

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 revisi 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