Contributions to Mammalogy and Zooarchaeology of Wallacea

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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).

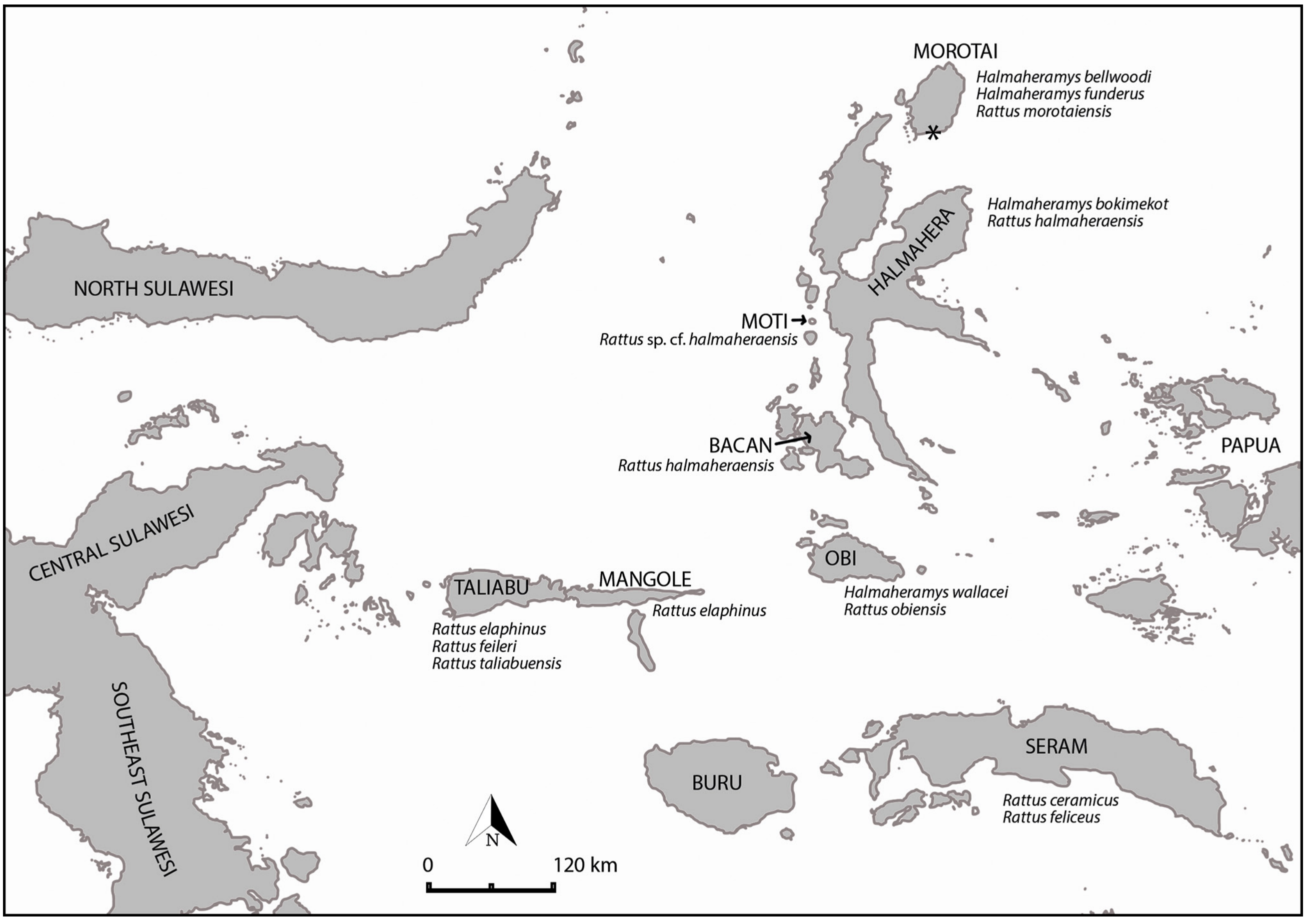

Figure 1. Map showing the location of the major islands and localities mentioned in the text, with Rattini species described from Moluccan islands to date. The star shows the location on Morotai of Daeo Cave no. 2, the archaeological site discussed in the paper, and the type locality for *Halmaheramys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

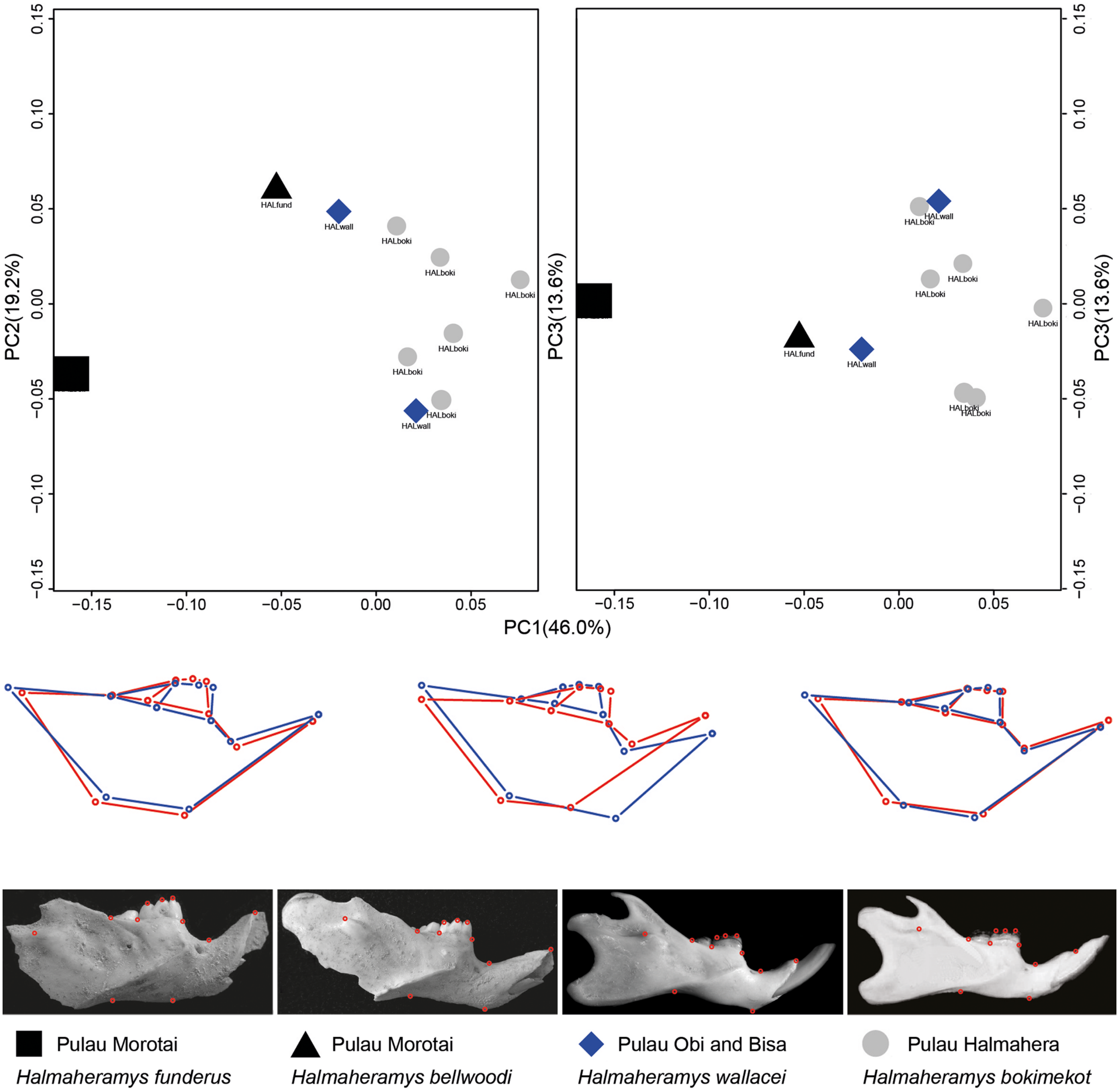

Figure 2. Two dimensional geometric morphometric comparisons of the mandibles of the four species of *Halmaheramys*. The first Principal Component (PC1) is plotted against the second (PC2) and third (PC3). Variance explained by each component is illustrated in parentheses for each component.

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

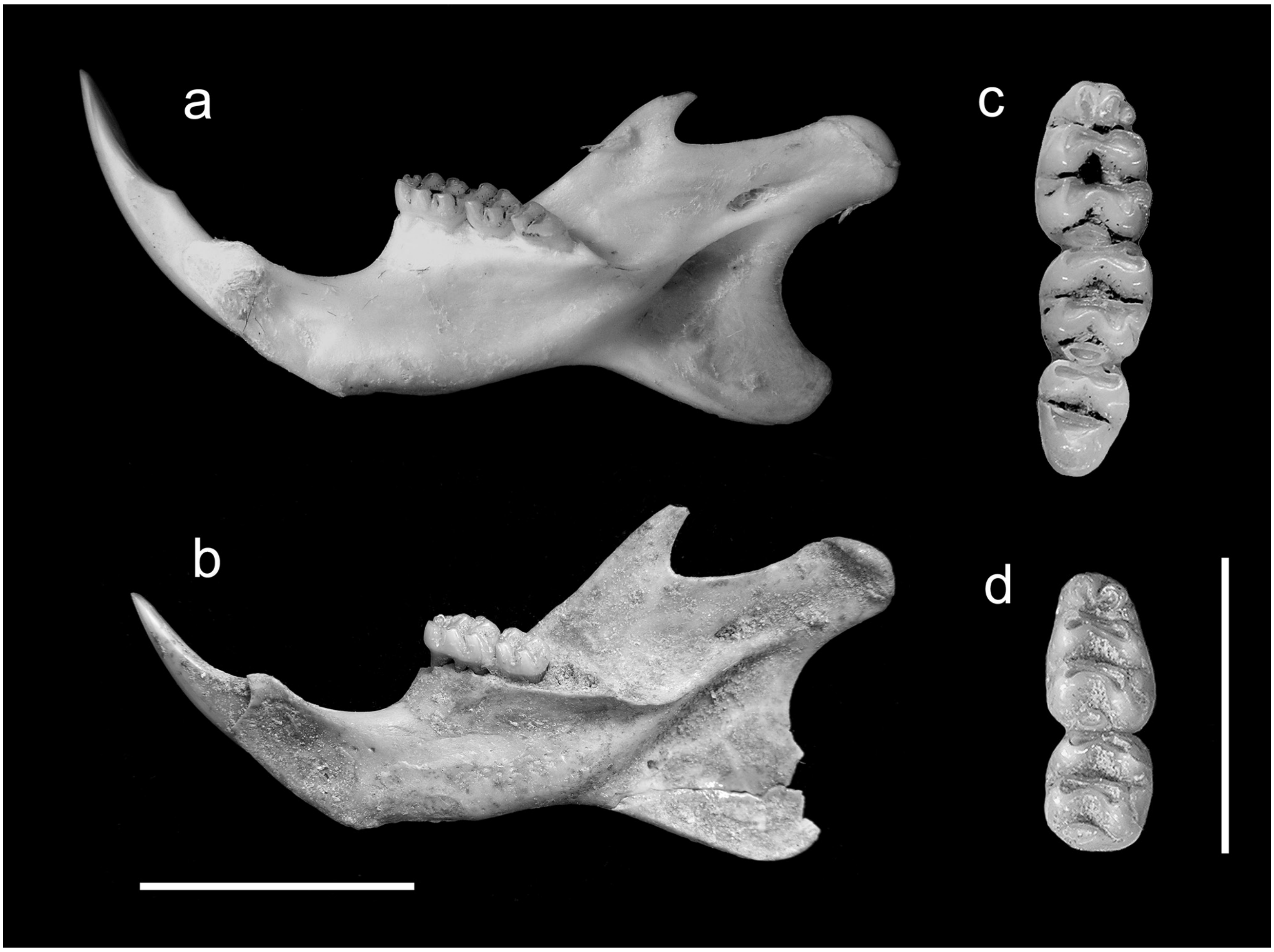

Figure 3. Subfossil specimen of *Rattus morotaiensis* from Morotai (AM F101473) compared with a modern specimen of the closely related *R. halmaheraensis* from Bacan (AM M.23653); (*a*) lingual side of right dentary AM M.23653; (*b*) lingual side of right dentary AM F101473; (*c*) occlusal view of right 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

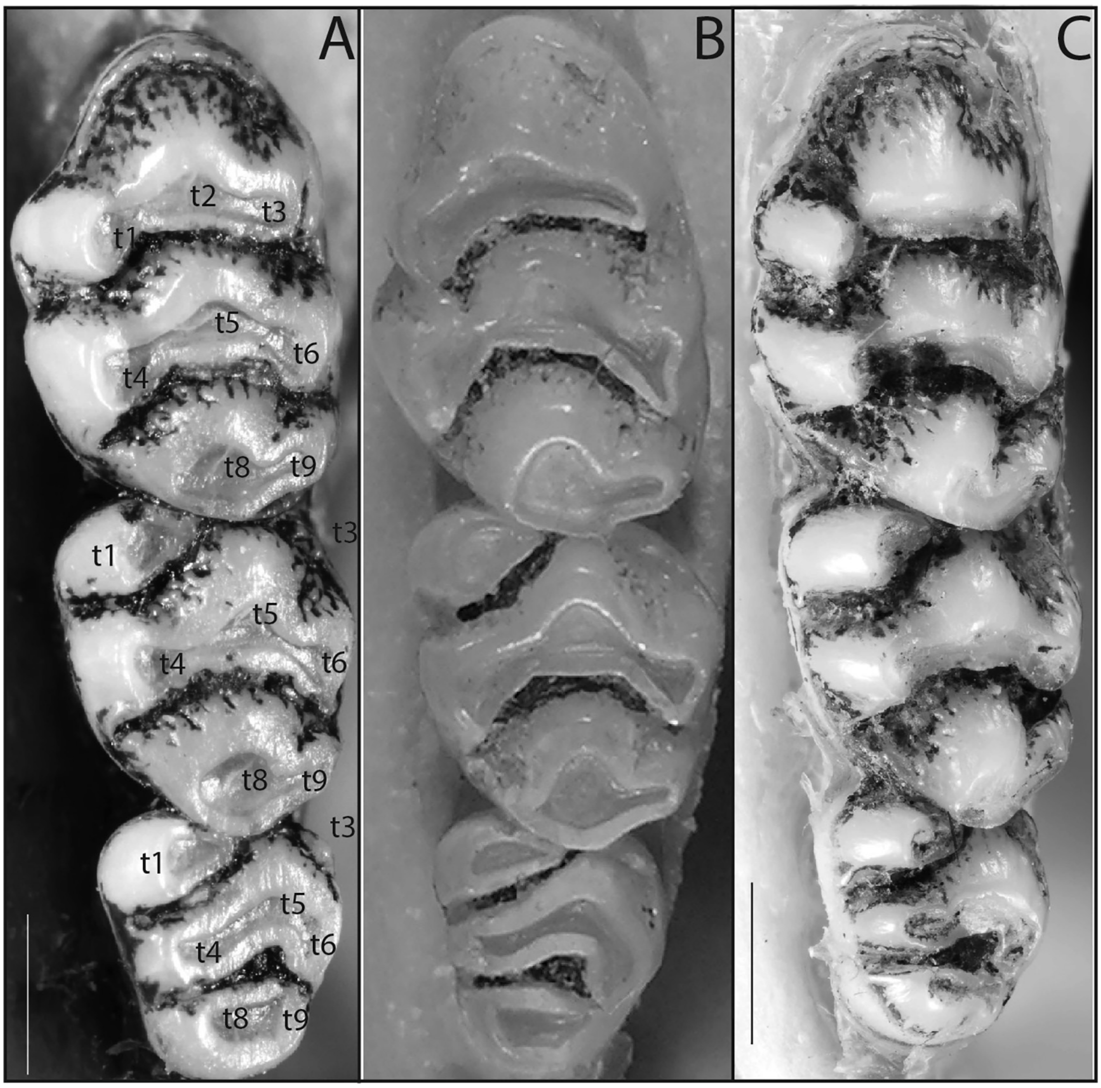

Figure 4. Upper molar rows of Moluccan *Rattus morotaiensis* species-group members (*A*) Modern *R. morotaiensis* from Morotai (USNM 277312, holotype); (*B*) Modern *R. halmaheraensis* from Bacan (AM M.23653); (*C*) Modern *R. halmaheraensis* from Halmahera (MZB 33270). All pictures to scale (cf. measurements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

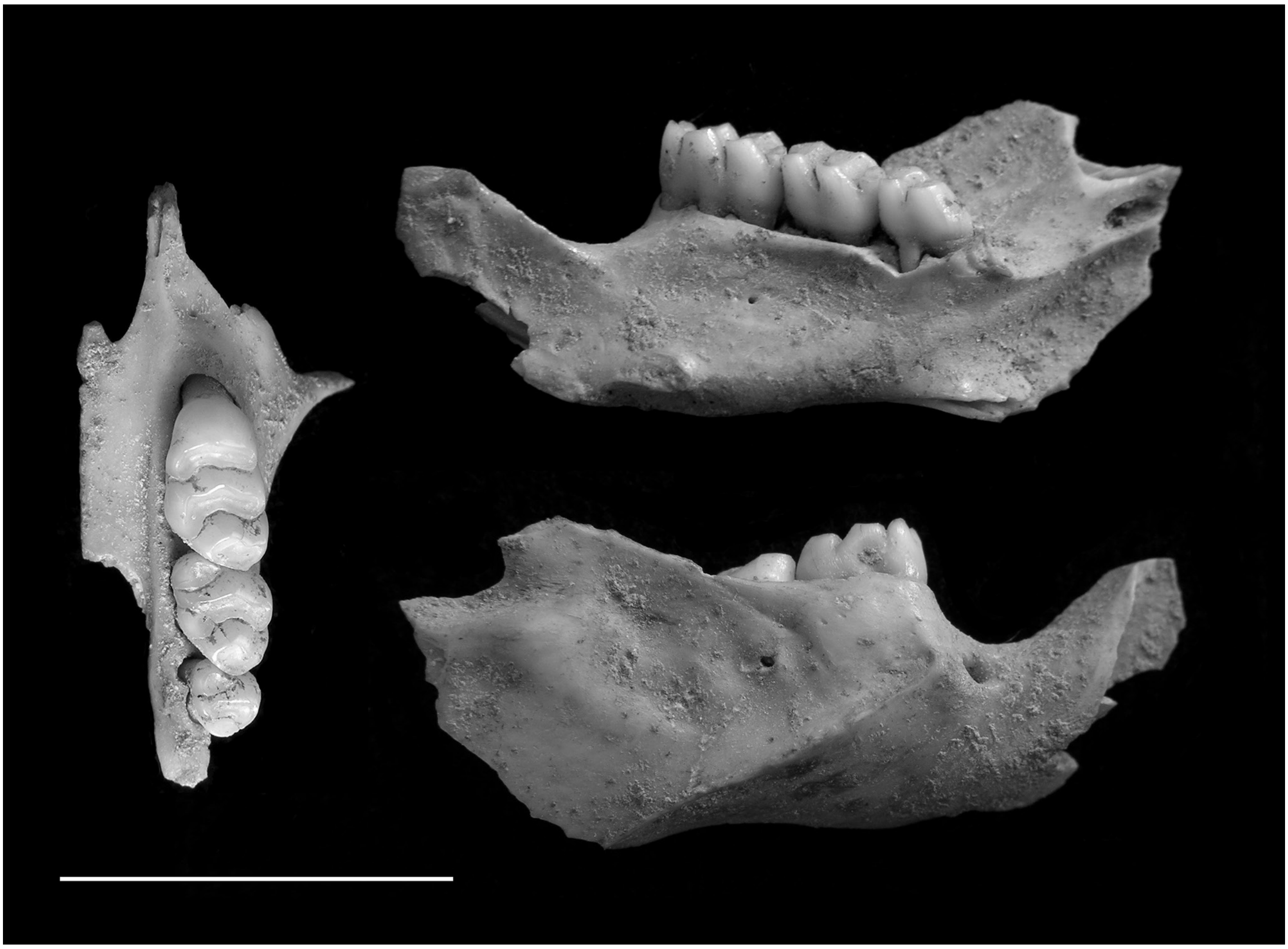

Figure 7. Subfossil specimens of *Halmaheramys funderus* sp. nov.; (*a*) ventral side of holotype left maxilla AM F101459; (*b*) lingual side of right dentary AM F101457; (*c*) labial side of right dentary AM F101457. Scale bar represents 10 mm.

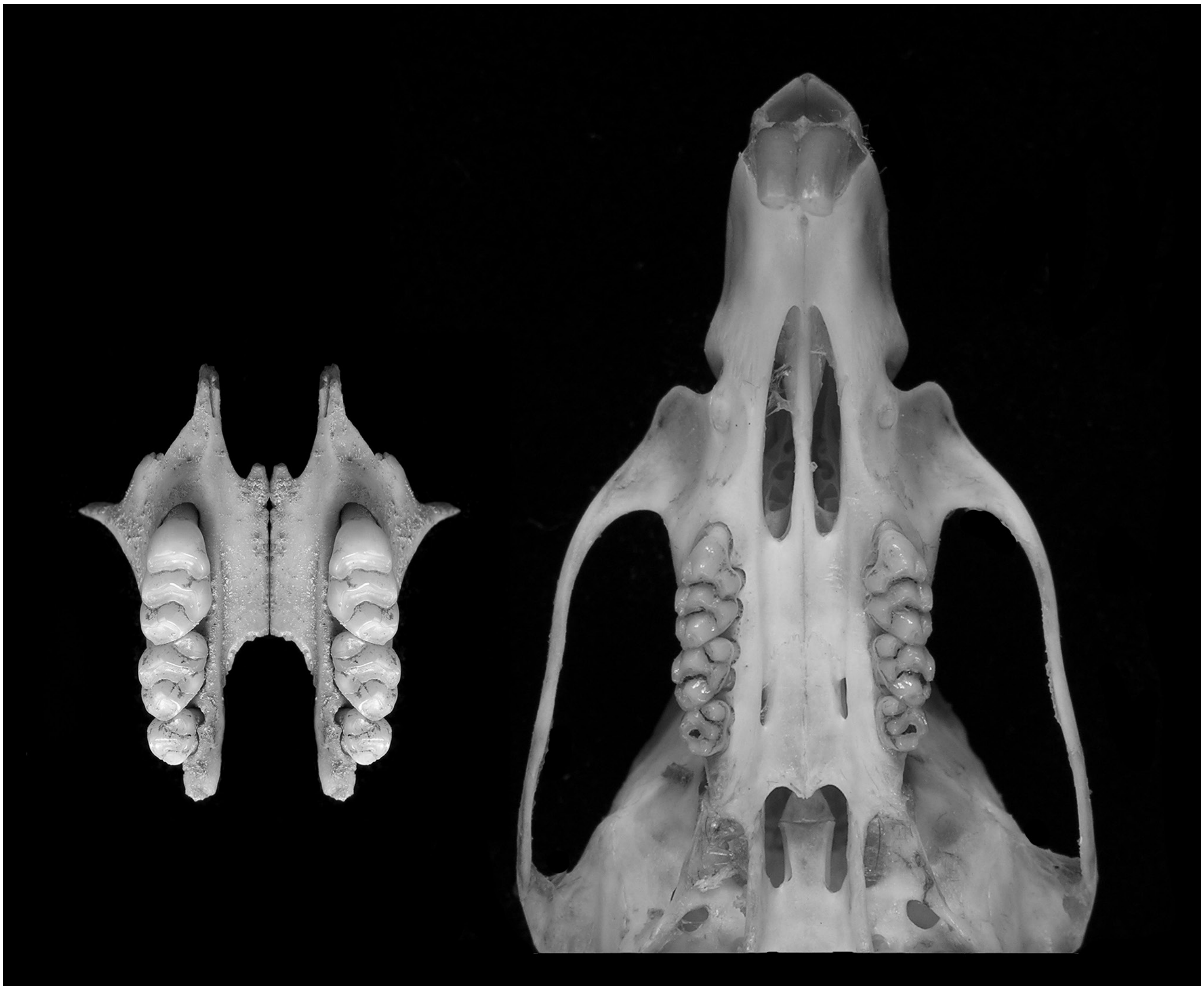

Figure 8. Palate of *Halmaheramys funderus* sp. nov. Reconstructed palatal region of *Halmaheramys funderus* (based on left maxilla and its mirror image), compared with the same region in a specimen of *Rattus rattus* (ANWC CM2768). The two specimens are scaled such that maxillary length (measured from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

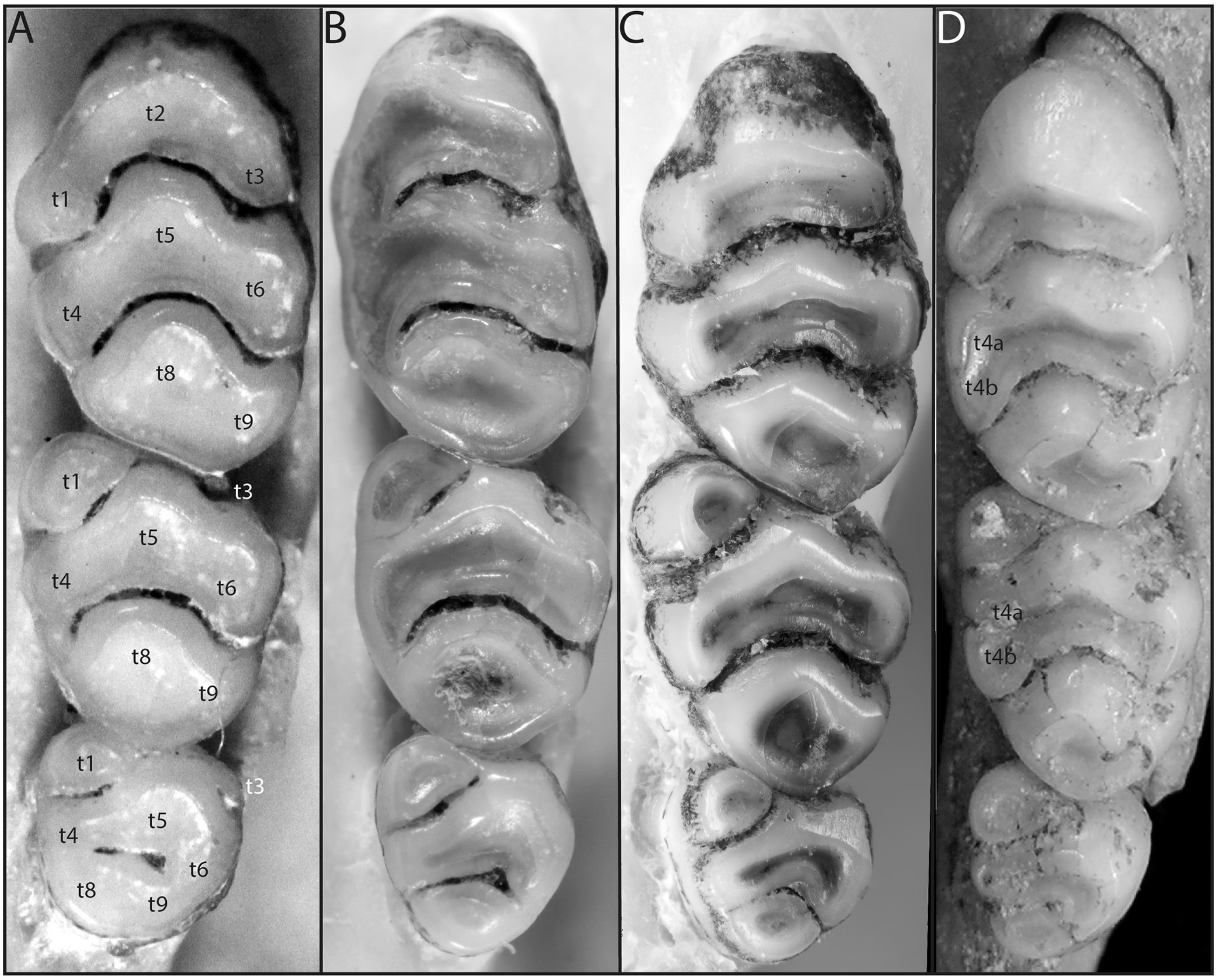

Figure 9. Upper molars of *Halmaheramys*. Occlusal views of the right maxillary upper molar rows of (*A, B*) *Halmaheramys wallacei,* (*A*) AM M.24389, Bisa, and (*B*) MZB 38227, Obi; (*C*) *Halmaheramys bokimekot* (MZB 33266, Halmahera); and (*D*) *Halmaheramys funderus* sp. nov. (AM F101459, Morotai, 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^{1}w = breadth of anteriormost upper molar; M$_1$w = breadth of anteriormost lower molar; M$_2$w = breadth of middle lower molar; M$_3$w = 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^{1}w	2.00	2.30	—	2.60
	1.89–2.04	2.10–2.40	—	2.60
	n = 6	n = 4	—	n = 1
M$_1$w	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$_2$w	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$_3$w	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.

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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

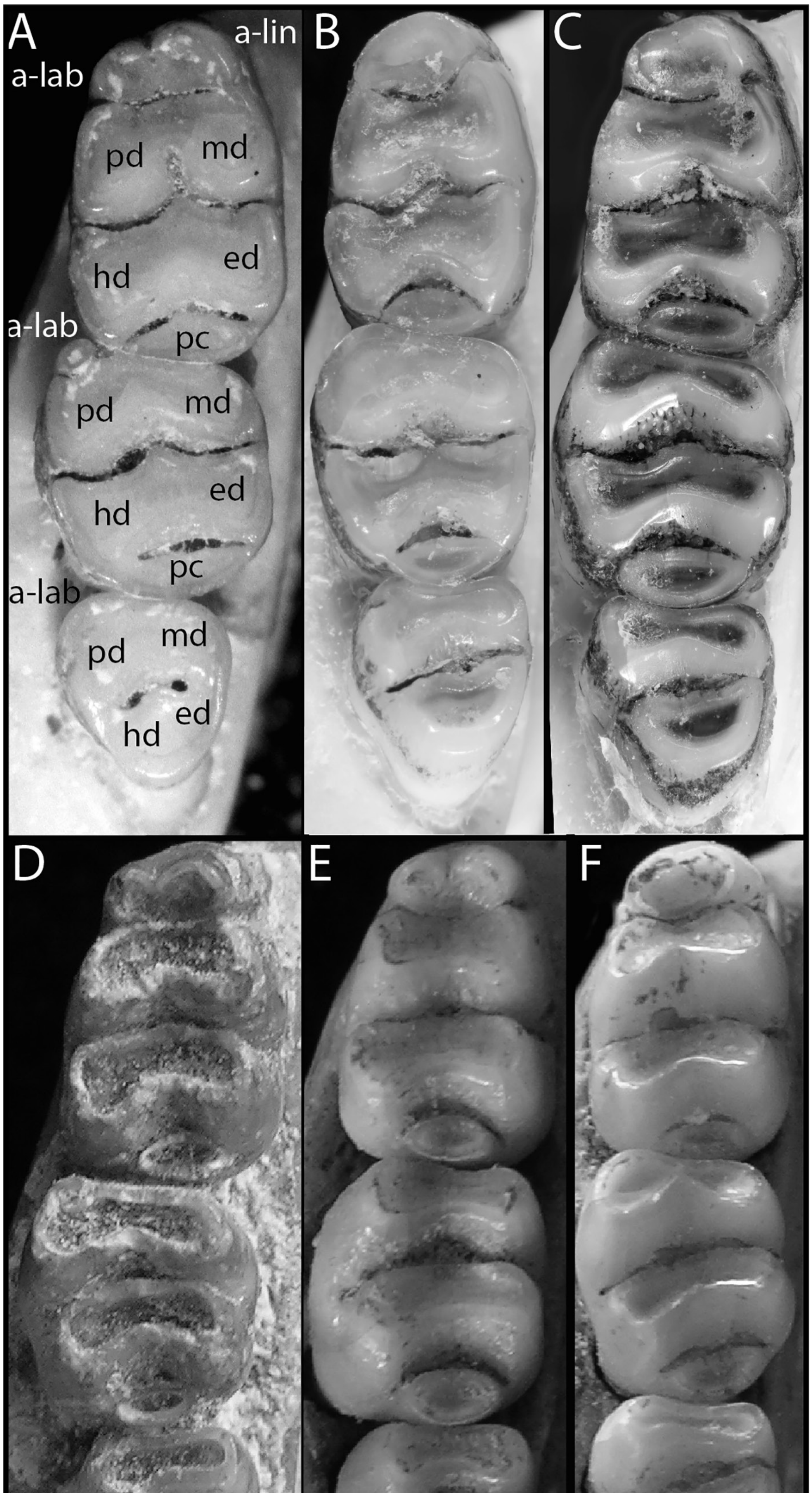

Figure 10. Lower molar comparisons of *Halmaheramys*. Occlusal views of the right lower molar rows of (*A, B*) *H. wallacei,* (*A*) AM M.24389, Bisa, and (*B*) MZB 38227, Obi; (*C*) *H. bokimekot* (MZB 33266, Halmahera); (*D–E*) *H. funderus* (AM F101463, AM F101457); and (*F*) *H. bellwoodi* sp. nov.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

Adams, D. C., F. J. Rohlf, and D. E. Slice. 2013. A field comes of age: geometric morphometrics in the 21st century. *Hystrix* 24: 7–14. https://doi.org/10.4404/hystrix-24.1-6283

Aplin, K. P., T. Chesser, and J. ten Have. 2003. Evolutionary biology of the genus *Rattus*: profile of an archetypal rodent pest. In *Rats, Mice and People: Rodent Biology and Management,* ed. G. R. Singleton, L. A. Hinds, C. J. Krebs, and D. M. Spratt, pp. 487–498. Canberra: ACIAR Technical Report 96.

Aplin, K. P., and K. M. Helgen. 2010. Quaternary murid rodents of Timor part I: new material of *Coryphomys buehleri* Schaub, 1937, and description of a second species of the genus. *Bulletin of the American Museum of Natural History* 341: 1–80.

Aplin, K. P., H. Suzuki, A. A. Chinen, R. T. Chesser, J. ten Have, S. C. Donnellan, J. Austin, A. Frost, J. P. Gonzalez, V. Herbreteau, F. Catzeflis, J. Soubrier, Y.-P. Fang, J. Robins, E. Matisoo-Smith, A. D. S. Bastos, I. Maryanto, M. H. Sinaga, C. Denys, R. A. Van Den Bussche, C. Conroy, K. Rowe, and A. Cooper. 2011. Multiple geographic origins of commensalism and complex dispersal history of black rats. *PLoS One* 6: e26357. https://doi.org/10.1371/journal.pone.0026357

Bellwood, P. 2019. The Indonesian-Australian archaeological research project in the Northern Moluccas. In *The Spice Islands in Prehistory: Archaeology in the Northern Moluccas, Indonesia*, ed. P. Bellwood, pp. 1–13. Canberra: ANU Press, Terra Australis 50.

Bellwood, P., G. Nitihaminoto, G. Irwin, Gunadi, A. Waluyo, and D. Tanudirjo. 1998. 35,000 years of prehistory in the northern Moluccas. *Modern Quaternary Research in Southeast Asia* 15: 233–275.

Bellwood, P., D. Tanudirjo, and G. Nitihaminoto. 2019. Investigations on Morotai Island. In *The Spice Islands in Prehistory: Archaeology in the Northern Moluccas, Indonesia*, ed. P. Bellwood, pp. 45–60. Canberra: ANU Press, Terra Australis 50.

Bellwood, P., A. Waluyo, Gunadi, G. Nitihaminoto, and G. Irwin. 1993. Archaeological research in the Northern Moluccas: interim results, 1991 field season. *Indo-Pacific Prehistory Association Bulletin* 13: 20–33.

Bookstein, F. L. 1991. Thin-plate splines and the atlas problem for biomedical images. In *Information Processing in Medical Imaging. IPMI 1991. Lecture Notes in Computer Science*, vol. 511, ed A. C. F. Colchester and D. J. Hawkes, pp. 326–342. Berlin, Heidelberg: Springer. https://doi.org/10.1007/BFb0033763

Brooks, T. M., S. L. Pimm, V. Kapos, and C. Ravilious. 1999. Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *Journal of Animal Ecology* 68: 1061–1078.

Camacho-Sanchez, M., J. A. Leonard, Y. Fitriana, M.-K. Tilak, and P.-H. Fabre. 2017. The generic status of *Rattus annandalei* (Bonhote, 1903) (Rodentia, Murinae) and its evolutionary implications. *Journal of Mammalogy* 98: 1340–1355. https://doi.org/10.1093/jmammal/gyx081

Corbet, G. B., and J. E. Hill. 1992. *The Mammals of the Indomalayan Region: a Systematic Review.* Oxford: Oxford University Press.

Dryden, I. L., and K. V. Mardia. 1998. *Statistical Analysis of Shape*. Chichester: John Wiley & Sons.

Ellen, R. 1997. The human consequences of deforestation in the Moluccas. *Civilisations* 44: 176–193.

Fabre, P.-H., Y. S. Fitriana, G. Semiadi, M. Pagès, K. Aplin, N. Supriatna, and K. M. Helgen. 2017a. New record of *Melomys burtoni* (Mammalia, Rodentia, Murinae) from Halmahera (North Moluccas, Indonesia): a review of Moluccan *Melomys*. *Mammalia* 82: 218–247.

Fabre, P.-H., A. Herrel, Y. Fitriana, L. Meslin, and L. Hautier. 2017b. Masticatory muscle architecture in a water-rat from Australasia (Murinae, *Hydromys*) and its implication for the evolution of carnivory in rodents. *Journal of Anatomy* 231: 380–397. https://doi.org/10.1111/joa.12639

Fabre, P.-H., M. Pagès, G. G. Musser, Y. S. Fitriana, J. Fjeldså, A. Jennings, K. A. Jønsson, J. Kennedy, J. Michaux, G. Semiadi, N. Supriatna, and K. M. Helgen. 2013. A new genus of rodent from Wallacea (Rodentia: Muridae: Murinae: Rattini), and its implication for biogeography and Indo-Pacific Rattini systematics. *Zoological Journal of the Linnean Society* 169: 408–447.

Fabre, P.-H., A. H. Reeve, Y. S. Fitriana, K. P. Aplin, and K. M. Helgen. 2018. A new species of *Halmaheramys* (Rodentia: Muridae) from Bisa and Obi Islands (North Maluku Province, Indonesia). *Journal of Mammalogy* 99: 187–208.

Fabre, P.-H., R. Portela-Miguez, M. E. Holden, Y. S. Fitriana, G. Semiadi, G. G. Musser, and K. M. Helgen. 2023. Review of Moluccan *Rattus* (Rodentia: Muridae) with description of four new species. In *Contributions to Mammalogy and Zooarchaeology of Wallacea*, ed. K. M. Helgen and R. K. Jones. *Records of the Australian Museum* 75(5): 673–718. https://doi.org/10.3853/j.2201-4349.75.2023.1783

Flannery, T. F. 1995. *Mammals of the South-West Pacific and Moluccan Islands*. Ithaca, New York: Cornell University Press.

Flannery, T. F., P. Bellwood, J. P. White, T. Ennis. G. Irwin, K. Schubert, and S. Balasubramaniam. 1998. Mammals from Holocene archaeological deposits on Gebe and Morotai Islands, Northern Moluccas, Indonesia. *Australian Mammalogy* 20: 391–400.

Flannery, T. F., P. Bellwood, P. White, A. Moore, Boeadi, and G. Nitihaminoto. 1995. Fossil marsupials (Macropodidae, Peroryctidae) and other mammals of Holocene age from Halmahera, North Moluccas, Indonesia. *Alcheringa* 19: 17–25.

Glover, I. 1986. Archaeology in eastern Timor, 1966–67. *Terra Australis* 11: 1–241.

Hall, R. 2002. Cenozoic geological and plate tectonic evolution of SE Asia and the SW Pacific: computer-based reconstructions, model and animations. *Journal of Asian Earth Sciences* 20: 353–431.
https://doi.org/10.1016/S1367-9120(01)00069-4

Hall, R. 2013. The palaeogeography of Sundaland and Wallacea since the Late Jurassic. *Journal of Limnology* 72: 1–17.
https://doi.org/10.4081/jlimnol.2013.s2.e1

Hall, R., M. G. Audley-Charles, F. T. Banner, S. Hidayat, and S. L. Tobing. 1988. Late Paleogene-Quaternary geology of Halmahera, eastern Indonesia: initiation of a volcanic island arc. *Journal of the Geological Society* 145: 577–590.
https://doi.org/10.1144/gsjgs.145.4.0577

Hall, R., G. Nichols, P. Ballantyne, T. Charlton, and J. Ali. 1991. The character and significance of basement rocks of the southern Molucca Sea region. *Journal of Southeast Asian Earth Sciences* 6: 249–258.
https://doi.org/10.1016/0743-9547(91)90071-5

Hasagawa, H., and Syaffrudin. 1995a. Nematode fauna of the two sympatric rats *Rattus rattus* and *R. exulans*, in Kao District, Halmahera Island, Indonesia. *Journal of the Helminthological Society of Washington* 62: 27–31.

Hasagawa, H., and Syaffrudin. 1995b. *Nippostrongylus marhaeniae* sp. n. and other nematodes collected from *Rattus* cf. *morotaiensis* in North Halmahera, Molucca Islands, Indonesia. *Journal of the Helminthological Society of Washington* 62: 111–116.

Helgen, K. M. 2002. Notes on a collection of mammals from the Moluccas, with new geographic records. *Mammalian Biology* 67: 51–54.

Helgen, K. M. 2003. A review of the rodent fauna of Seram, Moluccas, with the description of a new subspecies of mosaic-tailed rat, *Melomys rufescens paveli*. *Journal of Zoology (London)* 261: 165–172.

Helgen, K. M., and L. E. Helgen. 2009. Biodiversity and biogeography of the moss-mice of New Guinea: a taxonomic revision of *Pseudohydromys* (Rodentia: Murinae). *Bulletin of the American Museum of Natural History* 331: 230–312.
https://doi.org/10.1206/582-8.1

Hull, J. R., P. Piper, G. Irwin, K. Szabó, A. Oertle, and P. Bellwood. 2019. Observations on the Northern Moluccan excavated animal bone and shell collections. In *The Spice Islands in Prehistory: Archaeology in the Northern Moluccas,* Indonesia, ed. P. Bellwood, pp. 135–165. Canberra: ANU Press, Terra Australis 50.

Kellogg, R. 1945. Two rats from Morotai Island. *Proceedings of the Biological Society of Washington* 58: 65–68.

Koopman, K. F., and L. K. Gordon. 1992. Systematic notes on a collection of bats from Halmahera (Indonesia: Moluccas). *American Museum Novitates* 3035: 1–8.

Louys, J., M. B. Herrera, V. A. Thomson, A. S. Wiewel, S. C. Donnellan, S. O'Connor, and K. Aplin. 2020. Expanding population edge craniometrics and genetics provide insights into dispersal of commensal rats through Nusa Tenggara, Indonesia. In *Papers in Honour of Ken Aplin*, ed. Julien Louys, Sue O'Connor, and Kristofer M. Helgen. *Records of the Australian Museum* 72(5): 287–302.
https://doi.org/10.3853/j.2201-4349.72.2020.1730

Misonne, X. 1969. African and Indo-Australian Muridae: evolutionary trends. *Annales Musée Royal de l'Afrique Centrale, Tervuren, Belgique, Serie IN-8, Sciences Zoologiques* 172: 1–219.

Monk, K. A., Y. de Fretes, and G. Reksodiharjo-Lilley. 1997. *The Ecology of Nusa Tenggara and Maluku*. Oxford: Oxford University Press.

Musser, G. G. 1979. Results of the Archbold Expeditions. No. 102. The species of *Chiropodomys*, arboreal mice of Indochina and the Malay Archipelago. *Bulletin of the American Museum of Natural History* 162: 377–445.

Musser, G. G. 1981. Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bulletin of the American Museum of Natural History* 168: 225–334.

Musser, G. G. 1991. Sulawesi rodents: descriptions of new species of *Bunomys* and *Maxomys* (Muridae, Murinae). *American Museum Novitates* 3001: 1–41.

Musser, G. G. 2014. A systematic review of Sulawesi *Bunomys* (Muridae, Murinae) with the description of two new species. *Bulletin of the American Museum of Natural History* 392: 1–313.
https://doi.org/10.1206/863.1

Musser, G. G., and M. D. Carleton. 2005. Family Muridae. In *Mammal Species of the World: a Taxonomic and Geographic Reference*, third edition, ed. D. E. Wilson and D. R. Reeder, pp. 894–1531. Baltimore: Johns Hopkins University Press.

Musser, G. G., and L. A. Durden. 2014. Morphological and geographic definitions of the Sulawesian shrew rats *Echiothrix leucura* and *E. centrosa* (Muridae, Murinae), and description of a new species of sucking louse (Phthiraptera: Anoplura). *Bulletin of the American Museum of Natural History* 391: 1–87.
https://doi.org/10.1206/871.1

Musser, G. G., and L. R. Heaney. 1992. Philippine rodents: definitions of *Tarsomys* and *Limnomys* plus a preliminary assessment of phylogenetic patterns among native Philippine murines (Murinae, Muridae). *Bulletin of the American Museum of Natural History* 211: 1–138.

Musser, G. G., K. M. Helgen, and D. P. Lunde. 2008. Systematic revision of New Guinea *Leptomys* (Muridae, Murinae) with description of two new species. *American Museum Novitates* 3624: 1–60.

Musser, G. G., and C. Newcomb. 1983. Malaysian murids and the giant rat of Sumatra. *Bulletin of the American Museum of Natural History* 174: 327–598.

Musser, G. G., and C. Newcomb. 1985. Definitions of Indochinese *Rattus losea* and a new species from Vietnam. *American Museum Novitates* 1814: 1–32.

Pagès, M., Y. Chaval, V. Herbreteau, S. Waengsothorn, F.-F. Cosson, P. Hugot, S. Morand, and J. Michaux. 2010. Revisiting the taxonomy of the Rattini tribe: a phylogeny-based delimitation of species boundaries. *BMC Evolutionary Biology* 10 (184): 1–27.
https://doi.org/10.1186/1471-2148-10-184

Poulsen, M. K., and F. R. Lambert. 2000. Altitudinal distribution and habitat preferences of forest birds on Halmahera and Buru, Indonesia: implications for conservation of Moluccan avifaunas. *Ibis* 142: 566–586.

Rohlf, F. J., and D. Slice. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology* 39: 40–59.
https://doi.org/10.2307/2992207

Rowe, K. C., A. Achmadi, and J. Esselstyn. 2016. Repeated evolution of carnivory among Indo-Australian rodents. *Evolution* 70: 653–665.

Rowe, K. C., A. Achmadi, P.-H. Fabre, J. J. Schenk, S. J. Steppan, and J. A. Esselstyn. 2019. Oceanic islands of Wallacea as a source for dispersal and diversification of murine rodents. *Journal of Biogeography* 46: 2752–2768.
https://doi.org/10.1111/jbi.13720

Samuels, J. X. 2009. Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society* 156: 864–888.
https://doi.org/10.1111/j.1096-3642.2009.00502.x

Slice, D. E. 2007. Geometric morphometrics. *Annual Review of Anthropology* 36: 261–281.
https://doi.org/10.1146/annurev.anthro.34.081804.120613\

Stattersfield, A. J., M. J. Crosby, A. J. Long, and D. C. Wege. 1998. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation.* Cambridge, UK: BirdLife International.

Taylor, J. M., J. H. Calaby, and H. M. Van Deusen. 1982. A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinean region. *Bulletin of the American Museum of Natural History* 173: 177–336.

Thomas, O. 1920. On mammals from Ceram. *Annals and Magazine of Natural History* (series 9) 9: 422–431.

Turvey, S. T., T. E. Jeffree, A. A. Macdonald, K. Leus, R. J. Kennerley, Maharadatunkamsi, and A. C. Kitchener. 2023. Continued survival of the elusive Seram orange melomys (*Melomys fulgens*). *Mammalia* 87: 271–275. https://doi.org/10.1515/mammalia-2022-0135

Veatch, E. G., P.-H. Fabre, M. W. Tocheri, T. Sutikna, E. Wahyu Saptomo, G. G. Musser, and K. M. Helgen. 2023. A new giant shrew rat (Rodentia, Muridae, Murinae) from Flores, Indonesia and a comparative investigation of its ecomorphology. In *Contributions to Mammalogy and Zooarchaeology of Wallacea*, ed. K. M. Helgen and R. K. Jones. *Records of the Australian Museum* 75(5): 741–764. https://doi.org/10.3853/j.2201-4349.75.2023.1781

Wikramanayake, E., E. Dinerstein, C. J. Loucks, D. M. Olson, J. Morrison, J. Lamoreux, M. McKnight, and P. Hedao. 2002. *Terrestrial Ecoregions of the Indo-Pacific: A Conservation Assessment*. Washington, D.C.: Island Press.

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.