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## **Review of Moluccan Rattus (Rodentia: Muridae) with description of four new species**

Pierre-Henri Fabre, Roberto Portela Miguez, Mary Ellen Holden, Yuli S Fitriana,  
Gono Semiadi, Guy G Musser, Kristofer M Helgen

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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

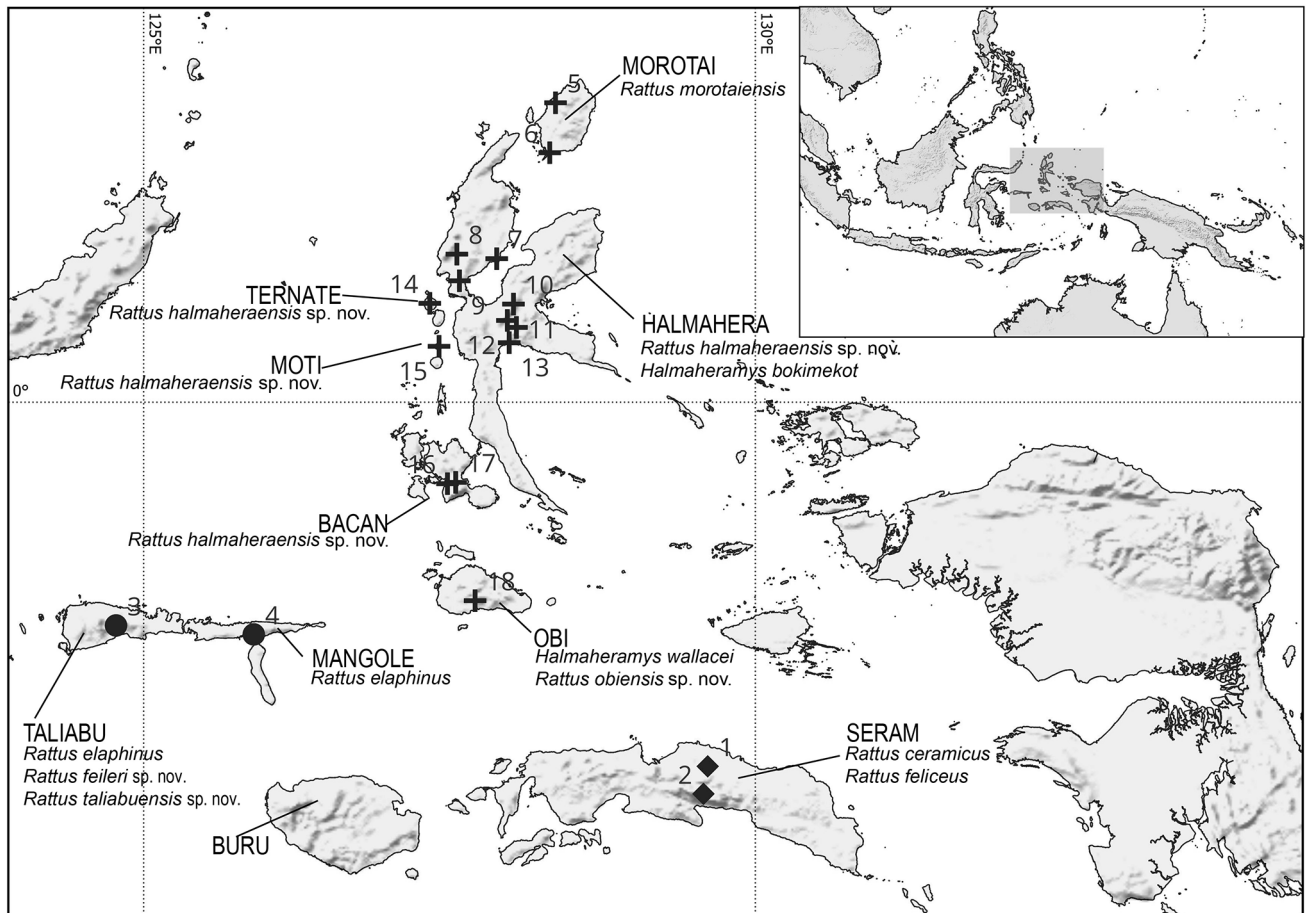
The Maluku Islands, also known as the Moluccas and the “Spice Islands”, form an archipelago within the Wallacean biogeographic region and comprise islands between Sulawesi and western New Guinea, from Morotai Island in the north to the Tanimbar Islands in the south (Monk *et al.*, 1997). Sporadic inter-island 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 Sulawesi 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*, *Baletomys*, *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: *Brcal* (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*, *Brcal*, *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 (Rodríguez *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).

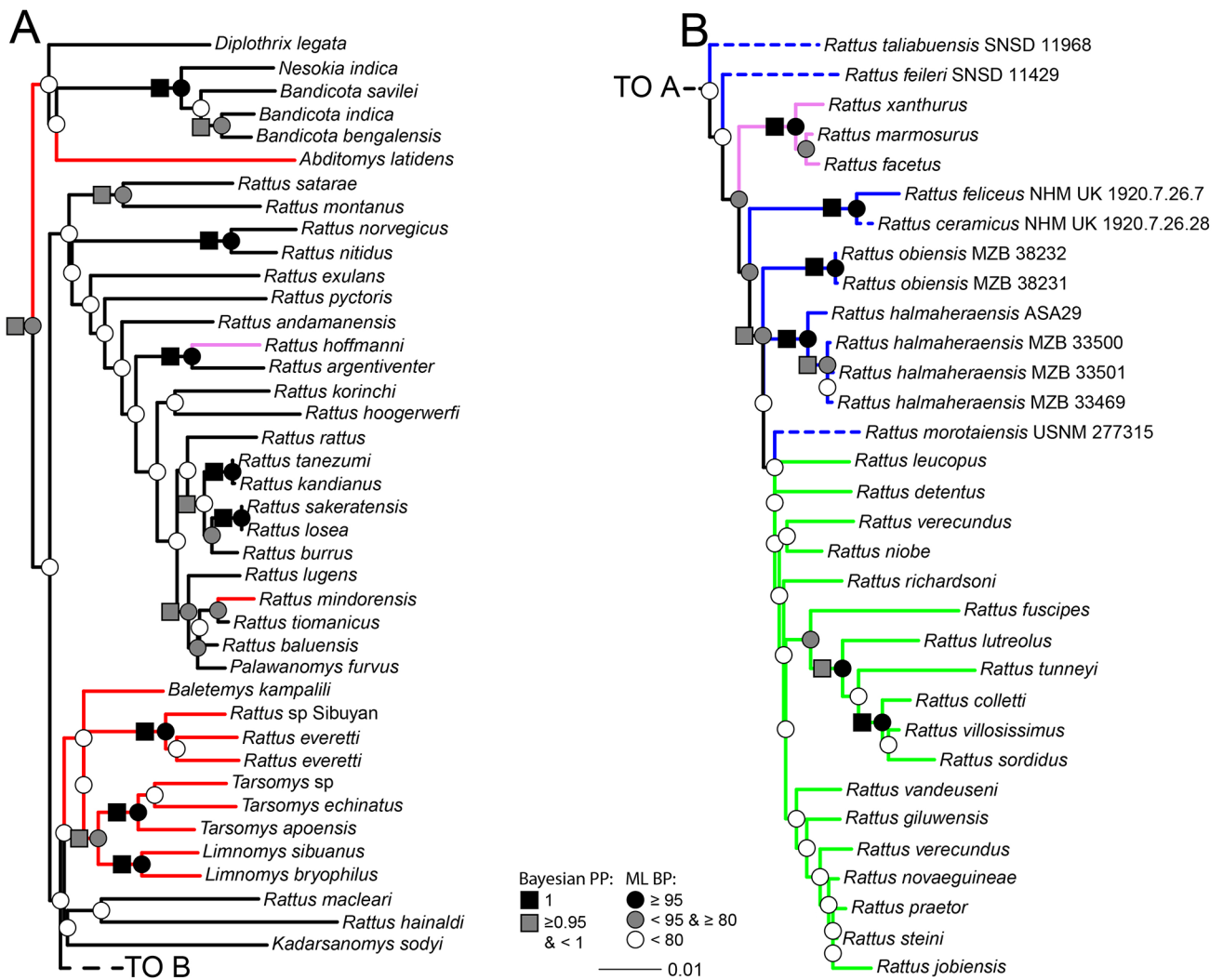
### Morphometric results

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 <i>R. taliabuensis</i> sp. nov.	—									
2 <i>R. feileri</i> sp. nov.	0.10	—								
3 <i>R. feliceus</i>	0.10	0.11	—							
4 <i>R. ceramicus</i>	0.09	0.11	0.04	—						
5 <i>R. halmaheraensis</i> sp. nov.	0.05–0.10	0.06–0.10	0.05–0.09	0.05–0.09	—					
6 <i>R. sp. cf. halmaheraensis</i> sp. nov. (Moti)	0.07	0.08	0.07	0.06	(<0.01)–0.07	—				
7 <i>R. obiensis</i> sp. nov.	0.10	0.10	0.10	0.09	0.05	0.04–0.07	—			
8 <i>R. facetus</i>	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 <i>R. xanthurus</i>	0.06	0.06	0.07	0.07	0.07	0.03–0.06	0.06	0.02–0.03	—	
10 <i>R. morotaiensis</i>	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  $\geq 95\%$ ; grey circles for ML bootstrap support  $< 95\%$  and  $\geq 80\%$ ; and white circles for ML bootstrap support  $< 80\%$ . Phylogenetic posterior probabilities (PP) are indicated by black squares for  $PP = 1$  and grey squares for  $1 > PP \geq 0.95$ . 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 (%)
<b>Seram</b>								
<i>Rattus ceramicus</i>	♂	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
<i>Rattus feliceus</i>	♂	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
<b>Taliabu</b>								
<i>Rattus elaphinus</i>	♂	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
<i>Rattus feileri</i> sp. nov.	♂	176	237	40	17	—	134	23
<i>Rattus taliabuensis</i> sp. nov.	♂	234	165	43	24	—	71	18
<b>Mangole</b>								
<i>Rattus elaphinus</i>	♂	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
<b>Morotai</b>								
<i>Rattus morotaiensis</i>	♂	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
<b>Halmahera</b>								
<i>Rattus halmaheraensis</i> 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
<b>Bacan</b>								
<i>Rattus halmaheraensis</i> sp. nov.	♂	200	224	39.5	18.7	158	112	20
<b>Obi</b>								
<i>Rattus obiensis</i> 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				
	<i>R. taliabuensis</i> sp. nov.		<i>R. elaphinus</i>		<i>R. feliceus</i>			<i>R. ceramicus</i>	
	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.

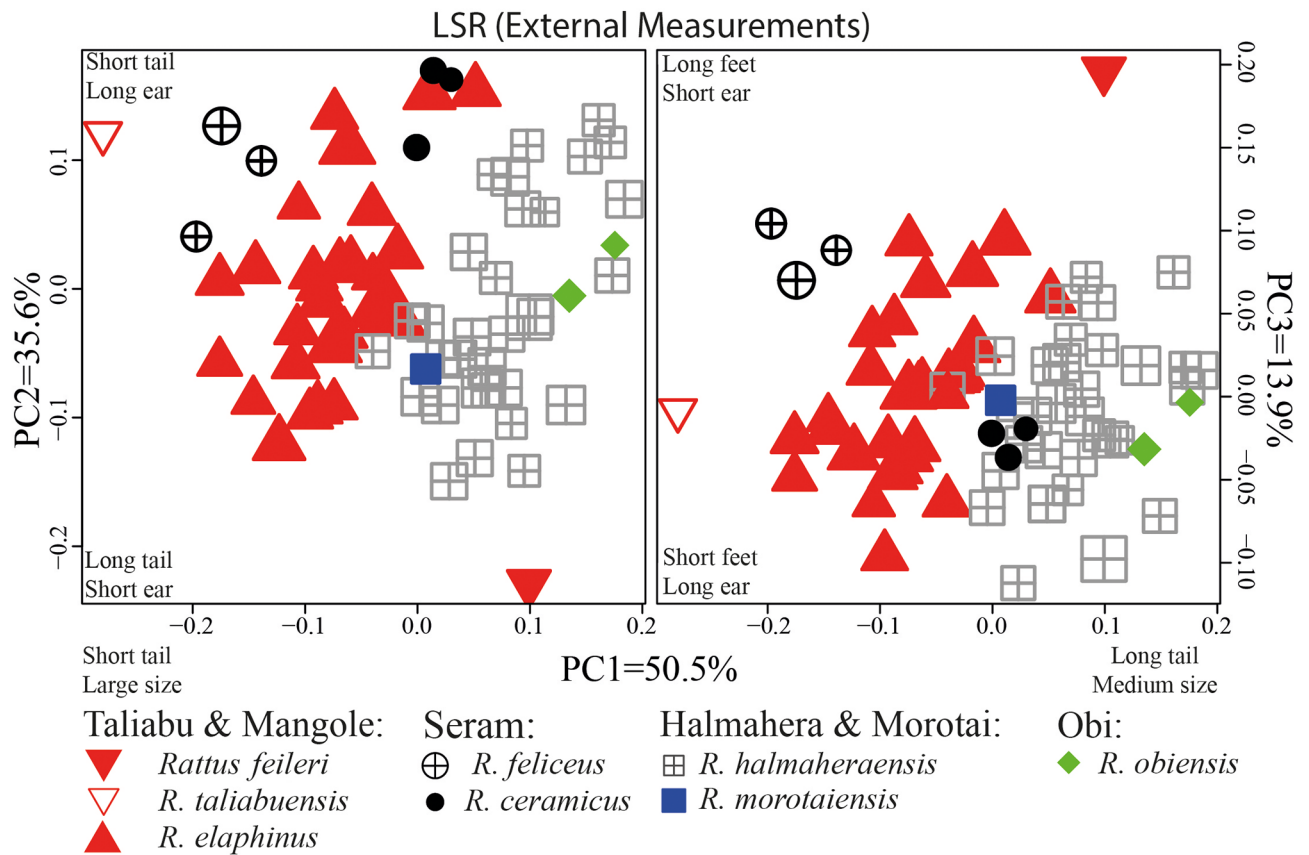
Dorsal shape analysis yielded a similar morphospace, but with less overlap between long-tailed and short-tailed rats. The PC1 axis separated (1) *Rattus* species with long rostra, wide lacrimal and zygomatic widths, and small braincases with a wide interparietal (*R. feliceus*, *R. ceramicus*, *R. elaphinus*, 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	
	<i>R. feileri</i> sp. nov.		<i>R. morotaiensis</i>			<i>R. halmaheraensis</i> sp. nov.			<i>R. obiensis</i> sp. nov.	
	SNSD	USNM				AM			MZB	MZB
	11429	277312				M.23652			38231	38232
Age	Young adult	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.

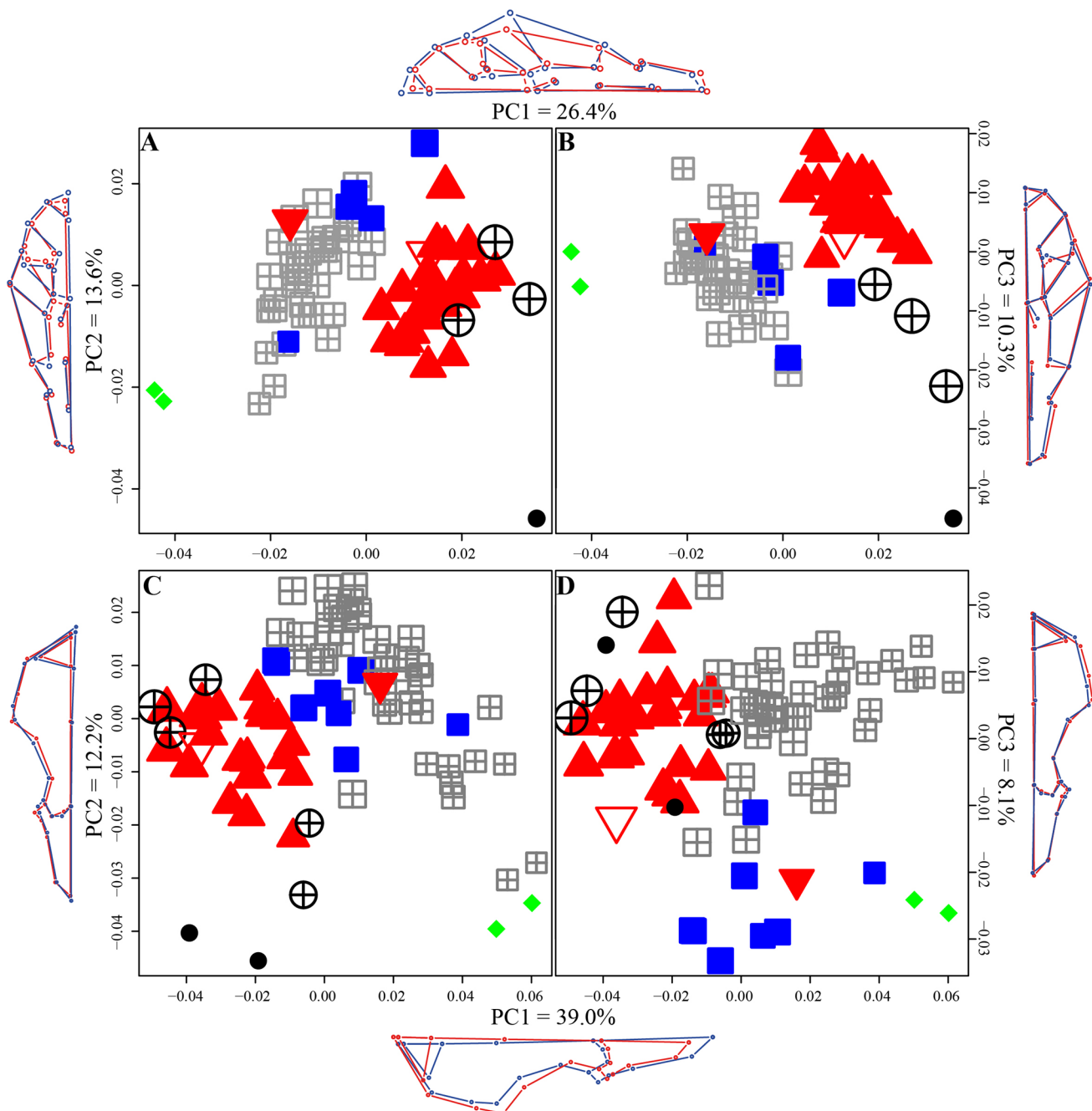
The pelage texture of *Rattus* species can be defined as spiny, bristly, harsh or soft-furred (cf. Emmons [2005: 254–255]). The length of the tail varies between species, both absolutely and relative to the length of the head and body. The tail is covered by overlapping rows of square scales; three hairs 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 tooththrows 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 stapedia 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 stapedia 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 stapedia artery branches from the common carotid artery, enters the periotic region through a large stapedia foramen, the infraorbital branch of the stapedia 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 stapedia 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 anteroconid 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

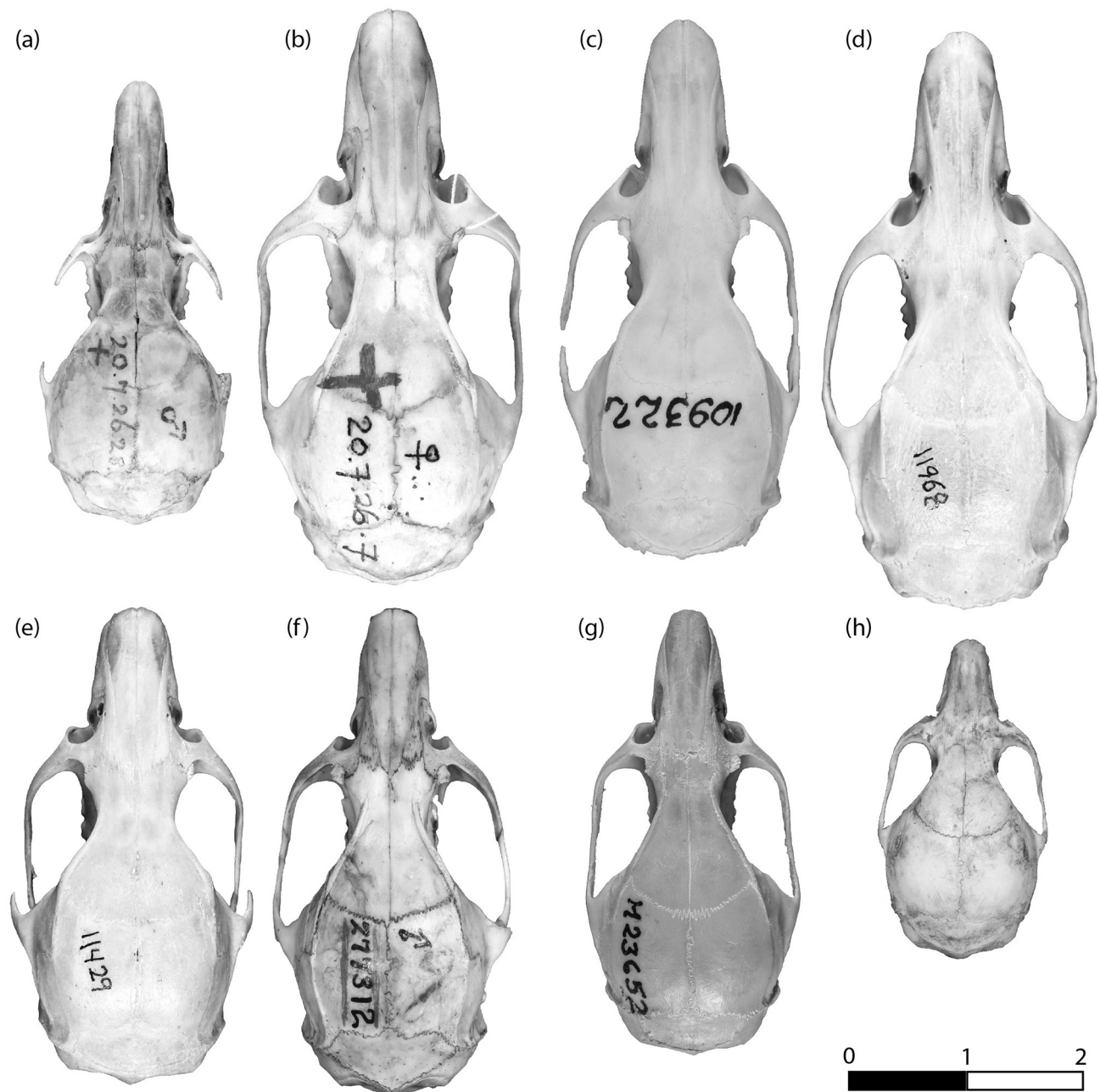
**Type material studied.** The type specimen (NHMUK ZD 1920.7.26.7) is an adult female collected at 6000 feet (1830 m) on Gunung Manusela, Seram Island, South Maluku (Figs 5–10). This specimen was caught by the Pratt brothers in February 1920 and described by Oldfield Thomas in the same year (Thomas, 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; Balette *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. aereus*, *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 antero-central 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.

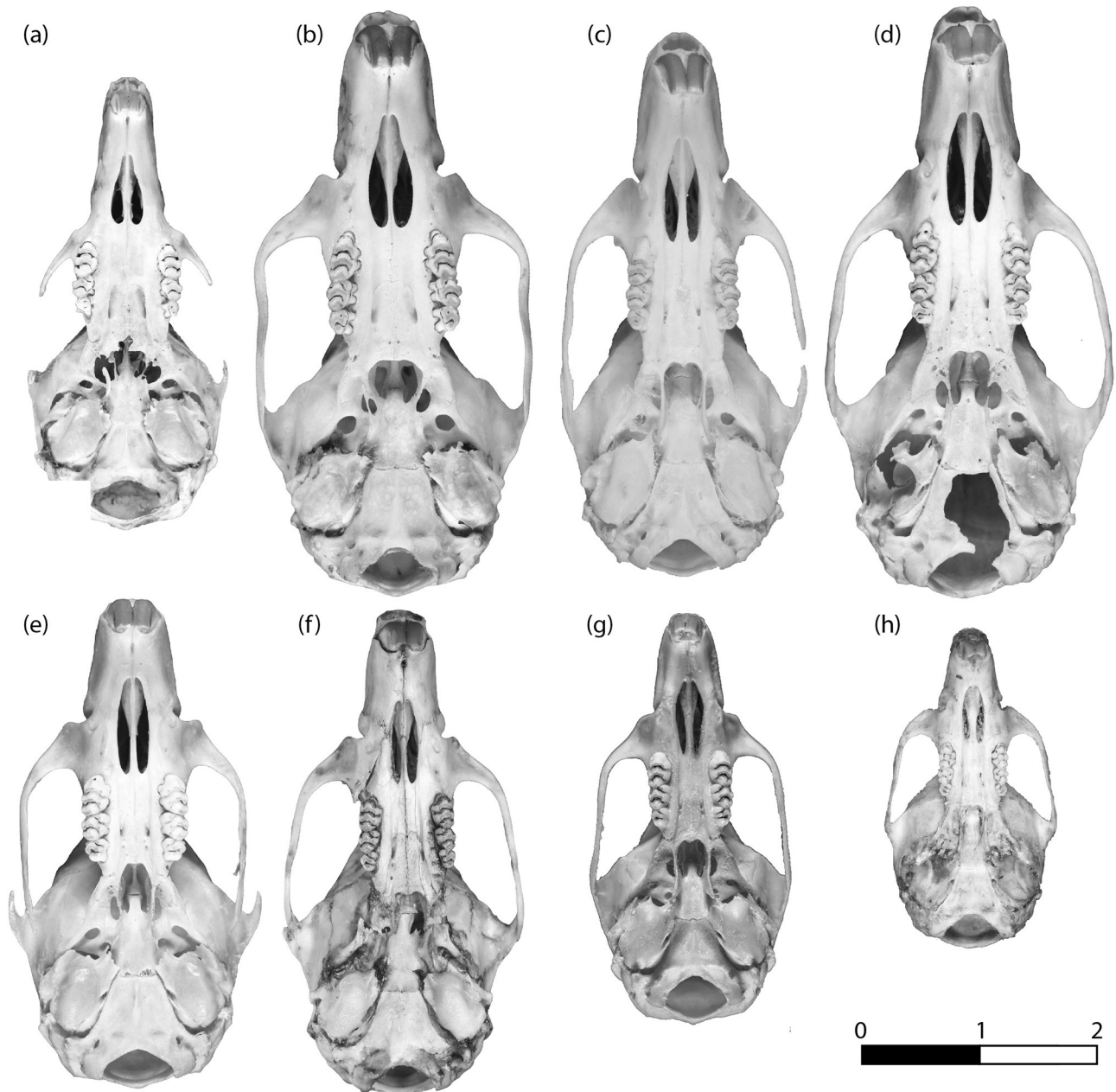
**Etymology.** We name this species in honour of German zoologist Alfred Feiler, who worked at the Staatliche Naturhistorische Sammlungen in Dresden until his retirement. Feiler kindly arranged the loan of Taliabu Island specimens to G. G. Musser, assisted K. M. Helgen on several visits to the museum 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 cusps as well as an anteroconid 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.

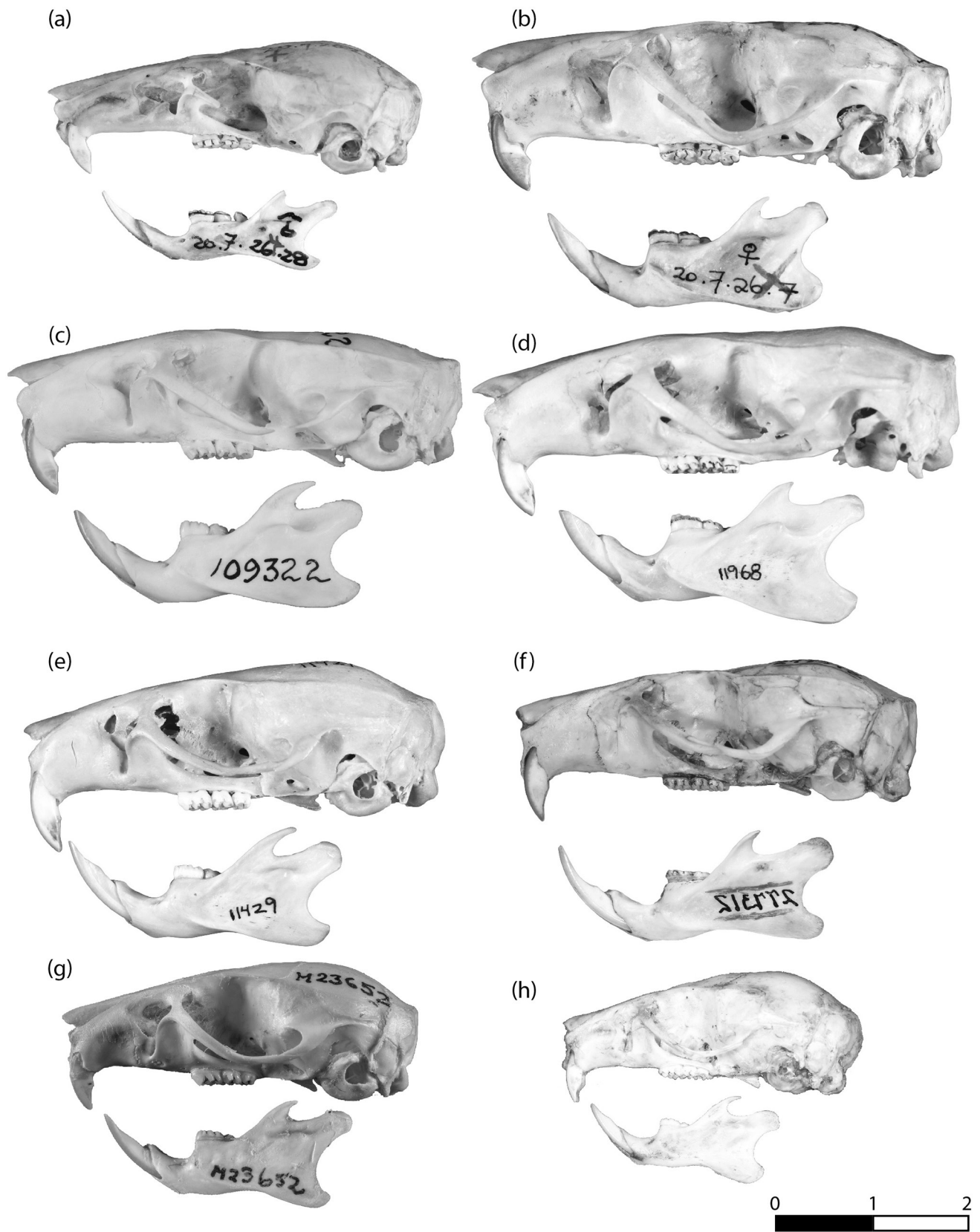
**Description and comparison with Taliabu *Rattus* and *R. morotaiensis*, *R. halmaheraensis* and *R. obiensis*.** *Rattus feileri* is of medium body size with a distinctive long tufted tail (Table 2 and Figs 11–12) and moderately long hind feet, and is similar in proportions to *Rattus halmaheraensis* 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 anteroconid 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

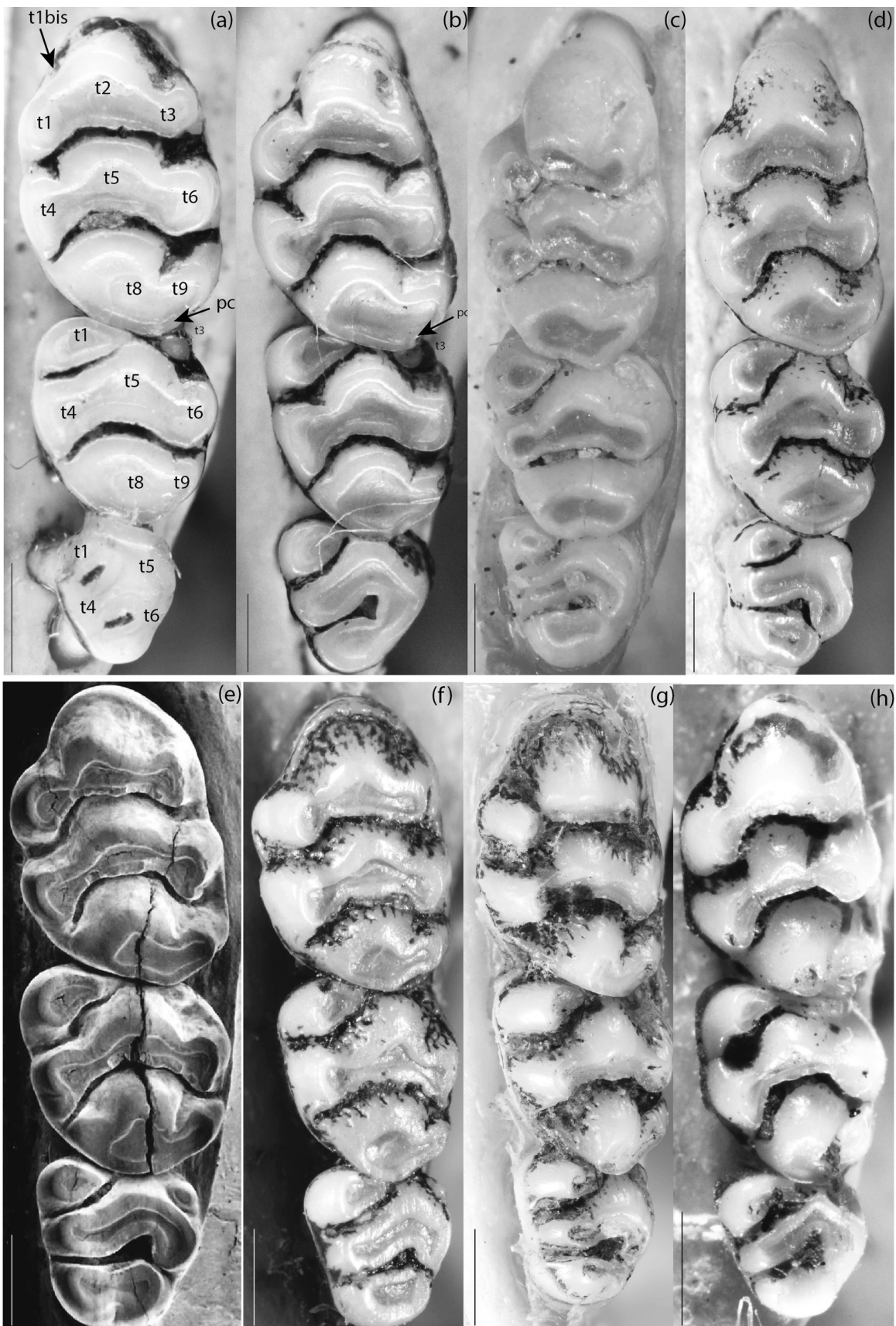
**Holotype:** The holotype is an adult (scrotal) male collected by the commercial collector J. J. Menden on 27 September 1938 on “Insel Taliaboe Molukken” (Taliabu Island, Maluku) and labelled SNSD 119968 (in Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde). Method of collection 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.** Oclusal 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 = antero-central; a-lab = anterolabial; md = metaconid, pd = protoconid, alc = anterolabial cusplet; plc = postero-labial 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.

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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

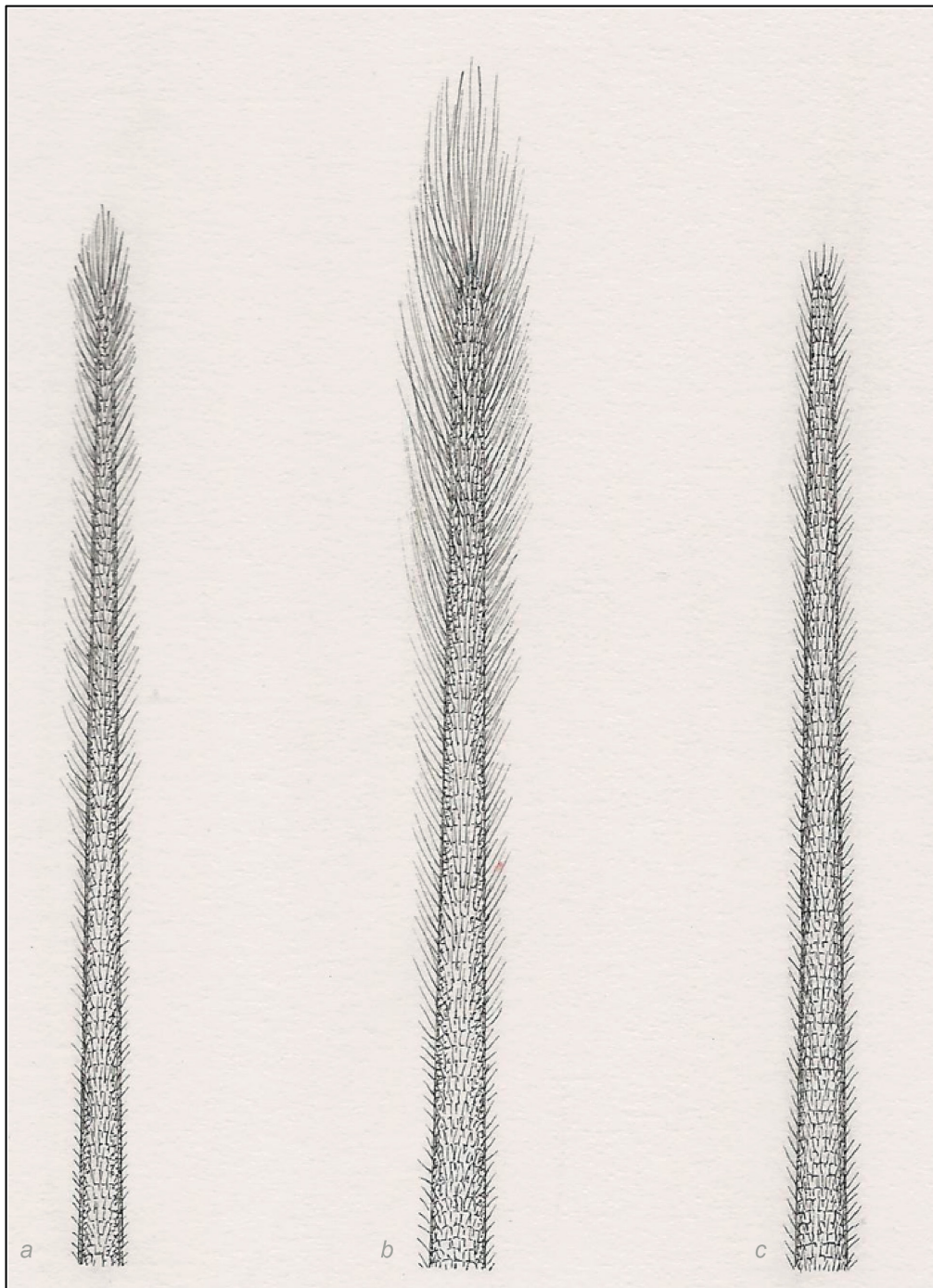


**Figure 11.** Dorsal and ventral views of study skins of (a, d) *Rattus feileri* sp. nov. (SNSD 11429 holotype); (b, e) *R. elaphinus* (AMNH 109322 paratype); and (c, f) *R. taliabuensis* sp. nov. (SNSD 11968 holotype). Scale bar 10 mm.

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 cusplets, 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.

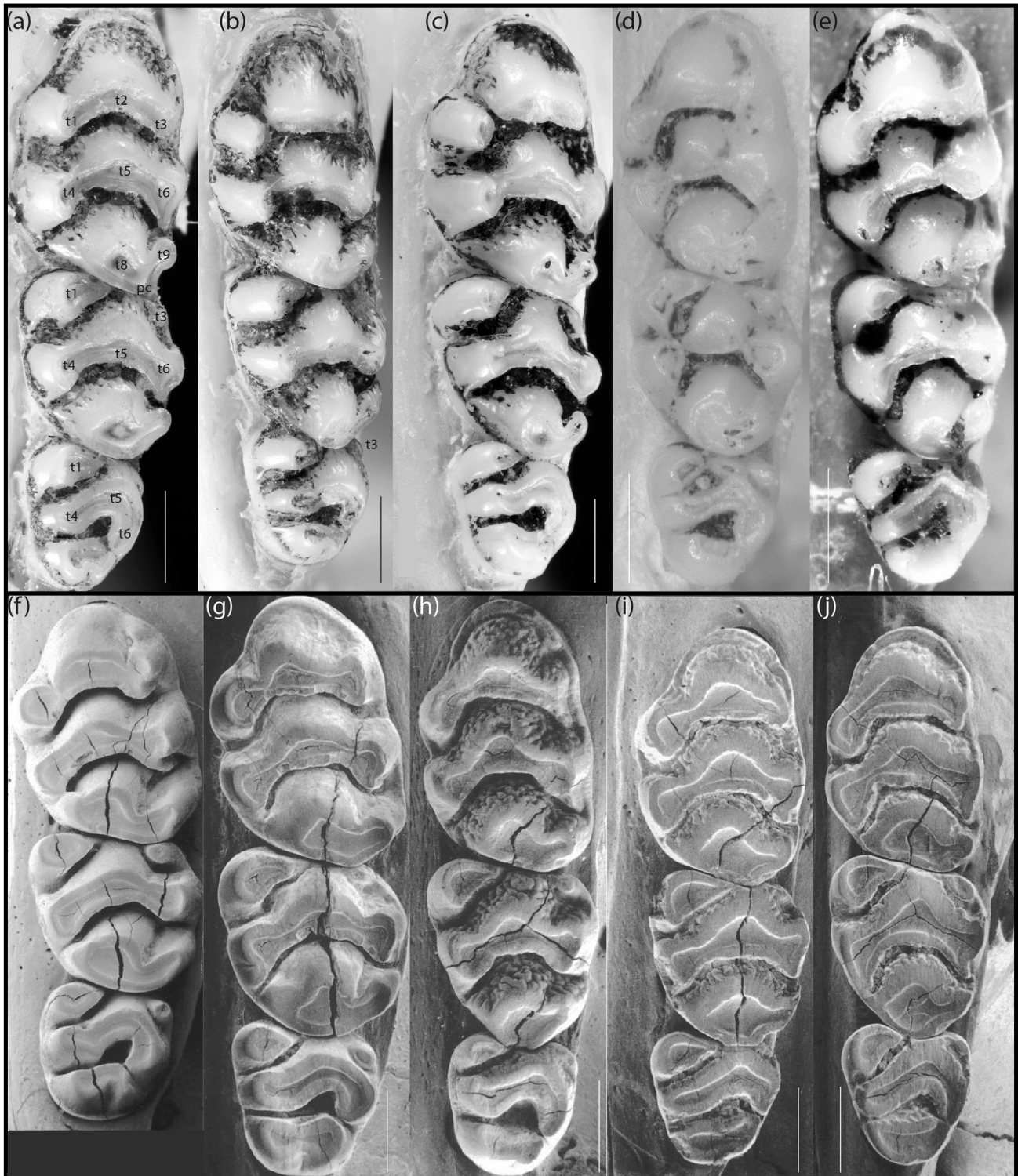
*Rattus obiensis* is a small rat with broad spiny hairs, characterized by the following features: (1) a long dark tail, which is longer than the head and body length (TL/HB = 128–130%; see also Table 2; Fig. 15 and Fig. 20); (2) long hind feet in proportion to the head and body length; (3) the palatal 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

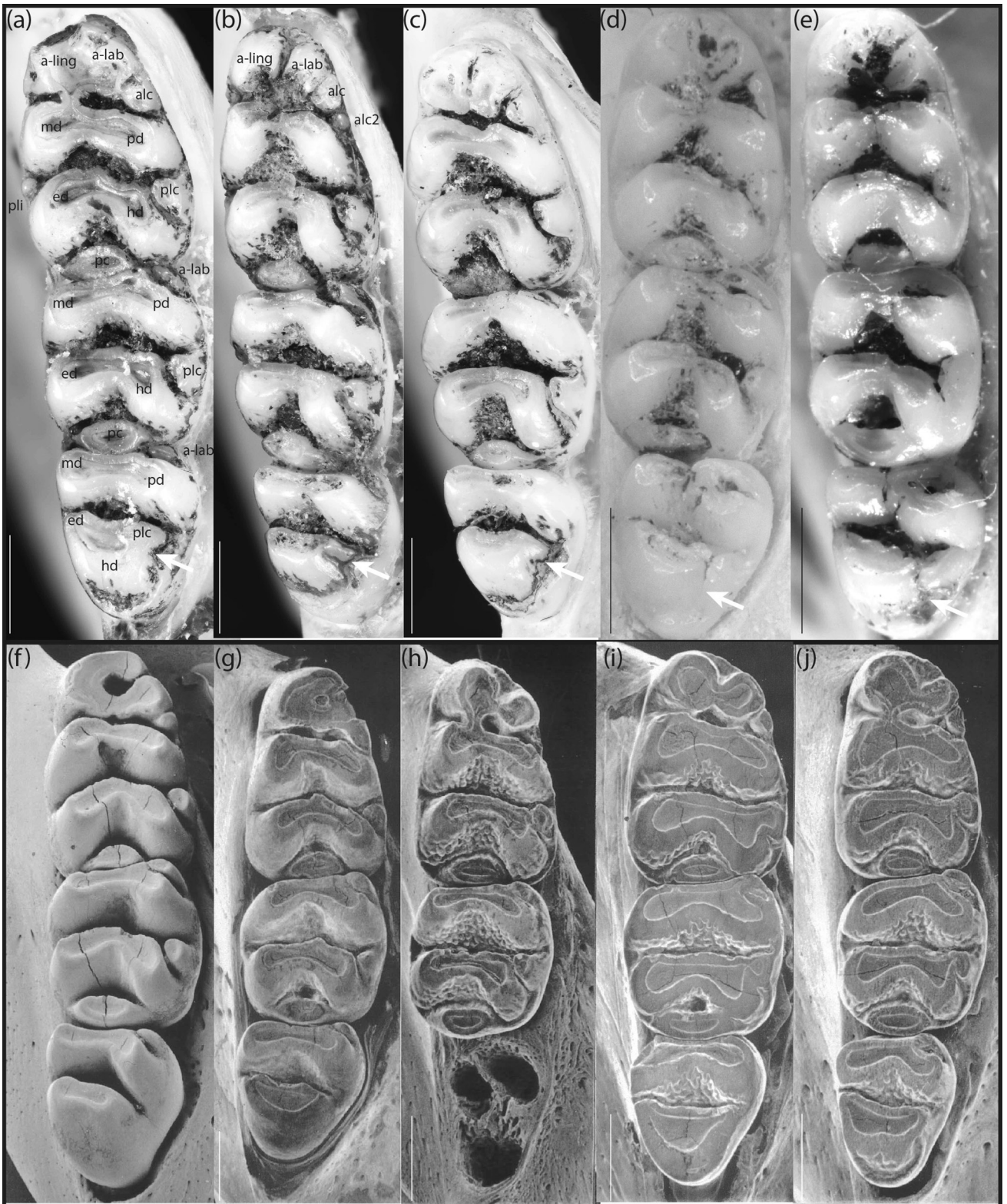
are bicoloured, with bases that are whitish grey and tips that are golden brown, buff, or greyish brown as in *R. halmaheraensis* of the same age. Some of the guard hairs are thickened and ivory coloured. The dorsal fur is darkest, becoming paler along the mid-line of the body, where the dorsum meets 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 cusps. 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 cusps on m3, present in *R. morotaiensis* but only in a minority of specimens of *R. halmaheraensis*, are present in both specimens of *R. obiensis*.

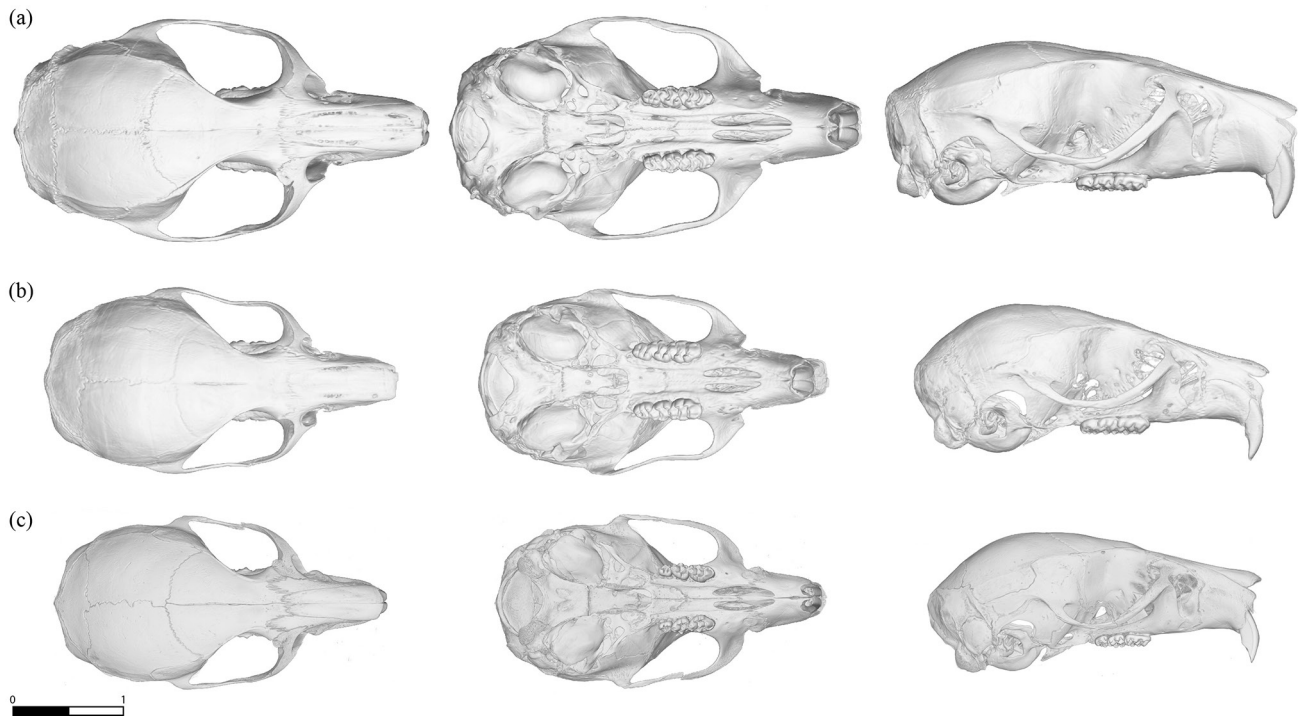
## Discussion

### 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*, *Baletomys*, *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.

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### 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, Piliانا village (3.20501°S 129.57604°E): 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.

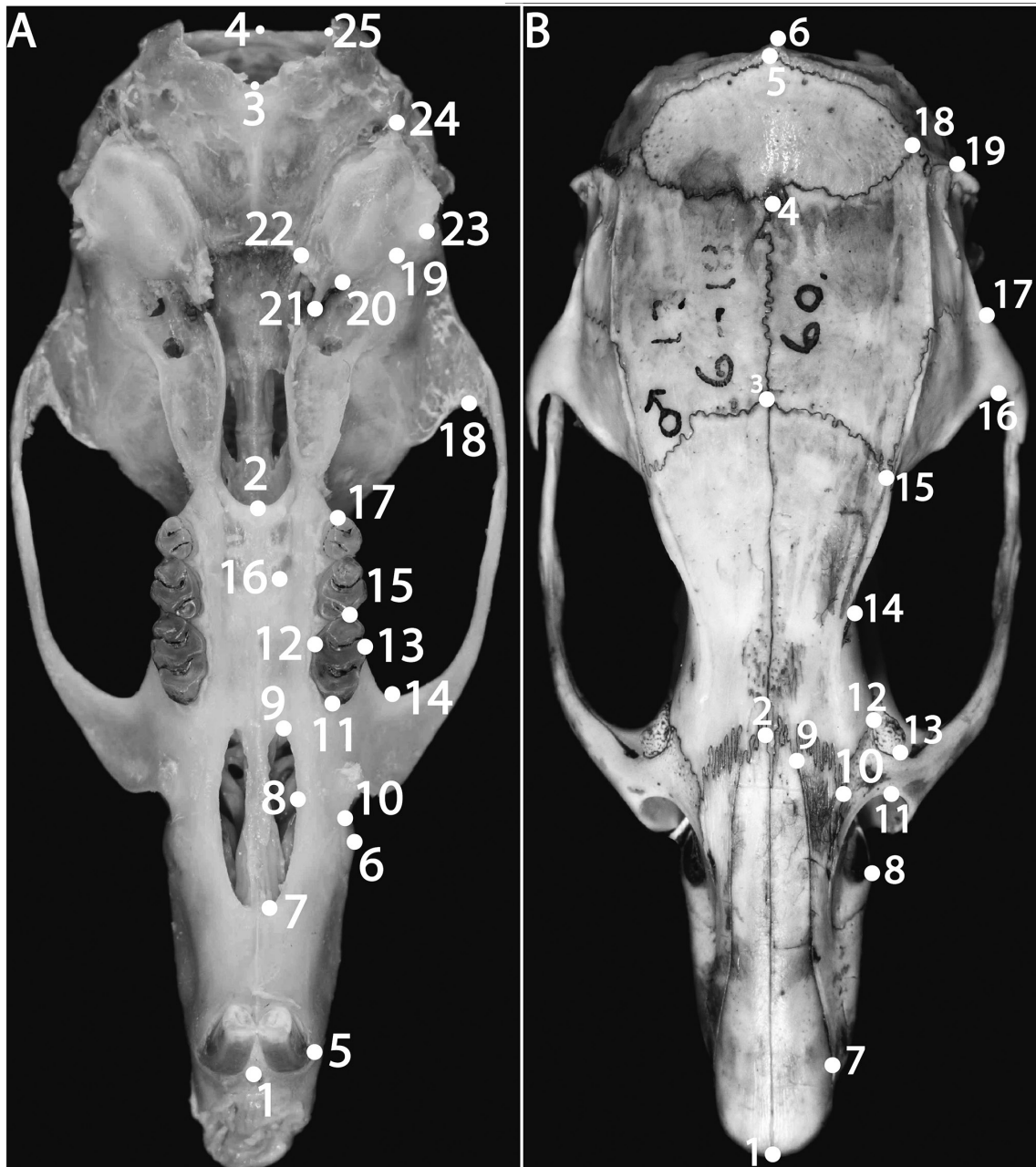
#### *Rattus halmaheraensis* sp. nov.

- (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.

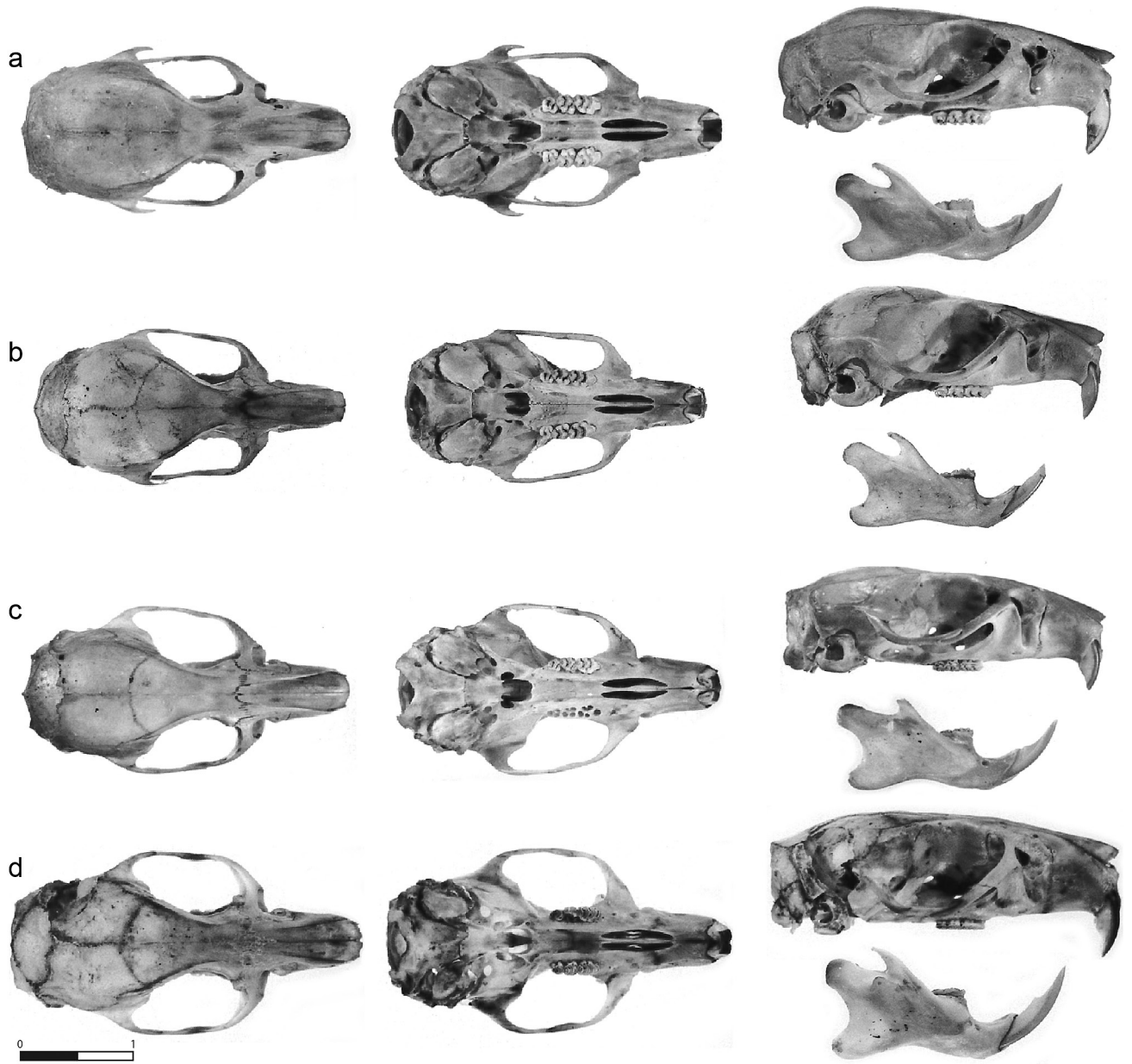
#### *Rattus obiensis* sp. nov.

- (18) Pulau Obi, Gunung Sere (1.624°S 127.709°E): MZB 38231–38232.
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## Appendix 2. Supplementary figures and tables.



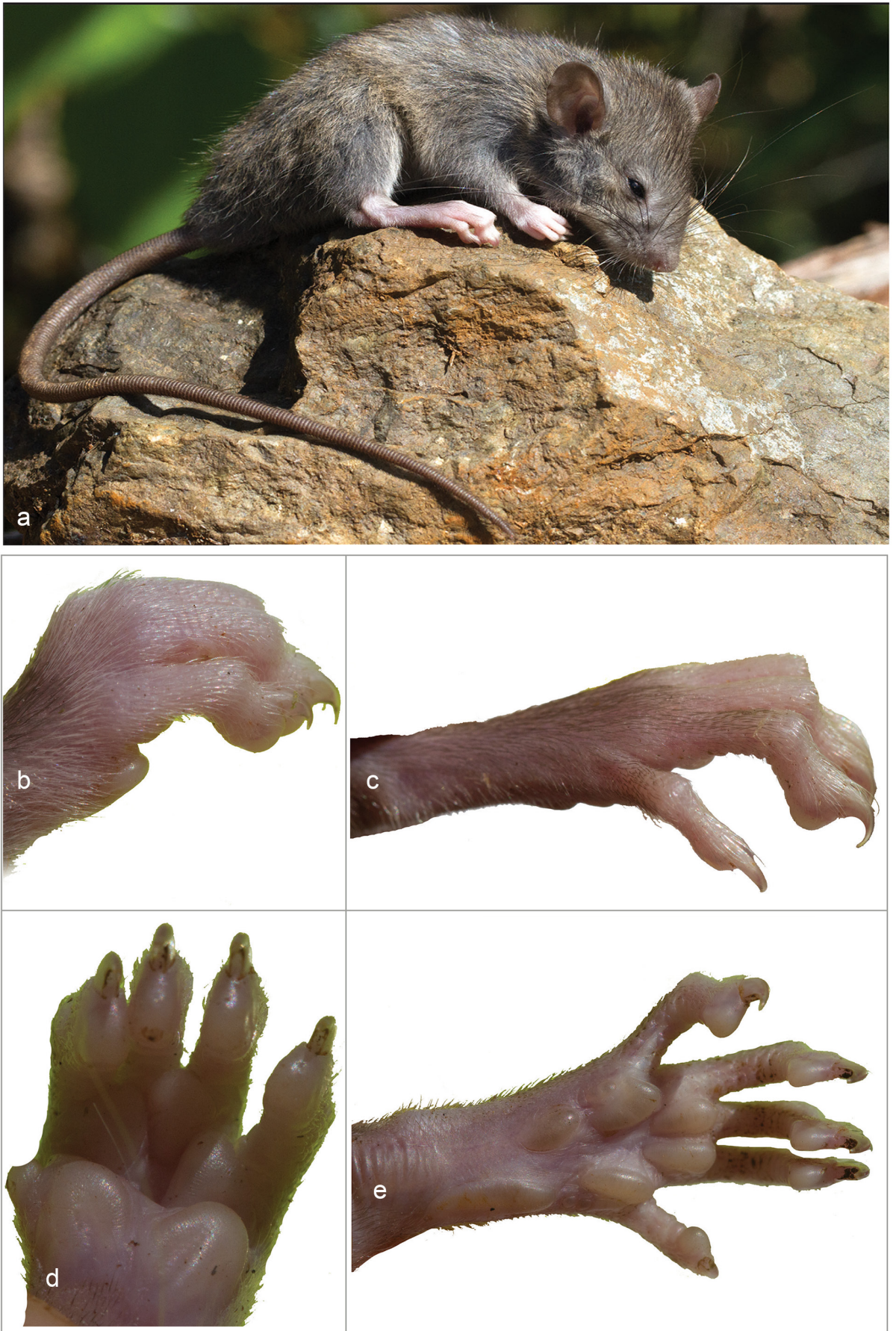
**Figure 17.** (A) Landmark locations on palatal side: (1) premaxillary bone between anterior margin of upper incisors, (2) posterior margin of the palatal bone, (3) anterior margin of the foramen magnum, (4) posterior margin of the foramen magnum, (5) lateral margin of the right incisor, (6) lateral 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	<i>Cytb</i>	BRCA1	GHR	IRBP	RAG1
<i>Abditomys latidens</i>	USNM 357244	United States National Museum	<i>this study</i>	na	na	na	na
<i>Baletemys kampalili</i>	FMNH 194804	Field Museum of Natural History	OM502714	na	OM502622	OM502591	OM502575
<i>Bandicota bengalensis</i>	T065	na	AM408336	na	AM910945	AM408331	na
<i>Bandicota indica</i>	ABTC 64912	South Australian Museum	KY753950	na	na	HM217713	na
<i>Bandicota savilei</i>	R1191	na	HM217385	na	na	HM217665	na
<i>Diplothrix legata</i>	HS 1163	na	AB033696	EU349670	EU349799	AB033706	EU349885
<i>Kadarsanomys sodyi</i>	MZB 34728	Museum Zoologicum Bogoriense	MG189671	<i>this study</i>	MG189687	MG189697	<i>this study</i>
<i>Limnomys bryophilus</i>	FMNH 148182	Field Museum of Natural History	OM502705	na	OM502616	OM502586	OM502570
<i>Limnomys sibuanus</i>	FMNH 206281	Field Museum of Natural History	OM502706	na	OM502617	OM502587	OM502571
<i>Nesokia indica</i>	Nind580	na	AF160605	—	—	—	—
<i>Palawanomys furvus</i>	FMNH 196056	Field Museum of Natural History	OM502717	na	OM502626	na	na
<i>Rattus andamanensis</i>	AMNH 272324	American Museum of Natural History	KY754124	na	na	HM217641	MF097929
<i>Rattus argentiventer</i>	MSB 93171	Museum of Southwest Biology	KY754125	na	na	HM217602	MF097930
<i>Rattus baluensis</i>	EBD 30360M	Estación Biológica de Doñana	NC_035621	na	na	na	na
<i>Rattus burrus</i>	USNM 111810	United States National Museum	Thomson <i>et al.</i> , 2018**	na	na	na	na
<i>Rattus ceramicus</i>	NHMUK ZD 1920.7.26.28	Natural History Museum (London)	<i>this study</i>	na	na	na	na
<i>Rattus colletti</i>	ABTC51642	South Australian Museum	na	HQ334408	na	HQ334596	HQ334665
<i>Rattus detentus</i>	PNGMAG274363	Australian Museum	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*
<i>Rattus everetti</i>	FMNH 142350	Field Museum of Natural History	DQ191485	na	na	DQ191513	na
<i>Rattus exulans</i>	NK 80010	na	NK 80010	na	DQ019074	KC953446	DQ023455
<i>Rattus facetus</i>	MVZ 225821	Museum of Vertebrate Zoology	MN273046	MN272962	MN272984	MN273005	MN273026
<i>Rattus feileri</i>	SNSD 11429	SNSD Dresden <sup>b</sup>	<i>this study</i>	na	na	na	na
<i>Rattus feliceus</i>	NHMUK ZD 1920.7.26.7	Natural History Museum (London)	<i>this study</i>	<i>this study</i>	<i>this study</i>	<i>this study</i>	<i>this study</i>
<i>Rattus fuscipes</i>	GI02R01/ABTC8644	South Australian Museum	na	HQ334429	na	HQ334620	HQ334683
<i>Rattus giluwensis</i>	ABTC87301	South Australian Museum	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*	Roycroft <i>et al.</i> , 2022*
<i>Rattus hainaldi</i>	WAM M35570	Western Australian Museum	Thomson <i>et al.</i> , 2018**	na	na	na	na
<i>Rattus halmaheraensis</i>	ASA M85	Museum Zoologicum Bogoriense	MN273047	MN272963	MN272985	MN273006	Roycroft <i>et al.</i> , 2022*
<i>Rattus halmaheraensis</i>	MZB 33500	Museum Zoologicum Bogoriense	<i>this study</i>	na	<i>this study</i>	<i>this study</i>	na
<i>Rattus halmaheraensis</i>	MZB 33501	Museum Zoologicum Bogoriense	<i>this study</i>	na	<i>this study</i>	<i>this study</i>	na
<i>Rattus halmaheraensis</i>	MZB 33469	Museum Zoologicum Bogoriense	<i>this study</i>	<i>this study</i>	<i>this study</i>	<i>this study</i>	na
<i>Rattus hoffmanni</i>	MVZ 225813	Museum of Vertebrate Zoology	KC878168	MK920935	KC878200	KC878238	MK920936
<i>Rattus hoogerwerfi</i>	ANSP 20319	Drexel University <sup>c</sup>	MN126561	na	na	na	na
<i>Rattus jobiensis</i>	NHMUK ZD 46.633	Natural History Museum (London)	<i>this study</i>	<i>this study</i>	<i>this study</i>	<i>this study</i>	<i>this study</i>
<i>Rattus kandianus</i>	ABTC 08529	South Australian Museum	JN675603	na	na	na	na
<i>Rattus korinchi</i>	RMNH 23151	Naturalis Museum	NC_049042	na	na	na	na
<i>Rattus leucopus</i>	ABTC42806 /KU 160770	SAM and KUM <sup>d</sup>	na	HQ334396	EU349825	HQ334582	HQ334652
<i>Rattus losea</i>	ABTC 118627	South Australian Museum	HM031715	na	na	na	na

Table 6. *Continued ...*

Table 6. Continued.

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

<sup>a</sup> Rnor\_6.0 reference Annotation Release 106.<sup>b</sup> SNSD—Staatliche Naturhistorische Sammlungen Dresden, Museum für Tierkunde.<sup>c</sup> The Academy of Natural Sciences of Drexel University.<sup>d</sup> South Australian Museum / Kansas University Museum.<sup>e</sup> The Commonwealth Scientific and Industrial Research Organisation.<sup>f</sup> 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.

Factors	(a) LSR				(b) Ventral skull				(c) Dorsal skull			
	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).

Factors	3pc						36pc						35pc					
	(a) LSR						(b) Ventral skull						(c) Dorsal skull					
	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					