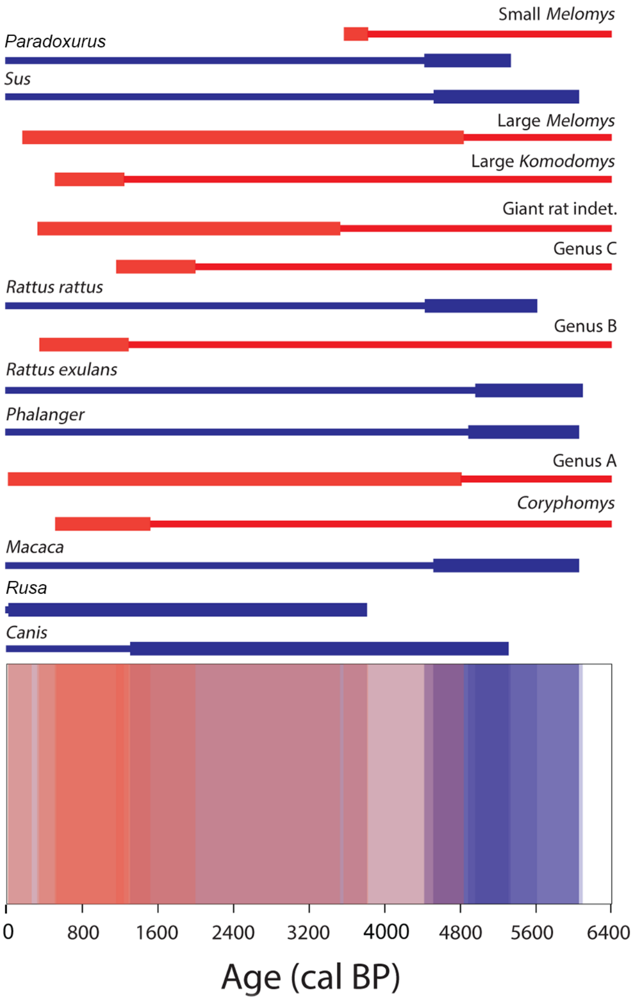

Figure 11. Top: Summary of LADs and FADs (see Table 1) for endemic or introduced taxa considered in this study (thicker band). Cooler colours indicate faunal introductions, warmer colours faunal extinctions; thinner band indicates that endemic fauna were present before the temporal period considered here or that introduced species are still present on the island today. Bottom: Colour spectrum indicating degree of overlap between LADs and FADs for endemic and introduced species, respectively. Purple colours in the spectrum indicate considerable overlap between introduced and endemic taxa; there is little likely overlap recorded at this temporal scale.

and mid-twentieth centuries and contained abundant faunal remains resulting from human subsistence. The assemblages contain a similar range of taxa to the earlier occupied cave sites but with a greater focus on introduced domestic species. Large endemic murids, however, are notably absent from these assemblages (see papers in O'Connor, McWilliam, & Brockwell, 2020).

If our interpretation is correct, giant rat remains from Lene Hara A and Uai Bobo 1 would then be considered the youngest material representing these taxa, and a staggered extinction scenario, from Genus C, Genus A, *Coryphomys*, and finally Genus B, the last giant rat taxa becoming extinct, may be suggested by this data. The late records of the murid extinctions, especially the Large *Melomys*, hints at the possibility that some of these species may still be extant, eking out an existence in poorly sampled remaining natural habitats. However, KPA did some modern trapping in an attempt to test this in the Nino Konis Santana National Park; one of the few remaining forested regions of Timor-Leste with some small patches of natural vegetation. He wasn't successful. Nor was Helgen, who also undertook mammal surveys and interviews with local villagers in Timor-Leste (Polhemus & Helgen, 2004; Trainor, 2010).

Faunal introductions of commensals and domesticates are not recorded prior to approximately 6000 years ago. Based on the modelled deposit ages, a suite of new taxa is recorded in the archaeological cave deposits approximately 6000 and 4800 years ago, including civets, pigs, Black and Pacific rats, cuscus, macaques, and dogs, although it must be emphasized that these oldest records are dated by association only. The oldest directly dated material from these sites—cuscus and civet—are considerably younger than the associated ages, at approximately 2800 cal BP (Table 1). Cuscus and dog remains which are directly dated from nearby Matja Kuru 2 similarly indicate introduction in the last 3000 years (O'Connor, 2015; see below), and new direct dating of a pig rib from this latter site (MK2 B16) has produced a date of 3356–3211 cal BP (S-ANU 58727, 3061 ± 21 BP). These records compare to regional faunal introductions in Wallacea and surrounding islands as follows and should be regarded as more reliable than the associated dates from the deposits.

Pigs have been recorded at about 3200 cal BP from Savidug Dune in the Batanes Islands, situated between Taiwan and Luzon (Piper *et al*., 2013). Dogs were recovered from the same site at about 2400 cal BP. Pig remains, likely domesticate, have been recovered from Nagsabaran, Philippines, around 4400 cal BP (Amano *et al*., 2013; Piper *et al*., 2009) while dogs occur from 2500 cal BP (Amano *et al*., 2013). A re-examination of the Minanga Sipakko faunal assemblage on Sulawesi has detected small numbers of domestic pig at *ca*. 3500 cal. BP (Anggraeni *et al*., 2014). At Leang Burung 1 in South Sulawesi, Simons & Bulbeck (2004) noted the presence of introduced cervids in stratigraphic contexts in the middle Holocene but suggested that the dog and common palm civet only arrived in the late Holocene. In the Malukus, pig bones were recovered from Uattamdi at *ca*. 3260 BP (ANU-9323) to 2330 BP (ANY-9322), with dog recovered in younger levels only (Bellwood *et al*., 1998). Pigs are present in Lapita sites in New Ireland, such as Kamgot, on Babase Island, by 3380–2950 cal BP (Matisoo-Smith, 2007).

At Liang Bua in Flores, van den Bergh *et al*. (2009) report pig, macaque, and civet by around 4000 cal BP. Deer, cattle, dog, and horse are only found in the uppermost levels of the site (van den Bergh *et al*., 2009). In Timor-Leste itself, a dog burial at Matja Kuru 2 is directly dated to 3064–2880 cal BP (Wk-34931) (Gonzales *et al*., 2013). Glover (1986) reported pig between Horizons VII and XIII at Uai Bobo 2, and he attributed a similar antiquity to cuscus, civet, and bovids based on their presence in Horizon VII. Our own modelling of the dates of this horizon suggests it dates from between 7069 and 6189 cal BP (SI). O'Connor (2015) questioned the antiquity of these faunal records based on the absence of these taxa from sites known by that time and suggested that disturbance at the site may have introduced these remains into older layers—she noted that none of the Uai Bobo 2 remains had thus far been directly dated. The results of our study support O'Connor's (2015) attribution of these remains to disturbance, as none of the introductions recorded in the ETAP sites approach this antiquity, even in the least conservative interpretation of the dates. A cuscus from Matja Kuru 2 has also been directly dated, returning ages of 3381–3231 cal BP (Wk-31505; O'Connor, 2015), which correlates with the other direct dates for this taxon from Matja Kuru 1 and Lene Hara (Table 1; O'Connor, 2015). Genetic analysis of cuscus material from Timor indicates that phalangerids on the island belong to *Phalanger orientalis*; however, neither the point of origin nor the timing of divergence of these introductions are clear (Kealy *et al*., 2020).

Louys *et al*. (2020) analysed modern Black and Pacific rat haplotype networks and craniometrics to understand dispersal of these murids into Nusa Tenggara. The two lineages examined in the Black rat species complex (RrC) points to an early dispersal into the Philippines for RrC Lineage II. RrC Lineage IV, present throughout Nusa Tenggara, suggested an original, more archaic dispersal event into the region followed by *in situ* production of genetic diversity. This was followed by a second, more recent dispersal into the islands. Louys *et al*. (2020) suggested that the Black rat arrived in Nusa Tenggara prior to the widespread dispersal of the Pacific rat from Flores, the Pacific rat's likely point of origin. The Pacific rat record followed the pattern found by others showing that, once dispersal began, a major haplotype group spread quickly through Nusa Tenggara and into the Pacific (Thomson *et al*., 2014; Matisoo-Smith *et al*., 2014; Hingston, 2015; West *et al*., 2017). In Flores, Black rats do not appear in the record of Liang Luar until about 400 years ago, while Pacific rats are recorded from at least 2500 BP (St Pierre, 2011). Both species are present in the Timor sites by about 4000 cal BP, although lack of direct dates prohibits us from determining whether the species arrived together, if one preceded the other, or the exact timing of these events.

Pleistocene Timor was host to numerous endemic mammal taxa, including diverse rodent and proboscidean species (Hoojer, 1969, 1972; Aplin & Helgen, 2010). At least some of Timor's giant rodents have considerable antiquity, from at least *ca*. 165 ka (Louys *et al.,* 2017), and we consider it likely that all small-bodied endemics were present on the island prior to human arrival. Today, Timor hosts only one extant endemic rodent, "*Komodomys" timorensis,* originally described from Mount Mutis in West Timor (Kitchener *et al*., 1991), and whose current conservation status is unknown (Clayton & Kennerley, 2017). Timorese proboscideans, two species of *Stegodon*, likely became extinct in the Middle Pleistocene, well before human arrival on the island (Louys *et al.*, 2016; Hidayah *et al.*, 2021). Murid extinctions, on the other hand, seem to have occurred only very recently. Similarly, Meijer *et al.* (2019) discuss avian extinctions on Timor, including the youngest date for an extinct large buttonquail, *Turnix* sp., directly dated to between 1395 and 1310 cal BP (S-ANU-55223, 95.4% probability range). The records from sites examined here suggest that extinction of the murid endemics did not quickly follow introduction of exotics (Fig. 10). There is a lag of several thousand years between the most likely point of exotic introductions and any ecological cascade due to those introductions. Ecological replacement and impacts are quick—on the scale of tens or perhaps at most hundreds of years (e.g., Okubo *et al.*, 1989; Morales *et al.*, 2013; Wood *et al.*, 2017). While further dating and modelling may close the gap between the dates of extinction of endemics and the introduction of invasives, implicating a principal ecological replacement extinction mechanism, based on current data we consider other extinction explanations more plausible.

Trainor (2010: 40–41) states "Timor's landscape was probably once a mixture of tropical forests and various savanna woodlands, with agriculture and burning practices over recent millennia causing extensive forest loss." While the exact timing of Timor's forest loss is unknown, both Wallace (1869) and Forbes (1885) comment on the lack of tropical forest when undertaking their respective surveys in the mid to late 19th century. Wallace notes that around Kupang there was "… nothing that can be called a forest, and the whole country has a parched and desolate appearance" (Wallace, 1869: 204). Forbes (1885) noted "Indeed, life of all kinds had been exceedingly conspicuous by its absence; save a scarlet *Trichoglossus* or a cockatoo flying across our path, and a few crows at Erlura, I had seen no birds, and the vegetation since crossing the Ligidoik river had been very poor indeed. A few casuarinas, acacias, gum-trees, and some rought-leaved *Compositae* being the only vegetable forms. The slopes on the other side looked somewhat more tree-dotted, however, but the bare red ground displayed itself over a large part of its area" (Forbes, 1885: 434); and "'The land of Timor is always falling,' is the natives' own account of the country"(Forbes, 1885: 433). In 1932, Georg Stein conducted an expedition into the previously unexplored high mountians of Timor-Leste but was disappointed by his findings, due to the presence of villages up to an altitude of 2300 m causing forests to "entirely disappear…" (Mayr's reconstruction of Stein's 1931–1932 Timor expeditions; Mayr, 1944: 131). In fact, Stein documents the presence of "… only open eucalyptus groves without undergrowth" (Mayr, 1944: 131). The Nino Konis Santana National Park, in Lautem district, retains the most extensive lowland forest on the island (FAO/UNDP, 1982; Trainor, 2010), however, even here little primary forest remains (Geoff Hope pers. comm. to SOC, 2000). Stone garden walling spanning kilometres, and the remains of earlier built settlements, attest to the extensive nature of past swiddening activities within the park (O'Connor *et al.*, 2020).

Understanding the nature of vegetation changes in Timor in the last few thousand years will be paramount to reconstructing the factors driving the late Holocene extinction record of this island. Unfortunately, few palaeobotanical studies of the island exist. Oliveira's (2008) palaeobotanical study at Bui Ceri Uato Mane in the Baucau region is one of the few that have been reported. He found no evidence of cereal crops in Timor's archaeological record, instead suggesting that tree crops and possibly tubers were in use throughout the Holocene. O'Connor (2015) similarly reviewed evidence for cereal in Timor's archaeological record and found limited and contentious examples only. Louys *et al.* (2020) suggested that rice cultivation in the drier parts of Nusa Tengarra may have been coincident with the arrival of Dong Son drums, from approximately the fifth century AD, as well as metal tools.

We have previously argued that the giant rat extinctions were likely associated with the introduction of metal tools into Nusa Tenggara because these facilitated widespread forest clearance (O'Connor & Aplin, 2007; O'Connor, 2015; Louys *et al.*, 2018; Miszkiewicz *et al.*, 2020). Historical records indicate that Timor was an important centre for white sandalwood export beginning approximately 1500 AD (McWilliam, 2005; O'Connor *et al.*, 2012) and metal tools would have greatly increased production of sandalwood at the expense of native forests. Deforestation may have been exacerbated by the introduced fauna through destruction of seedlings, seeds, and defoliation in a flora which had evolved in the presence of murids, but few other terrestrial mammals. Indeed, Glover (1986: 193–194) suggests that *Celtis* sp. seeds were found throughout his sequences, but decline and disappear at the same time as the giant rats, perhaps because the seeds were collected by the murids as food. Giant rats, although not a uniform taxonomic group, nevertheless plot on the C3 end of the carbon stable isotope spectrum (i.e., browsers and/or frugivores) (Louys *et al.*, 2018; Roberts *et al.*, 2020) and would have been particularly susceptible to loss of native forests. While we do not discount the obvious impacts of introduced competitors and predators, these may have been secondary compounding factors in extinction (Bergstrom *et al.*, 2023). The combination of new metal tools, a burgeoning sandalwood trade, introduction of rice agriculture, and the ecological impacts of introduced exotics likely removed almost all of Timor's endemic forests, and with them the giant rats that were dependent on them.

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Supplementary Information (SI)

Supplementary Information is published separately as a *figshare* dataset—"Supplementary information for Late Quaternary mammal introduction and extinction records from archaeological cave deposits in Timor-Leste" (see Louys *et al*., 2023).

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