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Murine rodents (Rodentia: Murinae) of the Myanmar-Thai-Malaysian peninsula and Singapore: taxonomy, distribution, ecology, conservation status, and illustrated identification keys

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Abstract. Based on field surveys undertaken between 2010 and 2013, museum studies in Thailand and the UK, and an extensive literature review, this paper provides information on the 28 species and 12 genera of murine rodents currently known from peninsular Myanmar, Thailand and Malaysia and Singapore. It incorporates a detailed summary of past research, 1851–2013, of the Murinae in the study area and includes descriptive characters of the external, cranial and dental morphology and measurements for each of the rodent species. It lists and maps the 93 murine taxa described from the peninsula, 84 of which are currently considered to be synonyms at species level. Each of the 389 different localities on the 28 distribution maps is numbered and linked to its source, either literature or museum specimen, and listed in the online gazetteer. The global conservation status of each species is obtained from the IUCN Red List. Remarks are made, where data are available, on the ecology, karyology, fossil history, sperm morphology, phylogeny, and taxonomic history and ambiguities. Recommendations are made for further research. A series of illustrated matrix keys is provided to assist with the identification of all the murine genera and species within the study area.

Key words. Taxonomy, distribution, identification keys, karyology, ecology, conservation status.

INTRODUCTION

With 2,277 species, the order Rodentia represents approximately 42 % of all mammal diversity (Musser & Carleton 2005). Geographically widespread and highly adaptable, rodents occupy a vast array of diverse ecological niches. They impact on the composition, structure, and succession of vegetation and fulfil many important ecosystem services, including assisting with nutrient cycling and the dispersal of seed and spores. Through their burrowing activities, they mix and aerate soils and with their high biomass, they provide an essential prey base for many predator species (Witmer 2004).

A minority of species causes significant problems to man. For example, in Asia, it is considered that in any one particular area between 5 and 10 % of rodent taxa are major agricultural pests (Aplin et al. 2003). As such, they eat crops in the field, typically reducing yields of rice by 5 to 10 % (Aplin et al. 2003), 6 % in pineapples (Joomwong 2007) and 5 % in oil palms (Aplin et al. 2003). They eat, spoil and contaminate stored food and post-harvest losses of 20 % are not unusual. They also carry diseases that can be transmitted either directly or indirectly to humans and livestock (Aplin et al. 2003; Chaval et al. 2010; Witmer 2004). Some of the most virulent diseases borne by rodents in Southeast Asia include: hantavirus, leishmania infection, leptospirosis, scrub typhus, toxoplasmosis and viral haemorrhagic fevers (Chaval et al. 2010; Herbreteau et al. 2012, http://www.ceropath.org/research/ rodent _borne_diseases).

Recognising the importance of rodents, both as biological entities and because of their association with man, the current paper, which is based on the unpublished work of Pimsai (2012), seeks to provide a baseline for future research of murines in peninsular Myanmar, Thailand, Malaysia and Singapore. The study area is illustrated in dark grey in Fig. 1 and all subsequent maps. It should be noted that although the northern boundary is clearly an artifact of geography, corresponding to the northern limit of peninsular Thailand, it also has zoogeographical significance approximating as it does to the Indochinese-Sundaic transition zone, although it is recognised that the exact location of this zone varies amongst different taxa and has been interpreted in different ways by different authors (Woodruff 2003, Woodruff &Turner 2009, Hughes et al. 2011).

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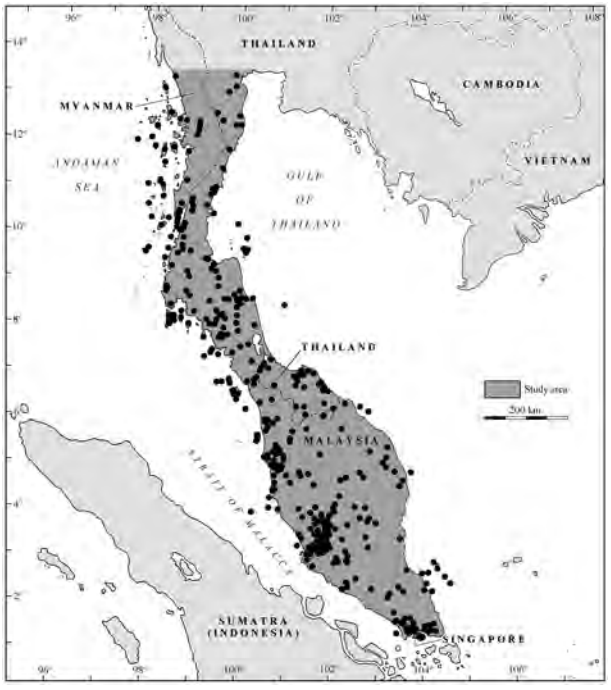

Fig. 1. Study area: peninsular Myanmar, Thailand and Malaysia, and Singapore. Localities from which specimen data were obtained are mapped and listed in the Gazetteer.

The paper focuses on the Murinae as this is the most speciose subfamily worldwide, with 561 species and 126 genera, within the largest Rodent family, the Muridae, 730 species and 150 genera (Musser & Carleton 2005). Within the study area, the Murinae, the rats and mice, have the highest population sizes, the greatest biomass, the greatest impact on man of all the rodents, and the richest diversity: 28 species and 12 genera (sensu Musser & Carleton 2005) – *Bandicota bengalensis* (Gray), *B. indica* (Bechstein), *B. savilei* Thomas, *Berylmys berdmorei* (Blyth), *B. bowersii* (Anderson), *Chiropodomys gliroides* (Blyth), *Hapalomys longicaudatus* Blyth, *Lenothrix canus* Miller, *Leopoldamys ciliatus* (Bonhote), *L. sabanus* (Jentink), *Maxomys inas* (Bonhote), *M. rajah* (Thomas), *M. surifer* (Miller), *M. whiteheadi* (Thomas), *Mus musculus* Linnaeus, *M. caroli* Bonhote, *Niviventer cameroni* (Chasen), *N. cremoriventer* (Miller), *N. fulvescens* (Gray), *Pithecheir parvus* Kloss, *Rattus andamanensis* (Blyth), *R. annandalei* (Bonhote), *R. argentiventer* (Robinson & Kloss), *R. exulans* (Peale), *R. norvegicus* (Berkenhout), *R. tanezumi* (Temminck), *R. tiomanicus* (Miller),and *Sundamys muelleri* (Jentink).

As a baseline, the paper seeks to put the complex taxonomy of the Murinae from the study region into context. This subfamily includes taxa from two tribes, the Murini and Rattini, and one ill-defined group, the 'Murinae *incertis sedis'* as defined by Lecompte et al. (2008). All 93 taxa described from the area are listed in Table 1. Of these, 44 were originally described as new species and 49 as subspecies. Forty-two were described from peninsular Malaysia (as understood today), 30 from peninsular Thailand, 19 from peninsular Myanmar and 2 from Singapore. Most were named at the start of the 20th Century, 65 between 1900 and 1919 and 19 between 1931 and 1941 with only six, from 1960 onwards. The most recent was described from Thailand in 1989. All but nine (*Berylmys berdmorei, Leopoldamys ciliatus, Maxomys inas, M. surifer, Niviventer cameroni, N. cremoriventer, Pithecheir parvus, Rattus annandalei,* and *R. tiomanicus* – highlighted in bold in Table 1) are considered today as synonyms, at species level. To further aid understanding of the taxonomy, the type locality of each taxon is plotted on the relevant distribution map.

The distribution maps are the first for all murine rodents from the study region that seek to give a higher level of geographical resolution by featuring spot localities rather than the more familiar shaded maps as available in Marshall (1988), Corbet & Hill (1992), and Francis (2008). Previously, some spot maps were available, as part of larger taxonomic studies, for certain species such as *Hapalomys longicaudatus* (Musser 1972), *Chiropodomys gliroides* (Musser 1979), *Sundamys muelleri* (Musser & Newcomb 1983) and *Bandicota* (Musser & Brothers 1994).

Literature sources for the maps were drawn from a large number of references dating back to Blyth (1851). These references, together with many others directly relating to murine rodents in the study area, are reviewed and summarised below. It is hoped that this review will provide a valuable starting point for all who wish to conduct further research on murine rodents in the study area.

The majority, approximately 60 % of the 115 publications included in the review is concerned with aspects of taxonomy. This is especially the case for papers and books published in the first one hundred years (1851–1950). During this time, all 40 publications were either exclusively, or primarily taxonomic and 30 included descriptions of new murine taxa (Table 1). Post 1950, researchers in the peninsula began to investigate additional aspects of murine rodents, including reproduction, behaviour, ecology, karyology, palaeontology, phylogeny, and the transfer of diseases between rodents and man.

A particular aim of this paper (*inter alia*) is to complement and support exciting new research looking at the phylogeny of rodents in the region based on combined mitochondrial and nuclear markers, for example Latinne et al. (2012, 2013b). The paper seeks to support the idea of a multi-approach to rodent identification as evinced by Chaval et al. (2010) by providing a detailed summary of the alpha taxonomy of the Murinae. It is hoped that the paper will facilitate future research of rodent taxonomy in Southeast Asia, and especially amongst in-country students and zoologists based in Thailand, Malaysia and

Myanmar, and will help promote studies that combine both morphometric and molecular approaches.

It is anticipated that the paper will assist those who wish to investigate further the taxonomy of species, the status of which has been questioned in a series of papers and on-line publications, for example *Berylmys berdmorei, Sundamys muelleri,* and *Rattus tiomanicus* (in Musser & Newcomb 1983), *Leopoldamys sabanus* (in Musser & Carleton 2005 and Balakirev et al. 2013) and *Niviventer fulvescens* (in Musser & Carleton 2005 and Balakirev et al. 2011), *Maxomys surifer* (in Gorog et al. 2004, Aplin et al. 2008c and Latinne et al. 2013b), and *Rattus tanezumi* (Heaney & Molur 2008 and Aplin et al. 2011). It is also in response to papers such as Francis et al. (2010), which although primarily concerned with bats, suggest that the number of mammal species currently recognised in Southeast Asia may represent only 50 % of the real diversity. In addition, it supports Waengsothorn et al. (2009) who highlight the need for further rodent research in Thailand.

This paper seeks to complement the taxonomic work of close colleagues working on other small mammal taxa in the region. This team of young taxonomists, based in the Prince of Songkla University (Thailand), National University of Laos, the Royal University of Phnom Penh (Cambodia), and the Institute of Ecology and Biological Resources (Vietnam), have studied extensively a range of taxa in mainland Southeast Asia. Together with members of the Harrison Institute, UK and other collaborating institutions, they have described several new species of bat (Douangboubpha et al. 2011, Soisook et al. 2013a and 2013b; Thong et al. 2012) and a new flying squirrel (Sanamxay et al. 2013). Additionally, they have undertaken many studies of small mammal diversity and distribution (extant and fossil) in the same area (Furey et al. 2012; Ith et al. 2011; Kingsada et al. 2011; Pearch et al. 2013; Thomas et al. 2013).

Correct identification of species is of primary importance to many studies (Chaval et al. 2010). Some species are considered agricultural pests whilst others, even within the same genus, are harmless or even beneficial, feeding on harmful invertebrates (molluscs and insects) and invasive weeds. Some species are the reservoir of zoonotic diseases deleterious to man, whilst others, closely similar in external morphology are not. To meet the challenges of murine identification within the study area, we have devised a series of keys that together, help with the identification of all 28 murine species. Those for the species are included in a series of Tables in the relevant sections of the text. Those for the genera are in Tables 25A, B & C. The diagnostic characters included in the matrix keys have been extracted from the generic and species descriptions. These matrices include a range of external, cranial and dental characters. Much of the information has been drawn from our own observations but none would have been possible without the detailed and inspiring work of past taxonomists and foremost amongst these are the studies of Musser (including Musser 1972, 1973a, 1973b, 1979, 1981; Musser et al. 1979; Musser & Brothers 1994; and Musser & Newcomb 1983).

Similarly, the ecological summaries in the text draw heavily on the studies of a range of previous authors, notably those of Medway (1969) and a series of papers by Harrison (dating from 1950 to 1966) and Lim (1966 to 1975). Conservation status is drawn from the on-line IUCN Red List (http://www.iucnredlist.org/). Of the 28 species, all but six are listed as of 'Least Concern'. The exceptions are one 'Endangered' species, *Hapalomys longicaudatus*; four 'Vulnerable' species, *Maxomys rajah, M. whiteheadi, Niviventer cameroni,* and *N. cremoriventer*; and one "Data deficient' species, *Pithecheir parvus*. However, each of the 28 species plays an important role in the ecosystems of the peninsula and each in its own way is an important subject for future research.

There are great opportunities for a whole range of future studies, not just in the peninsula but in Southeast Asia generally, including taxonomy (incorporating both morphometrics and genetic studies), phylogeny, phylogeography and palaeontology (looking at evolutionary histories), ecology and behaviour (especially linked to ecosystem services), as well as those concentrating on the role of rodents in disease transmission. It is our intention that the current study will provide a baseline to promote and facilitate this work in the Myanmar, Thailand and Malaysian peninsular and Singapore.

LITERATURE REVIEW OF MURINE RODENT RESEARCH 1851–2013

The first publication relevant to the current study is Blyth (1851) who described *Mus berdmorei* (= *Berylmys berdmorei*) from the Mergui (= Myeik) Archipelago (no exact locality). Subsequently, he published on two murines from Pinang (= Penang), Malaysia (Blyth 1865); one was a new taxon, *Mus rama* (Cantor in Blyth, 1865) (= *Mus musculus*) and the other was *Mus setifer* (*setifer* is currently referred to *Bandicota indica*, but these specimens are more probably referable to *B. bengalensis*). Three years later, Peters (1868) described a new taxon of pencil-tailed tree mouse, *Chiropodomys penicillatus* (= *C. gliroides*); the type locality is thought to be the Malaysian peninsula, although no details were given (Corbet & Hill 1992).

The first synthesis of mammal records from the region was provided by Flower (1900) who reported on 160 mammal species collected from Thailand and Malaysia. He included seven murine taxa from the Thai-Malay peninsula. Miller (1900a) described *Mus tiomanicus* (= *Rattus tiomanicus*) and *Mus obscurus* (renamed *M. pullus* Miller, 1901, = *Rattus exulans*) from Tioman Island. In the same year, Miller (1900b) published the first ma-

jor paper dedicated to the peninsular murines. He described seven new rat taxa, which had been collected in Trong (= Trang Province, Thailand). Of these, two are still recognised as valid species today: *Mus cremoriventer* (= *Niviventer cremoriventer*) and *M. surifer* (= *Maxomys surifer*). The other five are treated as synonyms (sensu Musser & Carleton 2005): *Mus vociferans* (= *Leopoldamys sabanus*), *M. ferreocanus* (= *Berylmys bowersii*), *M. validus* (= *Sundamys muelleri*), *M. asper* (= *Maxomys whiteheadi*), and *M. pellax* (= *Maxomys rajah*). All the type specimens are deposited in the United States National Museum.

Miller (1900c) reported on fourteen mammal species collected on the Batang Islands (today in Satun Province, Thailand) and Pulo Lankawi (today in Kedah Province, Malaysia). He described four new taxa, three geographical races and one species, of murines, *Mus vociferans lancavensis* (= *Leopoldamys sabanus*), *Mus surifer flavidulus* (= *Maxomys surifer*), *Mus surifer butangensis* (= *Maxomys surifer*) and *Mus pannosus* (= *Rattus tanezumi*).

Whilst Miller was publishing in America, in Britain, Bonhote (1900) described an isolated, endemic species, *Mus ciliata* (= *Leopoldamys ciliatus*), from Perak in Malaysia. He also recorded a number of additional localities for a range of murine taxa, including *Mus mettada* [*sic*] (= *Millardia meltada*) from Bukit, Jalor, Malaysia. This latter record is probably mistaken as the species is currently considered to be restricted to the Indian Subcontinent (Musser & Carleton 2005).

In 1900–1901, an extensive collection of mammals was made in the islands of the Mergui Archipelago (= Myeik Archipelago) off the west coast of Tennasserim (= Tanintharyi Province), Burma (= Myanmar). The specimens were presented to the United States National Museum. They included many murines, of which Miller (1903a) subsequently described nine as new species. Today, all are considered to be synonyms. Three, *Mus matthaeus*, *M. stridulus* and *M. lucas* are referable to *Leopoldamys sabanus*; *Mus gilbiventer* is referable to *Niviventer cremoriventer*; and *Mus luteolus*, *M. umbridorsum*, *M. bentincanus*, *M. casensis*, and *M. domelicus* are referable to *Maxomys surifer*. In the same paper, on the basis of nine specimens from Tioman Island, off the east coast of Malaysia, Miller described one new murid taxon, *Mus stridens* (= *Leopoldamys sabanus*).

Meanwhile, Bonhote (1903b) named a new species of rat from Bukit Besar, Jalor, Malaysia, *Mus bukit* (= *Niviventer fulvescens*). In a further paper, based on a collection from northern peninsular Malaysia, Bonhote (1903a) recorded an additional four rat species and described another three, of which one *Mus annandalei* (= *Rattus annandalei*) is still recognised as valid. Both *Mus jalorensis* (= *Rattus tiomanicus*) and *Mus griseiventer* (= *Rattus tanezumi*) are today treated as synonyms. A new taxon, *Mus jarak,* named by Bonhote (1905) from Malaysia, is currently referred to *Rattus tiomanicus*. In the following year, Bonhote (1906) provided additional data on ten murid taxa from southern peninsular Malaysia. This paper included the description of two new taxa, *Mus inas* (= *Maxomys inas*) and *Mus klossi* (= *Maxomys whiteheadi*). Thomas (1907) described two new species from Pinang (Penang), Malaysia, *Gunomys varillus* and *G. varius*, both are currently referred to *Bandicota bengalensis*.

Kloss (1908a) described two new murine taxa, *Mus villosus* (= *Rattus annandalei*) from Singapore and *Mus surifer microdon* (= *Maxomys surifer*) from Tioman Island, Malaysia. His subsequent paper on a provisional list of the mammals from the peninsular region was an update of Flower (1900) and included 31 murid taxa (Kloss 1908b).

Specimens collected from Tarutao Island (today in Satun Province, Thailand) and remitted to the Natural History Museum, London, included one new subspecies of murine, described by Thomas & Wroughton (1909) as *Mus vociferans tersus* (= *Leopoldamys sabanus*). Meanwhile, based on a collection from the Trengganu Archipelago, off the north-eastern coast of the Malaysian peninsula, Kloss (1911a) described two new subspecies, *Mus surifer grandis* and *M. s. flavigrandis,* both of which are today treated as synonyms of *Maxomys surifer*; more detailed descriptions of these two taxa, including measurements, were subsequently included in Kloss (1911b). Robinson & Kloss (1911a) described two new taxa, *Mus rattus rumpia* (= *Rattus tiomanicus*) and *Mus surifer leonis* (= *Maxomys surifer*) from Malaysia and Singapore respectively whilst Robinson & Kloss (1911b) included an additional new Malaysian murine taxon, *Mus muelleri foederis* (= *Sundamys muelleri*). The following year, Robinson (1912) described a further two new taxa, *Epimys surifer pemangilis* and *E. s. aoris,* both of which are also treated today as synonyms of *Maxomys surifer*. The specimens were deposited in the Selangor Museum.

Miller (1913) published a further review of 'Malaysian' mammals. It included fifteen new taxa of murine rodents from peninsular Myanmar, Thailand and Malaysia. Seven new taxa were published from the Mergui (= Myeik) Archipelago in Myanmar. All are now considered to be synonyms with three, *Epimys vociferans clarae, E. v. insularum,* and *E. stentor,* currently referred to *Leopoldamys sabanus* and four, *Rattus rattus fortunatus, R. r. exsul, R. r. insulanus,* and *R. r. dentatus* referred to *R. tanezumi.* A further two taxa, *Epimys gracilis* (marginally extralimital to the current study region) and *E. lepidus* were collected from the Tennasserim mainland (= part of Tanintharyi Division, Myanmar) both are currently considered to be synonyms of *Niviventer fulvescens.* Two taxa were described from what is today Satun Province, Thailand. One, *Epimys solus* (= *N. cremoriventer*), is from Tarutao Island and the other, *E. pannellus* (= *R. tanezumi*) from Butang Island. Of the four taxa from peninsular Malaysia, three, *Epimy rattus vicalana, E. roa,* and *E.*

tingius are now referred to *Rattus tiomanicus* and one, *R. victor*, to *Sundamys muelleri.*

Robinson & Kloss (1914) reported on a collection of specimens obtained from Thailand and Malaysia. Three new taxa of murids were described from Koh Samui, Thailand. All are today considered to be synonyms, namely, *Epimys jerdoni pan* (= *Niviventer fulvescens*), *E. surifer spurcus* (= *Maxomys surifer*) and *E. remotus* (= *R. andamanensis*). The two new taxa from peninsular Malaysia were *Epimys orbus* (= *N. fulvescens*) and *E. surifer manicalis* (= *M. surifer*). The specimens were donated to the Federated Malay States Museum.

Kloss (1916a) provided additional data on the distribution of four rodent taxa, which today are referred to *Maxomys surifer, Rattus tanezumi, Sundamys muelleri* and *Berylmys bowersii*. In two subsequent papers, Kloss (1916b) included the description of a new subspecies, *Pithecheirus melanurus parvus,* which is currently recognised as a distinct species, *Pithecheir parvus,* and Kloss (1916c) described *Epimys surifer eclipsis* (= *Maxomys surifer*). Robinson & Kloss (1916a) reported on six murine taxa from Kedah Peak.

Meanwhile, in peninsular Myanmar, Wroughton (1915) provided distribution and ecological data for nine murine taxa in southern Tenasserim (= Tanintharyi Division). Hinton (1919), in his extensive paper on the house rats of the Indian Subcontinent and Myanmar, described one new taxon of murid rodent, *Rattus rattus tikos* (= *Rattus tanezumi*), also from Tenasserim. Gyldenstolpe (1917) reported on the mammals collected on two Swedish expeditions to Thailand, including the peninsula and Gyldenstolpe (1919) summarised the mammals which had been recorded from Thailand, including many rodent taxa from the peninsula. Kloss (1919) included additional localities of *Rattus rajah surifer* (= *Maxomys surifer*) from peninsular Myanmar-Thailand and *R. r. neglectus* (= *R. rattus*) from peninsular Thailand. Lindsay (1926) reported on a collecting trip to the islands of the Mergui (= Myeik) Archipelago, which included records of five murine species.

Chasen & Kloss (1931) discussed aspects of *Rattus* taxonomy of specimens originating from islands in the Straits of Malacca. The paper included the description of a new taxon, *Rattus rattus payanus* (= *R. tiomanicus*) from Pulau Paya, off the west coast of Malaysia. Kloss (1931) described a new taxon, *Rattus canus malaisa* (= *Lenothrix canus*) from near Kuala Lumpur.

Chasen (1933) published on Malay *Rattus.* He included descriptions, ecological information and distribution data from Malaysia and Thailand for three taxa which are today referred to *Rattus tiomanicus, R. tanezumi* and *R. argentiventer*. Chasen (1936) reviewed some new and existing specimens of *Gunomys* (= *Bandicota bengalensis*) known from Penang Island, Malaysia. In the same year, Tate (1936) undertook a taxonomic review of the Muridae, with a study area extending from mainland Southeast Asia to New Guinea. Chasen (1937) provided information on a range of murines from the islands off the west coast of peninsular Thailand and described six subspecies of *Rattus tanezumi,* namely: *panjius, alangensis, lontaris, kadanus, moheius,* and *pipidonis.*

In Chasen (1940), an extensive work on 'Malaysian' mammals (in reality it included taxa from Malaysia, Thailand and Indonesia), 35 pages were devoted to the murid rodents. He included lists of species, subspecies, and synonyms. In addition, he named a number of new taxa, including *Rattus rapit cameroni*, which is today recognised as a distinct, endemic species, *Niviventer cameroni,* from the Cameron Highlands, peninsular Malaysia. Other new taxa included: *Rattus rattus robinsoni* (= *R. tanezumi*); *R. r. perhentianus* and *R. r. pemanggis* (both = *R. tiomanicus*); *R. sabanus dictatorius* and *R. s. salanga* (both = *Leopoldamys sabanus*); and *R. surifer puket, R. s. telibon, R. s. muntia* and *R. s. pidonis* (all = *Maxomys surifer*). Subsequently a supplement was published by Ellerman & Morrison-Scott (1955).

Sody (1941) reported on a collection of rats from the Indo-Malayan-Australian region, with particular emphasis on murines from Indonesia. The paper included one new taxon from the current study region, *Rattus rattus chaseni* (= *R. argentiventer*) from Krian, Perak, Malaysia. Meanwhile Ellerman (1941) published his monograph on the families and genera of living rodents with the murids included in volume 2. The exhaustive information contained in this treatise included a summary of generic characters and a list of subspecies and synonyms, many of which originated from peninsular Myanmar, Thailand and Malaysia.

In the 1950s, there was considerable interest in rodent behaviour, reproduction, and links to human disease. Working mostly in peninsular Malaysia, Harrison published prolifically (Harrison & Traub 1950; Harrison & Lim 1950 and Harrison 1952a, 1952b, 1954a, 1954b, 1955). Harrison (1956a) examined seasonality in rodent breeding rhythms and looked at age-weight ratios for eleven murine taxa from Malaysia to determine survival rates. He also recorded *Bandicota indica* from peninsular Malaysia and for the first time reviewed the discriminating characters between this species and *B. bengalensis* (Harrison 1956b). Harrison (1957a) looked at habitats and micro-habitats of various murine rodents in Malaysia. Additional papers by Harrison (1957b, 1957c, 1957d, 1958, 1961 and 1962) looked at various aspects of the behaviour, ecology and parasites of murine rodents.

Hill (1960) undertook a detailed review of Robinson's collections of 'Malaysian' mammals, which had been deposited in the Natural History Museum, London's collection. Despite the title, these specimens, including many rodents, originated not only from Malaysia but also from Thailand, Myanmar and Indonesia. Descriptions and measurements of the different taxa were included, numer-

ous localities were listed, and four new taxa were described, *Rattus rattus pharus, R. r. sribuatensis, R. r. kabanicus,* and *R. r. terutavensis,* all of which are now referred to *R. tiomanicus*.

Dhaliwal (1961), based on Searle & Dhaliwal (1961), reviewed the distribution and habitats of five species of *Rattus* (today referred to *R. annandalei, R. exulans, R. norvegicus, R. tanezumi,* and *R. tiomanicus*) in Singapore Island. Subsequently, he discriminated between two *Rattus* taxa, *diardii* (= *R. tanezumi*) and *jalorensis* (= *R. tiomanicus*) (Dhaliwal 1962 and 1963).

Medway (1964a) undertook a review of *Rattus inas* (= *Maxomys inas*) with information on its ecology, distribution and external and cranial characters. He compared specimens from peninsular Malaysia with those from Sabah. In the same year, he published on the marmoset rat, *Hapalomys longicaudatus*, from Malaysia (Medway 1964b). Rudd (1965) compared the weights of 10 murid taxa in the State of Selangor, examining individual and sexual variation. Harrison (1966) summarised nearly 20 years of research undertaken by the Institute of Medical Research, Kuala Lumpur in his rather informal book on the mammals of Malaysia and Singapore. Medway & Lim (1966) reviewed the taxonomy of three *Rattus* taxa: *tiomanicus, jalorensis* and *diardii.*

Lim et al. (1965) looked for the presence of parasitic nematodes in 14 species of murid rodent in the Kuala Lumpur area. Lim (1966) studied the predation of molluscs by wild rats since it was considered probable that land slugs and snails were intermediate hosts in the life-cycle of a nematode, which is the cause of *eosinophilic meningoencephalitis* in man. Medway (1967) provided detailed information on the breeding habits of *Chiropodomys gliroides* based on specimens collected from Selangor State, Malaysia.

Yong (1968) provided karyological data on four species of murines collected from peninsular Malaysia, namely: *Rattus bowersii ferreocanus* (= *Berylmys bowersii*), *R. muelleri validus* (= *Sundamys muelleri*), *R. edwardsi ciliatus* (= *Leopoldamys ciliatus*) and *R. sabanus vociferans* (= *L. sabanus*). Yong (1969a) and Yong (1969b) included the karyology of *R. berdmorei* (= *B. berdmorei*) from Thailand but without exact locality data. Yong (1969c) reported on rats from Kedah Peak, Malaysia and Harrison (1969) reported on the abundance and population density of mammals, including murine rodents, in Malayan lowland forests.

Meanwhile, Medway (1969) published his monograph on 'The wild mammals of Malaya', providing information on the distribution, identification, subspecies, habits and reproduction of all mammals from Malaysia and Singapore, including the murine rodents.

Yong (1970) included data on the external morphology, skull anatomy, habitat, breeding behaviour, karyology, serology and immunohaematology of *Rattus edwarsi* (specimens subsequently referred to *Leopoldamys ciliatus*) and *R. sabanus* (*L. sabanus*) from peninsular Malaysia. Yong & Dhaliwal (1970) discussed variation in pelage colour in *Rattus bowersii* (= *Berylmys bowersii*) from Malaysia. Marshall & Nongngork (1970) studied seven rat species on Koh Samui, Thailand with information on the discriminating characters and their ecology. Lim (1970) provided information on the ecology, diet, food preferences, and endoparasites of four species of murid rodent, *Rattus sabanus* (= *Leopoldamys sabanus*), *R. muelleri* (= *Sundamys muelleri*), *R. bowersii* (= *Berylmys bowersii*) and *R. edwardsi* (here considered to be *Leopoldamys ciliatus*) based on specimens collected throughout much of peninsular Malaysia.

Muul & Lim (1971) provided some valuable information on the distribution and ecology of four lesser known murid rodents, *Rattus edwarsi* (here considered to be *Leopoldamys ciliatus*), *R. annandalei, Lenothrix canus,* and *Pithecheir parvus* in Malaysia. Lim et al. (1971) published a review of the small mammals of Penang Island, Malaysia which included information on ten murid taxa. Yong (1971) described a new taxon, *Rattus tiomanicus tenggolensis,* from Pulau Tenggol, Malaysia.

Musser (1972) provided a detailed review of the genus *Hapalomys* including information on taxonomy, ecology, and distribution in Myanmar, Thailand and Malaysia. Yong et al. (1972) looked at the karology of *diardii* (= *R. tanezumi*) and *tiomanicus* and *jalorensis* (= *R. tiomanicus*). Musser (1973a) undertook a detailed review of *Rattus cremoriventer* (= *Niviventer cremoriventer*) and included information on taxonomy, distribution, and ecology. Markvong et al. (1973) studied the karyology of murids from throughout Thailand and included a rare record of *Rattus berdmorei* (= *Berylmys berdmorei*) from peninsular Thailand.

Yong (1973) undertook a study of the chromosomes of *Chiropodomys gliroides* from Malaysia. Lim & Muul (1975) studied the rare arboreal murine, *Pithecheir parvus,* in peninsular Malaysia and included information on the diagnostic characters, size, preferred habitats, distribution, habits of captive specimens, diet, and helminth infection. Langham & Ming (1976) included the first record of *Mus caroli* from peninsular Malaysia with information on the diagnostic characters and ecology. Medway & Yong (1976) studied aspects of rat systematics in peninsular Malaysia.

Marshall (1977b) provided a summary of the murid rodents of Thailand for Lekagul & McNeely (1977). He included illustrated keys, some synonyms, information on reproductive status, photographs of live animals and skulls, some measurements, short descriptions, distribution maps, and karyology. In the same year, Marshall (1977a) provided a detailed review of the genus *Mus* in Asia, including the Myanmar-Thai-Malaysian peninsula, with illustrated keys, information on karyology, distribu-

tion, diagnostic characters and ecology. Chan (1977) and Chan et al. (1978 and 1979) looked at protein variation and systematics in Malaysian rats. Tweedie (1978) provided a brief introduction to the rodents of Malaysia with a few measurements and some information on habits.

Musser et al. (1979) undertook a detailed revision of the genus *Maxomys*, with much data relevant to peninsular Myanmar, Thailand and Malaysia. In the same year, Musser (1979) also undertook a detailed study of the arboreal rat genus *Chiropodomys*, with information on the taxonomy, ecology and distribution. Fain et al. (1980) studied the parasitic mite fauna of Malaysian rodents. Yong et al. (1982) included information on the karyology of *Hapalomys* and *Pithecheir*. Musser (1981) published a detailed taxonomic paper which focused on two genera *Niviventer* and *Leopoldamys* with further comments on *Lenothrix* and *Maxomys*.

Abe (1983) reviewed the taxonomy of *Niviventer* from Thailand and included *bukit* in the synonymy of *N. fulvescens*. In the same year, Musser & Newcomb (1983) published a monograph on two genera, *Berylmys* and *Sundamys,* and also provided detailed information on 12 other genera known from the region, including 5 that are endemic to the Sunda Shelf. Langham (1983) studied the small mammals of peninsular Malaysia, including Kedah Peak.

Breed & Yong (1986) looked at the sperm morphology of 19 taxa of murid rodents from Malaysia. Marshall (1988) in the second edition of Lekagul & McNeely (1988) once again provided taxonomic, ecological, and distribution data on 36 species and 8 genera of murine rodents. Boonsong & Felten (1989) described a new species of bandicoot rat, *Bandicota bangchakensis* (= *B. savilei*) from Nakhon Si Thammarat, Thailand. (It should be noted that the publications of the Thai naturalist Boonsong Lekagul are sometimes referred to Boonsong and sometimes to Lekagul).

Corbet & Hill (1992) published a taxonomic monograph on the mammal fauna of Southeast Asia. They provided dichotomous and character matrix keys, a comprehensive list of synonyms and subspecies, and distribution maps. The book includes 12 genera and 23 species of Murinae from peninsular Myanmar, Thailand and Malaysia and Singapore. Musser & Brothers (1994) undertook a detailed review of the genus *Bandicota* in mainland SE Asia, including taxonomy, ecology and distribution. Three species were recognised as occurring in the study area, *B. bengalensis* (with a very restricted range), *B. savilei* and *B. indica*.

Chaimanee (1998) produced an invaluable, detailed monograph of the Plio-Pleistocene rodents of Thailand, which also included much information relevant to the extant species, especially their dentition. Chaimanee & Jaeger (2001) subsequently reviewed the evolution of *Rattus* and incorporated fossil data originating from peninsular Thailand. Gorog et al. (2004) looked at the phylogeography of three murine species, *Maxomys surifer, Leopoldamys sabanus,* and *M. whiteheadi* in the Sunda shelf. Francis (2008) published a guide to the mammals of South-east Asia. Maps and illustrations were provided for 26 of the murine species from the study region and were further supported with brief information on diagnostic characters, measurements, taxonomic notes, distribution, and ecology (two additional murine species were discussed but not illustrated).

Waengsothorn et al. (2009) included data about the rodent specimens held in the 'Centre for Thai National Reference Collections (CTNRC)'. They identified and mapped geographical areas of Thailand that have been well studied in the past and suggested priority areas for field research in the future. Most recently, there have been a series of papers on rodent-borne diseases in Thailand (Jittapalopong et al. 2008, 2011; Herbreteau et al. 2012). Meanwhile Pagès et al. (2010) looked at Rattini phylogeny, using DNA sequence information, to determine species boundaries. The results of this latter paper are designed to assist with medical health projects relating to murine rodents. Most recently, Pimsai (2012) undertook a study of the murine rodent fauna of peninsular Thailand and Malaysia, which is the basis for current paper. Achmadi et al. (2013) looked at the phylogeny, diversity and biogeography of Southeast Asian *Maxomys,* including specimens from peninsular Malaysia and Latinne et al. (2013b) looked at the diversity and phylogeny of Murinae associated with limestone karst throughout Thailand, including the peninsula. Pearch et al. (2013) undertook a review of small mammal fossil faunas from Thailand including rodents from peninsular Thailand.

METHODS

Species. The taxonomy of the 28 species and 12 genera follows Musser & Carleton (2005). Differences to this taxonomic opinion are noted in the text and particularly in the 'Taxonomic notes' for each species.

Material. Much of the data are based on the literature. However, additional specimens were collected in Thailand using cage traps and aluminium live traps, which were set both on the ground and in trees. The methodology followed Aplin et al. (2003). This new material was deposited as voucher specimens (dry skins and skulls) in the zoological collection of the Princess Maha Chakri Sirindhorn Natural History Museum, Prince of Songkla University, Thailand (PSUNHM).

An additional 165 specimens of 18 species were studied from 65 localities in Thailand and Malaysia (Pimsai 2012, Figure 18). The vast majority (61) of these localities were in Thailand, including 18 in peninsular Thailand, with only four localities in peninsular Malaysia. These

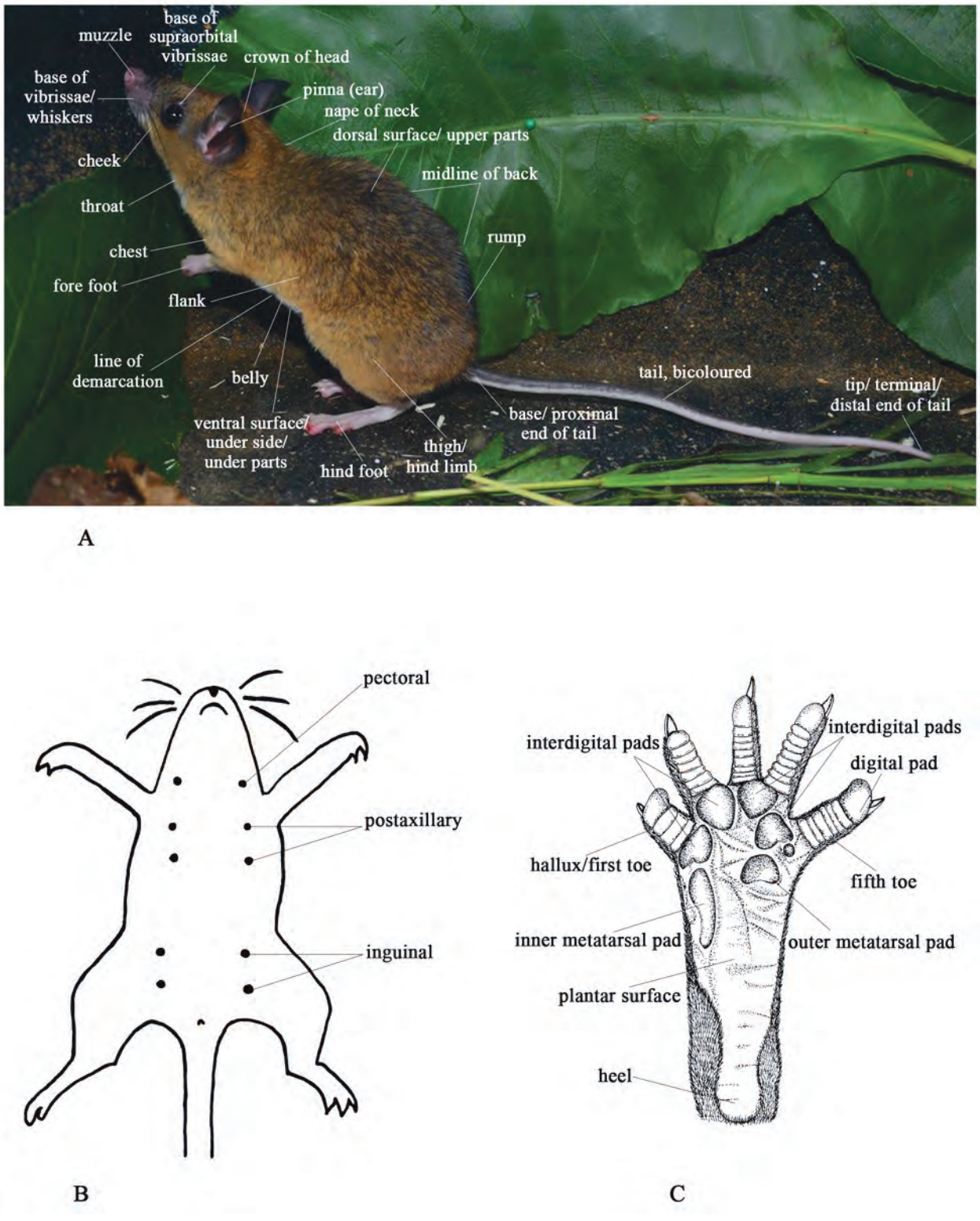

Fig. 2. (A): External characters of a murine rodent (*Maxomys surifer*), as referred to in the text; (B): arrangement of mammae in an adult female murine rodent (after Aplin et al. 2003, Figure 4.4); (C): the structure of the underside of a left hind foot (*Leopoldamys sabanus*).

specimens were held in the Centre for Thai National Reference Collections (CTNRC), Thailand Institute of Scientific and Technological Research (TISTR); the Harrison Institute, UK (HZM); and the Natural History Museum, London (BMNH).

Descriptions. Generic and species descriptions are based on personal observation (where specimens were available to the authors) and on the literature. Literature sources included original descriptions of the different taxa and subsequent taxonomic studies and monographs. The principal literature sources are listed at the beginning of each description.

Generic descriptions are restricted to the characters of species found within the study area. They do not include any additional characters of species which are found exclusively extralimitally. If only one species in a genus is found in the study area, the generic description is omitted.

Common terms used in the description of the external characters are illustrated in Fig. 2A. Where data are available, the arrangement of the mammae of each species is given, the terminology of which is given in Fig. 2B and follows Aplin et al. (2003). The structure of the hind feet for each genus is illustrated where specimens were available to the authors with sufficient resolution of structure to permit an accurate drawing. The nomenclature of the pads is illustrated in Fig. 2C. The different hair types, including 'spines' and guard hairs are illustrated in Fig. 3A–C. The section of tail of *Bandicota indica* shows the arrangement of the rows of scales, typical of many murine species (Fig. 3D). A photograph of *Maxomys surifer* is included to show a clearly defined demarcation on the flanks between the dorsal and ventral pelage (Fig. 3E); the photograph of the *Bandicota indica* specimen illustrates a pelage type that has no clear definition between the upper and lower parts (Fig. 3F).

Descriptions of the cranial and dental characters for each genus are supported in the text by a series of 12 drawings. Technical terms of features used in the generic/specific descriptions are lettered and numbered and linked to the drawings. This method has been adopted to assist all those using the paper who are not familiar with cranial and dental morphology. To assist further, the nomenclature of the cranial structures is also illustrated in Fig. 4A and the dental structures in Fig. 4B.

In general, the skull and teeth of young adult specimens (where available) were used for illustrative purposes, as it was considered that these were the most useful in helping to identify specimens caught in the field. However, it is appreciated that the morphology of the cusp patterns changes through time with young individuals often having much more clearly defined cusps than older individuals. Examples of these changes are illustrated in Fig. 5 for four different species (*Berylmys bowersi, Maxomys surifer, Rattus tanezumi,* and *Sundamys muelleri*). In addition, the dentition of a young *Lenothrix canus* is included in Fig. 4B, which can be related to the older individual in Fig. 18B. It is important that age-related differences in tooth morphology are borne in mind when using dental characters for identification purposes.

All drawings of the skulls and dentition were made by UP with a camera lucida and a stereo-microscope. One specimen of one species for each genus is illustrated.

Measurements. In the original study, Pimsai (2012) took a series of measurements from all specimens available to her in three Thai collections (see Material above). However, this original study was primarily focused on differences between genera and was less concerned with specific differences. For the current study, it was considered that the number of specimens measured was too small and their geographical origin too restricted for these measurements to be considered representative for many of the species. In addition, for some taxa, such as *Niviventer cameroni, Maxomys inas,* and *Pithecheir parvus,* no measurements were available in the initial study. Therefore, measurements included here are from a wide variety of literature sources, including many type descriptions. Usually more than one set of measurements is included for each species. These have been selected to represent different populations from different geographical areas and/or because they include additional measurements that are not included in the primary sources. All sources are listed in the caption for each Table.

It is appreciated that different researchers use different measuring techniques. In consequence, it is impossible to define measurements so that they exactly correspond to the method used by all the authors. However, the definitions given below follow what we consider to be best practice. For the cranial measurements (Fig. 6), we have primarily followed Musser (1979) and Harrison & Bates (1991). More measurements are included than those referred to directly in the current text. It is believed that the additional definitions will assist those working with supporting literature that does not include clear definitions of measurements. For the external characters, we have followed Aplin et al. (2003).

Head and body length (HB): from the tip of nose to the distal end of the anus;

Tail length (T): from the middle of the anus to the tip of the tail (not including hairs);

Ear length (E): taken inside the ear from the bottom of the notch to the furthest point along the rim/margin of the pinna;

Hind foot length (HF): from the back of the heel to the tip of the longest toe (not including the claws);

Mass: whole body mass of the specimen (in grams);

Greatest skull length (GSL): the greatest antero-posterior length of the skull, taken from the most projecting point at each extremity, irrespective of what structures form these points;

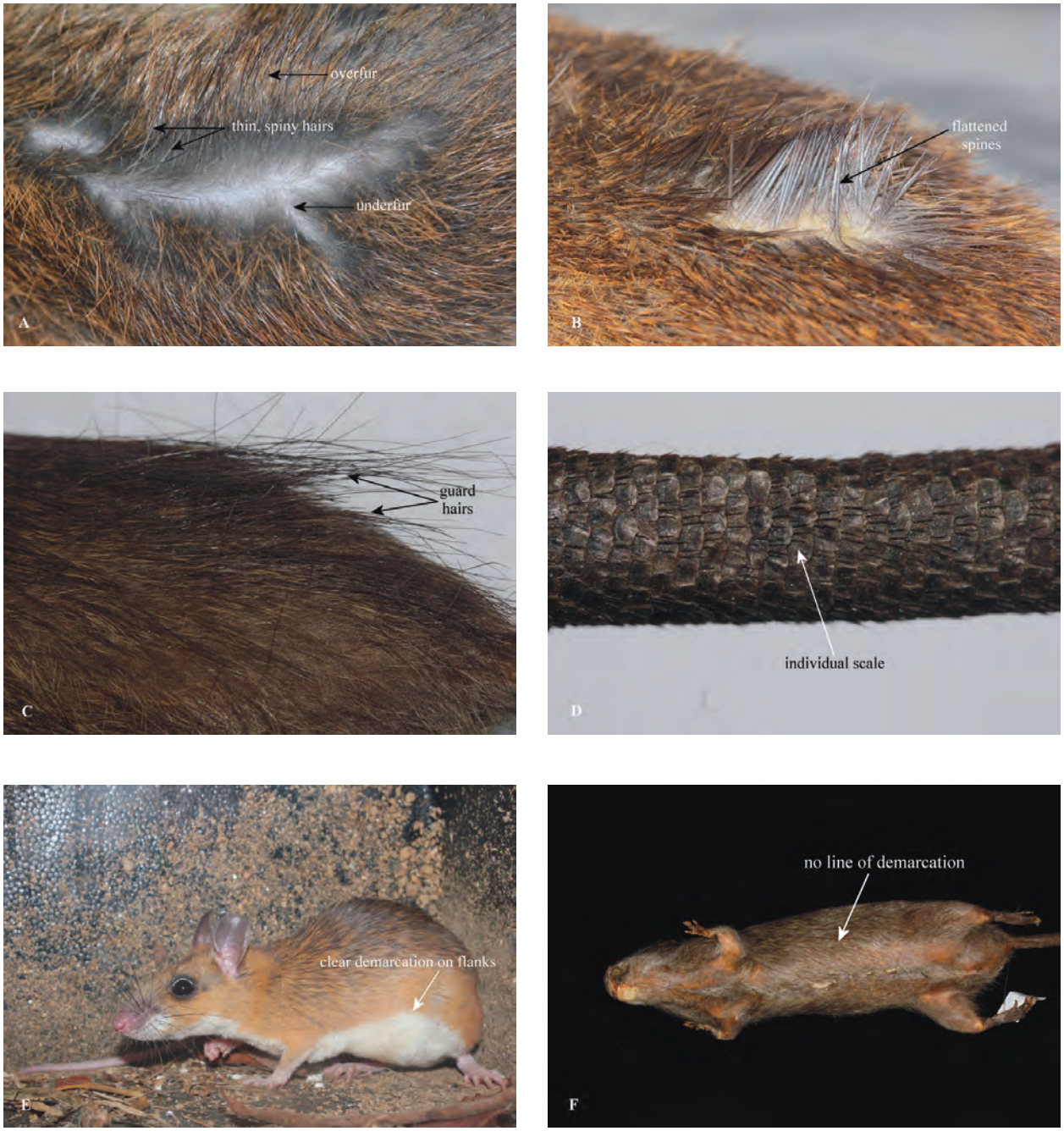

Fig. 3. Hair and tail of Murine rodents. (A): short (underfur) and long (overfur) hairs of *Rattus tanezumi*; (B): spines of *Maxomys surifer*; (C): guard hairs of *Bandicota indica*; (D): rows of scales on the tail of *Bandicota indica*; E: *M. surifer* – clear line of demarcation on the flank between upper and lower pelage; F: *Bandicota indica* – no line of demarcation on the flank between upper and lower pelage. Not to scale.

Occipital nasal length (ONL): the distance from the tip of the nasals to the posterior margin of the occiput (often but not always the same as GLS, especially in rodents with procumbent incisors);

Condylobasal length (CBL): from an exoccipital condyle to the anterior alveolar margin of the most forwardly projecting upper incisor tooth;

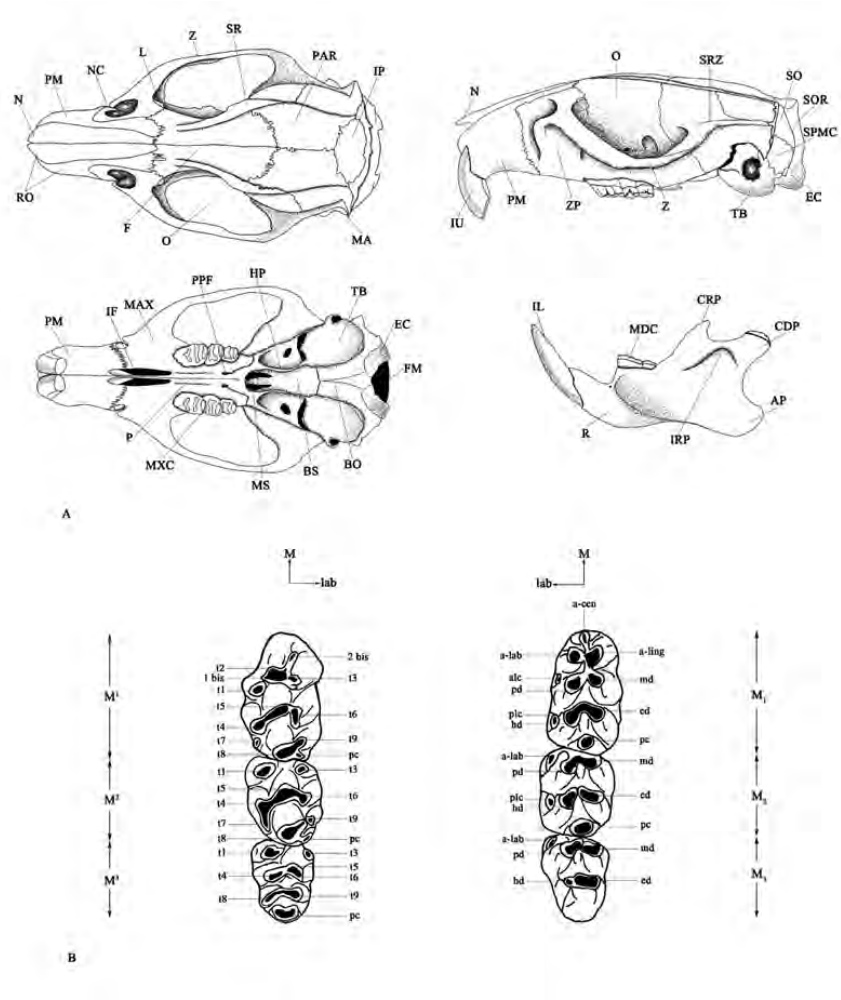

Fig. 4. Nomenclature of (A): cranial structures (based on *Bandicota indica*) and (B): dental structures – left upper molars, M^1–M^3, (on left) and left lower molars, M_1–M_3, on right of a young *Lenothrix canus* (following Musser & Newcomb 1983, Figure 2).
Skull: **AP**: angular process; **BO**: basiocciput; **BS**: basisphenoid; **CDP**: condylar process; **CRP**: coronoid process; **EC**: exoccipital condyle; **F**: frontal; **FM**: foramen magnum; **HP**: hamular process; **IF**: incisive foramina; **IL**: incisor, lower; **IP**: interparietal; **IRP**: incisor root process; **IU**: incisor, upper; **L**: lachrymal; **MA**: mastoid; **MAX**: maxilla; **MDC**: mandibular (lower) molars; **MS**: mesopterygoid space; **MXC**: maxillary (upper) molars; **N**: nasals; **NC**: nasolachrymal capsules; **O**: orbit; **P**: palate; **PAR**: parietal; **PM**: premaxilla; **PPF**: posterior palatine foramina; **R**: ramus of half mandible; **RO**: rostrum (premaxillae and nasals); **SO**: supraoccipital; **SOR**: supraoccipital ridge; **SPMC**: superior posterior mastoid chamber; **SR**: supraorbital ridge; **SRZ**: squamosal roots of zygoma; **TB**: tympanic bulla; **Z**: zygomatic arch; **ZP**: zygomatic plate.
Dentition: Cusps on upper molars are numbered according to Miller's (1912) scheme and referred to in the text with the prefix 't'; **a–cen**: anterocentral cusp; **a–lab**: anterolabial cusp; **alc**: anterior labial cusplet; **a–ling**: anterolingual cusp; **ed**: entoconid; **hd**: hypoconid; **md**: metaconid; **pc**: posterior cingulum; **pd**: protoconid; **plc**: posterior labial cusplet.

Zygomatic breadth (ZB): the greatest breadth across the zygomatic arches, regardless of where this point is situated along the length of the arches;

Interorbital breadth (IB): the least distance, as viewed dorsally, across the frontal bones between the orbital fossae;

Length of rostrum (LR): the distance from the tip of the nasal bones to the posterior margin of the zygomatic notch (the anterior edge of the dorsal maxillary root of the zygomatic plate);

Breadth of rostrum (BR): the greatest breadth across the rostrum;

Breadth of braincase (BB): the breadth of the braincase measured just above the squamosal roots of each zygomatic arch;

Height of braincase (HBC): the distance from the top of the braincase to the ventral surface of the basisphenoid bone;

Breadth of zygomatic plate (BZP): the least distance between the anterior and posterior edges of the zygomatic plate;

Length of nasals (LN): the distance from the anterior tip of the nasal bones to the most posterior suture between the nasal and frontal bones, measured parallel to the surface of the nasals;

Length of diastema (LD): the distance from the posterior alveolar margins of the upper incisors to the anterior alveolar margins of the first upper molars;

Length of incisive foramina (LIF): the distance from the anterior edge of one of the foramina to its posterior edge;

Palatal length (PL): the distance from the anterior alveolar margins of the incisors to the posterior edge of the palatal bridge;

Post palatal length (PPL): the distance from the posterior margins of the palatal bridge to the anterior margin of the foramen magnum;

Breadth of bony palate at first molars ($BBPM^1$): the least distance between the lingual edge of the alveolus of the first molar and the lingual edge of the alveolus of the opposite molar;

Breadth of bony palate at third molars ($BBPM^3$): the least distance between the lingual edge of the alveolus of

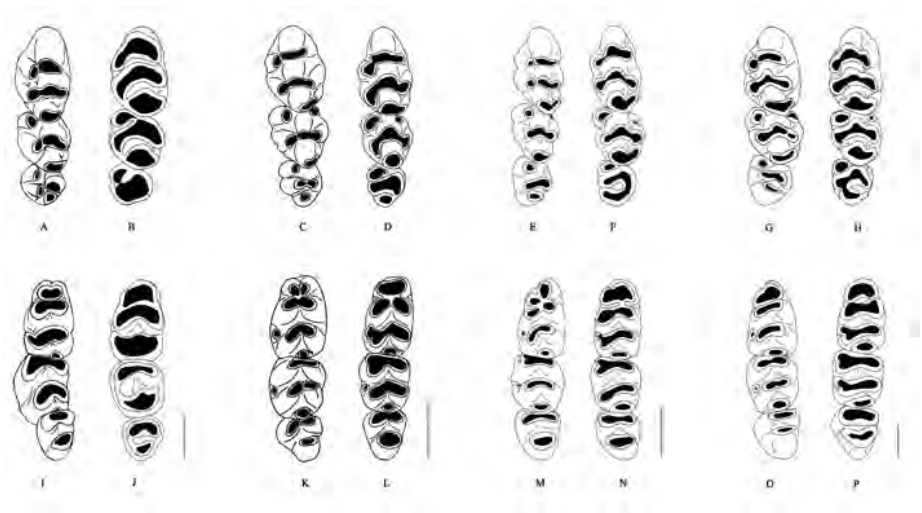

Fig. 5. Changes in dental morphology with age. A–H: left upper molars (M^1–M^3); I–P: left lower molars (M_1–M_3). In each pair, subadult teeth are on the left and adult teeth on the right. (A/I): *Berylmys bowersi*, subadult, (HZM 1.40111), Thailand; (B/J): *B. bowersi*, adult, (54–1287 CTNRC), Thailand; (C/K): *Maxomy surifer*, subadult, (54–5587 CTNRC), Thailand; (D/L): *M. surifer*, adult, (54–2919 CTNRC), Thailand; (E/M): *Rattus tanezumi*, subadult (54–5032 CTNRC), Thailand; (F/N); *R. tanezumi*, adult (54–4016), Thailand; (G/O): *Sundamys muelleri*, subadult, (54–642 CTNRC), Thailand; (H/P): *S. muelleri* adult (54–4392 CTNRC), Thailand. Scale = 2 mm.

the third molar and the lingual edge of the alveolus of the opposite molar;

Length of bullae (LB): the length of the bullae, anteroposteriorly;

Length of maxillary toothrow (ALM^1–M^3): the distance from the anterior edge of the alveolus of the first upper molar (M^1) to the posterior edge of the alveolus of the third upper molar (M^3);

Length of mandible (ML): the greatest distance from the most posterior part of the condyle to the most anterior part of the mandible, including the lower incisors/ not including the incisors (dependent on author);

Length of mandible toothrow (ALM_1–M_3): the distance from the anterior edge of the alveolus of the first lower molar (M_1) to the posterior edge of the alveolus of the third lower molar (M_3).

Distribution maps are based on literature records and on museum specimens studied personally by the authors or accessed through MaNIS (http://manisnet.org /portals.html). Each location on each map is included in the online gazetteer and is also linked to its source (museum specimen or literature), which is listed in Appendix I. Abbreviations of collections in the appendix are as follows: AMNH: American Museum of Natural History, New York, USA; BMNH: The Natural History Museum London (formerly the British Museum of Natural History), UK; FMNH: Field Museum of Natural History, Chicago, USA; NHM Thailand: The Natural History Museum, Thailand (specimens formerly in the Thailand Institute of Scientific and Technological Research [TISTR]); PSUNHM: Prince of Songkla University Natural History Museum, Hat Yai, Thailand; TTU: Texas Tech University, Lubbock, USA; UMMZ: University of Michegan, Museum of Zoology, USA; USNM: United States National Museum (Smithsonian), Washington. The maps and appendix were compiled by MP. The gazetteer was prepared by UP and MP.

Data for karyology are taken from the literature. Information on the fossil record is from Chaimanee (1998), Musser & Carleton (2005) and Pearch et al. (2013).

Conservation status is accessed from the web-based IUCN Red List and is individually referenced for each of the 28 species. Information on the ecology of the different species is based on personal observation in peninsular Thailand and on a wide variety of published references.

SYSTEMATIC SECTION

The descriptions of the 12 genera are provided to assist with the identification of murine rodents within the Myanmar-Thai-Malaysian peninsula and Singapore. Therefore (as noted in the Methods section above), they are restricted to the characters of species found within the study area. These descriptions omit characters of species that are entirely extralimital to this region. Where only one species in a genus is found in the study area, the generic description is omitted and the description is restricted to the species. Information provided for the genera and 28 species, including morphological characters, distribution and ecology, is based on personal observation (where data were available) and literature sources, which are listed in the relevant sections.

The generic and species matrix keys are based on the descriptions included below. They have been designed to assist those working in the field with live or newly sacrificed specimens as well as those conducting research in museums and/or laboratories with prepared voucher material.

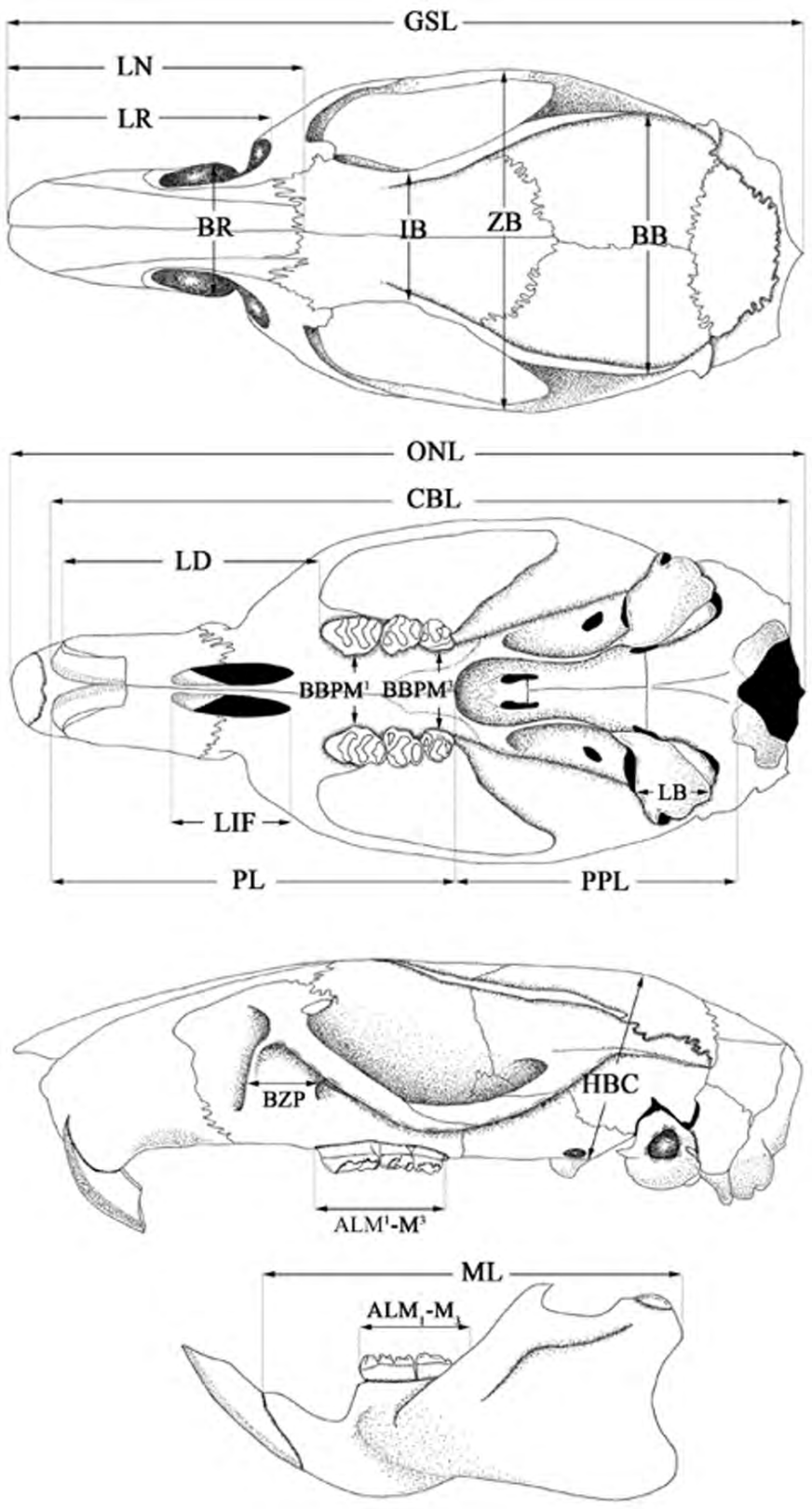

Fig. 6. Cranium and teeth of *Leopoldamys sabanus* (54–1319 CTNCR) showing limits of cranial measurement, which are defined in the text.

Genus *Bandicota*

Bandicoot rats

Bandicota Gray 1873: 418; type species *B. gigantea* Hardwicke, in *B. indica* (Bechstein).

Remarks. According to Musser & Carleton (2005), there are three species of extant *Bandicota* (*B. indica, B. bengalensis* and *B. savilei*) currently recognised, all of which occur in the study area of peninsular Myanmar, Thailand and Malaysia. A detailed study of the genus and its species is provided by Musser & Brothers (1994). Synonyms are listed in Musser & Carleton (2005).

Description (based on personal observation and Musser & Brothers 1994). The body size ranges from medium to large (Table 2). The tail is nearly always shorter than the head and body, almost hairless without a terminal tuft, unicoloured, brown to brownish-black (Fig. 3D). The dorsal pelage is grey-brown to almost black (Fig. 51F). The fur is long and coarse, without spines but with long guard hairs, which are most conspicuous on the lower black (Fig. 3C). The ventral pelage is slightly paler than the dorsal. However, there is no clear line of demarcation in colour between the hairs present on the upper and lower body. The hind feet have six or seven relatively small plantar pads (Fig. 7C) including interdigital pads (1), a very small outer metatarsal pad (2), and a kidney-shaped inner metatarsal pad (3). Females of *B. indica* and *B. savilei* have six pairs of mammae; females of *B. bengalensis* have up to 20 mammae.

In the skull, the rostrum is short and broad; the tips (Fig. 7Ai) of the nasals (ii) are triangular and about in line with the anterior surface of the incisors (xv) in *B. indica* and *B. savilei,* although they are posterior to the procumbent incisors (xxiv) of *B. bengalensis.* The interorbital area is narrowed (iii). The braincase is medium sized with prominent ridges (iv), which begin at the the supraoccipital (vi) and terminate in the interorbital region. The zygomata (v) are almost parallel or only slightly convergent anteriorly. The palate (xiii) is long, its length varies between species, and its posterior border (x) extends beyond the last (M^3) upper molars (ix). Therefore the postpalatal length, the distance from the back edge of the palate to the ventral margin of the foramen magnum (xii) is considerably shorter than the palatal length. The incisive foramina (vii) are elongated and often narrowed posteriorly; their posterior margins (viii) extend towards or pass slightly behind the front of the upper molar toothrows (*B. indica* and *B. savilei*) (xiv); in *B. bengalensis,* they extend further posteriorly between the first molars (M^1). The tympanic bullae are relatively large (xi). In each mandible, the coronoid process (xix) and the emargination (xxi) between the condylar (xx) and angular processes (xxii) are well-developed; the lower incisor root forms a very prominent process on the mandible (xxiii).

The upper incisors are opisthodont in *B. indica* and *B. savilei* and procumbent in *B. bengalensis* (Fig. 7) their enamel layers are orange, relatively pale in *B. bengalensis.* In the upper and lower molars, the initial cusp pattern found in juveniles is quickly lost through wear and subsequently appears as a series of simple laminae. The first upper molar (M^1) is relatively large; the first lamina comprises cusps t1, t2, and t3 (a), which are fused to form a plate; the second lamina also has t4, t5 and t6 (c) fused, although t4 (b) may look semi-separate in younger individuals; in the third lamina, cusps t8, t9 are fused making an oval wear surface (d). In the second upper molar (M^2), cusp t3 is absent; sometimes t1 (e) is fused with t4, t5, t6 (f) to form a plate (as illustrated in Fig. 7B), alternatively cusp t1 is prominent and not fused; on the third lamina (which may appear to be the second lamina, depending on the status of t1), cusps t8 and t9 (g) are fused making an oval wear surface. In the third upper molar (M^3), cusps t1, t4, t5, t6 (h) are fused making a large part of the molar; the second lamina, comprises t8 (i) only.

In the mandibular toothrow, the first lower molar (M_1) includes an anterocentral (j), anterolingual (l) and anterolabial cusp (k), which are fused together making a large lamina; the protoconid cusp (m) is fused with the metaconid (n); the hypoconid (o) is fused with the entoconid (p); the posterior cingulum is small (q) (absent in *B. bengalensis*). In the second lower molar (M_2), the anterolabial cusp (not seen in the specimen illustrated in Fig. 7B), the protoconid (r) and metaconid (s) and are fused; the hypoconid (t) is fused with the entoconid (u); the posterior cingulum (v) is small (absent in *B. bengalensis*). The third lower molar (M_3) is not greatly reduced when compared with M_2; the anterolabial cusp (w) is present and fused with the protoconid (x) and metaconid (y); the posterior lamina comprises the entoconid cusp (z).

Key to species for the three species currently known from peninsula Myanmar, Thailand, and Malaysia is included in Table 3.

Bandicota bengalensis

Lesser bandicoot rat

Arvicola bengalensis Gray 1835 (in 1830–35): pl. 21; Bengal, India.

Gunomys varius Thomas 1907: 204; Georgetown, Penang Island, Malaysia.

Gunomys varillus Thomas 1907: 205: Georgetown, Penang Island, Malaysia.

Description (based on personal observation and Chasen 1936 and Musser & Brothers 1994). Extralimitally this is the smallest of the three species of *Bandicota,* although specimens from Penang appear to be quite large (Table 2). The tail, which is shorter than head and body length, is virtually naked (although contrary to this, according to Thomas 1907, in specimens from Penang, the tail is 'well-clothed' in coarse hairs 2–3 mm in length). It is unicoloured, brownish to grey brown, with small scales, about 10–12 rows of scales/cm. The fur on the upperparts of the

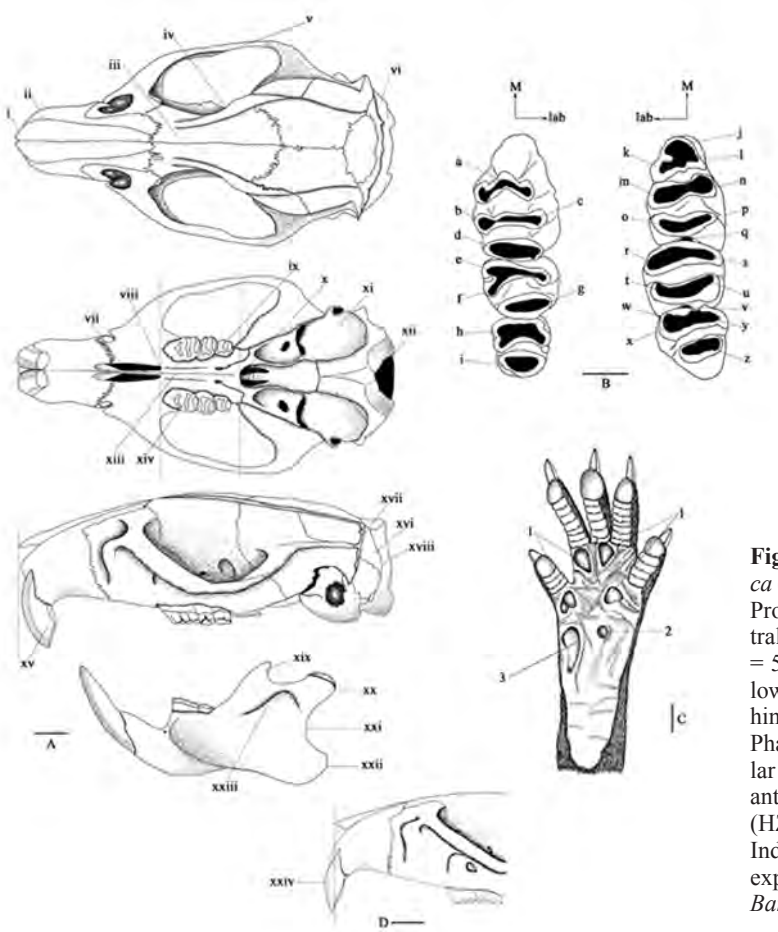

Fig. 7. Skull and dentition of *Bandicota indica* (54–2806 CTNRC), Ko Khram Yai, Chon Buri Province, Southeast Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *B. indica* (PSUZC–MM2012.199), Phato Watershed, Chumphon Province, peninsular Thailand (Scale = 5 mm). D: lateral view of anterior part of skull of *Bandicota bengalensis* (HZM 1.39650) Mandalay Division, Myanmar. Indicative numbers (i–xxiv) and letters (a–z) are explained in the text 'Description' for the genus *Bandicota.* M: mouth; lab: labial.

body is harsh in texture, and dark, an admixture of browns, greys, lighter buff, and black (based on extralimital specimens); it is described as mixed black and cream-buff, without brown tints; slaty grey at the base in the description of *varius* from Penang, Malaysia. There are moderately long, dark brown/black guard hairs. The head and dorsal line are particularly heavily pencilled in black. The underparts are dark grey (extralimital specimens) or alternatively in the description of *varius* from Penang, they are dull grizzled greyish, with slaty grey bases and dull whitish tips. There is no clear demarcation on the flanks between the upper and lower pelage. The hindfeet are shorter (in comparison to *B. indica*); brown to brownish grey in colour. There are 10 to 20 mammae (normally between 14 and 17): one pectoral, one postaxillary, one abdominal, and two inguinal pairs; higher counts are due to one additional postaxillary pair and variation in the number of abdominal mammae.

In extralimital material, the skull is smaller than those of *B. savilei* and *B. indica* (skulls illustrated in Musser & Brothers 1994, Figures 5 and 6). This is especially apparent in the shorter occipitonasal length (ONL), length of nasals and shorter length of the maxillary molars (ALM^1–M^3); however, in material from Penang skull size can be quite large (Table 2). Unlike in *B. savilei*, when viewed from above, the nasals do not conceal the nasal opening or the upper incisors. The upper incisors, which are pale orange to creamy in colour, are procumbent (Fig. 7Dxxiv) whereas they are opisthodont in *B. savilei* and *B. indica* (Fig. 7Axv).The incisive foramina of *B. bengalensis* are relatively long and extend posteriorly between the first upper molars (M^1). In the posterior part of the braincase, the posterolateral surface of the supraoccipital (Fig. 7Axvi) is greatly reduced with the supraocciptal ridge (xviii) fused with the dorsal third of the lambdoidal ridge (xvii). In *B. savilei* and *B. indica,* these two ridges are clearly separate (see Musser & Brothers 1994, Figure 8 for further details). In extralimital material, the crown width of the first molar (M^1) of *B. bengalensis* (2.41 mm, 2.13–2.75 mm) averages narrower than that of *B. savilei* (2.81 mm, 2.52–3.16 mm) and *B. indica* (3.38 mm, 3.02–3.65 mm) (Musser & Brothers, 1994, Table 3). The posterior cingulum (Fig. 7Bq and v) is absent in the first and second lower molars (M_1 and M_2) in *B. bengalensis* but is present in *B. indica* and *B. savilei.*

Karyology (based on extralimital specimens from five localities in India, Gadi & Sharma 1983). 2N= 42; NF= 58, 59 or 60; with six metacentric, two subtelocentric and 12 acrocentric chromosomes; the X chromosome is variably a submetacentric, acrocentric or subtelocentric; the Y chromosome is an acrocentric or submetacentric.

Sperm morphology. Information on the sperm morphology of a specimen from Penang, Malaysia is included in Breed & Yong (1986).

Fossil history. No fossil specimens of *B. bengalensis* are known from the study area (Pearch et al. 2013).

Taxonomic notes. The two taxa, *varius* and *varillus,* described from Penang, Malaysia (considered to be inadvertent human introductions, Chasen 1936; Musser & Carleton 2005 and others) are referred to *B. bengalensis* (Agrawal & Chakraborty 1976; Musser & Brothers 1994; for a contrary view of the taxonomy see Boonsong & Felten 1989).

Distribution and conservation status. *Bandicota bengalensis* is essentially a South Asian species with a range that extends from Pakistan, India, Sri Lanka, Nepal, and Bangladesh to Myanmar. Isolated populations in Penang Island, Malaysia and Indonesia are thought to be human introductions (Musser & Carleton 2005). In the study area, its range is restricted to peninsular Myanmar and Penang Island (Fig. 8).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, presumed large population, it occurs in a number of protected areas, has a tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Aplin et al. 2008f).

Ecology and reproduction. Virtually no ecological data are available for this species in the study area. Flower (1900, = *Nesocia* [sic] sp. inc.) noted that it had been collected in gardens, outbuildings and barracks in Penang, Malaysia, where it was common, causing damage to all kinds of field crops and also attacking stored grain. Extralimitally, it is common in both villages and towns where it is associated with agricultural areas. In Bangladesh, it is usually more frequently found in higher rainfall areas. It has a varied diet, with a preference for rice over wheat; it also consumes molluscs and crabs. It is a good swimmer and causes significant damage to deep-water rice crops. After harvest, it will frequently move from surrounding areas into villages when the fields no longer provide sufficient food. It has elaborate burrow systems (Posamentier 1989, Aplin et al. 2003). Males relocate their burrows more frequently than females. Most feed within an area of 12–40 m^2 around the burrow complex, although those living within a village generally move further (Aplin et al. 2003). Burrows are constructed in field bunds, vegetable gardens and orchards and in the floors and walls of buildings. The burrows have multiple chambers and entrances (sometimes as many as 12–16 per burrow) and

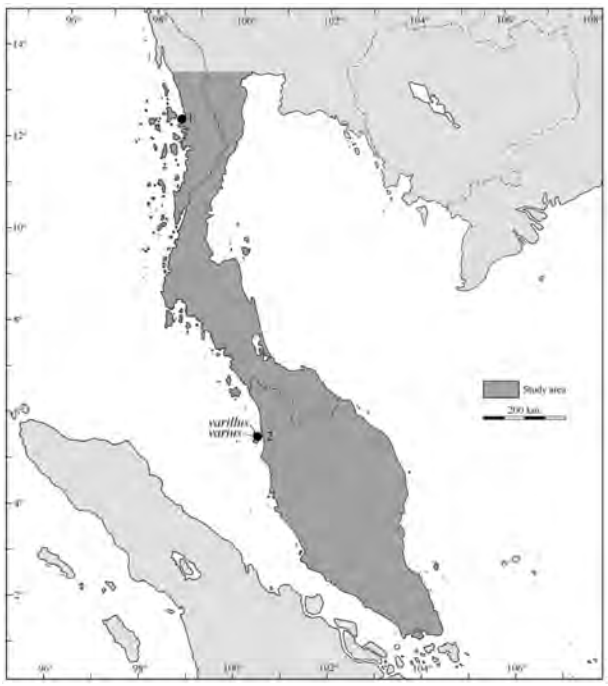

Fig. 8. Distribution of *Bandicota bengalensis* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Mergui (Myeik). **Malaysia:** 2. Georgetown, Penang Island. For full locality details, see Gazetteer and Appendix I.

may be used for several generations. Burrow entrances are either blocked during the day or left unblocked to facilitate escape. Since individuals of this species are very aggressive to each other, most burrows are usually occupied by a solitary adult male or female or females with young (Posamentier 1989, Aplin et al. 2003). However in areas of high density, many individuals may live in a burrow system. In India, breeding activity peaks in the dry season. The oestrus cycle is 3–5 days and the gestation period is 21–25 days. Sexual activity commences from about three months of age among females, slightly later in males. Litter size ranges from 1 to 19, with a mean of 6.2 young (Aplin et al. 2003).

Bandicota indica

Greater bandicoot rat; Large bandicoot rat

Mus indicus Bechstein 1800: 497; Pondicherry, India.

Description (based on personal observation and Musser & Brothers 1994). This is the largest of the three species of *Bandicota* (Table 2). The tail averages shorter than head and body length but is relatively longer that those of *B. savilei* or *B. bengalensis.* It is virtually naked, unicoloured, dark brown to black, with larger scales, about eight rows of scales/cm (Fig. 3D). The fur on the upperparts of the body is dark, blackish brown; the very long black guard hairs are particularly well-developed over the rump (Fig. 3C, Fig. 51F). The underparts are dark brownish grey; darker than in *B. savilei* and *B. bengalensis*. There is no

clear demarcation on the flanks between the upper and lower pelage. The hindfeet are much larger in comparison to the other two species and darker in colour, dark brown to black. There are 12 mammae (one pectoral, two postaxillary, one abdominal, and two inguinal pairs).

The skull averages larger than those of *B. savilei* and *B. bengalensis* (skulls illustrated in Musser & Brothers 1994, Figures 5 and 6 and in Marshall 1988, page 429) in all measurements but is particularly larger in occipitonasal length (ONL), nasal length (LN), length of diastema (LD), breadth of bony palate ($BBPM^3$) and length of the maxillary molar row (ALM^1–M^3) (Table 2). The incisive foramina extend to the anterior margin, or just posterior to the anterior margin of the first upper molars (M^1). Unlike *B. bengalensis*, in the posterior part of the braincase, the posterolateral surface of the supraoccipital (Fig. 7Axvi) is not greatly reduced (see Musser& Brothers 1994, Figure 8 for further details). In extralimital material, the crown width of the first upper molar (M^1) in *B. indica* (3.38 mm, 3.02–3.65 mm) exceeds that of *B. bengalensis* (2.41 mm, 2.13–2.75 mm) and *B. savilei* (2.81 mm, 2.52–3.16 mm) (Musser & Brothers 1994, Table 3). The posterior cingulum (Fig. 7Bq and v) is present on the first and second lower molars (M_1 and M_2); it is absent in *B. bengalensis.*

Karyology (based on extralimital specimens from five localities in India, Gadi & Sharma 1983). 2N= 42; NF= 66; there are seven metacentric, four subtelocentric, and nine acrocentric chromosomes; the X chromosome is a submetacentric; the Y chromosome is a submetacentric. Other extralimital specimens from Calcutta had a formula of 2N=44 (42–47); NF= 72, 74 (Gadi & Sharma 1983).

Fossil history. No specimens of *B. indica* are known from peninsular Thailand although the taxon has been recorded from a late middle Pleistocene site in north-eastern Thailand (Pearch et al. 2013).

Taxonomic notes. All specimens from the study area are referred to the nominate race.

Distribution and conservation status. *Bandicota indica* is known from India, Nepal, Myanmar, southern China, and Indochina. It has been introduced into the Malaysian peninsula and Indonesia (Musser & Carleton 2005). In the study region, it is known from peninsular Thailand and Malaysia (Fig. 9).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, tolerance of a broad range of habitats, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Aplin et al. 2008b).

Ecology and reproduction. In peninsular Thailand, *B. indica* was found in a range of habitats including secondary evergreen forest in Pet Buri Province and agricultural land in Trang Province, including rice fields (UP unpublished data). In peninsular Malaysia, *B. indica* was reported as 'attacking rice fields' in Kedah and Perlis (Harrison 1956b). Extralimitally, *B. indica* is found in field and village/urban habitats and is especially common around water sources. In most areas the population density is low and it can be considered only as a minor pest to agriculture. Indeed, where *B. indica* lives in low densities, its predation of invertebrates, including molluscs and crabs, may outweigh the limited damage it causes to crops. However, where it lives in high densities it can cause significant damage to rice and potato crops and also poultry and stored foodstuffs. When captured, it exhibits great ferocity (Aplin et al. 2003).

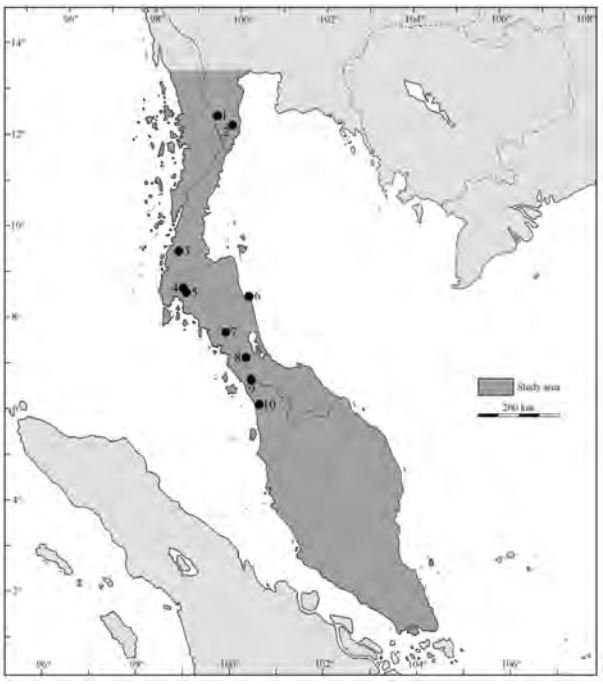

Fig. 9. Distribution of *Bandicota indica* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Pa La U; 2. Ban Na Pum; 3. Phato Watershed Conservation and Management Unit; 4. Klong Phraya Wildlife Sanctuary; 5. Khao Ying Mee; 6. Bang Chak; 7. Tan Ta Ya Phi Rom Temple; 8. Kam Phaeng Phet. **Malaysia:** 9. Perlis; 10. Kuala Jerlun. For full locality details, see Gazetteer and Appendix I.

In addition to human habitats, *B. indica* is also known from uncultivated marshy areas and forest patches. It is an excellent swimmer, allowing it to exploit a wide range of both aquatic and terrestrial foods, including molluscs, crustaceans, water lily fruit, water hyacinths, insects, earthworms, and field crops such as rice, vegetables, fruits and nuts. Its burrow systems range from short tunnels through to elaborate and extensive complexes with many chambers and entrances, that latter are sometimes below water. Large burrow complexes may cause considerable damage to buildings, dams and roadways. They contain numerous adults. Normally, individuals feed close to the burrow entrances. In India, breeding is shown to occur throughout the year, with a higher incidence of pregnan-

cy in the dry season. Litter size is 1 to 8 with a mean of 4.8, although larger litter sizes are also reported. The mean gestation period is 23 days (Aplin et al. 2003).

Bandicota savilei

Burmese bandicoot rat; Savile's bandicoot rat

Bandicota savilei Thomas 1916b: 641; Mount Popa, Myanmar, about 2500 feet.

Bandicota bangchakensis Boonsong & Felten 1989: 202; Bang Chak, Amphoe Muang, Nakhon Si Thammarat Province, Thailand, 8°30'N 100°00'E

Description (based on Musser & Brothers 1994). This is a medium-sized species, intermediate between the smaller *B. bengalensis* (based on extralimital specimens) and the larger *B. indica* (Table 2). The tail averages shorter than head and body length; it is relatively much shorter than in *B. indica.* It is virtually naked, unicoloured, brownish to greyish brown, with small scales, about 10–12 rows of scales/cm. The fur on the upperparts of the body is less coarse than that of *B. indica* and *B. bengalensis* and is paler, brownish in colour. There are long guard hairs. The underparts are grey buff, paler than in *B. indica* and *B. bengalensis*. There is no clear demarcation on the flanks between the upper and lower pelage. The hindfeet are relatively short in comparison to those of *B. indica.* They are brown or brownish grey. There are 12 mammae (one pectoral, two postaxillary, one abdominal, and two inguinal pairs).

In extralimital material, the skull is intermediate in size between the smaller *B. bengalensis* and the larger *B. indica* (skulls illustrated in Musser & Brothers 1994, Figures 5 and 6). Unlike in *B. bengalensis,* the nasals conceal the nasal opening and the upper incisors. The upper incisors are opisthodont; they are procumbent in *B. bengalensis.*The incisive foramina extend posteriorly between the first upper molars (M^1). Unlike in *B. bengalensis,* the posterolateral surface of the supraoccipital (Fig. 7Axvi) is not greatly reduced (see Musser & Brothers 1994, Figure 8 for further details). In extralimital material, the crown width of the first upper molar (M^1) (2.81 mm, 2.52–3.16 mm) is intermediate between the smaller *B. bengalensis* (2.41 mm, 2.13–2.75 mm) and the larger *B. indica* (3.38 mm, 3.02–3.65 mm) (Musser & Brothers 1994, Table 3). The posterior cingulum (Fig. 7Bq and v) is present on the first and second lower molars (M_1 and M_2); it is absent in *B. bengalensis.*

Fossil history. Within the study area, *B. savilei* has been recorded from the late middle Pleistocene locality of Khao Naphung in Thailand. The taxon is known from two further sites in Thailand, one in the west and one in the northeast of the country (Pearch et al. 2013).

Taxonomic notes. Musser & Brothers (1994) included *B. bangchakensis* from peninsular Thailand as a synonym of *B. savilei;* a view followed by Musser & Carleton (2005).

Distribution and conservation status. *Bandicota savilei* is known from Myanmar, Thailand, and Indochina. In the study region, it is known from peninsular Thailand (Fig. 10).

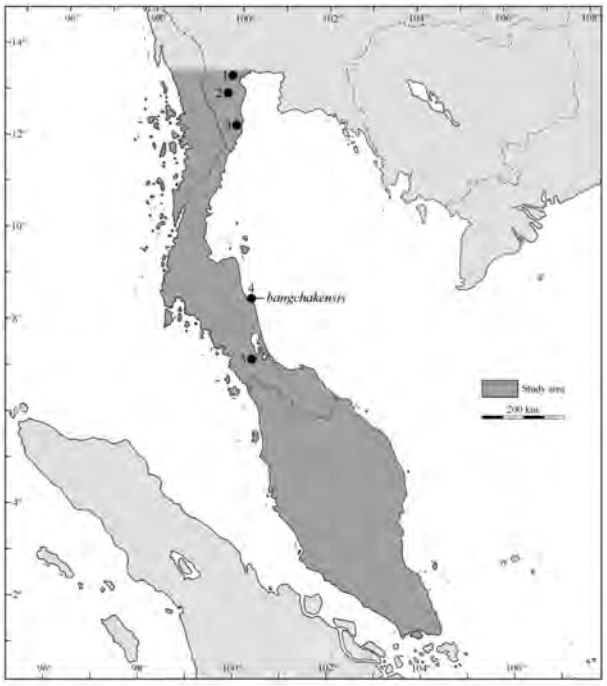

Fig. 10. Distribution of *Bandicota savilei.* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Pak Tho Khao Jeen; 2. Khao Rai; 3. Ban Na Pum; 4. Bang Chak; 5. Kam Phaeng Phet. For full locality details, see Gazetteer and Appendix I.

Its conservation status is listed by IUCN as 'Least Concern' in view of its "wide distribution, tolerance of a broad range of habitats, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Aplin 2008).

Ecology and reproduction. This is an adaptable species, present primarily in degraded habitats and regarded as a major agricultural pest in certain areas (Aplin 2008). Extralimitally, *B. savilei* is abundant in rice fields in Vietnam, although it avoids areas that frequently flood. This is in contrast to *B. indica*, which is more tolerant of aquatic habitats. An apparently 'natural' population of *B. savilei* is recorded from 'grass beneath teak forest' in Thailand (Marshall 1988). Large burrows are constructed in bunds and other elevated areas. Maize seems to be one of the favoured crops found in its diet. Few details are available concerning breeding behaviour. In Vietnam, a high proportion of females were found to be pregnant at the end of the dry season. In Myanmar, females have between five and eleven embryos (Aplin et al. 2003).

Genus *Berylmys*

Berylmys rats, White-toothed rats

Berylmys Ellerman 1947: 261; type species *Epimys manipulus* Thomas.

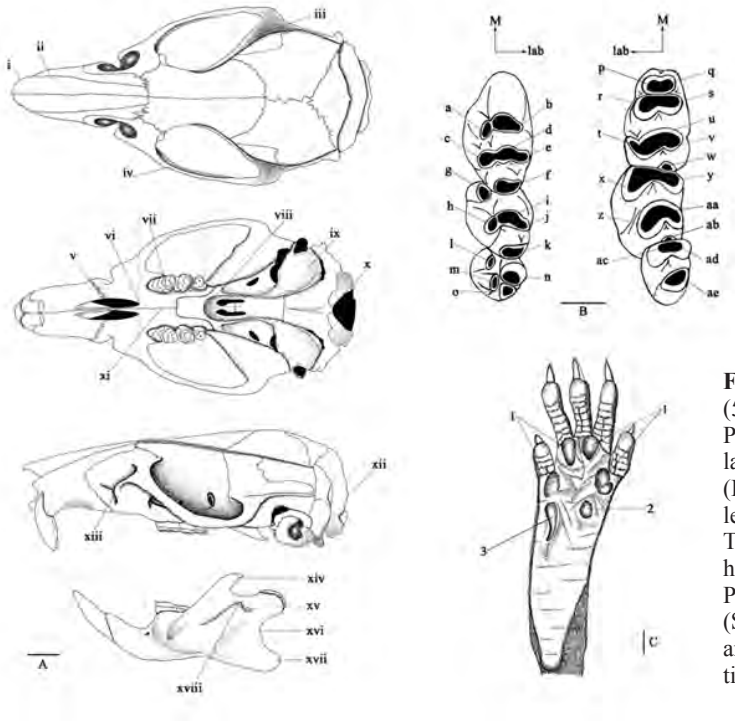

Fig. 11. Skull and dentition of *Berylmys bowersii* (54–1287 CTNRC), Doi Suthep–Pui, Chiang Mai Province, northern Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale 5 mm); (B): occlusal view of upper (left) and lower (right) left molars of *B. bowersii* (HZM.1.40111), Surat Thani, peninsular Thailand (Scale 2 mm); (C): left hind foot of *B. bowersii* (PSUZC–MM2012.200), Pak Jam, Trang Province, peninsular Thailand (Scale 5 mm). Indicative numbers (i–xviii) and (1–3) and letters (a–ae) are explained in the text 'Description' for genus *Berylmys*. M: mouth; lab: labial.

Remarks. According to Musser and Carleton (2005), there are four extant species of *Berylmys.* Two species are extralimital to the current study, namely *B. mackenziei* (Thomas), which occurs in north-east India, Myanmar, China and Vietnam and *B. manipulus* (Thomas), which is found in north-east India, northern and central Myanmar and southern China. Meanwhile, two species occur in the study area: *B. berdmorei,* which is essentially an Indochinese species and *B. bowersi*, which is found in both the Indochinese and Sundaic subregions (Musser & Carleton 2005). However, the taxonomy of *B. bowersi*, in particular, remains problematical. As noted below, Musser & Newcomb (1983) found considerable morphological variation amongst specimens referred to the species whilst Pagès et al. (2010) and Latinne et al. (2013b) recognised two distinct genetic lineages. Meanwhile, in Vietnam, Tran et al. (2009) described a new genus, *Pseudoberylmys*, which is considered by them to be closely allied to *Berylmys*.

Description (based on personal observation and Musser & Newcomb 1983; restricted to the two species occurring in the study area). Body size ranges from medium to large (Table 4). Tail colour varies between species, that of *B. bowersi* usually has a distinct white tip, which may extend for up to two-thirds of its length whereas the tail of *B. berdmorei* is either uniformly dark brown or sometimes slightly paler below. Tail length averages considerably shorter than head and body length in *B. berdmorei* but averages longer than head and body length in *B. bowersi.* The pelage is dense, smooth and stiff but not spiny; the hairs are rather uniform in length giving a brush-like texture (Fig. 51E). On the upper surface, the pelage is dark grey turning slightly browner in older individuals (especially in *B. bowersi*). The ventral pelage is white. The upper and lower surfaces are sharply demarcated from each other on the flanks. The ears are large and dark brown. The hind feet are long and narrow with 6 medium-sized pads (Fig. 11C); the interdigital (1), outer metatarsal (2) and inner metatarsal (3) pads are without ridges. Sexually adult males have cutaneous glandular areas in the midline of the stomach and inguinal region, which are stained with sebaceous secretions. Females of have four pairs of mammae in *B. bowersi* and five pairs in *B. berdmorei*.

The morphology of the skull in three different age classes (adult, young adult and juvenile) is illustrated for *B. bowersi* in Musser and Newcomb (1983, Figure 16). The nasals (Fig. 11Aii) are long, their anterior margins (i) are bluntly pointed or triangular. The braincase has weak lateral ridges in *B. bowersi* (iii). The ridges are better developed in *B. berdmorei.* The nasolachrymal canals are highly inflated (xiii). The zygomata (iv) are convergent, narrower anteriorly than posteriorly. The diastema (from the back of the upper canines to the front of the first upper molar) is very long, almost 30 % of skull length. The incisive foramina (v) are long; the posterior margins (vi) of the foramina are mostly situated in front of the anterior

margins of the first upper molar (M^1) (vii), occasionally they are level with the anterior margins or in a small minority of cases posterior to the front faces of M^1. The posterior border (viii) of the palate (xi) is about equal to, or even before, the posterior borders of the last upper molars (M^3). The distance from the back edge of the palate to the ventral margin of the foramen magnum (x) (postpalatal length) is shorter than palate length. The tympanic bullae (ix) are variable in size. The supraoccipital (xii) is large and slopes forward, especially in *B. berdmorei.* In each half mandible, the coronoid process (xiv) is well-developed and the posterior root of the incisor (xviii) is characteristically large, especially in *B. berdmorei*. The emargination (xvi) between the condylar (xv) and the angular (xvii) processes is well defined.

The enamel layers of the upper and lower incisors are white, pale yellow or pale orange. The upper incisors are orthodont or slightly procumbent. In the first upper molar (M^1), the first two rows of cusps form V-shaped laminae; in young individuals (as illustrated in Fig. 11B), cusp t1 (a) is separate from cusps t2 and t3 (b), which are fused; in older individuals cusps t1, t2 and t3 are all fused (Fig. 5B); cusps t4 (c), t5 (d) and t6 (e) are fused; there is one large cusp posteriorly (f), which represents cusps t8 and t9 (cusp t7 is absent). In the second upper molar (M^2), t1 (g) is large and prominent; t3 is always absent in *B. bowersi* and very occasionally present in *B. berdmorei*; cusps t4 (h) is separate in very young individuals but is usually fused with t5 (i) and t6 (j); the third row comprises cusps t8 and t9 (k), which are fused. The third upper molar (M^3) is rather small; t1 (l) is prominent; in young individuals, cusp t4 (m) is separate from t5 and t6 (n), which are fused; the last row has only t8 (o); sometimes cusp t4, t5, t6, and t8 are all fused (Fig. 5B).

In the mandibular toothrow, the first lower molar (M_1) is without an anterocentral cusp; the anterolabial cusp (p) is fused with the anterolingual cusp (q); in younger individuals, they are separate from the protoconid (r) and metaconid (s) but in older individuals all four cusps are fused; a posterior labial cusplet (t) is usually present and fused with the hypoconid (u) and the entoconid (v); the posterior cingulum (w) is visible in younger individuals. In the second lower molar (M_2), the protoconid (x) and metaconid cusps (y) are fused; an inconspicuous posterior labial cusplet is sometimes present (not illustrated); the hypoconid (z) and entoconid cusps (aa) are fused; a posterior cingulum is present in younger individuals (ab). The third lower molar (M_3) is rather small; the anterolabial cusp is absent; the protoconid (ac) is fused with the metaconid cusp (ad); the posterior lamina is constituted only by the entoconid cusp (ae).

Key to species for the two species currently known from the Myanmar-Thailand-Malaysia peninsula is included in Table 5.

Berylmys berdmorei

Berdmore's berylmys; Berdmore's white toothed rat

Mus berdmorei Blyth 1851: 173; Mergui (Myeik), Myanmar

Description (based on Musser & Newcomb 1983 and Francis 2008). This is a medium-sized, robust rat (Table 4). The tail is always shorter than the head and body length, averaging about 79 %, based on extralimital specimens from southeast Thailand; it is dark brown above; dark brown or greyish-white underneath; it lacks a pale tip. The fur on the upper parts of the body is iron grey. The under parts are white. The upper surfaces of the front and hind feet are white or grey and there are six plantar pads. Females have ten mammae, one pectoral pair, two postaxillary pairs and two inguinal pairs. The skull is characterised by its high braincase and large tympanic bullae (Fig. 11Aix), although in the holotype of *mullulus* (Thomas 1916a) from Myanmar, the bullae are smaller and the upper incisors slightly procumbent. Photographs of the skull of *B. berdmorei* are included in Musser & Newcomb (1983, Figures 17, 18, and 26) and Marshall (1988, 442).

Karyology (based on specimens from Thailand, Markvong et al. 1973, Musser & Newcomb 1983). 2N= 40, FN= 66; there are seven pairs of metacentric chromosomes, one pair of submetacentric chromosomes, five pairs of subtelocentric chromosomes, and six pairs of telocentric chromosomes; the X and Y sex chromosomes are telocentrics. A subsequent study of one female specimen from Thailand by Badenhorst et al. (2009) produced an essentially similar result, 2N= 40, FN= 64, with the karyotype comprising two large, four medium-sized and one small submetacentric pairs; one large, five medium-sized and one short acrocentric pairs of chromosomes. The Y chromosome was a small acrocentric.

Fossil history. No specimens are known from peninsular Thailand although the taxon has been recorded from a late middle Pleistocene site in north-eastern Thailand (Pearch et al. 2013).

Taxonomic notes. According to Musser & Newcomb (1983), the geographical variation in this species is little understood. Specimens from Vietnam and Southeast Thailand appear to average larger than those from southern Myanmar but very little is known about specimens from this latter region. The taxon *mullulus* (Thomas 1916a) from Thagata (just extralimital to the study area) is possibly a synonym of *B. b. berdmorei*. However, the holotype of *B. b. berdmorei,* which is in the collections of the Zoological Survey of India, is apparently badly damaged. Virtually nothing is known of the species within the study area of peninsular Myanmar, Thailand, and Malaysia.

Distribution and conservation status. *Berylmys berdmorei* is an essentially Indochinese species, including southern China, Thailand, Lao PDR, Cambodia, and southern Vietnam. In the study area, it occurs in peninsular Myanmar and Thailand, north of the Isthmus of Kra (Fig. 12).

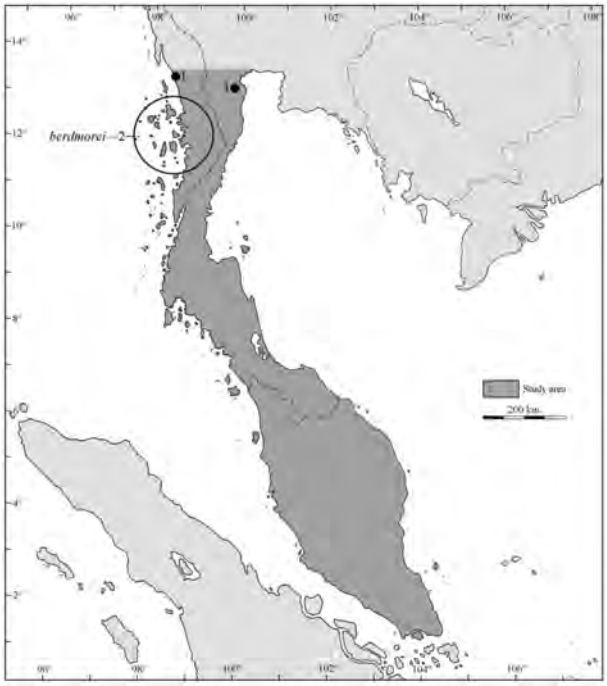

Fig. 12. Distribution of *Berylmys berdmorei* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Nathé Mine; 2. Mergui [Myeik] (no exact location). **Thailand:** 3. Phetchaburi. For full locality details, see Gazetteer and Appendix I.

Its conservation status is listed by IUCN as 'Least Concern' " in view of its wide distribution, tolerance of a degree of habitat modification, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Aplin et al. 2008g).

Ecology and reproduction. Little is known about this rat and nothing is recorded from the study area. Extralimitally, it is a terrestrial species that is known to inhabit forests from near sea level to at least 1,400 m, but is most common in upland areas where it is reported to favour swampy habitats. It is occasionally an agricultural pest, but generally avoids human habitations (Aplin et al. 2008g). In Southeast Thailand, it was found in lowlands at about 50 metres, where it was uncommon and sparsely distributed in swampy forests and marshy grass (Marshall 1988). In Vietnam, it was found in swampy forests and marshes from sea level to over 1000 metres (Lunde & Son 2001) and on Con Son Island, it was collected in forest at 300 metres (Van Peenan et al. 1970). In Lao PDR, it was moderately abundant in Luang Prabang Province. Here it lived both on the valley floor and adjacent slopes, where its burrows were located in small bamboo thickets and in fields planted with cassava and sweet potatoes; it is variously reported as damaging these crops. It was also found in an irrigated rice-field complex. Its burrows are several metres in length with two entrances and one central chamber. Burrows are occupied by individuals of both sexes (Aplin et al. 2003).

Berylmys bowersi

Bowers's berylmys, Bowers's rat

Mus bowersi Anderson 1879: 304; Hotha, Kakhyen Hills, west Yunnan, China, 4500 feet.

M. ferreocanus Miller 1900b: 140; Trang, peninsular Thailand, 3000 feet.

Description (based on personal observation and Musser & Newcomb 1983). This is the largest species of *Berylmys* (Table 4). The tails of specimens from the study area are dark above and below and usually have an extensive white tail tip of between half and two-thirds of the tail length. However, a recently collected specimen from Surat Thani Province has only the slightest indication of a pale tip (UP unpublished data) (Fig. 51E). The pelage is brownish grey on the upperparts; it is white on the underparts and is sharply demarcated on the flanks. The hind feet are dark above. Yong & Dhaliwal (1970) report an aberrant individual that had yellow pelage. There are eight mammae (one pectoral pair; one postaxillary pair and two inguinal pairs). The skull is characterised by its larger size in comparison to *B. berdmorei* but with relatively smaller tympanic bullae (although the bullae of *B. berdmorei mullulus* are also small). The upper incisors are orthodont, not procumbent as in *B. berdmorei*. Photographs of the skull of *B. bowersi* are included in Musser & Newcomb (1983, Figures 24 and 25) and Marshall (1988, p. 445).

Karyology (based on specimens from Thailand and Malaysia, Musser & Newcomb 1983). 2N= 40, FN= 66; there are seven pairs of metacentric chromosomes, one pair of submetacentric chromosomes, five pairs of subtelocentric chromosomes, and six pairs of telocentric chromosomes; the X and Y sex chromosomes are telocentrics. A study of one male and one female specimen from Thailand by Badenhorst et al. (2009) produced a comparable result, 2N= 40, FN= 64, with the karyotype comprising two large, four medium-sized and one small submetacentric pairs; and one large, five medium-sized and one short acrocentric pairs of chromosomes. The X chromosome was a medium-sized acrocentric; the Y chromosome was a small acrocentric.

Sperm morphology. Information on the sperm morphology of three specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. No specimens are known from peninsular Thailand (Pearch et al. 2013).

Taxonomic notes. Specimens from south of the Isthmus of Kra are referred to *B. b. ferreocanus* and are differentiated from Indochinese specimens by their larger skull size, relatively longer palate but shorter tympanic bullae; the tails have a greater proportion of white distally (Musser & Newcomb 1983). Pagès et al. (2010) and Latinne et al. (2013b) recognise two distinct genetic lineages, one

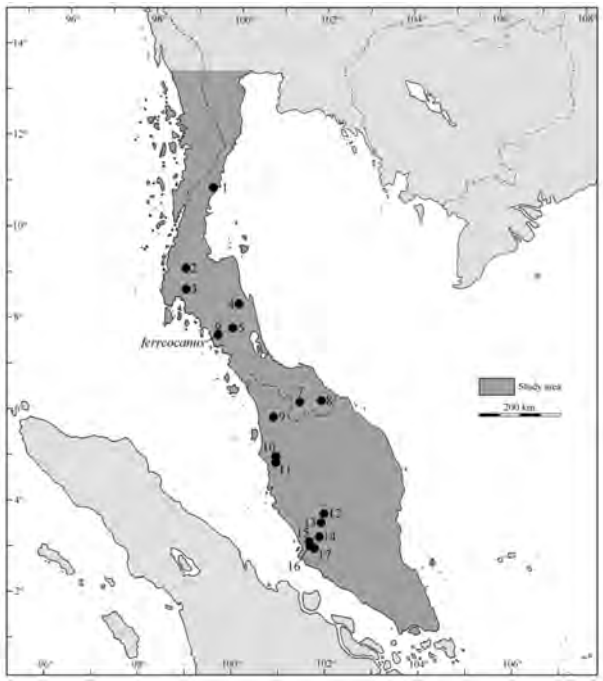

Fig. 13. Distribution of *Berylmys bowersii* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Maprit; 2. Rajjaprabha Dam; 3. Klong Phraya Wildlife Sanctuary; 4. Nakhon Si Thammarat Province; 5. Pak Jam; 6. Trang; 7. Yala Province; 8. Narathiwat Province. **Malaysia:** 9. Kedah State; 10. Maxwell's Hill; 11. Taiping; 12. Fraser's Hill; 13. Kampong Janda Baik; 14. Ulu Gombak, 20th mile Pahang Road; 15. Kepong; 16. Kuala Lumpur; 17. Ulu Langat. Not located: Yunong Jang. For full locality details, see Gazetteer and Appendix I.

from northern Thailand and one from Kanchanaburi Province and peninsular Thailand. However, the level of genetic difference between these two lineages is lower than that between *B. bowersi* and *B. berdmorei* (Latinne et al. 2013b).

Distribution and conservation status. *Berylmys bowersi* has a range that extends from northeast India to Myanmar, south China, Thailand, Lao PDR, Vietnam, and Sumatra. In the study area, it occurs in peninsular Thailand and Malaysia (Fig. 13).

Its conservation status is listed by IUCN as 'Least Concern' "as the species is widespread and locally abundant, at least in areas with suitable tree cover. It is present in several protected areas, and they are not likely to be declining at a rate to warrant listing in a threatened category" (Aplin et al. 2008a).

Ecology and reproduction. In peninsular Thailand, *B. bowersi* was collected in secondary evergreen forest in Surat Thani Province (approx. 400 m. a.s.l.) whilst others were trapped in lowland evergreen forest (UP unpublished data). In peninsular Malaysia, *B. bowersi* is a terrestrial species, which is most common in primary forest and which has also found in lower numbers in disturbed primary forest and secondary forest (Lim 1970). In peninsular Thailand, it was collected in Trang at an altitude of about 920 m (3000 feet) (Miller 1900b). In peninsular Malaysia, it is more abundant in highlands over 615 m (2000 feet) than in lowland areas (Harrison 1954a, 1957a, 1957b and Musser & Newcomb 1983) and most specimens are known from 1000–1500 m altitude (Lim 1970, Francis 2008). It tends to replace *Sundamys muelleri* in upland areas (Harrison 1954a). According to Medway (1969), it is generally found in gullies and valley bottoms on hillsides, rarely on the crests or ridges. Its abundance and population density were discussed by Harrison (1969). It seems to be equally abundant in dry and wet areas (Lim 1970). In contrast to *Bandicota indica*, it appears to be a docile animal (Medway 1969). Its diet is mostly restricted to vegetable matter (Harrison 1954a) although Medway (1969) suggests that it may also eat slugs and snails and Lim (1970) also found insects and even fish scales in the stomach of one individual. Its mean weight after ten months was estimated to be 350 g (Harrison 1956a). It is the least arboreal of all the *Berylmys* (Musser & Newcomb 1983) and its nest sites are found on the ground, in crevices among rocks, in holes in fallen logs, in holes in the banks of forest pathways, along forest streams, and in the holes at the bases of trees in the dry parts of the forest floor (Lim 1970). Litter size is 2 to 5 with a mean of 4. Typically it lives for about six months in the wild (Harrison 1955; Medway 1969). Extralimitally, in Lao PDR, *B. bowersi* appears to be strictly forest dwelling, although it is occasionally trapped in cropping areas (Aplin et al. 2003).

Genus *Chiropodomys*

Tree mice

Chiropodomys Peters 1868: 448; type species *C. penicillatus* Peters (in *C. gliroides*).

Remarks. *Chiropodomys* are small arboreal mice, which are relatively common in Southeast Asia. Six extant species have been described, of which only one, *C. gliroides*, occurs in the study region of the Myanmar-Thai-Malaysian peninsula. With the exception of *C. gliroides*, the other five taxa have relatively restricted distributions. Synonyms of the extant species are included in Musser (1979) and Musser & Carleton (2005).

Description. The generic description is omitted since there is only one species of this genus in the study area.

Chiropodomys gliroides

Pencil-tailed tree mouse

Mus gliroides Blyth 1856: 721; Cherrapunji, Khasi Hills, Assam, India.

Chiropodomys penicillatus Peters 1868: 448; probably peninsular Malaysia.

Description (based on personal observation and Musser 1979). This is a small arboreal rat with a long tail (Table 6), which has a well-defined tuft of hairs at the tip. The

fur is thick, short (6–8 mm in length), and soft. Guard hairs are abundant but short, scarcely extending beyond the dense coat. In specimens from peninsular Malaysia, the pelage is brightly coloured, reddish brown on the upper parts, with an orange-red (ochraceous) flank stripe. The underside of the head and belly is white and is clearly demarcated from the upper surface. The head is wide and the face is short. The eyes are large and prominent; they are encircled by a dark ring and are densely surrounded by thin lashes. The cheeks are buffy; the facial whiskers are long. The ears are thin, brown and finely haired. In specimens from north of the Isthmus of Kra (10° 30'N), the upper pelage tends to be paler; there is usually no flank stripe; and the belly fur is tinged with cream. Specimens from Bankachon in southern peninsular Myanmar exhibit intermediate characters between the northern, Indochinese form, and the southern, Sundaic form. The fore feet are white. The hind feet are white variably tinged with brown. Both the fore and hind feet are highly specialised for climbing (drawings of fore and hind feet are included in Musser 1979, Figure 13). In the hind foot (Fig. 14C), the first digit (hallux) (4) of the each hind foot is much shorter than the others and ends in a large fleshy pad (3) in which a small, nearly flat nail is embedded; the other digits are slender and terminate in smaller pads, which have short, thin, sharp claws. The fifth toe (2) appears to be always flexed and capable of being bent over towards the hallux. The interdigital (1) and inner metatarsal pads (5) are grossly enlarged; the outer metatarsal pad (3) is crescent shaped. Both the palmar (fore foot) and plantar (hind foot) pads are naked and unpigmented. The tail is long but not prehensile; it is hairy and tipped with a well-developed tuft of hairs (see Marshall 1988, page 424), which are about 4–5 mm in length. It is uniformly brown or dark brown in colour. Females have two pairs of mammae in the inguinal region.

The skull is wide and short. The rostrum is short and broad; the anterior margins of the nasals (Fig. 14Ai) are bluntly rounded. The interorbital area (ii) is broad and the lachrymal bones (iii) are well-developed. The braincase is wide and rounded with prominent supraorbital ridges (iv). The palate (xi) is broad; its posterior border (viii) extends just beyond the last (M^3) upper molars (vii). Therefore the distance from the back edge of the palate to the ventral margin of the foramen magnum (x) (postpalatal length) is shorter than the palatal length. The incisive foramina (v) are short and wide in specimens from the Malay Peninsula and islands on the Sunda Shelf and long and thin in material from Indochina (as illustrated here). When long, their posterior margins (vi) extend to, or slightly pass the front margins of, the first molar teeth (M^1) (xii). The tympanic bullae (ix) are moderately developed.

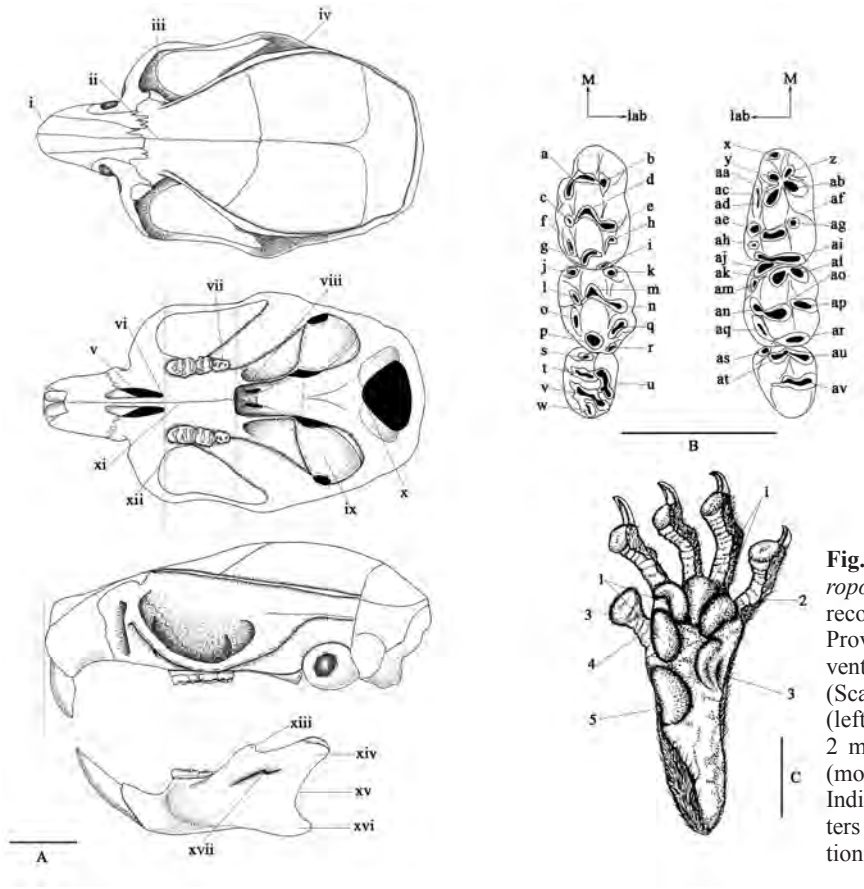

Fig. 14. Skull and dentition of *Chiropodomys gliroides,* (no specimen number recorded), Phu Phan District, Sakon Nakhon Province, north–east Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *C. gliroides* (modified from Hill 1960) (Scale = 5 mm). Indicative numbers (i–xvii) and (1–5) and letters (a–av) are explained in the text 'Description' for *C. gliroides*. M: mouth; lab: labial.

Each half mandible is short with a small coronoid process (xiii) and a shallow emargination (xv) between the condylar (xiv) and angular processes (xvi); the posterior root of the lower incisor (xvii) is indicated but not well-developed. Photographs of the skull are available in Musser & Newcomb 1983, Figure 102 and Marshall 1988, page 425).

The enamel layers of the upper and lower incisors are either orange or pale yellow and without grooves; the upper incisors are orthodont. The upper and lower molars are relatively small in relation to the size of the skull; all upper molars have three roots. In the first upper molar (M^1), cusps t1 and t2 (Fig. 14Ba) and t3 (b) are variably fused or separated in different individuals; on the second row, cusps t4 (c), t5 (d) and t6 (e) are all separate from each other in younger individuals; on the third row, cusps t7 (f), t8 (g) and t9 (h) are also separate; a posterior cingulum (i) is present. The second upper molar (M^2) includes a large and prominent anterior lingual cusp (t1) (j) and anterior labial cusp (t3) (k); on the second row, cusps t4 (l), t5 (m) and t6 (n) are separate; on the third row, cusps t7 (o), t8 (p) and t9 (q) are separate; the posterior cingulum (r) is present; sometimes cusp t8 fuses with the posterior cingulum. The third upper molar (M^3) is elongated; the anterior lingual cusp (t1) (s) is large and prominent; cusp t3 is absent; cusp t4 (t) is separate from t5 and t6 (u), which may be fused; in the last row, t8 and t9 (v) are fused; a posterior cingulum (w) is present.

In the mandibular toothrow, all the lower molars have two large roots. The first lower molar (M_1) has an anterocentral cusp (x); the anterolabial cusp (y) is separate from the anterolingual cusp (z); the protoconid (aa) is separate from the metaconid cusp (ab); an anterior labial cusplet (Cv2) (ac) and a posterior labial cusplet (Cv3) (ad) are present; the hypoconid (af) is larger than the entoconid cusp (ag); labial cusplet 4 (Cv4) (ae) and labial cusplet 5 (Cv5) (ah) are also present; the posterior cingulum (ai) is well-developed. In the second lower molar (M_2), the anterolabial cusp is large and prominent (aj); the protoconid (ak) is similar in size to the metaconid cusp (al); labial cusplets Cv3 (am), Cv4 (an), and Cv5 (aq) are present; the hypoconid (ao) is larger than the entoconid cusp (ap); the posterior cingulum (ar) is well-developed. The third lower molar (M_3) is relatively large; the anterolabial cusp (as) is present; the protoconid (at) is the same size as the metaconid cusp (au); the posterior lamina comprises the entoconid cusp (av) only.

Karyology. 2N= 42; there are 18 pairs of acrocentric autosomes and two pairs of metacentric-submetacentric autosomes, the X chromosome is a metacentric and the Y chromosome is a subacrocentric (Yong 1973; Yong et al. 1982).

Sperm morphology. Information on the sperm morphology of a specimen from peninsular Malaysia is available in Breed &Yong (1986).

Fossil history. In Thailand, it is known from 12 late Pliocene to late middle Pleistocene sites and one Holocene site, including six localities in the peninsula (Pearch et al. 2013).

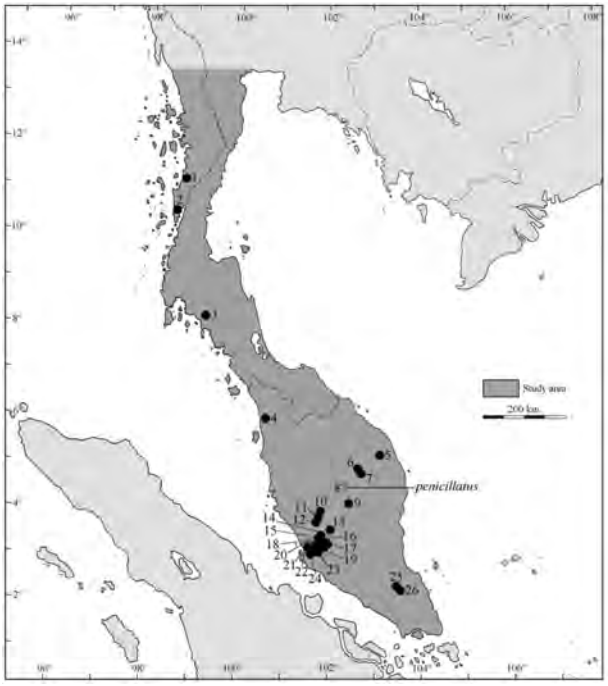

Fig. 15. Distribution of *Chiropodomys gliroides* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. 5 miles south of Karathuri; 2. Bankachon. **Thailand:** 3. Trang Province. **Malaysia:** 4. Kedah Peak; 5. Gunong Kutu; 6. Gunong Tahan; 7. Telom River; 8. Malaysian peninsular (no exact locality); 9. Gunong Mengkuang; 10. Gunong Benom; 11. Bukit Kutu; 12. Semangko Pass; 13. Bentong Forest; 14. 16th mile of Pahang Road, Kuala Lumpur; 15. Jaram; 16. Bukit Lagong; 17. Gombak Forest Reserve; 18. Kepong Forest Reserve; 19. Ulu Gombak; 20. Kuala Lumpur; 21. Tanjong Rabok; 22. Ulu Langat; 23. Ulu Langat Forest Reserve; 24. Bukit Mandol; 25. Tamok; 26. Bakok. For full locality details, see Gazetteer and Appendix I.

Distribution and conservation status. *Chiropodomys gliroides* has a range that extends from western China to northeast India, Myanmar, Thailand, Lao PDR, Vietnam, Malaysia, Indonesia. In the study area, it is known from peninsular Myanmar, Thailand and Malaysia (Fig. 15).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, presumed large population, it occurs in a number of protected areas, has a tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Lunde et al. 2008a).

Ecology and reproduction. This is primarily an arboreal rodent, although it also descends to the ground (Medway 1969). According to Hill (1960) it has been collected at altitudes ranging from 585 metres (1900 feet) to 1630 metres (5300 feet) in peninsular Malaysia, where it occurs in most types of forest but is most common in areas in

which bamboo is abundant (Medway 1969). By day, it nests in hollow trees or the internodal spaces of large bamboos. These bamboos are of any age, from standing green stems to old dead lengths lying on the ground. To reach the internodal space of an intact standing bamboo, it gnaws a neat circular entry hole of about 25 mm in diameter. Leaves of a variety of different plants are brought into the internodal space as nesting material (Medway 1969).

Gestation is thought to last 21 days. The young are weaned at 17 days of age and reach adult size and apparent maturity within 100 days (Medway 1967). Pregnancies are unevenly distributed through the year, with according to Harrison (1955) most (18 %) occurring between January-March. However, Medway (1967) found 20 %, 50 %, and 36 % of females collected in Selangor were pregnant in December, January and April respectively, with pregnant females found in all months except for June and July. Litter size is 1 to 3 individuals (mean 2.2). Adult size is attained at about 100 days (Medway 1969).

Genus *Hapalomys*

Marmoset-mice

Hapalomys Blyth 1859: 296; type species *H. longicaudatus* Blyth.

Background. *Hapalomys* is a Southeast Asian arboreal rat (illustrated in Abramov et al. 2012, Figure 2). According to Musser & Carleton (2005) there are two living species, *H. longicaudatus* and *H. delacouri* Thomas. *H. delacouri* is a small bodied species and is confined to Hainan Island (South China), north Lao PDR and southern Vietnam. The larger *H. longicaudatus* has wider distribution and is known from Myanmar, southwest and peninsular Thailand, and peninsular Malaysia. However, Abramov et al. (2012), on the basis of new karyotypic data, suggest that specimens from northern Lao PDR and Vietnam may be referable to a third species, *H. pasquieri* Thomas. Several new fossil species of *Hapalomys* have been described from Thailand (Chaimanee 1998) and China (Zheng 1993). The geographical origin of the genus is not clear (Musser & Newcomb 1983).

Description. The generic description is omitted since there is only one species of this genus in the study area.

Hapalomys longicaudatus

Greater marmoset rat

H. longicaudatus Blyth 1859: 296; Sitang River, Tenasserim, Myanmar.

Description (based on personal observation and Musser 1972). This is a medium-sized rat (Table 7), which is well adapted for climbing in bamboo and small branches (see Musser 1972, Figures 1 and 2 for photographs of live animals). Fur on the upperparts is thick, soft and woolly; it is greyish-brown or brown. There is an ochraceous (yellowish-orange-brown) strip on the flanks, which separates the dorsal surface from the essentially white underparts, although in some individuals there may be a pale yellowish-brown tinge on the hairs in the axillary, inguinal and abdominal areas. The face is dark, greyish-brown, including the cheeks. The ears are dark brown and relatively small compared to the size of the head. The feet are large, adapted for gripping and characteristic in shape (not illustrated here; photographs included in Musser 1972, Figures 4 and 5). The hind feet, which are brown with paler hairs on the toes, are broad and wide with long, well-spaced digits; there are large, ridged, interdigital and metatarsal pads on the soles of feet, and broadened pads near the tip of the toes. The first digit (hallux) is semi-opposable, with a flattened nail instead of a pointed claw. The tail is longer than head and body, brown throughout, well haired on the distal third, and ending in a tuft of hairs. Females have four pairs of mammae, including one pectoral, one postaxillary, and two inguinal pairs.

In the skull, the rostrum is medium sized and wide; the nasals (Fig. 16Aii) scarcely extend in front of the incisors (xiv) and have blunt tips (i). The nasolacrimal capsules (iii) are large and inflated. The interorbital area (v) is wide. The braincase is broad, inflated, and, in adults, has prominent, well-developed ridges (iv) that form a flange of bone overhanging the supraorbital region. The posterior border (x) of the palate (xiii) is about in line with the posterior borders of the last upper molars (M^3) (ix), or in some cases anterior to the posterior borders of M^3. The distance from the posterior border of the palate to the ventral margin of the foramen magnum (xii) (postpalatal length) is shorter than palatal length. The incisive foramina (vi) are narrow; their posterior margins (vii) are situated well in front of the anterior margins of the first molars (M^1) (vii). The tympanic bullae (xi) are large and globular. Each half mandible is medium-sized, elongate and with a small coronoid process (xv); the lower incisor root forms a prominent process on the mandible (xvi). Photographs of the skull are available in Musser & Newcomb 1983, Figure 102 and Marshall 1988, page 423).

The enamel layers of the incisors are orange. The upper incisors are orthodont relative to the rostrum. The upper and lower molars have a characteristic morphology. The anterior border of the first upper molar (M^1) has two cingular conules (Fig. 16Ba and b); on the first row, cusps t1 (c), t2 (d) and t3 (e) are separate from each other; on the second row, cusps t4 (f), t5 (g) and t6 (h) are separate; on the third row, cusps t7 (i), t8 (j) and t9 (k) are separate. In the second upper molar (M^2), the anterior lingual cusp (t1) (l) and anterior labial cusp (t3) (m) are prominent; on the second row, cusps t4 (n), t5 (o) and t6 (p) are separate; on the third row, cusps t7 (q), t8 (r) and t9 (s) are separate. In the third upper molar (M^3), the anterior lingual cusp (t1) (t) is prominent; cusp t3 is absent; cusps t4 (u) and t5 (v) are separate; in the last row, t8 (w), t9 (x) and the posterior cingulum (y) are fused.

In the mandibular toothrow, the first lower molar (M_1)

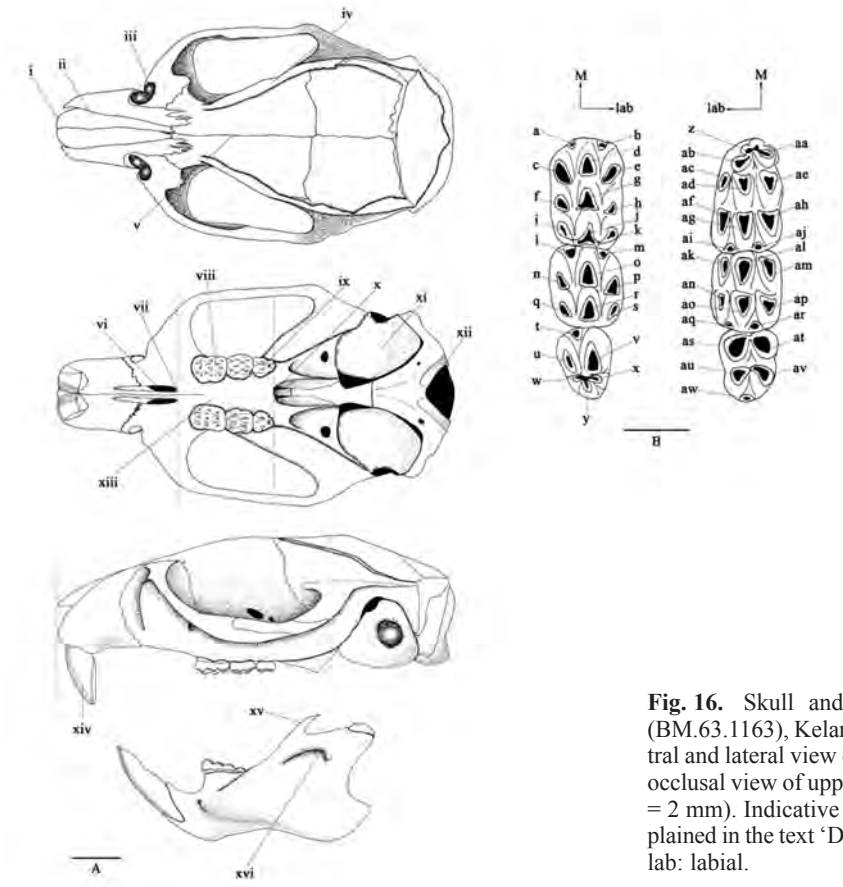

Fig. 16. Skull and dentition of *Hapalomys longicaudatus* (BM.63.1163), Kelanton, peninsular Malaysia. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm). Indicative numbers (i–xvi) and letters (a–aw) are explained in the text 'Description' for *H. longicaudatus*. M: mouth; lab: labial.

has a small anterocentral cusp (z), which is fused to the anterolingual cusp (aa) in Fig. 16B; the anterolabial cusp (ab) is separate; a labial cusplet (Cv3) (ac) is present; the protoconid (ad) is separate from the metaconid cusp (ae); a labial cusplet (Cv5) (af) is present; the hypoconid (ag) is separate from the entoconid cusp (ah); there are two small but well-developed cusplets (ai and aj) on the posterior border of the tooth. In the second lower molar (M_2) a labial cusplet (Cv3) (ak) is present; the protoconid (al) is separate from the metaconid cusp (am); a labial cusplet (Cv5) (an) is present; the hypoconid (ao) is separate from the entoconid cusp (ap); there are two small cusplets (aq and ar) on the posterior cingulum. In the third lower molar (M_3), the anterolabial cusp is absent; the protoconid (as) is the same size as the metaconid cusp (at) and the hypoconid (au) is the same size as the entoconid cusp (av); there is a posterior cingulum (aw).

Karyology (based on specimens from peninsular Malaysia, Yong et al. 1982). 2N= 50; there are 23 pairs of acrocentric autosomes and one pair of subacrocentric autosomes, the X chromosome is a metacentric and the Y chromosome a subacrocentric.

Sperm morphology. Information on the sperm morphology of a specimen from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. Fossil specimens of *H. longicaudatus* from the middle Pleistocene are known from four localities in Thailand, including two sites in the peninsula (Pearch et al. 2013).

Taxonomic notes. Musser (1972) undertook a detailed review of the genus, including a comparison of *H. longicaudatus* with *H. delacouri*. Currently, *H. longicaudatus* is considered to be monotypic with no subspecies described.

Distribution and conservation status. According to Musser & Carleton (2005), *H. longicaudatus* is known from Southwest China, southeast Myanmar, and southwest Thailand. However, Lunde (2008) referred the Chinese population to *H. delacouri*. Within the study area, it has been recorded from relatively few localities in peninsular Myanmar, Thailand and Malaysia (Fig. 17).

The conservation status of *H. longicaudatus* is listed by IUCN as 'Endangered' because "its area of occupancy is highly restricted to undisturbed bamboo habitat within

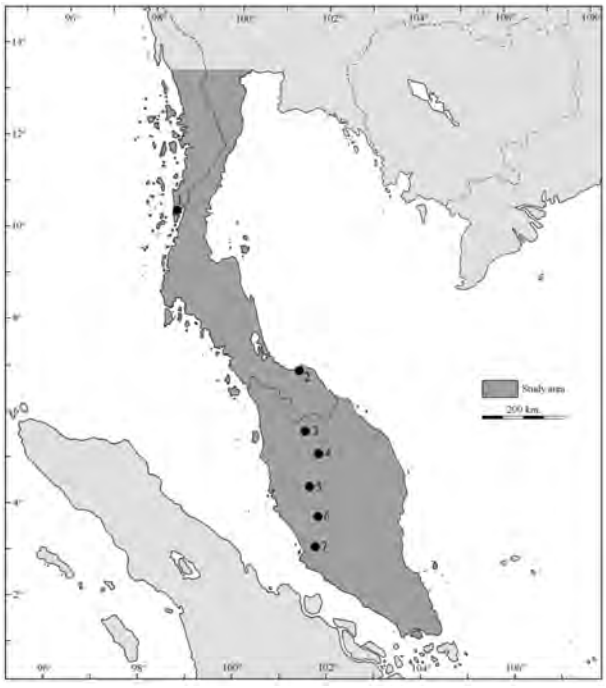

Fig. 17. Distribution of *Hapalomys longicaudatus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Bankachon. **Thailand:** 2. Pattani. **Malaysia:** 3. Belatop: 4. Ulu Kelantan; 5. Kelanta; 6. Genting Semangko (Semangko Pass); 7. Kuala Lumpur (near). For full locality details, see Gazetteer and Appendix I.

evergreen lowland forest and is probably less than 500 km^2, its distribution is severely fragmented, and the extent of its remaining habitat is probably declining". It is thought to be possibly extinct in Thailand and Myanmar (Aplin & Lunde 2008a).

Ecology and reproduction. According to Medway (1969), *H. longicaudatus* is an arboreal species associated with the bamboo *Gigantochloa scortechinii.* During the day, it sleeps in nests in the internodal spaces of standing green, or dead, bamboo stems. Access to these spaces is through holes, which the rat gnaws in the outer wall of the bamboo; these entrances, which characteristically have a 10 mm strip of bamboo skin removed from around them, can be at any height above the ground. In contrast to the holes made by *Chiropodomys,* those of *H. longicaudatus* are larger, some 35 mm in diameter. The nests are lined exclusively with leaflets of bamboo. The diet consists entirely of parts of bamboo, with the flowering shoots being especially favoured. Further information on the behaviour, ecology and diet of this species in Malaysia is included in Medway (1964b). Little is known of the species in Thailand, although a specimen from Khwae Noi River in southwestern Thailand was caught in bamboo jungle (Musser 1972). Similarly, a specimen from Bankachon in peninsular Myanmar was also found among bamboos, together with *Chiropodomys* (Musser 1972).

Genus *Lenothrix*

Lenothrix rats

Lenothrix Miller 1903b: 466; type species *L. canus* Miller.

Background. The genus *Lenothrix* includes only one species, the Sundaic rodent, *Lenothrix canus*.

Generic description. The generic description is omitted since the genus is monospecific.

Lenothrix canus

Sundaic lenothrix; Grey tree rat; Hoary rat

Lenothrix canus Miller 1903b: 466, pl. 18; Tuangku Island, Banjak Islands, Sumatra.

Rattus canus malaisia Kloss 1931: 105; near Kuala Lumpur, Selangor, Malaysia.

Description (based on Miller 1903b, Kloss 1931, Musser 1981, Musser & Newcomb 1983). This is medium-large arboreal rat (Table 8) with a body mass of 81–220 g (Muul & Lim 1971). The fur, which is without spines, is characterised by its woolly texture. The underfur is fine, dense and woolly, about 12 mm in length in the mid-part of the back. There are also slender, straight cylindrical hairs which are about 25 mm in length and in addition some weak, flattened hairs, which are most abundant on the flanks and underparts, but are mostly inconspicuous. The colour of the upper surface is grey or grey-brown. It is darkest in the midline of the back, where there are some black hairs. It is palest on the shoulders and flanks. The demarcation between the upper surface and the belly is reasonably well-defined on the flanks. The belly is creamy-white or creamy-buff. The sides of the muzzle are white; the vibrissae are shiny black. The ears are relatively small and blackish, virtually naked except for some minute hairs. The fore and hind feet are white. The hind feet (not illustrated), which are brown with some white hairs, are short, broad and adapted for climbing in trees. Most of the plantar surface of each foot is taken up by large interdigital and metatarsal pads that are textured with high ridges and deep grooves. The pads at the end of the digits are swollen, especially on the first toe (the hallux), which has a small nail-like claw; the other digits have short, recurved, sharp claws. The two outer digits are semi-opposable. The tail is very long but not prehensile. It is black at the base and has an extensive white tip, sometimes up to half or more of its length. It is covered with very short hairs, which turn white and increase in size towards the tip, where they are some 5 mm in length. In the mid-part of the tail, there are 11 rings/cm, but the rings are not clearly defined over much of the tail. According to Musser (1981), there are ten mammae: one pectoral pair; two postaxillary pairs, and two inguinal pairs. However, Kloss (1931) suggested that there are eight mammae: three pectoral pairs and one inguinal pair.

In the skull, the rostrum is long and the anterior margins of the nasals (Fig. 18Ai) are rounded or blunt. The interorbital area (ii) is relatively narrow whereas the or-

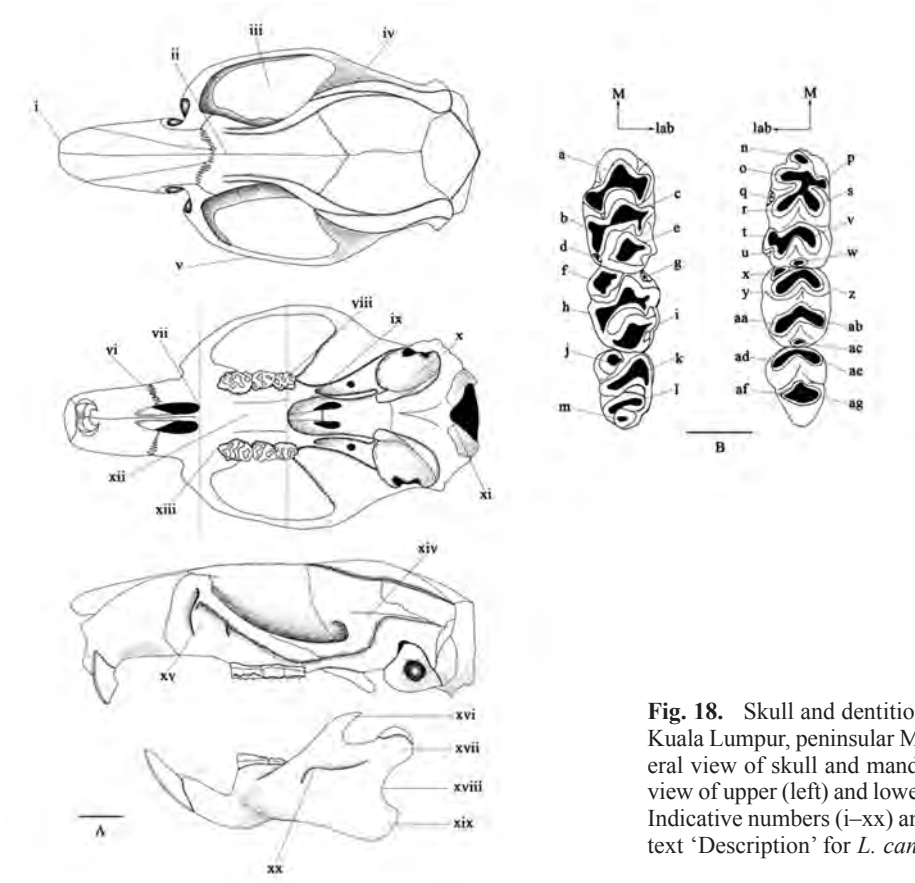

Fig. 18. Skull and dentition of *Lenothrix canus* (BM.49.630), Kuala Lumpur, peninsular Malaysia. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm). Indicative numbers (i–xx) and letters (a–ag) are explained in the text 'Description' for *L. canus*. M: mouth; lab: labial.

bital area (iii) is large. The braincase has very well-developed lateral ridges (iv), especially over the posterior part of the orbit, where the ridges are flange-like. The zygomatic plates (xv) are narrow; the zygomata (v) are considerably broader than the braincase. Squamosal roots (xiv) of the zygomata are set in the mid-part of the sides of the braincase. The posterior margin (ix) of the palate (xii) ends before or in line with the last upper molars (M^3) (viii); the distance from the posterior margin of the palate to the ventral margin of the foramen magnum (xi) (postpalatal length) is shorter than the palatal length. The incisive foramina (vi) are short and wide; their posterior margins (vii) end well in front of the anterior margin of the first molars (M^1) (xiii). The tympanic bullae are moderately developed (x). Each half mandible has a large coronoid process (xvi); the posterior root of the lower incisor (xx) and the emargination (xviii) between the condylar (xvii) and angular (xix) processes are clearly defined. Photographs of the skull are available in Musser (1981, Figure 44) and Musser & Newcomb (1983, Figure 94).

The enamel layers of the incisors are white or pale yellow; the upper incisors are opisthodont or almost orthodont relative to the rostrum. In young individuals most of the cusps are separate from each other (Fig. 4B); in older individuals (Fig. 18B) they become fused. In the first upper molar (M^1), cusps t1, t2 and t3 (a) are separate in young individuals but become fused with age; on the second row, cusps t4 (b) t5 and t6 (c) are variably fused in older individuals; cusp t7 (d) is separate from cusps t8 and t9 (e), which are fused. There is a small posterior cingulum visible in young individuals (Fig. 4B). In the second upper molar (M^2), the anterior lingual cusp (t1) (f) is large and prominent and there is a small t3 (g); on the second row, cusps t4, t5 and t6 (h) are fused; on the third row, cusp t8 and t9 (i) are fused in older individuals; there is also a small posterior cingulum visible in younger specimens. The third upper molar (M^3) is narrower than the second upper molar (M^2) but only a little shorter; the anterior lingual cusp (t1) (j) is large and prominent; cusp t3 is very small and in older individuals is fused with cusps t4, t5 and t6 (k) (Fig. 18B); the last row has t8 and t9 (l) are fused together; the posterior cingulum is well-developed (m).

In the mandibular toothrow, the first lower molar (M_1) has an anterocentral cusp (n), an anterolabial cusp (o) and an anterolingual cusp (p); there is a small anterior labial cusplet (q); the protoconid (r) is separate from the metaconid cusp (s) in younger individuals; the posterior labial cusplet (t) is separate in younger individuals (Fig. 4B) and fused with the hypoconid (u) and entoconid (v) in old-

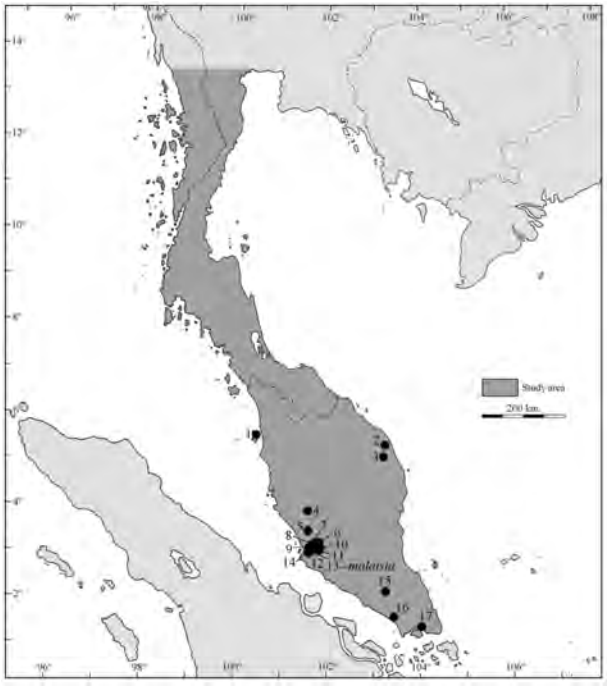

Fig. 19. Distribution of *Lenothrix canus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Malaysia:** 1. Muka Head Forest Reserve, Penang Island; 2. Lerek; 3. Kuala Berang; 4. Gunong Benom; 5. Bukit Kutu; 6. Ulu Gombak; 7. Bukit Lagong; 8. Subang; 9. Bukit Lanjang Forest Reserve; 10. Kuala Lumpur; 11. Pahang Road, 16 miles N.E. of Kuala Lumpur; 12. Kepong, 8 miles N.W.of Kuala Lumpur; 13. Sungei Buloh; 14. Bukit Mandol; 15. Kemidak; 16. Tamok; 17. Kudong. For full locality details, see Gazetteer and Appendix I.

er individuals (Fig. 18B); the posterior cingulum (w) is well-developed. In the second lower molar (M_2), the anterolabial cusp (x) is prominent; the protoconid (y) is fused with the metaconid cusp (z); the hypoconid (aa) is separate from the entoconid cusp (ab) in younger individuals (Fig. 4B); the posterior cingulum is well-developed (ac). In the third lower molar (M_3), the anterolabial cusp is present (Fig. 4B) or absent (Fig. 18B); the protoconid (ad) is separate from the metaconid cusp (ae) in younger individuals; the posterior lamina comprises a very small hypoconid (af) and a large entoconid cusp (ag) (the two are fused in the older specimen in Fig. 18B).

Karyology (based on specimens from Malaysia, Yong 1969a; Musser 1981). 2N = 46, FN = 63 (in males) and 62 (in females); there are three pairs of small metacentric chromosomes, five pairs of subtelocentric chromosomes, 14 pairs of telocentric chromosomes; the X chromosome is a submetacentric and the Y chromosome a telocentric.

Sperm morphology. Information on the sperm morphology of two specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. No specimens are known from Thailand (Pearch et al. 2013).

Taxonomic notes. Although *Lenothrix* was treated as a subgenus of *Rattus* (Ellerman 1949, Medway 1969), subsequent authors (Misonne 1969; Medway & Yong 1976) followed Miller (1903b) and included it in its own separate genus. Musser (1981) provided an exhaustive list of distinguishing characters. Kloss (1931) described a new subspecies *L. c. malaisia,* to which he referred specimens from peninsular Malaysia and Sarawak. However, the validity of this race is not clear and requires further study.

Distribution and conservation status. *Lenothrix canus* is a Sundaic species, which is found in peninsular Malaysia, Tuankul Island, and Borneo, including Sarawak, Sabah, and southwest Kalimantan (Musser & Carleton 2005). Its distribution in the study area is illustrated in Fig. 19.

Its conservation status is listed by IUCN as 'Least Concern' since it has a "wide distribution, presumed large population, occurrence in a number of protected areas, tolerance to some degree of habitat modification, and because it is unlikely to be declining at nearly the rate required to qualify for listing in a threatened category" (Ruedas et al. 2008b).

Ecology and reproduction. This is primarily an arboreal rodent, which in peninsular Malaysia has been collected from the foothills of Selangor (Medway 1969) where it was common in the forests of Bukit Lagong, Bukit Kutu, and Bukit Lanjang and also in the lowland secondary forests at Subang and Meru. In addition, it was abundant in the Kampong rubber plantations on Bukit Mandol and was trapped in primary and disturbed primary forests in Pahang and Johor (Muul & Lim 1971). Extralimitally, it is considered to be a common species in primary rain forest in the Mount Kinabalu National Park in Sabah (Wells et al. 2004); it was also collected in primary and secondary forest in Sarawak (Kloss 1931). Mean litter size is 3.0 with a range of 2 to 6 (Harrison 1955). Average life span in the wild is five months (Harrison 1956a).

Genus *Leopoldamys*

Long-tailed giant rats

Leopoldamys Ellerman 1947: 261; type species *Mus sabanus* Thomas.

Remarks. *Leopoldamys* is a rather large and semi-arboreal rat, which according to Musser & Carleton (2005) is represented by six living species, of which two, *L. sabanus* and *L. ciliatus,* are found in the study area of peninsular Myanmar, Thailand and Malaysia. The distribution of the genus is mapped in Musser (1981, page 265). With the exception of *L. sabanus,* and to a lesser extent *L. edwardsi,* the other four taxa appear to have relatively restricted ranges. *Leopoldamys milleti* (Robinson & Kloss) is currently thought to be restricted to the Langbian Mountains of Vietnam; *Leopoldamys neilli* (Marshall) is endemic to central and northern Thailand; *L. siporanus* (Thomas) is endemic to the Mentawai Archipelago of Indonesia; and

L. ciliatus is confined to peninsular Malaysia and the highlands of Sumatra.

However, for an alternative view see Balakirev et al. (2013). They recognise 8 species. Three, *L. ciliatus, L. siporanus* and *L. milleti,* have geographical ranges comparable to those outlined in Musser & Carleton (2005). However, they consider *L. sabanus* to be restricted to Borneo; specimens formerly referred to *L. sabanus* in the lowlands of the Malacca Peninsula, northward to southwestern Thailand are assigned to *L. vociferans* (Miller); and specimens from the lowlands of eastern and central Indochina are now included in *L. revertens* (Robinson & Kloss). The taxon *neilli* is considered to be a junior synonym of *L. herberti* (Kloss). *Leopoldamys edwardsi* has a range that includes China and northern Vietnam (northward of 21°N). However, it should be noted that this new taxonomic treatment is contrary to that of Latinne et al. (2012, 2013a, 2013b).

Description (based on personal observation and Musser 1981; restricted to the two species [sensu Musser & Carleton 2005] occurring in the study area). *Leopoldamys* is characterised by its large size, long tail, which greatly exceeds head and body length (Tables 9 and 11), and smooth fur, which is without spines. The guard hairs on the back are soft and about equal in length to the overfur, or only slightly longer. The dorsal pelage is sharply demarcated from the pale underparts, which are white to creamy white (Fig. 51D). The tail is usually unicoloured, brown (sometimes slightly paler below) in *L. ciliatus* and bicoloured in *L. sabanus*. When bicoloured, its upper surface is brown, sometimes mottled brown and the lower surface is pale, tending to white (above and below) towards the tip. The hind feet are long and slender, each with six plantar pads (Fig. 20C); the interdigital pads (1) are medium sized; the outer metatarsal pad (2) is rounded and the inner metatarsal pad (3) is elongated. Females have eight mammae: one pectoral pair, one postaxillary pair, and two inguinal pairs (Musser 1981), although according to Medway (1969) there are two pectoral pairs and two inguinal pairs.

The skull is long and narrow. The nasals are long with rounded, blunt anterior margins (Fig. 20Ai). The interorbital area is broad (vi) and each lachrymal bone (ii) is small. In lateral view, the braincase is low; it has well-developed supraorbital ridges (iii), which extend posteriorly to the supraoccipital (v). The zygomata (iv) are virtually parallel to each other. The zygomatic plates (xv) do not extend much beyond the anterior root (xvi) of each zygoma; meanwhile the squamosal root (xvii) is set high on the side of the braincase. The palate (xiii) is wide and scored by shallow palatine grooves; its posterior border (x) ends before, or in line with, the last upper molars (M^3) (ix). The distance from the back edge of the palate to the ventral margin of the foramen magnum (xii) (postpalatal length) is shorter than the palatal length. The incisive foramina are short and broad (vii); their posterior margins (viii) end well in front of the anterior margin of the first upper molars (xiv). The tympanic bullae are small (xi) and pressed against the squamosal bones (xviii). Each half mandible has a small coronoid process (xx) and a shallow emargination (xxii) between the condylar (xxi) and angular processes (xxiii). The process of the lower incisor root (xxiv) is little developed.

The upper incisors (xix) are strongly opisthodont and the enamel layers of the upper and lower incisors are bright orange. In the first upper molar (M^1), cusps t1 and t2 (Fig. 20Ba) are fused with t3 (b); cusps t4, t5 and t6 (c) are also fused; on the third row, cusps t8 (d) and t9 (e) are fused; there is no posterior cingulum. In the second upper molar (M^2), cusp t1 (f) is rounded and large; cusp t3 is mostly, but not always, absent; cusps t4, t5 and t6 (g) are fused; there is a large t8 (h). In the third upper molar (M^3), the anterior lingual cusp (t1) (i) is large and prominent; cusp t3 is absent in *L. ciliatus* but occasionally present in some specimens of *L. sabanus* from Malaysia; cusps t4, t5 and t6 (j) are fused; the last row comprises only t8 (k); in older individuals, t8 becomes fused with t4, t5 and t6 (Fig. 20B); there is no posterior cingulum.

In the mandibular toothrow, the first lower molar (M_1) is without an anterocentral cusp; the anterolabial cusp (l) and anterolingual cusp (m) are fused; in the second row, the protoconid (n) cusp is fused with the metaconid cusp (o); in the third row, the posterior labial cusplet (p) is separate in young individuals but otherwise is fused with the hypoconid (q) and entoconid cusps (r); the posterior cingulum (s) is well-developed. In the second lower molar (M_2), the anterolabial cusp is very occasionally present in *L. ciliatus* but absent from *L. sabanus* (Fig. 20B); the protoconid (t) is fused with the metaconid cusp (u); the posterior labial cusplet (v) is always present, separate in young individuals, it is fused in older individuals (Fig. 20B) with the hypoconid (w) and entoconid cusps (x); the posterior cingulum (y) is well-developed. In the third lower molar (M_3), the anterolabial cusp is absent; the protoconid (z) is fused with the metaconid cusp (aa); the posterior lamina is constituted only by the entoconid cusp (ab), although sometimes there is also a small hypoconid.

Key to species for the two species currently recognised in the Myanmar-Thai-Malaysian peninsula is included in Table 10.

Leopoldamys ciliatus

Sundaic mountain leopoldamys

Mus ciliata Bonhote 1900: 879; Mount Inas, Perak, Malaya.

Description (based on Bonhote 1900, Yong 1970). This is a large rat with a long tail (Table 9). The mean weight of 30 males and 30 females from peninsular Malaysia was 300 g and 284 g respectively (Lim 1970), with a range (both sexes) of 204–395 g (Muul & Lim 1971). The fur is short and without long, protruding guard hairs. On the

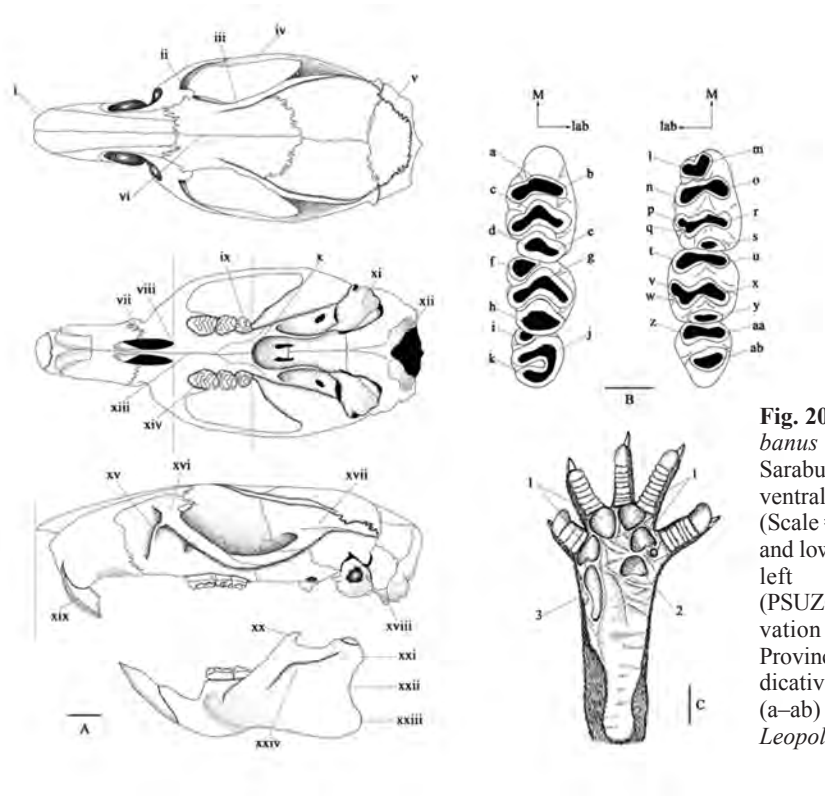

Fig. 20. Skull and dentition of *Leopoldamys sabanus* (54–1319 CTNCR), Phu Num Tok, Saraburi Province, central Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *L. sabanus* (PSUZC–MM2012.201) Phato Watershed Conservation and Management Unit, Chumphon Province, peninsular Thailand (Scale = 5 mm). Indicative numbers (i–xxiv) and (1–3) and letters (a–ab) are explained in the text 'Description' for *Leopoldamys.* M: mouth; lab: labial.

upper surface, it is dark brown or greyish, comprising a light grey under-fur intermixed with longer hairs, which are pale at their bases and dark at their tips; the flanks are fawn coloured, without a reddish brown stripe. The fur is without spines, the guard hairs are grey with black or brown tips. The underparts are yellowish-white and clearly demarcated from the flanks; frequently there is a median dark patch (brown or grey) on the chest between the forelimbs (Medway 1969, = *R. edwardsi*). The ears are moderately long, naked and uniformly rounded. The whiskers are very long and numerous. There are two very long supraorbital bristles/hairs, which exceed 70 mm in length (hence the species name) and which differentiate this species from *L. sabanus* (bristle length = 40 mm). The fore and hind feet are a uniform brown, sometimes with an irregular longitudinal whitish stripe. The hind feet are long in comparison to those of *L. sabanus.* The tail is long, significantly longer than head and body length (Medway 1969, Musser & Newcomb 1983), although in the original description of *ciliatus*, the tail (315 mm) is considered to be only slightly longer than head and body (290 mm) (Table 9). It is usually unicoloured, brown, and with many short, stiff bristles; occasionally specimens have an unpigmented patch at the tip or the entire underside pale. The skull and teeth, which are illustrated in Musser & Newcomb (1983, Figure 115, = *L. edwardsi*), closely conform to the generic description provided above. According to Bonhote (1900), the skull is similar to that of *L. sabanus* but is slightly longer (where the two are sympatric) and with a greater depth of braincase and less prominent supraorbital ridges.

Karyology. 2N = 42, FN = 56 (male and female); there are three pairs of small metacentric chromosomes, four pairs of subtelocentric chromosomes, and 13 pairs of telocentric chromosomes; the X and Y chromosomes are telocentrics (= *Rattus edwardsi* in Yong 1969a; = *Leopoldamys edwardsi* in Musser 1981).

Sperm morphology. Information on the sperm morphology of two specimens (listed as *L. edwarsi*) from peninsular Malaysia is included in Breed &Yong (1986).

Fossil history. Currently, there are no records of fossil *L. ciliatus* from the study area (Pearch et al. 2013).

Taxonomic notes. This taxon was formerly included in *L. edwardsi* by Musser (1981) and Corbet & Hill (1992). However, Musser & Carleton (2005) considered that *L. edwardsi* was restricted to the Indochinese region, whereas specimens from the Sundaic region were referable to *L. ciliatus*.

Distribution and conservation status. *Leopoldamys ciliatus* is known from the highlands of Sumatra and peninsular Malaysia, where its range is illustrated in Fig. 21.

Its conservation status is listed by IUCN as 'Least Concern' since it has a "wide distribution, presumed large population, it occurs in a number of protected areas, has a tol-

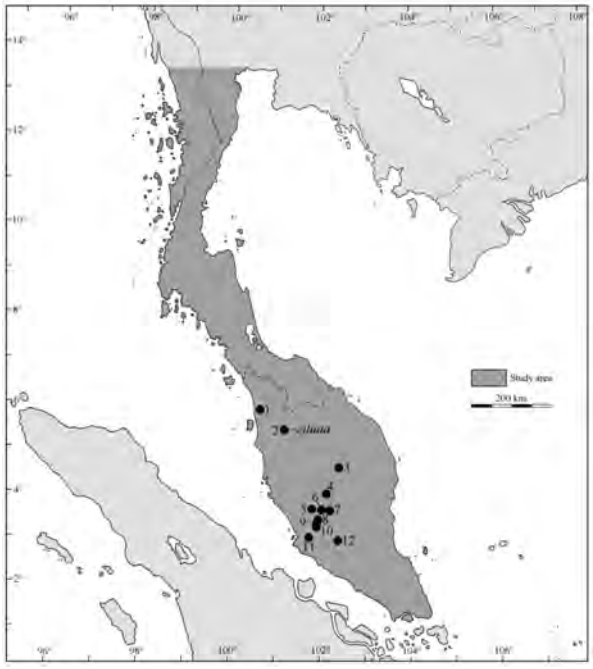

Fig. 21. Distribution of *Leopoldamys ciliatus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Malaysia:** 1. Kedah Peak; 2. Mt. Inas; 3. Gunong Tahan; 4. Gunong Benom; 5. Bukit Kutu; 6. Gunong Menkuang; 7. Bukit Fraser (above Semangko Pass); 8. Gunong Ulu Kali; 9. Gunong Bunga Buah; 10. Ulu Gombak, 20th mile [of] Pahang Road; 11. Ulu Langat Forest Reserve; 12. Jelebu District. For full locality details, see Gazetteer and Appendix I.

erance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Musser et al. 2008a).

Ecology. In peninsular Malaysia, *L. ciliatus* occurs in montane forests with a rather peaty floor, which is carpeted with mosses and has many crevices at the base of trees and rocks (Yong 1970, = *R. edwardsi*). It is mainly confined to altitudes in excess of 1075 metres (3500 feet) and as such does not usually overlap with *L. sabanus* (Yong 1970, Lim 1970, = *R. edwardsi*). The lowest altitude it was encountered was at 615 metres (2000 feet) at Kampong Janda Baik in Pahang (Yong 1970). Lim (1970) suggests that it is restricted to primary forests and although primarily a ground-dweller, also climbs trees; its nests were found in tree holes (nearly two metres above the ground) and in fallen logs. He also suggested that it prefers drier, well-drained areas although it may visit wetter areas. It is a terrestrial and possibly arboreal, omnivorous species which occurs in primary and degraded tropical moist forest. It occurs in the montane forests of Sumatra and peninsular Malaysia usually above 1000 m (Musser et al. 2008a). Its diet includes insects, fruit and vegetable matter (Lim 1970).

Leopoldamys sabanus

Indomalayan leopoldamys; Long-tailed giant rat

Mus sabanus Thomas 1887: 269; Mount Kinabalu, Borneo, Indonesia.
Mus vociferans Miller 1900b: 138; Trang, peninsular Thailand, 1000 feet.
M. stridens Miller 1903a: 28; Tioman Island, East Malaysia.
M. stridulus Miller 1903a: 29; Bentinck Island, Mergui Archipelago, Myanmar.
M. matthaeus Miller 1903a: 29; St Matthew Island, Mergui Archipelago, Myanmar.
M. lucas Miller 1903a: 30; St Luke Island, Mergui Archipelago, Myanmar.
E. stentor Miller 1913: 19; James Island, Mergui Archipelago, Myanmar.
Mus vociferans lancavensis Miller 1900c: Langkawi Island, Malaysia.
M. v. tersus Thomas & Wroughton 1909: 535; Teratau Island, southwest Thailand.
Epimys v. insularum Miller 1913: 19; Domel Island, Mergui Archipelago, Myanmar.
E. v. clarae Miller 1913: 20; Clara Island, Mergui Archipelago, Myanmar.
R. s. dictatorius Chasen 1940: 165; Penang Island, Malaysia.
R. s. salanga Chasen 1940: 166; Junk Seylon Island, Southwest Thailand.

Description (based on personal observation and Miller 1900b; Miller 1900c; Miller 1903a; Thomas and Wroughton 1909; Miller 1913; Chasen 1940 and follows the taxonomy of Musser & Carleton 2005). This is a large rat with a very long tail (Tables 9 and 10). The pelage on the upper surface is short and the black guard hairs, which are some 15 mm in length, scarcely extend beyond the over-fur. The colour varies from darker forms (*vociferans, tersus, matthaeus*) to paler forms (*stridulus, lucas, lancavensis*). In general, the mainland form (*vociferans*) has grey under-fur on the dorsal surface, which is overlain with golden-orange/yellow hairs, which are grizzled with black (Fig. 51D). The black is most conspicuous on the back and the rump and least apparent on the flanks. There is a clear division between the orange-brown flanks and the ventral surface. The belly and the inner side of the legs are dull white to yellowish-white to the hair bases (*vociferans*) or creamy buff (*lancavensis, stridulus*), although in some forms the yellow is more pronounced (*stridens, matthaeus*). The ears are rounded. The muzzle is comparable to the upper surface in colour and the cheeks are orange-buff, like the flanks. The whiskers are black and long. The supraorbital bristles are about 40 mm in length. The fore and hind feet are white, irregularly marked with brown. The footpads are well-developed for climbing. The tail is characteristically long, always much longer than the head and body (Tables 9 and 11). In general it averages more than 140 % of head and body length, although there is some individual and possible geographical variation. The tail is bicoloured in the basal half, dark brown above and whitish (unpigmented) below. The half nearer the tip is usually, but not always, whitish (unpigmented) above

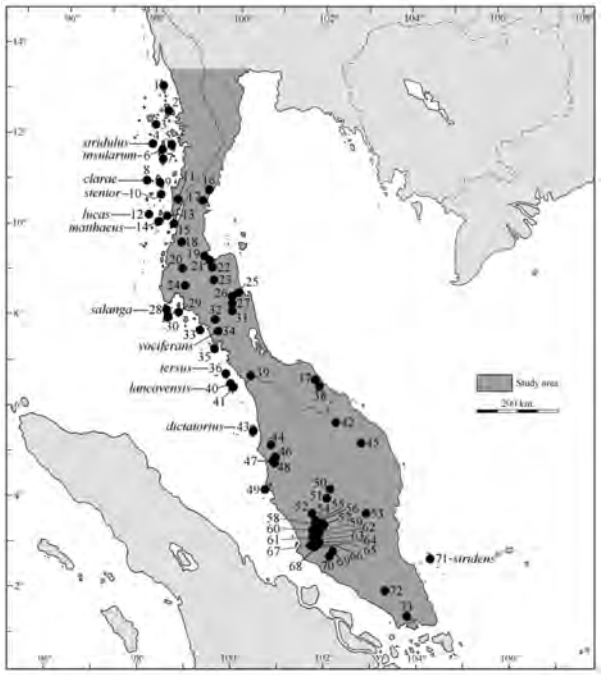

Fig. 22. Distribution of *Leopoldamys sabanus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Tavoy Island; 2 King's Island; 3. Ross Island 4. Bentinck Island; 5. Kisseraing Island; 6. Domel Island; 7. Malcolm Island; 8. Clara Island; 9. Sullivan Island; 10. James Island; 11. Bankachon; 12. St. Luke Island; 13. Hastings Island; 14. St. Matthew Island; 15. Victoria Island. Not located: Helfer Island. **Thailand:** 16. Maprit; 17. Chumpann; 18. Phato Watershed Conservation and Management Unit; 19. Tha Chang; 20. Rajjaprabha Dam; 21. Khao Nong; 22 .Khao Tha–Phet; 23. Ban Plai Nam; 24. Klong Phraya Wildlife Sanctuary; 25. Krung Ching; 26. Khao Luang; 27. Nongkok; 28. Junk Seylon Island; 29. Telok Poh, Pulau Panjang; 30. Klong Tun Sai; 31. Khao Phu Khao Ya National Park; 32. Lam–ra; 33. Pasir Raja, Pulau Lontar; 34. Trang; 35. Pulau Telibon; 36. Teratau Island; 37. Ban Thon; 38. Ban Ya Kan. **Malaysia:** 39. Kaki Bukit; 40. Langkawi Island; 41. Sungei Kilim; 42. Kedah Peak; 43. Penang Island; 44. Ulu Selama; 45. Ulu Trengganu; 46. Maxwell's Hill; 47. Taiping; 48. Gunong Ijan; 49. Pangkor Besar Island; 50. Genting; 51. Gunong Benom; 52. Binting Bidai; 53. Jenka; 54. Klang Gates; 55. Ginting Bidai; 56. 16th. mile of Pahang Road, Ulu Gombok; 57. Fraser's Hill; 58. Kuala Kubu; 59. Genting Simpah; 60. Templer Park; 61. Kampong Janda Baik; 62. Ulu Gombak, 20th mile [of] Pahang Road; 63. Bukit Lagong Forest Reserve; 64. Bukit Lanjang; 65. Kampong Janda Buah; 66. Kuala Lumpur; 67. Cheras; 68. Ulu Langat; 69. Bukit Lantar; 70. Bukit Tangga; 71. Tioman Island; 72. Karang; 73. Mount Pulai. For full locality details, see Gazetteer and Appendix I.

and below. It is coarsely, conspicuously and uniformly annulated with 7 to 8 rings of scales/cm in the mid-part and with numerous short stiff bristles. The skull (Fig. 20A) essentially conforms to the generic description above, with some individual and geographical variation. Photographs of the skull are available in Musser & Newcomb 1983, Figure 115 and Marshall 1988, page 484).

Karyology (based on specimens from Malaysia, Yong 1969a; Musser 1981). 2N = 42, FN = 54 (male and female); there are two pairs of small metacentric chromosomes, four pairs of subtelocentric chromosomes, and 14 pairs of telocentric chromosomes; the X and Y chromosomes are telocentrics.

Sperm morphology. Information on the sperm morphology of four specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. There are seven localities of fossil *L. sabanus* in Thailand including two late middle Pleistocene sites in the peninsula (Pearch et al. 2013).

Taxonomic notes. According to Musser (1981) and Musser & Carleton (2005), considerable morphological variation is apparent between populations from the Indochinese and Sundaic subregions and among insular populations from the Sundaic subregion. This may indicate the presence of more than one species. Subsequently, Latinne et al. (2013b) suggested that *L. sabanus* (sensu stricto) is essentially confined to the Sundaic subregion.

Distribution and conservation status. *Leopoldamys sabanus*, as currently understood, is widespread. It ranges from Bangladesh to Myanmar, Thailand, Indochina and Indonesia. Its range in the Myanmar-Thai-Malaysian peninsula is illustrated in Fig. 22. For a contrary view of its distribution in Thailand, see Latinne et al. (2013b), who suggested that it was restricted to southern Thailand with a northern limit of Kanchanaburi Province.

Its conservation status is listed by IUCN as 'Least Concern' since it has a "wide distribution, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category. Additional taxonomic studies will reveal this taxon to be comprised of several species for which a review of the Red List assessment will be necessary" (Lunde et al. 2008b).

Ecology and reproduction. *Leopoldamys sabanus* is mostly nocturnal and unlike *L. ciliatus* is mainly found in lowland forest, especially evergreen forest habitats up to 1200 metres although it has been found above this elevation at Maxwell's Hill, Perak (up to 1380 metres) and on the slopes of Mount Kinabalu (up to 3100 metres) in Sabah, Malaysia (Marshall 1988; Francis 2008; Lunde et al. 2008b). Yong (1970) states that it seems to be confined to dipterocarp forests with a hard substratum carpeted with fallen leaves and the trees without crevices at the base. Lim (1970) suggests that its altitudinal range does not overlap with that of *L. ciliatus* and that it prefers disturbed primary forest and secondary forest to pristine primary forest; its nests were found in tree holes and in burrows in the ground. According to Medway (1969), it is mostly ground dwelling and favours well drained areas. However, it is able to climb freely and Gorog et al. (2004) and Wells et al. (2004) noted that it was a semi-arboreal rat that forages on the ground as well as in the canopy and amongst

lianas. According to Lim (1970), the diet consists of insects, fruit, and other vegetable matter (as well as snails). In South Asia, it is a nocturnal and subterranean species, which occurs in tropical, subtropical, wet montane temperate forests (Molur et al. 2005).

The young are born in short burrows dug into sloping hillsides. There are one or two entrances and the nest chamber is lined with broad leaves, most of which are collected from surrounding shrubs and woody undergrowth. In Selangor, Malaysia pregnant females were recorded in all months, but most frequently from July to September and least frequently from January to March. Mean litter size is 3.1 (1 to 7) (Medway 1969).

Genus *Maxomys*

Maxomys rats

Maxomys Sody 1936: 55; type species *Mus bartelsii* Jentink.

Remarks. *Maxomys* is an essentially Sundaic genus of rodents. With the exception of *M. rajah, M. surifer, M. whiteheadi*, the other 14 species have relatively restricted geographical ranges. Eleven are variously distributed in the large and small islands on the Sunda shelf and the Thai-Malay peninsula, south of the Isthmus of Kra. Only one of these, *M. surifer*, extends north of the isthmus into Indochina. A single species, *M. moi* Robinson & Kloss, is endemic to Laos and Vietnam. One species, *M. pagensis* Miller, occurs on the Mentawai Islands, off the fringe of the Sunda Shelf. Four species, *M. hellwaldii* Jentink*, M. dollmani* Ellerman*, M. musschenbroekii* Jentink*,* and *M. wattsi* Musser, are found on Sulawesi and are the only members of this genus found to the East of Wallace's line (Musser et al. 1979). Four species, *M. inas, M. rajah, M. surifer,* and *M. whiteheadi*, occur in the Myanmar-Thai-Malaysian peninsula and Singapore (Musser & Carleton 2005). Aspects of the phylogeny, diversity and biogeography of the genus were reviewed by Gorog et al. (2004) and Pagès et al. (2010). Most recently, Achmadi et al. (2013) recognised two putative new species from Sulawesi and Latinne et al. (2013b) identified four highly divergent genetic lineages within *M. surifer.*

Description (based on personal observation and Musser et al. 1979; restricted to the four species occurring in the study area). The body size ranges from small to medium (Table 12). The tail is shorter to slightly longer than the head and body. It is finely scaled in all species; it is dark above and paler below, sometimes with the portion nearest to the tip white (unpigmented) above and below, but is without a terminal pencil of hairs. The dorsal pelage over the head and body is short, soft, dense, and spiny (Figs 2A, 3B, 3E, and 51A). The hind feet are always long and narrow, with smooth and naked plantar surfaces (Fig. 23C), usually with five, smooth pads (four interdigital and one inner metarsal), lacking the outer metatarsal pad, in *M. inas* and *M. whiteheadi*. If present, as in *M. surifer* and *M. rajah*, this pad is small and rounded (2); the inner metarsal pad (3) is similar in size to the interdigital pads (1). In all local species, females have four pairs of mammae: one pectoral, one postaxillary and two inguinal pairs.

In the skull, the rostrum is long and wide (Fig. 23Aii) and the nasals (v) extend in front of the upper incisors (xi-ii). The anterior border of each nasal is triangular anteriorly (i). The lachrymal bones (iii) are relatively large. The zygomata are virtually parallel with each other (vi). The braincase has well-defined ridges on the dorso-lateral margins (iv). The palate is relatively short (but exceeds the postpalatal length); its posterior border (ix) is in line with, or slightly anterior to, the posterior borders of the last upper molars (M^3) (xii). The incisive foramina are short, wide and heart-shaped (vii); their posterior margins (viii) are situated well in front of the anterior margins of the first molars (xi). The tympanic bullae are small (x). In each half mandible, the coronoid process (xiv) is small; the emargination (xvi) is shallow between the condylar (xv) and angular (xvii) processes.

The incisors have an orange enamel layer; the upper incisors (xiii) are opisthodont. In the first upper molar (M^1), cusp t1 (Fig. 23Ba) is separate in younger individuals (Fig. 5C), but subsequently fuses with cusps t2 and t3 (b); on the second row, cusp t4 (c) may or may not (Fig. 23B) be separate from cusps t5 and t6 (d), which are fused; the third row has one large medial cusp which is representative of both t8 and t9 (e) (cusp t7 is missing). In the second upper molar (M^2), cusp t1 (f) is prominent and large; cusp t3 (g) is usually present in *M. rajah, M. surifer* and *M. whiteheadi* but is often absent in *M. inas*; in younger individuals, cusp t4 (h) is separate from cusps t5 and t6 (i), which are fused (Fig. 5C); in older individuals t4, t5 and t6 may be fused, as in Fig. (23B); cusps t8 and t9 (j) are fused. In the third upper molar (M^3), cusp t1 (k) is rounded and large; cusp t3 is usually absent; cusp t4 (l) is separate from cusps t5 and t6 (m) in younger individuals but fused in older individuals (Fig. 5C & D); there is a single cusp in the third row (n).

In the mandibular toothrow, the first lower molar (M_1) comprises an anterolabial (o) and anterolingual cusp (p), which are separate in younger individuals (Fig. 5K) but are fused together in older *Maxomys*; the protoconid (q) and metaconid cusp (r) are well-defined; there is a posterior labial cusplet (s) which is separate in young individuals (Fig. 5K) but is fused with the hypoconid (t) and entoconid cusps (u) in older individuals; there is a posterior cingulum (v) in *M. rajah* and *M. surifer* but this is mostly absent in *M. inas* and *M. whiteheadi.* In the second lower molar (M_2), there is usually an anterolabial cusp (w) in all local species except *M. whiteheadi;* it is adjacent to the protoconid (x) and metaconid cusps (y); in *M. rajah* and *M. surifer,* there is also usually a posterior labial cusplet (z) adjacent to the hypoconid (aa) and entoconid cusps (ab) but this is generally absent in *M. inas* and *M. whiteheadi*; there is a posterior cingulum (ac). In the third low-

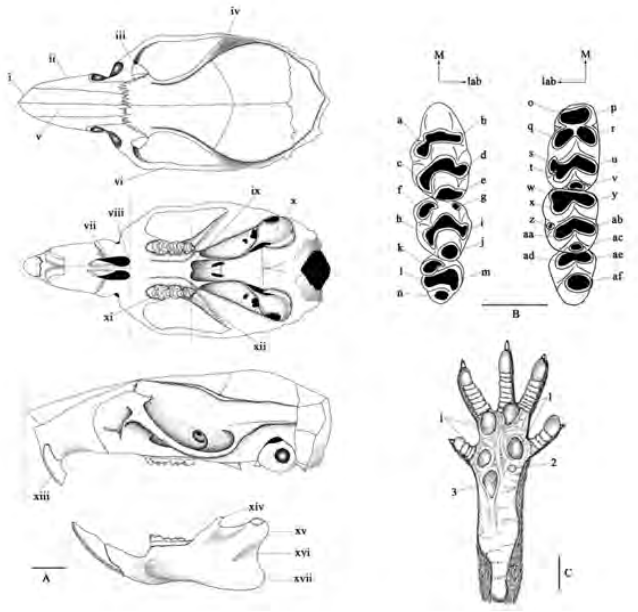

Fig. 23. Skull and dentition of *Maxomys surifer* (54–2919 CTNCR), Pong Nam Ron District, Chanthaburi Province, Southeast Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *M. surifer* (PSUZC–MM2012.202), Phato District, Chumphon Province, peninsular Thailand (Scale = 5 mm). Indicative numbers (i–xvii) and (1–3) and letters (a–af) are explained in the text 'Description' for *Maxomys.* M: mouth; lab: labial.

er molar (M_3), the anterolabial cusp is absent; the metaconid (ad) and protoconid cusps (ae) are fused and the posterior lamina is constituted only by the entoconid cusp (af). In *M. rajah,* a posterior cusplet is also usually present.

Key to species of the four species currently recognised in the study area (sensu Musser & Carleton 2005) is included in Table 13. However, recent research indicates that there are additional distinct genetic lineages of *Maxomys* within peninsular Thailand that may prove to be discrete species (Latinne et al. 2013b).

Maxomys inas

Malayan mountain maxomys; Malayan mountain spiny rat
Mus inas Bonhote 1906: 9; Mount Inas, Perak, Malaysia.

Description (based on Bonhote 1906, Medway 1969, Francis 2008). This is a medium-sized rat (Table 12) with a mass of 55–105 g (Medway 1969). On the upper surface, the fur is long and thickly interspersed with stiff, flattened spines. It is a uniform, rich yellow-reddish-brown (ochraceous rufous) grizzled with black. On the ventral surface, it is grey washed with chestnut to pale yellow-brown (ochraceous) to pinkish buff. The demarcation between the upper and lower surfaces is not well defined. The upper surfaces of the fore- and hind feet are brownish white. There are five plantar pads on the hind feet. In the type description, the tail is described as being rather shorter than head and body length (Bonhote 1906) but in Hill (1960), Medway (1969) and Musser et al. (1979), the measurements appear about equal, whereas according to Francis (2008) it is slightly longer. The tail is almost naked and bicoloured, dark above and paler below. The skull is medium-sized (Table 12).

Karyology (based on specimens from Malaysia, Yong 1969a; Musser et al. 1979). 2N= 42, FN= 83; there are ten pairs of metacentric chromosomes and ten pairs of submetacentric chromosomes; the X chromosome is a metacentric and the Y chromosome is an acrocentric.

Sperm morphology. Information on the sperm morphology of two specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. Currently, there is no fossil record of *M. inas* in the study area (Pearch et al. 2013).

Taxonomic notes. Although described as a discrete species, this taxon was treated subsequently by Chasen (1940) as a subspecies of *Rattus alticola* Thomas (= *Maxomys alticola*) described from Borneo. Later, it was recognised again as a distinct species by Medway (1964a), Corbet & Hill (1992) and Musser & Carleton (2005).

Distribution and conservation status. *Maxomys inas* is endemic to peninsular Malaysia, where its range is illustrated in Fig. 24.

Its conservation status is listed by IUCN as 'Least Concern' since it "has a relatively wide distribution in montane parts of the Malay Peninsula (though it may occur further north), and there are not believed to be any major threats to the species at present" (Lunde & Aplin 2008).

Ecology and reproduction. According to Musser & Carleton (2005), it is essentially restricted to montane habitats in peninsular Malaysia above 900 metres. In Pahang, Malaysia, it was collected at altitudes ranging from approximately 1080 metres to 1630 metres (3500 feet to 5300 feet) (Hill 1960). Litter size in one individual was 3 (Medway 1969). Its diet includes caterpillars (Medway 1964a, 1969).

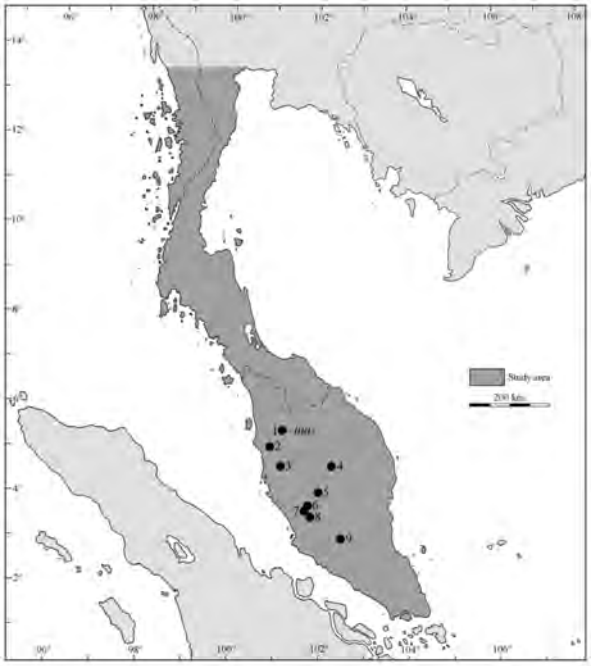

Fig. 24. Distribution of *Maxomys inas* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Malaysia:** 1. Mt. Inas; 2. Maxwell's Hill; 3. Mt. Brinchang; 4. Gunong Tahan; 5. Gunong Benom; 6. Bukit Fraser; 7. Bukit Kutu; 8. Gunong Menkuang; 9. Jelebu District. For full locality details, see Gazetteer and Appendix I.

Maxomys rajah

Rajah maxomys; Rajah spiny rat

Mus rajah Thomas 1894: 451; Mount Batu Song, Sarawak, Borneo, Malaysia.

Mus pellax Miller 1900b: 147; Trang, peninsular Thailand.

Description (based on Miller 1900b, Hill 1960, Medway 1969 and Musser et al. 1979). This is a medium-large rat (Table 12) with a mass of 80–265 g (Medway 1969). The pelage is harsh with many conspicuous spines. The back and crown of the head are brown (light brown to dull buff brown) without any reddish tinge, although the shoulders and flanks are more ochre in colour. The midline of the back is often, but not always, darker. However, there are relatively few black hairs and the numerous spines are grey not black. There is a clear division on the flanks between the dorsal and ventral surfaces; the latter is white to the base of the hairs and often has a dark longitudinal streak in the midline of the belly (Medway 1969). The inner side of the legs and upper surface of the feet are white. There are six plantar pads, including a small outer metatarsal pad. The face is brown and there are moderately conspicuous grey-brown eye-rings. The ears are dark brown, and there is a white spot between the ears in a minority of specimens of the local form, *pellax*. The tail is reported to average slightly longer than head and body length in Hill (1960), Medway (1969) and Pimsai (2012) and slightly shorter in Musser et al. (1979) (Table 12). It is bicoloured, but not sharply, light brown above and whitish (unpigmented) below, the colours becoming indefinite near the tip. There are about ten rings of scales/cm in the midpart of the tail; the hairs are reduced in length near the tip. The skull is medium-large (Table 12) and is essentially similar to that of *M. surifer* in all characters, with the possible exception of the upper molar toothrow, which is slightly longer on average in *M. rajah*. Photographs of the skull are included in Marshall (1988, page 449).

Karyology (based on specimens from peninsular Malaysia, Yong 1969a, Musser et al. 1979). 2N= 36, FN= 56; there are six pairs of metacentric chromosomes, three pairs of submetacentric chromosomes, and eight pairs of acrocentric chromosomes, both the X and Y chromosomes are metacentrics.

Fossil history. There are no records of fossil *M. rajah* from peninsular Thailand (Pearch et al. 2013).

Taxonomic notes. The taxonomic status of *Maxomys rajah* has varied over time. Some suggested that *rajah* and *surifer* were conspecific (Ellerman & Morrison-Scott 1951 & 1955, Harrison 1957a) whilst others treated them as separate species (Chasen 1940, Sody 1941, Ellerman 1949, Hill 1960, Yong 1972, Corbet & Hill 1992, Musser & Carleton 2005). Hill (1960) provides a detailed comparison of the local race *pellax* with the nominate form from Sarawak.

Distribution and conservation status. *Maxomys rajah* is known extralimitally from Riau Archipelago, Sumatra and Borneo (Musser & Carleton 2005); in the study area it is found in southern peninsular Thailand-Malaysia and Singapore (Fig. 25).

Its conservation status is listed by IUCN as 'Vulnerable' because of "a population decline, estimated to be more than 30 % over the last ten years, inferred from extensive loss and degradation of its lowland forest habitat" (Aplin et al. 2008e).

Ecology and reproduction. According to Francis (2008), this is a nocturnal and predominantly terrestrial rodent. It lives in burrows in forest, the entrances of which are loosely plugged with leaves (Yong 1972). It generally occupies higher, better drained sites than *M. surifer* (Harrison 1957a, Medway 1969). It is common in appropriate habitat. Nor (2001) recorded 34 specimens between 500 and 1100 m on Mount Nuang, Ulu Langat, Selangor Province, Malaysia. Yong (1972) collected specimens on Gunong Benom between 215 and 770 metres; it tends to avoid interacting with *M. surifer* and the two species are seldom found in the same location. In Trang Province, Thailand, it was collected at an altitude of about 310 metres and had an average litter size is 3.3 (2–5, n= 3) (Harrison 1955). In Narathiwat Province, near the Malaysian border it was collected in tropical rain forest at approximately 200 metres a.s.l. (UP unpublished data).

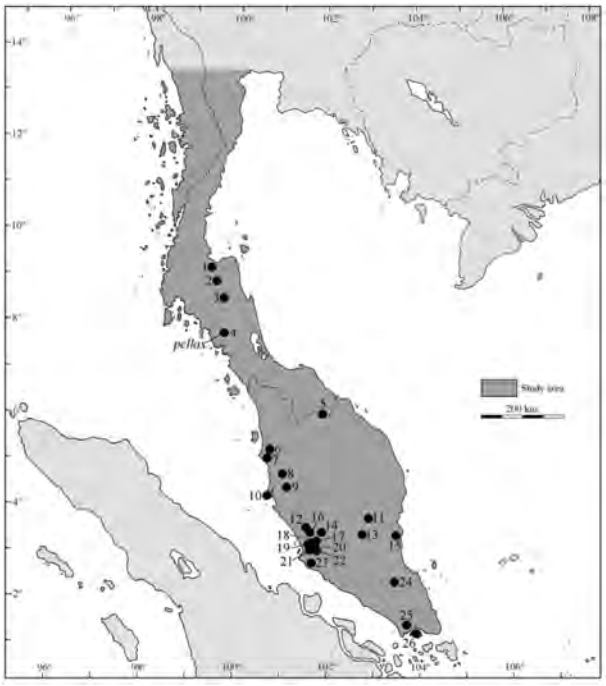

Fig. 25. Distribution of *Maxomys rajah* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Khao Tha-Phet; 2. Ban Plai Nam; 3. Khao Luang; 4. Trang; 5. Hala Bala Wildlife Research Station. **Malaysia:** 6. Ulu Selama; 7. Krian Road; 8. Runuk Tanjong; 9. Jeram Kawan; 10. Pulau Pangkor Besar; 11. Jenka; 12. Rawang; 13. Kampong Awak; 14. Ulu Gombak, 20th mile [of] Pahang Road; 15. Bukit Bangkong; 16. Bukit Lanjang Forest Reserve; 17. Klang Gates; 18. Bukit Lagong; 19. Subang Forest Reserve; 20. Kuala Lumpur; 21. Chera; 22. Ulu Langat Forest Reserve; 23. Bukit Dantai; 24. Bekok; 25. Pulai. **Singapore:** 26. Singapore Island. For full locality details, see Gazetteer and Appendix I.

Maxomys surifer

Indomalayan maxomys, Red spiny maxomys, Red spiny rat

Mus surifer Miller 1900b: 148; Trang, peninsular Thailand.
Mus luteolus Miller, 1903a: 36; St Matthew Island, Mergui Islands, Myanmar.
Mus umbridorsum Miller 1903a: 37; Loughborough Island, Mergui Islands, Myanmar.
Mus casensis Miller 1903a: 38; Chance Island, Mergui Islands, Myanmar.
Mus bentincanus Miller 1903a: 38; Bentinck Island, Mergui Islands, Myanmar.
Mus domelicus Miller 1903a: 39; Domel Island, Mergui Islands, Myanmar.
Mus surifer flavidulus Miller 1900c: 189; Langkawi Island, Malaysia.
Mus surifer butangensis Miller 1900c: 190; Adang Island, Butang Islands, west Thailand.
Mus surifer microdon Kloss, 1908a: 145; Tioman I, Malaysia (pre-occupied by *Mus microdon* Peters, 1852) = *Epimys surifer binominatus* Kloss 1915: 223.
Mus surifer flavigrandis Kloss 1911a: 119; East Perhentian Island, East Malaysia.
Mus surifer grandis Kloss 1911a: 119; Great Redang Island, East Malaysia.
Mus surifer leonis Robinson & Kloss 1911a: 170; Singapore Island.
Epimys surifer pemangilis Robinson 1912: 593; Pemanggil Island, East Malaysia.
Epimys surifer aoris Robinson 1912: 594; Aor Island, East Malaysia.
Epimys surifer manicalis Robinson & Kloss 1914: 230; Koh Pennan (Island), Northeast Malaysia.
Epimys surifer spurcus Robinson & Kloss 1914: 230: Koh Samui (Island), Thailand.
Epimys surifer eclipsis Kloss 1916c: 53; Koh Kra (Island), Thailand.
Rattus surifer puket Chasen 1940: 169; Junk Seylon Island, Western Thailand.
Rattus surifer telibon Chasen 1940: 170; Telibon Island, Western Thailand.
Rattus surifer muntia Chasen 1940: 170; Muk (=Muntia) Island, Trang, Western Thailand.
Rattus surifer pidonis Chasen 1940: 171; Pipidon Island, Western Thailand.

Description (following the taxonomy of Musser & Carleton 2005 and based on personal observation and Miller 1900b, Miller 1900c, Miller 1903a, Kloss 1908a, Kloss 1911a, Robinson & Kloss 1911a, Robinson 1912, Robinson & Kloss 1914, Chasen 1940, Medway 1969). This is a medium-large rat (Tables 12 and 14; Figs 2A, 3E, and 51A) with a mass of 139–284 g (Medway 1969). The fur is characteristically harsh and includes numerous spiny hairs (Fig. 3B). The underlying colour is a bright reddish brown, which is paler in some specimens and darker in others (Fig. 3E). These colours are variably grizzled with black, which is heavy in some geographical forms and may almost combine to produce a dark stripe down the midline of the back. In some, it is darkened on the shoulders, back and rump; in others it is blackish brown on the posterior half of the back, less so on the shoulders and head. The flanks range in colour from orange-brown to buff; there is always less grizzling compared to the upper surface. There is a clear division between the flanks and the under surface, which is white to the base of the hairs in some specimens but yellowish-white to creamy/dirty buff in others (Fig. 3E). There is occasionally an indistinct buff patch on the centre of the abdomen. The throat has a band of darker hairs in some specimens; this ranges in colour and size from narrow, about 18 mm, and yellow to darker, yellowish-orange-buff and about 30 mm in width. In many individuals, there is no colour band or an indistinct band. The muzzle sometimes has a whitish or yellowish-buff patch at the base of the whiskers. The cheeks are yellowish-orange. There is sometimes a dark ring of hairs around the eye. The outer surfaces of the legs are comparable in colour to the flanks. In some individuals, the fore and hind limbs are encircled with yellowish-brown, separating the white inner portion from the foot. In other individuals, this ring is only present on the

hind or fore limbs or is absent. The feet are white or dull white. The hindfeet have six pads, including a small, rounded outer metatarsal pad (Fig. 23C1).

The tail is variable in length (Table 12), although mostly it is about equal to the head and body. However, in some populations, it is generally longer and in others, it is often shorter (Table 14). It is bicoloured, dark brown above and pale (dull white) below (Fig. 2A). Usually, there is a pale tip, which is equal to one quarter or more than one third of the tail length. There are 12 rings of scales/cm in the midpart of the tail; the rings become narrower and less regular near the tip, where the sparse hairs become more numerous but shorter; there is no pencil of hairs. The skull is medium-large (Table 12) and photographs are included in Marshall (1988, page 451).

Karyology (based on specimens from Malaysia, Yong 1969a). 2N= 52, FN= 66; there are four pairs of metacentric chromosomes, two pairs of submetacentric chromosomes, and 19 pairs of acrocentric chromosomes; both the X and Y chromosomes are metacentrics. For Thai specimens, Markvong et al. (1973) report that there are five pairs of metacentric chromosomes, one pair of submetacentric chromosomes, 19 pairs of acrocentric chromosomes, with the X chromosome being a metacentric and the Y chromosome a submetacentric (Musser et al. 1979).

Sperm morphology. Information on the sperm morphology of two specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. Fossil specimens dating back to the late Pliocene have been collected from seven localities in Thailand including four in the peninsula (Pearch et al. 2013).

Taxonomic notes. It is generally accepted that *Maxomys surifer,* as currently understood, is a complex of cryptic species, requiring further taxonomic revision (Gorog et al. 2004, Aplin et al. 2008c, Achmadi et al. 2013), with Latinne et al. (2013b) recognising four highly divergent genetic lineages. Hill (1960) provides descriptions (mostly with measurements, see Table 14) and further information on the following named forms from the study area: *aoris, binominatus, butangensis, casensis, flavidulus, flavigrandis, grandis, leonis, luteolous, manicalis, muntia, pemangilis, pidonis, puket, spurcus, surifer* and *telibon*. Previously the taxon *surifer* was included by Harrison (1957a) in *M. rajah,* although he noted several distinguishing characters between *rajah pellax* and *rajah surifer.*

Distribution and conservation status. *Maxomys surifer* is widely distributed, ranging from Myanmar to Indochina and south-west China to Indonesia (Musser & Carleton 2005); in the study area it is found in the Myanmar-Thailand-Malaysia peninsula and Singapore (Fig. 26).

Its conservation status is listed by IUCN as 'Least Concern' because it is a "very widespread species, it has a presumed large population, no major threats, and occurs in many protected areas" (Aplin et al. 2008c).

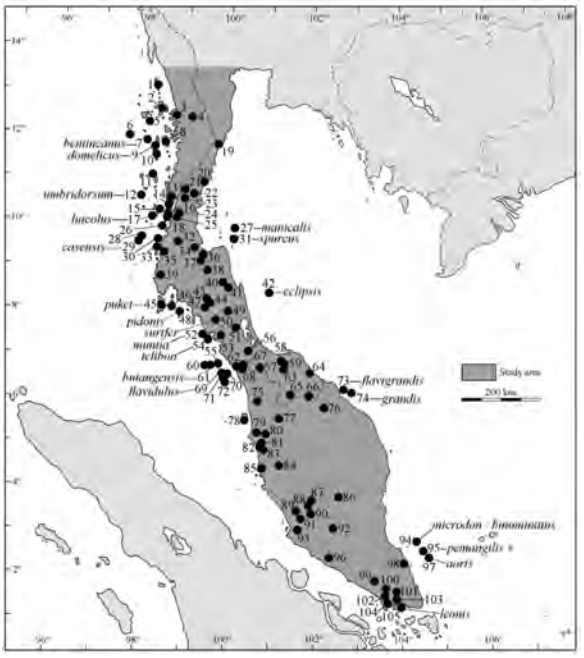

Fig. 26. Distribution of *Maxomys surifer* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Tavoy Island; 2. King's Island; 3. Tenasserim River; 4. Thaget; 5. Ross Island; 6. Sir John Hayes Island; 7. Bentinck Island; 8. Kisseraing Island; 9. Domel Island; 10. Malcolm Island; 11. Lampi Island; 12. Loughborough Island; 13. Maliwun; 14. Bankachon; 15. Hastings Island; 16. Victoria Point; 17. St. Matthew Island; 18. Victoria Island. Not located: Taok Plateau. **Thailand:** 19. Tap–Li; 20. Maprit; 21. Marmok; 22. Ban Na; 23. Tasan; 24. Lam Nam Kra Buri National Park; 25. Ban Bang Non; 26. De Lisle Island; 27. Koh Pennan; 28. Koh Surin Nua; 29. Chance Island (Koh Surin Tai); 30. Koh Yam Yai; 31. Koh Samui; 32. Phato Watershed Conservation and Management Unit; 33. Koh Rah; 34. Tha Chang; 35. Thung Chalee Wildlife Sanctuary; 36. Ban Kok Klap; 37. Khao Nong; 38. Plai Nam; 39. Khao Lak; 40. Khao Luang; 41. Nongkok; 42. Koh Kra; 43. Song Hong; 44. Chong; 45. Junk Seylon [Phuket Island]; 46. Koh Yoa Yai; 47. Lam–ra; 48. Pipidon Island; 49. Pak Jam; 50. Trang; 51. Gap; 52. Koh Muk; 53. Nam Tok Ton Te; 54. Telibon Island; 55. Koh Tarutao; 56. Kuan Khao Wang Forest Park; 57. Khao Num Kang National Park; 58. Nam Tok Sai Khao; 59. Na Pra Du; 60. Pulo Rawi; 61. Pulo Adang; 62. Wang Bla Chan; 63. Sam Yak A–Sen; 64. Ban Thon; 65. Goah Tanah; 66. Hala Bala Wildlife Research Station. **Malaysia:** 67. Pelarit; 68. Padang Sireh; 69. Pulo Langkawi; 70. Sungei Kilim, Pulau Langkawi; 71. Sungei Kubong, Pulau Langkawi; 72. Dayang Bunting; 73. E. Perhentian Island; 74. Great Redang Island; 75. Gurun; 76. Kedah Peak; 77. Temengoh; 78. Telok Bahang, Penang Island; 79. Ulu Selama; 80. Lenggong; 81. Maxwell's Hill; 82. Bukit Gantang; 83. Gunong Ijan; 84. Jeram Kawan; 85. Tanjong Hantu; 86. Kota Tongkat; 87. Bentong; 88. Ginting Bidai; 89. Rawang; 90. Ulu Gombak, 20th. mile [of] Pahang Road; 91. Bukit Lagong; 92. Ayer Kring; 93. Cheras; 94. Tioman Island; 95. Pemanggil Island; 96. Bukit Tampin; 97. Pulau Aur; 98. Bukit Besar; 99. Si Karang; 100. Kangka Kuli; 101. Kangka Ketcho; 102. Pulai; 103. Johore Bahru; 104. Pelepak. **Singapore:** 105. Changi. For full locality details, see Gazetteer and Appendix I.

Ecology and reproduction. *Maxomys surifer* is locally common to quite rare depending on the population surveyed (Aplin et al. 2008c). In Thailand, it was found in a range of habitats including primary forest in Ranong Province and in the various islands that comprise Tarutao National Park, Satun Province. In Trang and Surat Thani Provinces it was found in secondary forest at approximately 126 metres a.s.l. In Chumphon and Songkhla Provinces, it was trapped in evergreen rain forest at approximately 50 metres a.s.l. It appears to be less associated with human habitation than *Rattus tanezumi* (UP unpubl. data).

In peninsular Malaysia, it is common in the forests of the lowlands and hills up to at least 1450 metres (Medway 1969). It is nocturnal and mostly terrestrial, living in burrows in primary and secondary forests, and also found in rice fields and gardens, especially if the gardens are adjacent to forests, but not in heavily disturbed areas (Corbet & Hill 1992, Francis 2008). It is not found in trees and it is not commensal (Chaimanee 1998). The natural diet consists of vegetable material, including fruits and fallen fruit, supplemented by insects, slugs, and small vertebrates. The young are born in nest chambers lined with fresh green leaves cut from surrounding shrubs and undergrowth. The burrows are short and have one or two entrances. Mean litter size is 3.3 (2–5) (Medway 1969).

Maxomys whiteheadi

Whitehead's maxomys

Mus whiteheadi Thomas 1894: 452; Mt Kinabalu, northern Borneo, Malaysia.
Mus asper Miller 1900b: 145; Trang, peninsular Thailand.
Rattus klossi Bonhote 1906: 9; Johore, Malaysia.

Description (based on personal observation and Miller 1900b, Bonhote 1906, Medway 1969). This is a small rat (Table 12) with a mass of 35–75 g (Medway 1969). The fur on the upper surface is a reddish-brown, grizzled with dark brown in some specimens. The fur bases are grey. There are numerous grey spines with dark tips; these are particularly abundant on the back and are less numerous on the flanks and belly. The crown of the head, shoulders and back are darker brown; the flanks are yellow-brown to buff. The underside, which is not sharply demarcated from the dorsal surface is grey or dull buff, fading to buffy grey on the chin and inner side of the legs; the hairs are dusky at their bases. In the form *klossi*, the belly is apparently a paler, creamy buff. There is sometimes a tawny spot on the chest. The muzzle is brown, greyish on the sides and there is a dark ring around the eyes. On average, the tail is shorter than the head and body (Table 12), it is bicoloured and without a white tip; the tip is also without a pencil of hairs. The hind foot usually has 5 pads; very occasionally a small outer metatarsal pad is present. The skull is small (Table 12); photographs are included in Marshall (1988, page 447).

Karyology (based on specimens from Malaysia, Yong 1969a, Musser et al. 1979). 2N= 36, FN= 71; there are eight pairs of metacentric chromosomes and nine pairs of submetacentric chromosomes, the X chromosome is a metacentric and the Y chromosome is an acrocentric.

Sperm morphology. Information on the sperm morphology of a specimen from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. There are no published records of fossil *M. whiteheadi* from Thailand (Pearch et al. 2013).

Taxonomic notes. There is little consistent geographical variation in this species (Robinson & Kloss 1918, Corbet & Hill 1992).

Distribution and conservation status. *Maxomys whiteheadi* is known extralimitally from Sumatra, Borneo and adjacent islands (Musser & Carleton 2005). In the study area, it is found in peninsular Thailand and Malaysia (Fig. 27).

Its conservation status is listed by IUCN as 'Vulnerable' since it is "believed to have undergone a decline of more than 30 % over the last ten years as inferred from rate of forest loss in the region, particularly in the lowlands of Sumatra and Borneo" (Aplin et al. 2008d).

Ecology and reproduction. This is a nocturnal and mainly terrestrial rodent, which lives in tall and secondary lowland forests. It is also found in plantations, rice paddies and disturbed areas but only if adjacent to forest. It is most common in forested lowlands and foothills, but has also been collected in mountains (Medway 1969; Aplin et al. 2008d). According to Medway (1969), it requires a canopy of either forest trees or bushes in scrub. In Thailand, it was collected in tropical rain forest in Narathiwat Province (approximately 200 metres. a.s.l.) and in primary forest in Phattalung Province (approximately 95 metres a.s.l.) (UP unpublished data). Its diet includes ants and other insects as well as plant matter (Francis 2008). There is no significant seasonal variation in reproductive activity. Litter size is 1–6 (mean = 3.0, n = 57) (Harrison 1955). On average, individuals are thought to survive for about 3.5 months in the wild (Harrison 1956a, Medway 1969).

Genus *Mus*

Mice

Mus Linnaeus, 1758: 59; type species *M. musculus* Linnaeus.

Background. According to Musser & Carleton (2005), there are 38 species of extant *Mus*, which belong to four subgenera: *Coelomys* Thomas, *Mus, Nannonmys* Peters, and *Pryomys* Thomas. With the exception of *Mus musculus,* which has a worldwide distribution thanks to its close association with man, all other species are confined to Africa, Europe and/or Asia and most have relatively restricted ranges. In Southeast Asia, six species, *booduga* (Gray), *cervicolor* Hodgson, *cookii* Ryley, *fragilicauda* Auffray, *pahari* Thomas, and *shortridgei* (Thomas) are confined to the Indochinese subregion and three species,

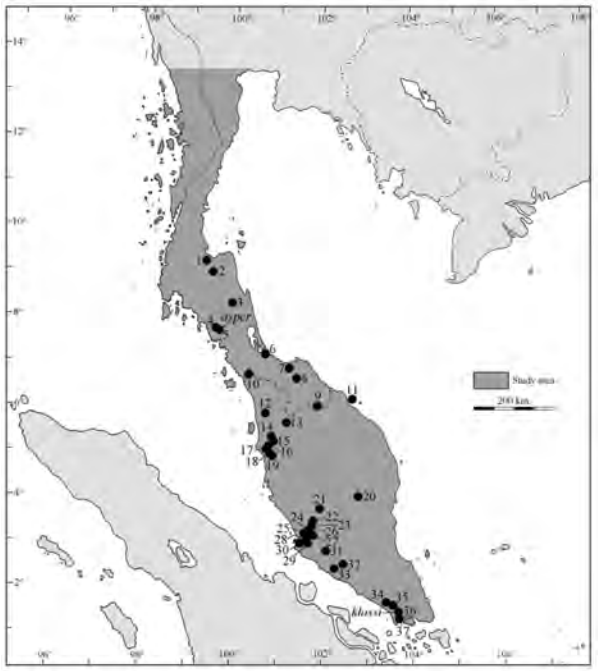

Fig. 27. Distribution of *Maxomys whiteheadi* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Khao Tha–Phet; 2. Ban Plai Nam; 3. Khao Phu Khao Ya National Park; 4. Ban Khao Chong; 5. Trang; 6. Khao Ram; 7. Ban Lam Mai; 8. Bang Lang Dam; 9. Hala Bala Wildlife Research Station. **Malaysia:** 10. Pelarit; 11. E. Perhentian Island; 12. Kedah Peak; 13. Temengoh; 14. Ulu Selama; 15. Lenggong; 16. Tredoh Peak; 17. Semangoh [Semangko]; 18. Gunong Semanggul; 19. Bukit Gantang; 20. Labong Edan; 21. Bentong; 22. Ginting Bidei; 23. Ulu Gombak, 20th mile [of] Pahang Road; 24. Bukit Lagong; 25. Bukit Lanjang Forest Reserve; 26. Kepong; 27. Gombak; 28. Subang Forest Reserve; 29. Kuala Lumpur; 30. Cheras; 31. Bukit Tangga; 32. Nyalas; 33. Padang Tuan; 34. Tamok Forest Reserve; 35. Mount Lun Chun; 36. Mount Pulai; 37. Pelepak. Not located: Sap Patchung. For full locality details, see Gazetteer and Appendix I.

crociduroides (Robinson & Kloss), *terricolor* Blyth (probably an inadvertent human introduction), and *vulcani* Robinson & Kloss, to the Sundaic subregion. A further two species, *M. musculus* and *M. caroli*, occur in both the Indochinese and Sundaic subregions (both may be inadvertant human introductions to the Sundaic subregion) and are present in the study area of peninsular Myanmar-Thailand-Malaysia and Singapore.

Description (based on personal observation and Marshall 1988; Aplin et al. 2003; restricted to the two species occuring in the study area). The body size is small. The tail is about as long, or longer in some *M. caroli,* as the head and body (Table 15). Tail colour varies between species. In *M. musculus,* it is uniformly dark brown, in *M. caroli,* it is clearly bicolour, dark above and pale below. In the two local species, the dorsal pelage is without spiny hairs; it varies from dark grey to deep brown to dark brown. The ventral pelage is uniformly white or white with grey bases in *M. caroli*; it is greyish brown and not clearly demarcated from the upper surface on the flanks in *M. musculus* (in specimens from the study region). The hind feet (Fig. 28C) are elongated. Each has six pads; the interdigital pads (1) are small and situated towards front of the foot; the outer metatarsal pad (2) is especially small; the inner metatarsal pad (3) is elongated. Females have five pairs of mammae.

In the skull, the nasals (Fig. 28Aii) are short; their anterior margins (i) are rounded or blunt and usually extend in front of the upper incisors (xii), although not in *M. caroli*. The lachrymals (iii) are small. The braincase is small with low, indistinct, ridges (iv). The incisive foramina (v) are long; their posterior margins (vi) usually extend well beyond the front margins of the anterior molars (M^1) (vii), although in *M. caroli,* they are shorter and only reach the anterior borders of M^1. The posterior border (viii) of the palate (xi) extends beyond the last molar (M^3). The distance from the posterior border of the palate to the ventral margin of the foramen magnum (x) (postpalatal length) is slightly shorter than palatal length. The tympanic bullae (ix) are medium-sized. The coronoid process (xiii) of each half mandible is narrow and hooked backwards; the emargination (xv) between the condylar (xiv) and angular processes (xvi) is well-developed.

The enamel layers of the incisors are orange (dark orange in *M. caroli*). The upper incisors are opisthodont (xii) (procumbent in *M. caroli*). The first upper molar (M^1) is large, equal to or exceeding the combined lengths of the second (M^2) and third molars (M^3). In M^1, cusp t1 (a) is sometimes fused (especially in older individuals) and sometimes separate from t2 (b) and t3 (c), which are fused; cusps t4 (d), t5 (e) and t6 (f) are variably separate or fused with one another depending on the individual; posteriorly, there is one large medial cusp, which includes t8 (g) and a small t9 (h) (cusp t7 is missing). In the second upper molar (M^2), cusp t1 (i) is large and prominent; a very small cusp t3 is sometimes present or absent as in Fig. 28B; on the second row cusps t4 (j), t5 (k) and t6 (l) are variably fused or separate, depending on the individual; the third row comprises cusp t8 (m) and a small cusp t9 (n), which are fused in older individuals. The third upper molar (M^3) is small; cusp t1 (o) is relatively large and prominent; cusps t4, t5, t6 (p) are fused; the last row has only t8 (q); sometimes cusp t4, t5, t6, t8 are fused making a large part of the molar, especially in a worn tooth (as in Fig. 28B).

In the mandibular toothrow, the first lower molar (M_1) is without a anterocentral cusp; there is an anterolabial cusp (n), an anterolingual cusp (s), a protoconid (t) and a metaconid (u); the hypoconid (v) and entoconid cusps (w) are often fused; the posterior cingulum (x) is well-developed. In the second lower molar (M_2), there is sometimes

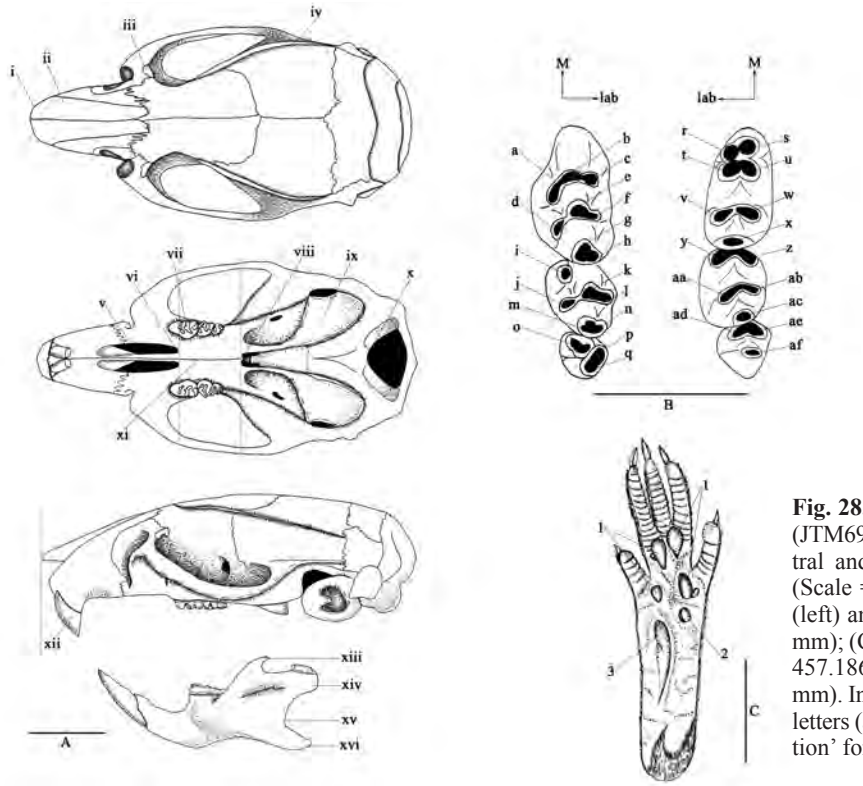

Fig. 28. Skull and dentition of *Mus musculus* (JTM6912), no data, Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *M. musculus* (HZM 457.18657), Beesham, Pakistan (Scale = 5 mm). Indicative numbers (i–xvi) and (1–3) and letters (a–af) are explained in the text 'Description' for *Mus*. M: mouth; lab: labial.

an indistinct indication of an anterolabial cusp, otherwise it is absent; the protoconid (y) is fused with the metaconid cusp (z); the hypoconid (aa) is fused with the entoconid cusp (ab); the posterior cingulum (ac) is well-developed. The third lower molar (M_3) is small; the anterolabial cusp is absent; protoconid (ad) is fused with the metaconid cusp (ae); the posterior lamina comprises the entoconid cusp (af).

Key to species for the two species of *Mus* currently known from peninsula Myanmar, Thailand, and Malaysia is included in Table 16.

Mus caroli

Ryukyu mouse; Long-tailed rice-field mouse

Mus caroli Bonhote 1902: 627; Okinawa, Ryukyu Islands.

Description (based on Bonhote 1902, Marshall 1977a, Marshall 1988, Aplin et al. 2003). This is a small species which has a mean mass of 11.0 g (Marshall 1977a). Characteristically, its tail is distinctly bicoloured, with the upper part, very dark, almost black; its length is variably reported as equal to, or exceeding, head and body length (Table 15). The fur on the upperparts of the body is light fulvous-brown (brownish-yellow) to brownish-grey. The underparts are white with a clear line of demarcation on the flanks. According to Bonhote (1902), the fur is soft and moderately long and is entirely free from spines, although Aplin et al. (2003) suggest that the fur on the back and flanks contains narrow spines and varies in texture from soft to moderately stiff. The hind feet are variously described as white (Bonhote 1902), white or white peppered with dark hairs (Aplin et al. 2003) or dark grey to white (Marshall 1988). The chin and lips are white. The skull has procumbent upper incisors, which are dark orange. The nasal bones do not hide the incisors when viewed from above. The incisive foramina are relatively short; their posterior borders are about in line with the anterior borders of the first upper molars (M^1).

Karyology. 2N= 40, based on specimens from northern Thailand; the karyotype is illustrated in Markvong et al. (1973, Figure 6). Badenhorst et al. (2009) reported that *M. caroli* has a 2N= 40 acrocentric karyotype (NFa= 38).

Fossil history. Specimens are known from one late Pliocene/early Pleistocene site in western Thailand (just north of the study area) and one late middle Pleistocene site in northeastern Thailand (Pearch et al. 2013).

Taxonomic notes. Corbet & Hill (1992) suggested that on the basis of shared characters, such as the pure white ventral pelage, specimens from peninsular Thailand are possibly referable to *M. caroli ouwensi* Kloss from eastern Java.

Distribution and conservation status. *M. caroli* has a range that extends from Japan to China, Vietnam, Lao PDR, Cambodia and Thailand. Specimens from Malaysia and Indonesia may represent inadvertent introductions by humans (Musser & Carleton 2005). In the study area, it is recorded from peninsular Thailand and Malaysia (Fig. 29).

Its conservation status is listed by IUCN as 'Least Concern' "because of its wide distribution, presumed large population, occurrence in protected areas, tolerance to some degree of habitat modification, no known major threats, and because it is unlikely to be declining at nearly the rate required to qualify for listing in a threatened category" (Aplin & Lunde 2008b).

Ecology and reproduction. *Mus caroli* inhabits rice fields and other agricultural grassy areas and can subsist on invertebrates (Marshall 1977a). It is most often associated with man-made habitats and is only rarely collected in natural habitats; the latter include pine-grass savannah and dipterocarp forest. Others have been found in grass and sedge close to water (Marshall 1988). Information on its occurrence in Kedah, Malaysia is included in Langham & Ming (1976). In northern Thailand, it was found in pine savannah (Marshall 1977a). In Myanmar, it is known from rice and hay fields and also grassy areas in deciduous forest (Corbet & Hill 1992). It nests inside paddy-field dikes and its globular nest is made of dried grass (Marshall 1977a). Litter size is 5 to 6 (Marshall 1988).

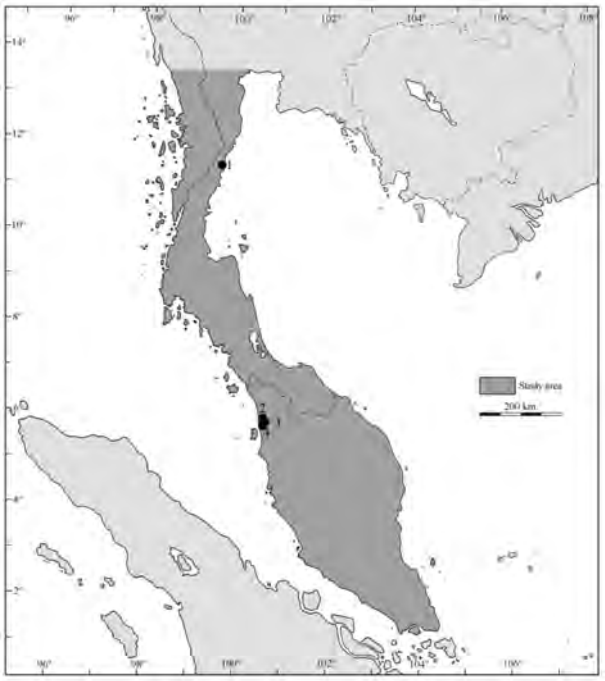

Fig. 29. Distribution of *Mus caroli* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Prachuapkhirikhan. **Malaysia:** 2. Titi Batu; 3. Teroi Tua; 4. Kampong Perigi. For full locality details, see Gazetteer and Appendix I.

Mus musculus

House mouse

M. musculus Linnaeus, 1758: 62; Upsala, Sweden.

Description (based on personal observation and Marshall 1988; Aplin et al. 2003). This is a small species with a mean mass of 13.1 g (Marshall 1977a). In material from the study area, it has a unicoloured, dark brown, tail (occasionally the undersurface of the tail may be slightly paler), which is about equal in length to the head and body. The dorsal pelage is dark greyish-brown to brown; the underparts are a slightly paler greyish-brown (in local material; elsewhere the belly may be white). In consequence, there is no clear line of demarcation on the flanks. The fur is soft throughout without spines. The hind feet are brown, except for the toes which are paler. The skull (Fig. 28A) has opisthodont, orange, upper incisors and relatively long incisive foramina, the posterior borders of which are about in line with the mid-part or posterior borders of the first upper molars (M^1). The nasal bones hide the incisors when viewed from above.

Karyology. 2N= 40 based on specimens from Thon Buri, Bangkok, Thailand; there are 40 telocentric chromosomes and the karyotype is illustrated in Markvong et al. (1973, Figure 9).

Fossil history. There are no fossil records of *M. musculus* from Thailand (Pearch et al. 2013).

Taxonomic notes. According to Corbet and Hill (1992), specimens from Southeast Asia are provisionally referred to *M. m. castaneus* Waterhouse 1843.

Distribution and conservation status. *Mus musculus* is closely associated with humans and has an almost worldwide distribution (Musser & Carleton 2005). In the study area, it is recorded from very few localities in peninsular Thailand and Malaysia (Fig. 30). However, it is highly probable that this simply reflects a lack of collecting effort and reporting rather than a natural scarcity and that nearly every house in the major cities has a population of *M. musculus* (Guy Musser pers. comm.).

Its conservation status is listed by IUCN as 'Least Concern' since it is "a widespread and abundant species that thrives in anthropogenic habitats" (Musser et al. 2008c).

Ecology and reproduction. *Mus musculus* is a commensal species that in Southeast Asia is essentially confined to houses, food stores, and out-buildings, although it is occasionally found in village gardens and animals pens. It is not found in cropping areas. Its diet is very varied and it can cause significant damage to stored foods. It nests in a variety of sites, including burrows excavated in the walls and floors of buildings or under piles of straw or piles of grain bags. In Malaysia, it has an average gestation period of 20 days. Mean litter size is 4.3 infants (1 to 7). Sexual maturity is attained after 35 days (Aplin et al. 2003; Medway 1969).

Genus *Niviventer*

Niviventer rats

Niviventer Marshall 1976: 402; type species *Mus niviventer* Hodgson.

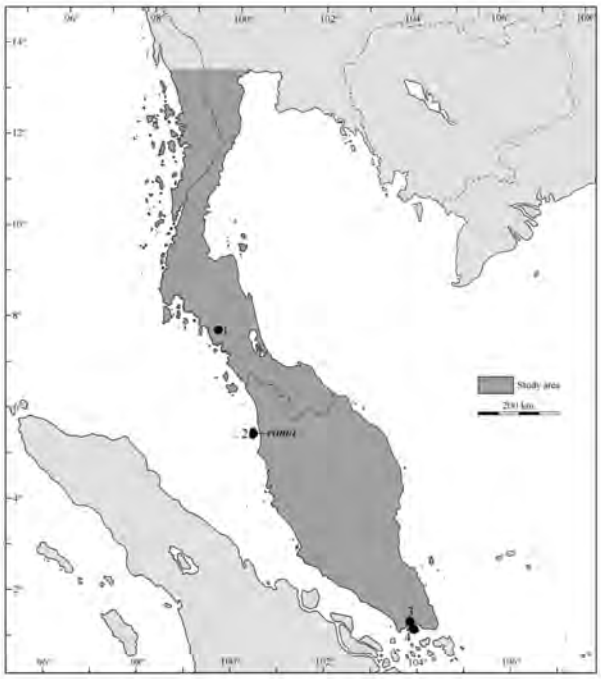

Fig. 30. Distribution of *Mus musculus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Trang Province. **Malaysia:** 2. Penang [Island]; 3. Johore Bahru. **Singapore:** 4. Singapore Island. For full locality details, see Gazetteer and Appendix I.

Remarks. There are 16 extant species of *Niviventer*, which are divided into two divisions the *Niviventer andersoni*-Division and the *Niviventer niviventer*-Division (Musser 1981). The former, includes two species and is restricted to China. The latter includes the remainder of the taxa, most of which have geographically restricted ranges but two, *N. cremoriventer* and *N. fulvescens,* are more widespread. These two taxa, together with *N. cameroni*, a Malaysian endemic, occur in the study area. Synonyms of the extant species are included in Musser & Carleton (2005); for a contrary view of species delimitations see Balakirev et al. (2011)

Description (based on personal observation and Musser 1981; restricted to the three species occurring in the study area). This is a medium-sized rat (Table 17). The pelage is dense, with flattened, grooved spines and guard hairs of variable length. The dorsal pelage is greyish-brown to reddish-brown. The ventral pelage is uniformly white or cream-coloured and is sharply demarcated on the flanks from the dorsal surface. The tail is usually longer than head and body length, with longer hairs at the tip, which form an indistinct tuft/pencil in some species. The tail is usually bicoloured but is monocoloured in one local species, *N. cremoriventer* (Fig. 51B). The hind foot of the genus is usually long and slender but is short and broad in *N. cremoriventer*. There are six plantar pads (Fig. 31C); the interdigital (1), outer metatarsal (2) and inner metatarsal (3) pads are all moderately developed. Females have four pairs of mammae (one pectoral pair, one postaxillary pair, and two inguinal pairs).

The skull is long, slender and often flattened. The nasals (Fig. 31Aii) are long with rounded or blunt anterior margins (i) that extend in front of the upper canines (xvi). The interorbital area is narrow (vii). There are well defined ridges (v) on the lateral margins of the braincase (vi). The zygomatic arches (iv) are narrow, not exceeding the width of the braincase; the zygomatic plates (xvii) are also narrow; the squamosal roots (xviii) of the zygomata are situated moderately high on the braincase. The lachrymal bones (iii) are small and inconspicuous. The palatal bridge (xv) is short; its posterior border (xii) is situated either before, in line with, or just beyond (as illustrated in Fig. 31A) the posterior margins of the last upper molars (M^3) (xi). Therefore the distance from the back edge of the palate to the ventral margin of the foramen magnum (xiv) (postpalatal length) is shorter than the palate length. The incisive foramina (viii) are long and narrow; their posterior margins (ix) extend to, or slightly pass, the front margins of the first upper molars (M^1) (x). The tympanic bullae (xiii) are very small relative to the size of the skull. In each half mandible, the coronoid process (xix) is small; the emargination (xxi) between the condylar (xx) and angular (xxii) processes is relatively shallow; the lower incisor root forms an indistinct process on the mandible (xxiii).

The upper incisors are orthodont or opisthodont (depending on species but also showing individual variation within species, for example both types are found in *N. fulvescens*) and the enamel layer is smooth and orange. The first upper molar (M^1) is long, narrow and with a simple cusp pattern; cusps t1, t2, t3 (Fig. 31Ba) are fused; in the second row t4, t5 and t6 (b) are also fused; on the third row, cusp t7 is absent; cusp t8 (c) is enlarged and there is no posterior cingulum. In the second upper molar (M^2), cusp t1 (d) is rounded and large; cusp t3 is mostly absent; cusps t4, t5, t6 (e) are fused; on the third row, cusps t7 and t9 are absent; cusp t8 (f) is large. In the third upper molar (M^3), cusp t1 (g) is rounded and large; cusp t3 is always absent; in the youngest individuals, t4 is separate from t5 and t6, which are separate from t8, however in all older individuals, t4, t5, t6 and t8 (h) are fused (as illustrated here).

In the mandibular toothrow, the first lower molar (M_1) is without an anterocentral cusp; the anterolabial cusp (i) is fused with the anterolingual cusp (j); the protoconid (k) is fused with the metaconid cusp (l); in a minority of individuals there is a small, separate posterior labial cusp (m) that becomes fused (as illustrated in Fig. 31B) with the hypoconid (n) and the entoconid cusp (o); the posterior cingulum (p) is well-developed. In the second lower molar (M_2), there is sometimes an anterolabial cusp (not

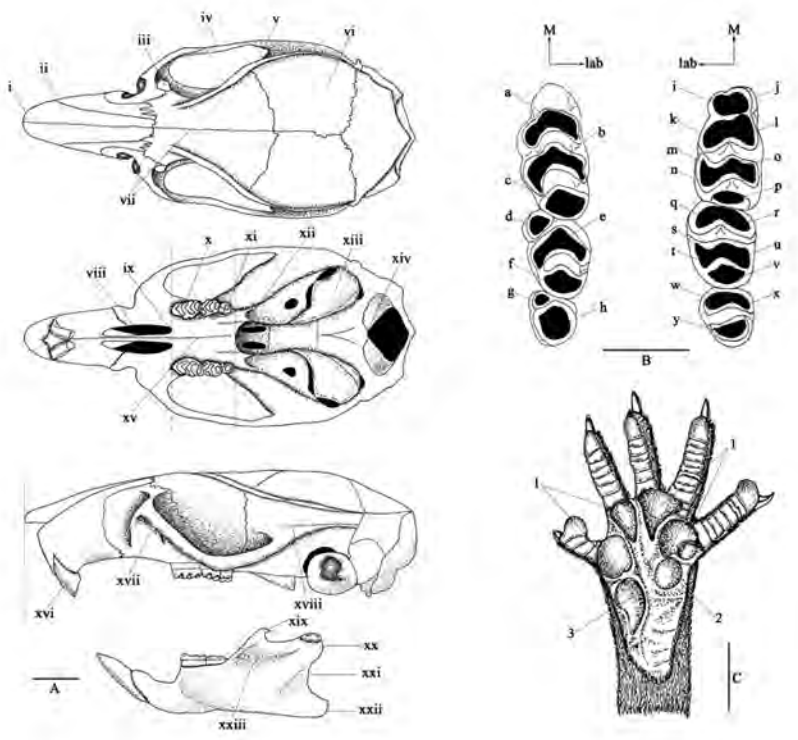

Fig. 31. Skull and dentition of *Niviventer fulvescens* (54–7179 CTNCR), Phuluang Wildlife Research Centre, Loei, northern Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *N. fulvescens* (PSUZC–MM2012.203), Na Thawi District, Songkhla Province, peninsular Thailand (Scale = 5 mm). Indicative numbers (i–xxiii) and (1–3) and letters (a–y) are explained in the text 'Description' for *Niviventer*. M: mouth; lab: labial.

illustrated in Fig. 31B), which, when present, is fused with the protoconid (q) and metaconid cusps (r); in a minority of individuals there is a small, separate posterior labial cusp (s) that becomes fused with the hypoconid (t) and entoconid cusps (u) in older individuals; the posterior cingulum (v) is well-developed. In the third lower molar (M_3), the anterolabial cusp is absent; the protoconid (w) and metaconid cusps (x) are fused; the posterior lamina is constituted only by the entoconid cusp (y).

Key to species for the three species currently known from the Myanmar-Thai-Malaysian peninsula (sensu Musser & Carleton 2005) is included in Table 18. However, the findings of Pagès et al. (2010) and Balakirev et al. (2011) question the taxonomy of this genus, as understood here, and in consequence, future revisions may change species definitions.

Niviventer cameroni

Cameron Highlands niviventer; Cameron Highlands white-bellied rat

Rattus rapit cameroni Chasen 1940: 176; Cameron Highlands, Pahang, Malaysia, c. 5000 ft (1524 metres).

Description (based on Chasen 1940; Medway 1969 = *Rattus fulvescens*, and Musser 1981 = *N. rapit cameroni*). This is a medium sized rat (Table 17). The upperparts are bright reddish brown; the fur is mixed with many spines and long black guard hairs; the underparts are white. The tail is bicoloured, brown above and white (unpigmented) below from the base to the tip (although Medway 1969 suggests that it is dark brown on the underside near the base); the tail is without a conspicuous tuft. The skull is large with a long and robust rostrum and well-developed incisive foramina; the tympanic bullae are small. The teeth are large. Photographs of the skull are available in Musser 1981, Figure 10).

Sperm morphology. Information on the sperm morphology of two specimens (listed as *Niviventer rapit*) from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. No fossil material of *N. cameroni* has been recorded from Thailand (Pearch et al. 2013).

Taxonomic notes. *Niviventer cameroni* was originally described as a subspecies of *rapit* by Chasen (1940), a view followed by Musser (1981) and Corbet & Hill (1992). However, Musser & Carleton (2005) treat it as a distinct species based on its larger cranial and dental measurements and its tail, which is without a conspicuous tuft.

Distribution and conservation status. *Niviventer cameroni* is endemic to the Cameron Highlands of peninsular Malaysia (Fig. 32).

Its conservation status is listed by IUCN as 'Vulnerable' "because its extent of occurrence is less than 10,000 km^2, its distribution is severely fragmented, and there is continuing decline in the extent and quality of its forest habitat" (Musser & Ruedas 2008).

Ecology and reproduction. The holotype was collected at an altitude of about 1524 metres (5000 feet) in the Cameron Highlands. It is now known from elevations ranging from 1524 to 2012 metres in these Highlands in

Fig. 32. Distribution of *Niviventer cameroni* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Malaysia:** 1. Cameron Highlands. For full locality details, see Gazetteer and Appendix I.

primary montane tropical forest (Musser & Carleton 2005). It is not known if the species can persist in disturbed or modified habitats (Musser & Ruedas 2008).

Niviventer cremoriventer

Pencil-tailed rat, Dark-tailed tree rat.

Mus cremoriventer Miller 1900b: 144; Trang, south Thailand, 3000ft.

M. gilbiventer Miller 1903a: 35; Sullivan Island, Mergui Islands, Myanmar.

E. solus Miller 1913: 22; Teratau Island, southwest Thailand.

Description (based on personal observation and Musser 1973a). This is a largely arboreal, small rat (Table 17) with a mass 50–105 g (Medway 1969). The upper pelage is dense and with fine overhairs (up to 20 mm) and numerous flattened, grooved, semi-rigid spines (up to 20 mm) and longer guard hairs (35–40 mm). The colour is bright orange to reddish-brown or yellowish, reddish brown, which is grizzled with black along the rump and back; it is palest on the flanks and brightest on the shoulders and thighs (Fig. 51B). The underparts are white to cream buff; the pelage is shorter (8 to 10 mm) and includes some flattened, flexible spine-like hairs. The upper and lower-parts of the body are clearly demarcated along the flanks, where often there is a thin, orange strip. The tail is considerably longer than the head and body and is dark brown, above and below (Fig. 51B); it is quite hairy, with a conspicuous tuft/pencil of hairs extending 5 to 8 mm beyond the tail tip. The face is short, the eyes are ringed in brownish-orange fur, and the ears are large, covered in short, fine hairs, and are pale to dark brown in colour. The upper surfaces of the front and hind feet have short, fine, white hairs; the claws of the hind feet are about 4 to 5 times the size of those of the front feet; the hind foot of *N. cremoriventer* is illustrated in Musser (1973a, Figure 1). Females have four pairs of mammae. The skull is small and compact; it is illustrated in Musser (1981, Figure 10). The rostrum is short, broad and blunt. The incisive foramina tend to terminate in line with or before the anterior borders of M^1. The tympanic bullae are very small.

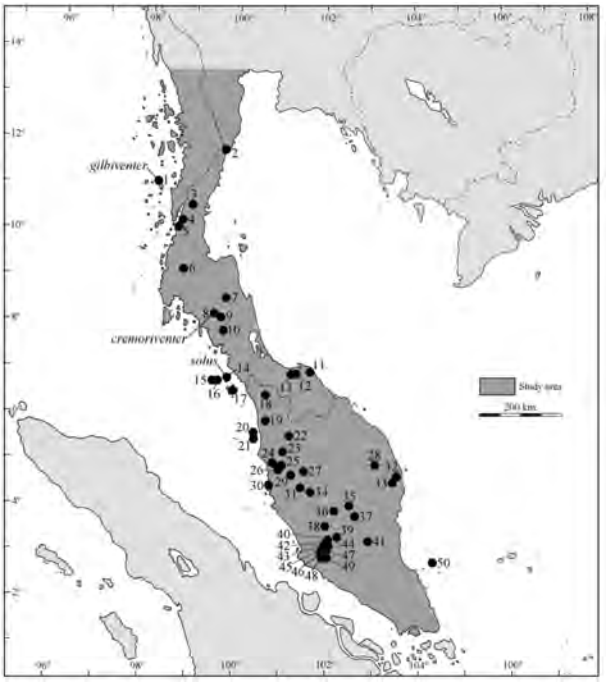

Fig. 33. Distribution of *Niviventer cremoriventer* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Sullivan Island. **Thailand:** 2. Khlong Wan [Tapli]; 3. Tasan; 4. Ban Bang Nawn; 5. Ban Bang Non; 6. Khlong Saeng; 7. Khao Luang; 8. Trang; 9. Chong; 10. Muang; 11. Khao Num Kang National Park; 12. Pattani; 13. Nam Tok Sai Khao; 14. Tarutau Island; 15. Koh Rawi; 16. Pulo Adang. **Malaysia:** 17. Pulo Langkawi; 18. Bukit Besar; 19. Kedah Peak; 20. Penang Island; 21. Telok Bahang; 22. Temengoh; 23. Lenggong; 24. Gunong Semanggul; 25. Gunong Ijau; 26. Maxwell's Hill; 27. Gunung Kerbau; 28. Kuala Berang; 29. Brinchang Peak; 30. Tanjong Hantu; 31. Lubok Tamang; 32. Tanjong Dungan; 33. Bukit Besi; 34. Kuala Tahan; 35. Tahan; 36. Genting; 37. Gunung Sinyom; 38. Tanjong Malim; 39. Genting Sempat; 40. Ulu Gombok; 41. Lubok Tamang; 42. Bukit Lagong; 43. Bukit Lagong Forest Reserve; 44. Kuala Lumpur; 45. 27 km. north–east of Kuala Lumpur; 46. Kepong; 47. Bukit Mandol; 48. Subang; 49. Pahang Road, 16 miles north–east of Kuala Lumpur; 50. Tioman Island. For full locality details, see Gazetteer and Appendix I.

Karyology (based on specimens from peninsular Malaysia, Yong 1969a; Musser 1973a). 2N= 46, FN= 54 with one pair of subterminal autosomes, 18 pairs of acrocentric autosomes, and three pairs of metacentric autosomes; the X and Y chromosomes are acrocentric.
Fossil history. No fossil material of *N. cremoriventer* has been recorded from Thailand (Pearch et al. 2013).
Taxonomic notes. Specimens from the study area are referred to the nominate form, *N. c. cremoriventer.* The two island taxa, *gilbiventer* and *solus,* are discussed in detail by Musser (1973a) who treats them as synonyms of the nominate form. According to Latinne et al. (2013b), mitochondrial markers (a 85 bp cytb fragment) clearly discriminate between *N. cremoriventer* and *N. fulvescens.*
Distribution and conservation status. *Niviventer cremoriventer* is found in peninsular Thailand and Malaysia, and some offshore islands; including the Myeik Archipelago of Myanmar, Anambas Islands, Sumatra, Nias, Billiton, Bangka, Borneo, Java, Bali, and small islands off the northern tip of Sabah (Musser and Carleton 2005). Its distribution in the study area is mapped in Fig. 33.

Listed as 'Vulnerable' because of a "population decline, estimated to be more than 30 % over the last ten years, inferred shrinkage in distribution, and habitat destruction and degradation" (Ruedas et al. 2008e).
Ecology and reproduction. On Tarutao Island and Rawi Island, off the west coast of peninsular Thailand, *N. cremoriventer* was collected in primary forest (UP, unpublished data). However, in Malaysia, it is reported as being common in secondary-growth forests but uncommon or absent in primary forest. It is nocturnal and mostly arboreal; most specimens have been trapped between two and four metres off the ground, although occasionally they are trapped at ground level (Musser 1973a). Its diet comprises vegetable matter, fruits and insects. It becomes sexually mature at a weight of about 50 g; litter size varies from 2 to 5, with a mean number of 3.7 (Harrison 1954b).

Niviventer fulvescens

Indomalayan niviventer; Chestnut white-bellied rat
Mus fulvescens Gray 1847: 18; Nepal.
Mus bukit Bonhote 1903b: 125; Bukit Besar, Jalor, Malaysia, 2500 feet.
Epimys lepidus Miller 1913: 20; Bok Pyin, South Tenasserim, Myanmar.
Epimys orbus Robinson & Kloss 1914: 228; Khao Nawng, Bandon, Southern Thailand, 3500 feet.
Epimys jerdoni pan Robinson & Kloss 1914: 229; Samui Island, Thailand.

Description (based on personal observation and Bonhote 1903b; Medway 1969 = *Rattus niviventer*; Musser 1981; Abe 1983). *Niviventer fulvescens* is the medium size rat (Table 17) with a mass of 70 g (Medway 1969). The upperparts have yellowish-brown to orange-brown pelage, which is grey at the base. This is intermixed with many short, flattened spines, which vary in colour from white to dark brown and are variably tipped with black. There are short black guard hairs, which are especially abundant on the lower back. The underparts are white or yellowish-white. There is a sharp line of demarcation on the flanks. The tail is bicoloured, but not always markedly so, dark brown above and white below; it has fine silky hairs which are longer at the tip. The tail is usually longer, sometimes considerably longer than head and body length. The cheeks, sides of the head and neck are yellowish-orange-brown without dark grizzling. White extends on to the wrists but not on to the ankles. The upper surfaces of the fore and hind feet are dirty white, each with a brown median strip, which does not reach the base of the digits. The skull is medium-sized with a robust rostrum and relatively short incisive foramina; as with all *Niviventer,* the tympanic bullae are small. The teeth are unremarkable. Photographs of the skull are available in Musser 1981, Figure 11).
Sperm morphology. Information on the sperm morphology of a specimen (listed as *Niviventer bukit*) from peninsular Malaysia is included in Breed & Yong (1986).
Fossil history. *Niviventer fulvescens* is known from six fossil localities in Thailand dating back to the early to late middle Pleistocene. Three of the localities are in the peninsula (Pearch et al. 2013).
Taxonomic notes. Corbet & Hill (1992) referred specimens from north of the Isthmus of Kra to *N. fulvescens* and those from the south to *N. bukit*; this view was contrary to Abe (1983), who considered *bukit* to be the local subspecies of *N. fulvescens* in the Thai peninsular. This latter view was followed by Musser & Carleton (2005) but was challenged by Balakirev et al. (2011), who treated *bukit* as a discrete species with an Indochinese and Sundaic distribution. Pagès et al. (2010) also suggested that there was more species diversity within *fulvescens* than currently recognised. Over the years, *N. fulvescens* has been confused with *N. confucianus, N. niviventer,* and *N. tenaster.* Musser & Carleton (2005) recommend further research, especially with DNA sequences, to determine the relationships of all these closely related taxa. Latinne et al. (2013b) discriminated between this species and *N. cremoriventer* using mitochondrial markers (a 85 bp cytb fragment).
Distribution and conservation status. *Niviventer fulvescens* has a range that extends from Nepal and northern India to Bangladesh, south China, Myanmar, Thailand, and Indochina. It is also known from peninsular Myanmar-Thailand-Malaysia, Sumatra, Java and Bali (Musser & Carleton 2005). Its distribution in the study area is mapped in Fig. 34.

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, presumed large population, it occurs in a number of protected areas, has a tolerance of a degree of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Musser et al. 2008b).

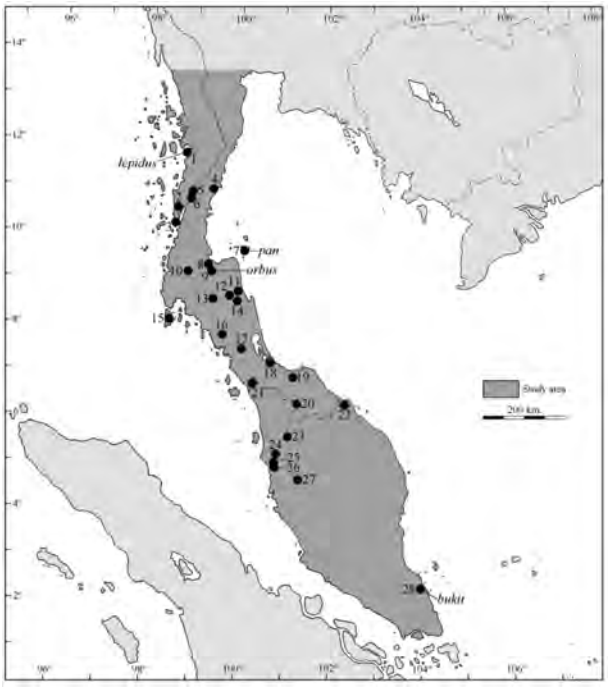

Fig. 34. Distribution of *Niviventer fulvescens* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Bokpyin; 2. Bankachon; 3. Victoria Point. **Thailand:** 4. Khao Mon; 5. 30 km. west of Chumphon; 6. Tap-Li; 7. Koh Samui; 8. Ao Ko; 9. Khao Nawng; 10. Khlong Saeng; 11. Ban Phi Tham; 12. Khao Luang; 13. Tang Pran; 14. Nongkok; 15. Tone Sai Waterfall National Park; 16. Trang; 17. Nam Tok Tamot; 18. Khao Ram; 19. Nam Tok Sai Khao; 20. Mae Wad. **Malaysia:** 21. Pelarit; 22. Kota Bharu; 23. Temengoh; 24. Lenggong; 25. Maxwell's Hill; 26. Taiping; 27. Mt. Brinchang; 28. Bukit Besar. For full locality details, see Gazetteer and Appendix I.

Ecology and reproduction. *Niviventer fulvescens* was collected in tropical rain forest in Songkhla Province at approximately 150 metres a.s.l. (UP unpublished data). Marshall (1988 = *Rattus bukit*) suggested that it was common in the lowland evergreen forest of peninsular Thailand; it was found in a similar habitat at Bankachon in peninsular Myanmar (Wroughton 1915). In northern Thailand, *N. fulvescens* was found in evergreen, pine and deciduous forests and on the Korat Plateau it was common in evergreen forest and secondary forest (Marshall 1988). According to Francis (2008), it is a mostly nocturnal species, which is found in forest habitats, gardens and disturbed areas with vegetation. It is active both on the ground and in trees, climbing on large lianas and vines.

Genus *Pithecheir*

Woolly tree rats, Pithecheir rats
Pithechir [sic] Müller 1839: 12 (*nomen nudum*).
Pithecheir Lesson 1840: 264; type species *Pithecheir melanurus* Lesson.

Remarks. *Pithecheir* is a medium-sized arboreal rat which is endemic to the Sundaic subregion. There are two extant species, *P. parvus*, which is restricted to the Malaysian peninsula and *P. melanurus* Cuvier, which is found in Java (Musser & Carleton 2005).
Description. The generic description is omitted since there is only one species of this genus in the study area.

Pithecheir parvus

Monkey-footed rat, Malayan woolly tree rat
Pithecheir melanurus parvus Kloss 1916b: 250; Bukit Kutu, Selangor, Malaya, 3400ft.
Description (based on personal observation and Kloss 1916b, Misonne 1969; Medway 1969 and Musser & Newcomb 1983). This is a medium-sized rat, which together with *P. melanurus,* is one of the most arboreal murine rodents of the Sundaic region. The tail is naked, uniformly brown and prehensile distally (towards the tip); it averages 113 % of head and body length (Table 19). The fur is very long, soft and without spines. On the upper surface, the pelage is brownish-red, most richly coloured on the head and upper back; the hair bases are slate-grey. The underparts are creamy-white. The chin, flanks and lower parts of the hind limbs are buffy-brown. There is a clear line of demarcation between the upper and lower surfaces. The ears are short and translucent; whitish at the base. The feet are brown above and highly adapted for climbing (hence the English name 'monkey-footed rat'); the hind feet (not illustrated) are short and broad with very large interdigital and metatarsal pads; the first toe (hallux) is widely separated from the others with an enlarged pad at the tip, which has a very short claw; all four other toes also have enlarged pads at the tips. There are two pairs of inguinal mammae.

The skull is elongated and medium-sized. The nasals (Fig. 35Aii) extend beyond the anterior border of the incisors (xii); their anterior margins (i) are rounded and blunt. The interorbital area (iii) is wide. The braincase is wide and when viewed from the side is of medium height; in older individuals, it has strongly developed supraorbital ridges (v), which form thin flanges of bone overhanging the orbital areas. They extend posteriorly as strong ridges on the braincase. The zygomata (iv) are robust and broader than the braincase but not as widely flared as in *Lenothrix*; the zygomatic plate is very narrow (xiii). The incisive foramina (vi) are medium-sized and relatively broad; their posterior margins (vii) end well in front of the anterior margin of the first molars (M^1) (viii). The posterior border (x) of the palate ends before or in line with the posterior border of the last upper molars (M^3) (ix). Palatal length slightly exceeds postpalatal length. The tympanic bullae (xi) are very large. Each half mandible has a small coronoid process (xiv); the lower incisor root is moderately prominent (xv). Photographs of the skull are available in Musser & Newcomb (1983, Figure 94).

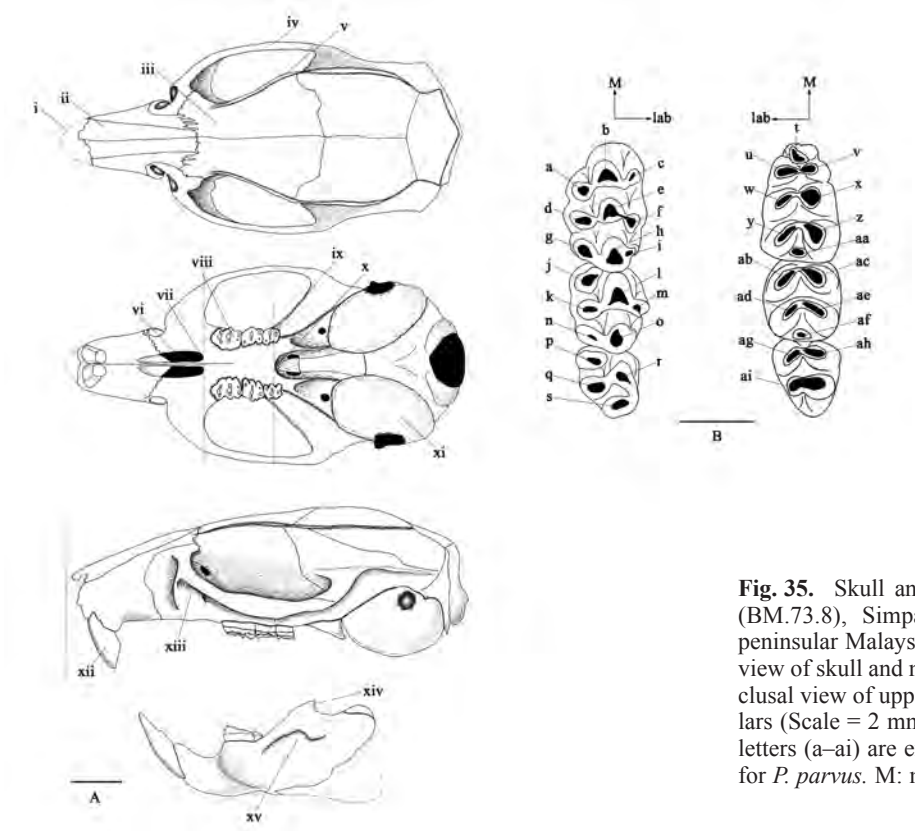

Fig. 35. Skull and dentition of *Pithecheir parvus* (BM.73.8), Simpang Pertang, Negeri Sembilan, peninsular Malaysia. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm). Indicative numbers (i–xv) and letters (a–ai) are explained in the text 'Description' for *P. parvus*. M: mouth; lab: labial.

The enamel layers of the incisors are orange. The upper incisors are opisthodont (xii). In the first upper molar (M^1), the first row comprises three separate cusps, t1 (Fig. 35Ba), t2 (b) and t3 (c); on the second row, cusps t4 (d), t5 (e) and t6 (f) are separate or variably fused, depending on the age of the individual; on the third row, cusp t7 (g) is separate from t8 (h) and t9 (i), which is small. In the second upper molar (M^2), the anterior lingual cusp (t1) (j) is large and prominent; t3, if present, is small (not present in the tooth illustrated in Fig. 35B); on the second row, cusps t4 (k), t5 (l) and t6 (m) are separate; on the third row, cusp t7 (n) is separate from t8 (o), which is essentially fused with a very small t9 (not present in the tooth illustrated in Fig. 35B). In the third upper molar (M^3); the anterior lingual cusp (t1) (p) is large and prominent; cusp t3 is absent; cusp t4 (q) is separate from cusps t5 and t6 (r), which are fused; in the last row, cusp t7 is absent; cusps t8 and t9 (s) are fused.

In the mandibular toothrow, the first lower molar (M_1) has an anterocentral (t), anterolabial (u) and anterolingual cusp (v); the protoconid (w) is smaller than the metaconid cusp (x); the hypoconid (y) is smaller than the entoconid cusp (z); there is a posterior cingulum (aa). In the second lower molar (M_2), the anterolabial cusp is absent; the protoconid (ab) and metaconid cusps (ac) and the hypoconid (ad) and entoconid cusps (ae) are separate; there is a posterior cingulum (af). In the third lower molar (M_3), the anterolabial cusp is absent; there is a protoconid (ag) and metaconid cusp (ah); the posterior lamina comprises a fused hypoconid and entoconid cusp (ai).

Karyology (based on specimens from Malaysia, Yong et al. 1982). 2N= 50; 16 pairs of acrocentric autosomes, one pair of subacrocentric autosomes and seven pairs of metacentric-submetacentric autosomes, the X chromosome is a metacentric and the Y chromosome a subacrocentric.

Sperm morphology. Information on the sperm morphology of a specimen from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. Specimens dating back to the early Pleistocene have been collected from two localities in peninsular Thailand (Pearch et al. 2013).

Taxonomic notes. Measurements included by Kloss (1916b) for the type specimen are small (Table 19) and probably represent a juvenile or very young adult.

Distribution and conservation status. *Pithecheir parvus* is endemic to peninsular Malaysia (Fig. 36).

Its conservation status is listed by IUCN as 'Data Deficient' "since, although it has been recorded over a reasonably wide area, it is uncertain if the species can persist in modified habitats. If it can be found at disturbed sites, it could be a Least Concern species, however, if it is largely confined to primary or undisturbed forest, it may qualify for a threat category" (Aplin et al. 2008h).

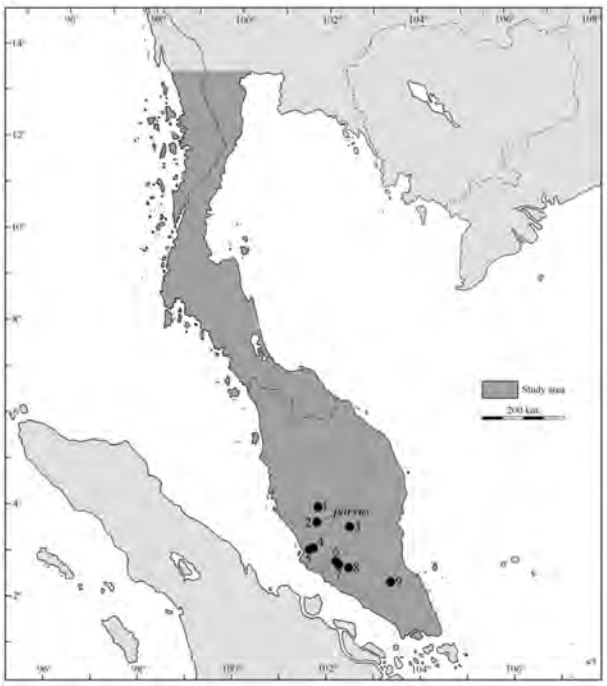

Fig. 36. Distribution of *Pithecheir parvus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Malaysia:** 1. Gunong Benom; 2. Bukit Kutu; 3. Sungei Jengka Forest Reserve; 4. Subang Forest Reserve; 5. Meru Forest Reserv; 6. Bukit Perangoh; 7. Tanah Wat Forest; 8. Ayer Bangi; 9. Labis Forest Reserve. For full locality details, see Gazetteer and Appendix I.

Ecology and reproduction. The holotype of *P. parvus* was collected at an elevation of about 1050 metres (3400 feet) on Bukit Kutu in Selangor, Malaysia (Kloss 1916b). Subsequently, it was collected from the same locality by Muul & Lim (1971) and from other secondary and lowland forests. The latter authors also obtained a specimen from Gunong Benom, Pahang in primary forest at about 550 metres (1800 feet) elevation. According to Chaimanee (1998), *P. parvus* lives in dense forests up to 1600 metres elevation but Aplin et al. (2008h) suggest that the upper limit is 1200 metres. With its prehensile tail and specialised hind feet, this is an arboreal species, which is found in the forest understorey and in the crowns of short palms and tree ferns. It constructs large globular nests (Lim & Muul 1975; Musser & Newcomb 1983).

Genus *Rattus*

Rats

Rattus Fischer 1803: 128; type species *Mus decumanus* Pallax (currently included in *Rattus norvegicus*).

Remarks. *Rattus* is the most diversified extant genus of rodents with 64 species. Most species (59 of the 64) have relatively restricted distributions, the exceptions are *R. argentiventer, R. exulans, R. norvegicus, R. tanezumi and R. tiomanicus*, which together with *R. andamanensis* and *R. annandalei* are the seven species currently known from the Myanmar-Thai-Malasian peninsula (Musser & Carleton 2005). Synonyms of the extant species are included in Musser et al. (1979) and Musser & Carleton (2005).

Description (based on the seven species occurring in the study area). The body size ranges from small (*exulans*) to large (*norvegicus*) (Table 20). The tail is usually brown above and below (Fig. 51C) but in *R. norvegicus* is slightly bicoloured, paler below. Tail length averages less than the head and body in some species, *R. argentiventer* and *R. norvegicus*, is about equal to, or slightly exceeds it in others, *R. exulans, R. tanezumi* and *R. tiomanicus*, and considerably exceeds it in *R. andamanensis* and *R. annandalei*. However, these are average measurements and there is much individual variation and some geographical variation (see for example Tables 22 and 23). Some species, *R. andamanensi, R. argentiventer, R. exulans R. tanezumi,* and *R. tiomanicus* have pelage that includes spiny hairs (to various degrees), whereas in others, *R. norvegicus* and *R. annandalei,* they are absent. The dorsal pelage is grey-brown, olive-brown, yellowish-brown/orange and variably speckled with black. The ventral pelage is also variable in colour, from white to yellowish-white to grey. The hind-feet have six pads (Fig. 37C). Four are interdigital (1), these are smooth in some species (*argentiventer*), whilst in others they are ridged to assist with climbing (for example *tiomanicus* and *tanezumi*); the outer metarsal pad (2) is smaller and the inner is kidney-shaped (3). The number of mammae varies between species; one has two axillary pairs and two inguinal pairs (*exulans*), others have three axillary pairs and three inguinal pairs; *R. annandalei* is variable with four, five, or six pairs.

In the skull, the rostrum (Fig. 37Avi) is long and wide; the nasals have rounded or blunt tips (i) and extend in front of the incisors (xv), sometimes far enough to form a short tube. The nasolacrimal capsules (ii) are large and inflated. The lachrymals (iii) are small. The braincase is medium-sized. There are well-developed supraorbital ridges (iv), which extend posteriorly along the lateral margins of the braincase. The zygomatic arches (v) are robust and narrower slightly anteriorly, such that they are broader where they attach to the braincase. The zygomatic plate (xvi) is narrow. The palate (xiv) is long; the length of palate varies between species; its posterior border (xi) extends beyond the last upper molars (M^3) (x). Therefore the distance from the back edge of the palate to the ventral margin of the foramen magnum (xiii) (postpalatal length) is shorter than palate length. The incisive foramina (vii) are long and relatively narrow; their posterior margins (viii) extend to, or slightly pass, the anterior margins of the first molars (M^1) (ix). The tympanic bullae (xii) are relatively large. The coronoid process (xvii) of the mandible and the emargination (xix) between the condylar (xviii) and angular (xx) processes are well-developed. The process of the lower incisor root (xxi) is moderately developed.

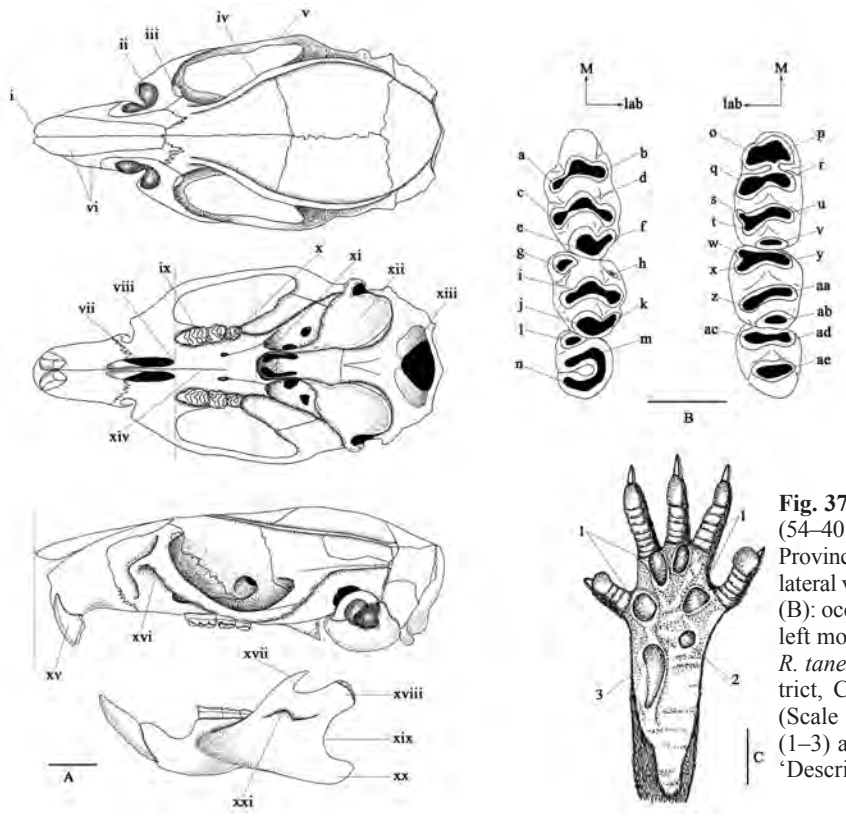

Fig. 37. Skull and dentition of *Rattus tanezumi* (54–4016 CTNCR), Kaeng Khoi District, Saraburi Province, central Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *R. tanezumi* (PSUZC–MM2012.204), Phato District, Chumphon Province, peninsular Thailand (Scale = 5 mm). Indicative numbers (i–xxi) and (1–3) and letters (a–ae) are explained in the text 'Description' for *Rattus*. M: mouth; lab: labial.

The enamel layers of the incisors are orange. The upper incisors are opisthodont (xv) or sometimes orthodont relative to the rostrum (vi). In the first upper molar (M^1), cusp t1 (Fig. 37Ba) is separate (in young individuals, see Fig. 5E) from cusps t2 and t3 (b), which are fused; on the second row, cusp t4 (c) is separate or fused with cusps t5 and t6 (d), which are fused; on the third row, there is a large medial cusp, t8 (e), fused to a small lateral one, t9 (f); cusp t7 is missing. In the second upper molar (M^2), cusp t1 (g) is large and prominent; most (but not all) specimens have a small cusp t3 (h); in the second row, cusps t4, t5 and t6 (i) are fused (in the youngest of individuals with newly erupted teeth, t4 is separate from t5 and t6, which are just fused); the third row comprises a larger t8 (j) and a smaller t9 (k), which are fused; t7 is absent. In the third upper molar (M^3), cusp t1 (l) is large and prominent; cusp t3 is usually absent in most species; cusps t4, t5, t6 (m) are fused, even in young individuals; the last row has only t8 (n); in worn teeth, sometimes cusps t4, t5, t6, t8 are fused making a large part of the molar (as illustrated in Fig. 37B).

In the mandibular toothrow, the first lower molar (M_1) is without an anterocentral cusp; in the oldest individuals, the anterolabial (o) and anterolingual cusps (p) and the protoconid (q) and metaconid cusps (r) are all fused, whereas in younger individuals they are all separate; in the youngest individual of *R. tanezumi* seen, there is also an anterior labial cusp (not illustrated in Figs 5M or 37B) and a posterior labial cusp (s); the hypoconid (t) is fused with the entoconid cusp (u); the posterior cingulum (v) is well-developed. In the second lower molar (M_2), the anterior labial cusp (w), the protoconid (x) and the metaconid cusp (y) are fused; a posterior labial cusplet is present (see Fig. 5M) but may be fused with hypoconid (z) (as in Fig. 37B), which is in turn fused with the entoconid cusp (aa); the posterior cingulum (ab) is well-developed. In the third lower molar (M_3), the anterolabial cusp is absent; the protoconid (ac) is fused with the metaconid cusp (ad); the posterior lamina comprises the entoconid (ae).

Key to species for the seven species of *Rattus* currently known from peninsular Myanmar- Thailand- Malaysia and Singapore is shown in Table 21. It should be noted that differentiating between *Rattus* species, and especially *R. tanezumi* and *R. tiomanicus*, is often difficult using morphometric characters. This is further complicated by the fact that the taxonomy still requires further refinement with recent molecular studies showing that there are, for example, at least four distinct lineages of *Rattus* in peninsular Thailand, the identification of which are not determined (Latinne et al. 2013b). If these lineages are true species, then it is highly probable that *R. tanezumi,* and possibly *R. tiomanicus,* are complexes of morphologically cryptic species. As noted by Pagès et al. (2010), further research incorporating molecular data from the holotypes of the different *Rattus* taxa, especially those of the numerous synonyms, would be the most suitable way to

determine accurately the taxonomy of this genus in Southeast Asia.

Rattus andamanensis
Indochinese forest rat
Mus (leggada) andamanensis Blyth 1860: 103; Andaman Islands.
Epimys remotus Robinson and Kloss 1914: 231; Samui Island, East peninsular Thailand.

Description (based on Robinson & Kloss 1914, Aplin et al. 2003 = *R. sikkimensis*): This is a moderately large, arboreal rat (Table 20) with a mean mass of 221 g (Marshall 1988). The pelage on the upper parts is somewhat shaggy and includes thin, flexible, grooved, spiny-hairs. The colour is an admixture of yellow-orange and sooty brown, darkest on the back, where the long black guard hairs are most numerous; the flanks are browner, with the dark grey hair roots more prominent. The under parts are creamy white, sharply demarcated from the flanks. The hind feet are large and have silky, whitish hairs, darker brown in the mid-part; they have large well-developed interdigital and metatarsal pads, which are covered with fine lamellae/ridges (to assist with climbing). The ears are large for *Rattus*. The tail is long and unicoloured, brownish-black; on average, it considerably exceeds head and body length. The vibrissae are characteristically long (up to 60 mm in length), thick and black. There are six pairs of mammae: one pair pectoral, two pairs postaxillary, three pairs inguinal (Marshall 1988). The skull is strongly ridged and broad; the sides of the braincase are slanted, not vertical as in *R. tanezumi* (Corbet & Hill 1992). The rostrum is robust and relatively short for its width. The incisive foramina are long, extending to the anterior border of the first (M^1) molar or between the anterior roots of the M^1. Photographs of the skull are available in Musser & Newcomb 1983, Figures 110 and 111, = *R. sikkimensis*) and Marshall 1988, page 470, = *R. remotus*).
Karyology. 2N= 42 (based on specimens from Samui Island, Thailand); autosomal pairs 1, 4, 9, and 13 are subtelocentric; autosomal pair number 11 is heteromorphic; the karyotype is illustrated in Markvong et al. (1973: Fig. 17).
Fossil history. Specimens referred to *R. koratensis* and *R. sikkimensis* (see Taxonomic notes, below) and dating back to the early Pleistocene are known from nine localities in Thailand, including three in the peninsula (Chaimanee 1998, Pearch et al. 2013).
Taxonomic notes. The taxonomy of this species is complex. Specimens from Thailand have been variously referred to *remotus* by Marshall (1988) and Corbet & Hill (1992), *koratensis* Kloss by Chaimanee (1998) and *sikkimensis* by Chaimanee (1998) and Musser & Newcomb (1983). Aplin et al. (2003) include both names. However, following Musser & Carleton (2005), specimens from the study area are here referred to *R. andamanensis*.

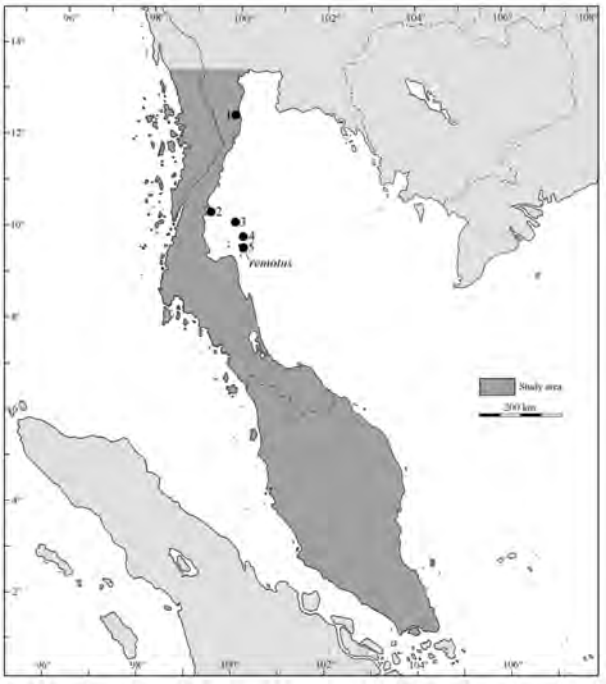

Fig. 38. Distribution of *Rattus andamanensis* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Ban Pa Lau; 2. Koh Kra; 3. Koh Tau; 4. Koh Pha–ngan; 5. Koh Samui. For full locality details, see Gazetteer and Appendix I.

Distribution and conservation status. *Rattus andamanensis* has an extensive range from eastern Nepal to northeast India, Bhutan, southern China, Myanmar, northern Thailand, and Indochina; it is also known from the Andaman and Nicobar Islands. In the study area, it occurs in one locality in northern peninsular Thailand and four islands in the Gulf of Thailand (Fig. 38).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, presumed large population, occurrence in several protected areas, tolerance of habitat modification, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Aplin et al. 2008i).
Ecology and reproduction. In peninsular Thailand, the holotype was collected in the hills of Koh Samui (Robinson & Kloss 1914), where it is also reported from evergreen forest (Markvong et al. 1973). According to Marshall (1988), it is found in orchards and secondary forest in Koh Samui; it shares this habitat with *Niviventer fulvescens* and *Rattus tanezumi* (= *Rattus bukit* and *Rattus rattus robinsoni* respectively in Marshall 1988). It is considered to be arboreal (Aplin et al. 2003).

Rattus annandalei
Annandale's rat, Singapore rat
Mus annandalei Bonhote 1903a: 30; Sungkai, South Perak, Malaysia.
Mus villosus Kloss 1908a: 146; Singapore Island.

Description (based on Bonhote 1903a; Kloss 1908a). This is a medium-large rat (Table 20) with a mass of 145–250 g (Medway 1969), 120–260 g (Muul & Lim 1971). The fur is moderately soft and without spines. The upper body is grizzled yellowish-brown (fulvous) to buff-brown. It is darker posteriorly owing to the prevalence of long black guard hairs, which attain 40 mm on the rump. It is also darker down the middle of the back. The flanks are paler, owing to the grey basal hair showing through and the absence of dark annulations to the hairs. In some individuals there is a narrow band (4 mm) of pure buff on the flanks. The under parts are white, tinged with yellow; the line of demarcation on the flanks is well marked in some individuals, less so in others. The buffy white of the chest and belly extends to the wrists and to the upper lip behind and below the whiskers. In males, there is a brown prescrotal patch. The forearms and thighs are greyish-brown; the inner sides of the fore limbs are white and of the hind limbs, including the ankles, are dark brown. The feet are dark brown. In general, the tail is considerably longer than the head and body and is a uniform black in colour, covered in short stiff hairs. The ears are somewhat elongated and naked. There are two or three pairs of pectoral and two or three pairs of inguinal mammae (Medway 1969). The skull is elongated and has noticeably large tympanic bullae. The incisive foramina tend to be short and extend to the anterior border of the first (M^1) molar. Photographs of the skull are included in Musser & Newcomb (1983, Figures 110 and 111).

Fossil history. There are no records of fossil *R. annandalei* from Thailand (Pearch et al. 2013).

Taxonomic notes. According to Medway (1969), specimens from Perak are referable to *R. a. annandalei* whereas those from Selangor and to the south are comparable to *R. a. bullatus* Lyon 1908, which was described from Rupat Island, east of Sumatra.

Distribution and conservation status. *Rattus annandalei* has a relatively restricted range; it is found in eastern Sumatra; Padang and Rupat Islands off the east coast of Sumatra; peninsular Malaysia and Singapore. Its distribution in the study area is illustrated in Fig. 39.

Its conservation status is listed by IUCN as 'Least Concern' "as although it is probably undergoing decline due to the conversion of forested habitat to agricultural lands in parts of its range, it is unlikely to be declining fast enough to warrant listing in a higher category of threat" (Aplin & Lunde 2008c).

Ecology and reproduction. In Perak in peninsular Malaysia, it was apparently uncommon (Chasen 1940). Medway (1969) suggested that it was localised, confined to secondary woodland and scrub. However, in Selangor, it was common in lowland secondary forests and in kampong rubber estates; here it was trapped in the lower branches of trees and also on the ground. None was taken in deep forest (Muul & Lim 1971). In Singapore, it was widespread (Harrison 1966). According to Corbet & Hill (1992), it is not an agricultural pest.

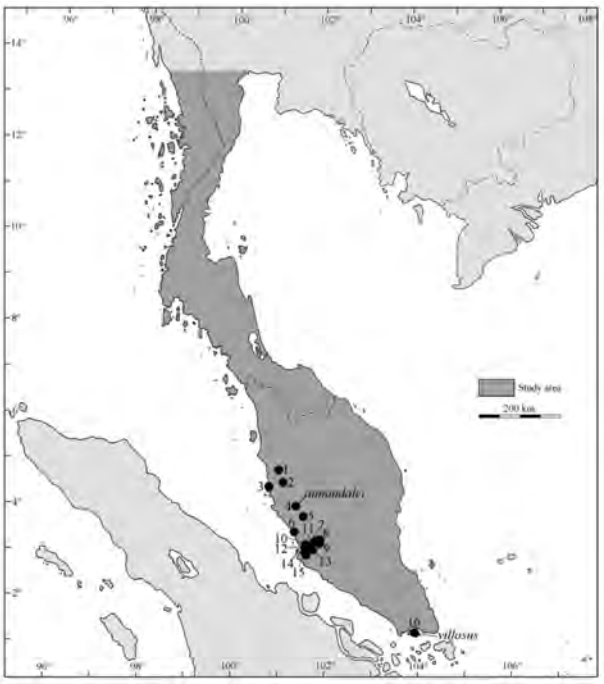

Fig. 39. Distribution of *Rattus annandalei* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Malaysia:** 1. Taiping; 2. Bruas; 3. Tanjong Tuan (= Tanjong Hantu); 4. Sungkai; 5. Tanjong Malim; 6. Kuala Selangor; 7. Bukit Cherakah; 8. Bukit Lagong; 9. Bukit Lanjang; 10. Meru; 11. Subang Forest Reserve; 12. Cheras; 13. Kuala Lumpur; 14. Klang; 15. Bukit Mandol. **Singapore:** 16. Botanical Gardens. For full locality details, see Gazetteer and Appendix I.

Rattus argentiventer

Ricefield rat

Epimys rattus argentiventer Robinson & Kloss 1916b: 274; Pasir Ganting, West coast of Sumatra, 2°7'S.

R. r. chaseni Sody 1941: 269; Krian, Perak, Malaya.

Description (based on Musser 1973b, Aplin et al. 2003). This is a medium-sized rat with a robust body and a relatively short tail, which usually averages shorter than head and body length (Table 20). The pelage feels soft and sleek to the touch; it includes thin, pale, flexible, grooved, spiny-hairs. The guard hairs are black and relatively short and inconspicuous. The upper parts are yellowish brown speckled with black, giving a characteristic 'salt and pepper' effect. Although some specimens are more greyish and others have more yellowish and brown hues, the 'salt and pepper' effect is always distinctive. The underparts are silvery grey (never creamy), with white hair tips and grey bases; the midventral region is often a buffy-brown; the throat is white. The flanks and sides of the head are paler than the head and back; this colour extends to the

upper surface of the fore and hind feet. The hind feet are long and narrow and have six pads, four interdigital and two metatarsal; these pads are small and smooth relative to those in *R. tiomanicus* and *R. tanezumi*, with the lamellae/grooves scarcely indicated (hind foot illustrated in Musser 1973b, Figure 2). The cheeks are grey. In front of each ear is a tuft of orange hairs. These tufts are clearly visible in young individuals; they may be less conspicuous in some adults that have longer pelage (Guy Musser pers. comm.). The tail is unicoloured, dark above and below; it is usually but not always shorter than the head and body. Females have six pairs of mammae: one pectoral, two postaxillary, one abdominal, and two inguinal. The skull has a short, broad and deep rostrum, which curves conspicuously downwards. The interorbital region is narrow; the braincase is oval. The incisive foramina are long and wide; posteriorly they terminate between the first upper molars (M^1), a point much further back than in *R. tanezumi*. The tympanic bullae are relatively large. The dentition is robust. Photographs of the skull are included in Musser & Newcomb (1983, Figures 110 and 111) and Marshall (1988, page 468).

Karyology. 2N= 42 (based on specimens collected in rice fields in the Bangkok area); autosomal pairs 1 to 9 are subtelocentric; the karyotype is illustrated in Markvong et al. (1973, Figure 16).

Sperm morphology. Information on the sperm morphology of two specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. *Rattus argentiventer* is known from a single late middle Pleistocene site in north-eastern Thailand (Pearch et al. 2013).

Taxonomic notes. The taxon *argentiventer* was described originally as a subspecies of *Rattus rattus* (= *R. tanezumi*). However, this view was rejected by Musser (1973b) and was not followed by subsequent authors, including Corbet & Hill (1992), Musser & Carleton (2005) and Maryanto (2003). The taxon *chaseni* is included as a synonym (Maryanto 2003), although the tail is uncharacteristically long (Table 20).

Distribution and conservation status. *Rattus argentiventer* has an extensive range from Thailand and Indochina to Malaysia, Indonesia, and the Philippines. Within the study area, it is known from peninsular Myanmar, Thailand and Malaysia (Fig. 40).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, adaptability to disturbance, large population, its occurrence in a number of protected areas, the absence of threats, and because the population is considered to be stable" (Ruedas et al. 2008a).

Ecology and reproduction. In Thailand, *R. argentiventer* was collected in secondary evergreen forest in Surat Thani Province at approximately 400 m. a.s.l. (UP unpublished data). In Malaysia, it is restricted to ricefields, scrub, grassland and young plantations; it is absent from the forest interior (Medway 1969). Aplin et al. (2003) suggest that it avoids village habitats except as a vagrant but is found in gardens and orchards; it favours areas that are regularly flooded. Both sexes dig burrows in well drained soil, in bunds between flooded paddies, or in and around raised vegetable gardens and orchards. The burrows of females tend to be more extensive than those of males. One burrow can house two or more litters from the same female (Medway 1969, Aplin et al. 2003). Its diet includes a high proportion of insects, including termites in grassland and grasshoppers in rice fields; it also feed on young rice plants, grasses, paddy weeds, grass seeds and cereal grains. It may feed on some vertebrates and snails. It is a pest of young oil palms (Harrison 1954a, 1962, Lim 1966, Medway 1969). Typically crop losses in rice growing areas to *R. argentiventer* may be 10–20 % but chronic losses of 30–50 % may occur in areas that are particularly favourable to this rodent or where the multiple cropping

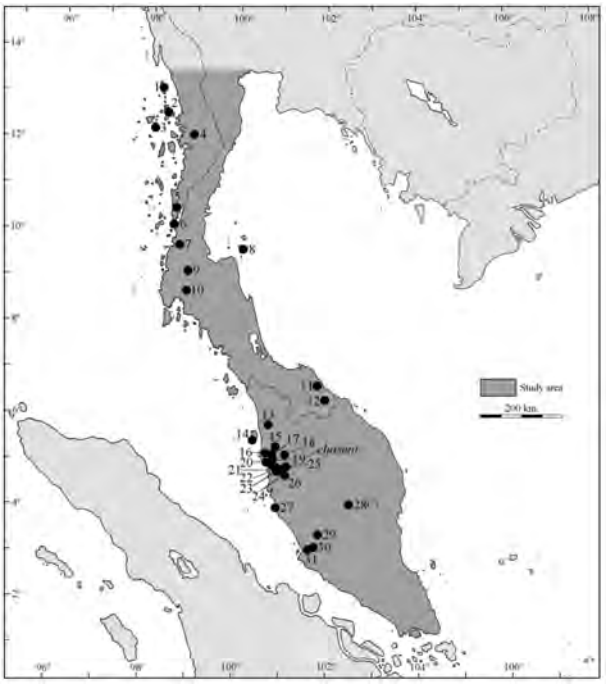

Fig. 40. Distribution of *Rattus argentiventer* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Tavoy Island; 2. King's Island; 3. Ross Island; 4. Tenasserim Town; 5. Maliwun; 6. Victoria Point. **Thailand:** 7. Ban Kam Phuan; 8. Khao Phlu (base of), Koh Samui; 9. Rajjaprabha Dam; 10. Klong Phraya Wildlife Sanctuary; 11. Bangnara; 12. Rangae. **Malaysia:** 13. Kedah Peak; 14. Kampong Pulau Betong; 15. Bagan Triang; 16. Parit Buntar; 17. Tanjong Piandang; 18. Briah; 19. Krian; 20. Kuala Kurau; 21. Telok Anson; 22. Bagan Serai; 23. Gunong Semanggul; 24. Maxwell's Hill; 25. Selensing; 26. Taiping; 27. Bagan Datoh; 28. Pahang (State); 29. Sungei Tua; 30. Kuala Lumpur; 31. Cheras. For full locality details, see Gazetteer and Appendix I.

of rice provides a continuous supply of food. On average 10% of females are pregnant without seasonal variation. Mean litter size is 6.0 and ranges from 5 to 7 (Harrison 1961, Medway 1969). However Aplin et al. (2003) suggest that breeding patterns are closely linked to rice production, with the first litter as the rice reaches booting stage, the second litter during the ripening stage, and the third litter shortly after harvest. At certain times nearly 100 % of females may be pregnant. Females usually become pregnant at a point when body weight reaches 60–120 g. Males usually reach sexual maturity at 90+ g (estimated at about 59 days). The gestation period is 20–26 days. In the wild, on average females give birth to about 6 infants.

Rattus exulans

Polynesian rat

Rattus exulans Peale 1848: 47; Tahiti, Pacific Ocean.
Mus obscurus Miller 1900a: 213; Tioman Island, Malaysia. Preoccupied by *M. obscurus* Waterhouse 1837 (= *Akodon obscurus*) = *M. pullus* Miller 1901: 178.

Description (based on personal observation, Miller 1900a, Medway 1969, Corbet & Hill 1992, Aplin et al. 2003). This is a small rat, which is superficially similar to a large mouse (Table 20). The fur is rather short, about 8 mm in the middle of the back, and there are numerous well-developed, slender, grooved, pale, hair-like spines; these bristles are best developed on the upper surface, whilst on the ventral surface they are scarcely evident. The dorsal surface is grey-brown to brown intermixed with dull yellowish-red buff; the head and lower back tend to be browner than the rump, flanks, shoulders and legs. The ventral surface of the body and the inner side of the legs are pale, irregularly washed with brownish yellow. The bases to the hairs are slate-grey throughout the body. The feet are grey. The tail is uniformly dark brown. It is annulated with about 16 rings/cm in the midpart of the tail; these rings are obscurely divided into scales. The tail has very short hairs, which do not obscure the rings nor form a pencil (tuft) of hairs at the tip. The hind feet have six well-developed pads; the proportionately larger interdigital and metarsal pads clearly distinguish this species from a large *Mus* (Fig. 28C). The whiskers (vibrissae) on the head are long. According to Medway (1969), there are four pairs of mammae; two pairs pectoral and two pairs inguinal; Aplin et al. (2003) state that there are one pair pectoral, one pair postaxillary and two pairs inguinal. The skull is the smallest of all the *Rattus* in the study region (Table 20). Unlike *Mus* (Fig. 28B), the length of the anterior upper molar (M^1) in *R. exulans* is less than the combined lengths of the second and third molars (M^2 and M^3). Photographs of the skull are included in Musser & Newcomb (1983, Figures 110 and 111) and Marshall (1988, page 474).

Karyology. 2N= 42 (based on specimens collected in Chiang Mai, northern Thailand); autosomal pairs 1 to 11 are subtelocentric; the karyotype is illustrated in Markvong et al. (1973, Figure 19). According to Badenhorst et al. (2009), the diploid number is 2N= 42 and and the autosomal fundamental number (NFa) = 54, 58 or 59.

Sperm morphology. Information on the sperm morphology of two specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. There are no recorded fossil specimens of *R. exulans* from Thailand (Pearch et al. 2013).

Taxonomic notes. According to Corbet & Hill (1992), geographical variation in this widely distributed species is not significant, mainly affecting the ventral pelage, which ranges from light to dark grey with a variable amount of brown in the hair tips. Extralimitally, montane forms tend to be slightly darker with longer, softer pelage and flattened spines absent or sparse. In the study of Pagès et al. (2010), *R. exulans* formed a discrete monophyletic group.

Distribution and conservation status. *Rattus exulans* has an extensive range from Bangladesh through Southeast Asia to Taiwan, Indonesia, the Philippines, New Guinea, the Southwest Pacific islands, and islands off northern Australia. Its distribution is probably caused by a combination of inadvertent human introductions and possibly some natural rafting (Musser & Carleton 2005). Within the study area, it is known from peninsular Thailand and Malaysia and Singapore (Fig. 41).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, tolerance of a broad range of habitats, presumed large population, and because it is unlikely to be declining fast enough to qualify for listing in a more threatened category" (Ruedas et al. 2008c).

Ecology and reproduction. *Rattus exulans* is variably described as being a 'ground rat' (Medway 1969) and as 'highly arboreal' (Aplin et al. 2003). According to Corbet & Hill (1992), it is a common pest species found in houses, granaries, cultivated areas, scrub and forest, usually on the ground. In Thailand, it is reported from houses, markets, the vicinity of houses and also rice paddies close to buildings (Marshall 1988). In field surveys for the current study, it was found in a forest near buildings and in secondary evergreen forest in Surat Thani Province (approximately 400 metres. a.s.l.). Specimens were also collected in rain forest in Narathiwat Province (approximately 200 metres a.s.l.) and in a building in Songkhla Province (UP unpublished data). Extralimitally, in mainland Southeast Asia and Bangladesh, it has been found to coexist with *R. tanezumi* in village houses. It climbs around in tall grasses or low trees and on the walls and roofs of houses. It usually constructs a nest of leaves and grass in dense grass and situated some 200 mm or more above the ground. Inside buildings, nests are usually located in roof thatch and less often in piles of straw or other material on the ground (Aplin et al. 2003). In Malaysia, 23–29 % of females were pregnant, with little seasonal variation. Mean

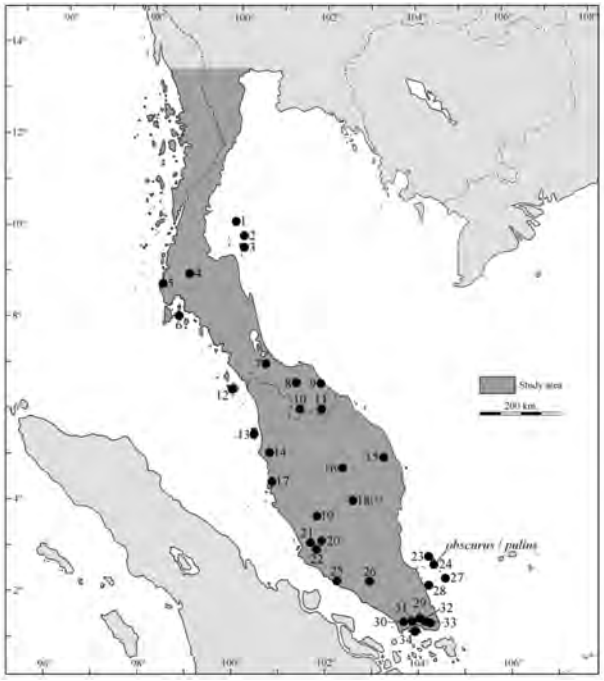

Fig. 41. Distribution of *Rattus exulans* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Koh Tao; 2. Ban Tai; 3. Ban Bang Khla, Kho Samui; 4. Rajjaprabha Dam; 5. Khao Lak; 6. Koh Yao Yai; 7. Prince of Songkla University; 8. Muang Yala; 9. Ban Thon; 10. Biserat; 11. Hala Bala Wildlife Research Station. **Malaysia:** 12. Langkawi Island; 13. Penang Island; 14. Maxwell's Hill; 15. Bukit Jong; 16. Aring; 17. Tanjong Hantu; 18. Pahang (State); 19. Semangko Pass; 20. Klang Gates; 21. Kuala Lumpur; 22. Ulu Langat; 23. Tulai Island; 24. Tioman Island; 25. Malacca; 26. Segamat; 27. Aur Island; 28. Tinggi Island; 29. Tebraun; 30. Pelepak; 31. Johore Bahru; 32. Kangka; 33. Pasir Gudang. Not located: Gomok (Johore State). **Singapore:** 34. Tanglin. For full locality details, see Gazetteer and Appendix I.

litter size is 4.3 (1 to 8) (Harrison 1955, Medway 1969). Mean length of life in the wild is thought to be 3.2 months (Harrison 1956a).

Rattus norvegicus

Norway rat

Mus norvegicus Berkenhout 1769: 5; Great Britain.

Description (based on personal observation, Medway 1969, Marshall 1988, Corbet & Hill 1992, Aplin et al. 2003, Francis 2008). This is a large rat (Table 20) with a mass of between 150–400 g (Medway 1969). It has short fur, which is slightly stiff but is without bristles; it has long guard hairs. It is grey-brown to brown on the dorsal surface; pale-brown or grey on the ventral surface; there is often a white patch on the chest. There is no clear line of demarcation between the colour on the flanks and the belly. Black (melanistic) individuals are quite common in some areas. The nose is long and broad and the eyes and ears are relatively small. The tail is almost always shorter than the head and body. It is usually weakly bicoloured, dark above and slightly paler below, sometimes mottled in appearance. The front and hind feet are large, with poorly developed foot pads and inconspicuous ridges. In contrast to the dark feet of *Bandicota,* those of *R. norvegicus* are mostly white (dark hairs in melanistic individuals). There are six pairs of mammae with three pairs pectoral and three pairs inguinal. The skull is robust, medium-large to very large in some individuals with long incisive foramina. The skull ridges are well-defined in older individuals and characteristic in shape; they are relatively straight and situated close to one another, which gives the impression of a relatively narrow braincase. The toothrows are long. Photographs of the skull are included in Marshall (1988, page 462) and Musser & Newcomb (1983, Figures 110 and 111).

Karyology. 2N= 42, FN= 62 (based on specimens from Thailand); seven pairs of metacentric chromosomes; four pairs of subtelocentrics; nine pairs of telocentrics; the X and Y sex chromosomes are telocentrics (Musser & Newcomb 1983).

Fossil history. There are no recorded fossil specimens of *R. norvegicus* from Thailand (Pearch et al. 2013).

Taxonomic notes. Wild populations of this species are thought to have inhabited Southeast Siberia, northern China and parts of Japan. However, inadvertent human introductions worldwide have obscured wild geographical patterns.

Distribution and conservation status. *Rattus norvegicus* has a worldwide distribution but is more common in the colder latitudes of the Northern and Southern Hemispheres. In the warmer climates of the tropics it is restricted to habitats that have been highly modified by humans (Musser & Carleton 2005). Within the study area, it is recorded from Thailand and Malaysia and Singapore (Fig. 42) but is probably considerably more widespread in urban areas than this map suggests.

Its conservation status is listed by IUCN as 'Least Concern' as it is "a common species with no major threats" (Ruedas 2008).

Ecology and reproduction. According to Medway (1969), *R. norvegicus* is confined to ships, harbours and neighbouring built-up areas. It is apparently unable to compete with native rats in rural habitats. Aplin et al. (2003) describe it as a terrestrial, burrowing species with poor climbing skills, which is often found close to water, such as along rivers and major irrigation canals. It occurs in urban areas, where it lives in and around buildings and animal yards, feeding on refuse and stored food. Occasionally, it is found in cultivated areas but the level of damage to crops is not known in Southeast Asia. It is a communal species that constructs large and complex burrow systems that may be occupied for many years. Its nests are lined with leaves and other soft material and are con-

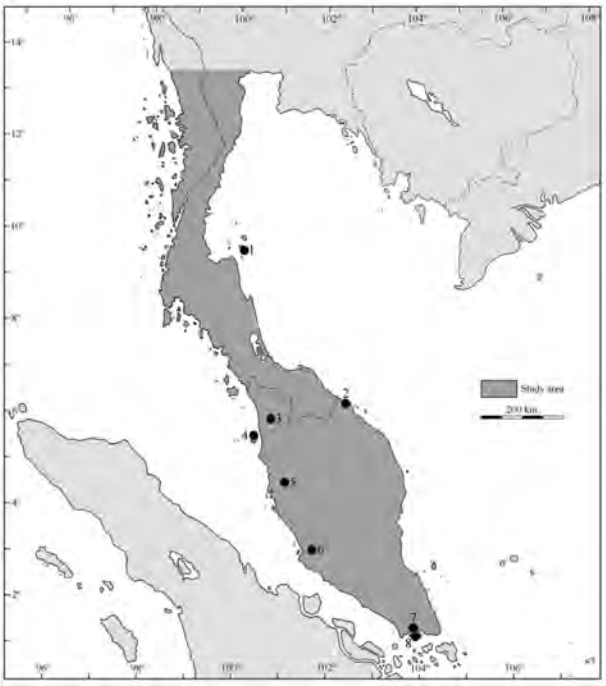

Fig. 42. Distribution of *Rattus norvegicus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Koh Samui. **Malaysia:** 2. Kota Bharu; 3. Gurun; 4. Georgetown, Penang Island; 5. Gunong Ijau; 6. Kuala Lumpur; 7. Johore Bahru. **Singapore:** 8. Singapore Island. For full locality details, see Gazetteer and Appendix I.

structed within the burrow. No data are available on litter size in Southeast Asia. In India, mean litter size is 8.1. The gestation period is 22 to 24 days.

Rattus tanezumi

Oriental roof rat, Oriental house rat, Oriental ship rat

Rattus tanezumi Temminck 1844: 51; Japan (possibly from near Nagasaki on Kyushu Island).
Mus griseiventer Bonhote 1903a: 30; Perak, Malaysia.
Mus pannosus Miller 1900c: 190; Adang Island, Butang Islands, Thailand.
Epimys panellus Miller 1913: 8; Rawi Island, Butang Islands, Thailand.
Epimys rattus dentatus Miller 1913: 14; Hastings Island, Mergui Islands, Myanmar.
Epimys rattus insulanus Miller 1913: 14; Helfer Island, Mergui Islands, Myanmar.
Epimys rattus exsul Miller 1913: 15; James Island, Mergui Islands, Myanmar.
Epimys rattus fortunatus Miller 1913: 15, Chance Island, Mergui Islands, Myanmar.
Rattus rattus tikos Hinton 1919: 400; Tenasserim Town, Myanmar.
Rattus rattus panjius Chasen 1937: 85; N Panjang Island, western peninsular Thailand.
Rattus rattus alangensis Chasen 1937: 87; Alang Yai Island, western peninsular Thailand.
Rattus rattus lontaris Chasen 1937: 88; Lontar Island, western peninsular Thailand.
Rattus rattus kadanus Chasen 1937: 89; Kadan Island, western peninsular Thailand.
Rattus rattus moheius Chasen 1937: 91; Pipidon Island, western peninsular Thailand.
Rattus rattus pipidonis Chasen 1937: 92; Pipidon Island, western peninsular Thailand.
Rattus rattus robinsoni Chasen 1940: 154; Samui Island, eastern peninsular Thailand.

Description (based on personal observation and Bonhote 1903a, Chasen 1937, Medway & Lim 1966, Medway 1969, Musser & Califia 1982, Marshall 1988, Corbet & Hill 1992, Aplin et al. 2003, Francis 2008). This is a medium-large rat (Tables 20 and 22, Fig. 51C) with a mass of 85–240 g (Medway 1969). The dorsal pelage includes thin, flexible, grooved, spine-like hairs, these are pale basally with black tips and are more evident in older individuals. The extent of the spines varies between populations – for example, they are scarcely evident in the island form *lontaris*. There are long guard hairs that extend well beyond the overhairs and are conspicuous over the lower part of the back and rump; these are mostly black, although some are also paler for part of their length. In general, the upperparts are grizzled olive brown, sometimes with greyish or reddish-orange tones, sometimes there is darkening on the midline of the back and the crown of the head; some individuals are paler, others are darker. The underparts vary in colour from grey to brown-grey to creamy-white, sometimes with a yellowish tinge. Medway & Lim (1966) suggest that the colour of the ventral pelage may be related to habit, with those living in urban areas in mainland Malaysia having greyish-brown hairs on the belly and those on Singapore Island, which occupy rural as well as urban areas having variably coloured belly hairs from greyish-brown to pale grey. The feet are brown, although the hairs on the toes are white. The hind feet are moderately broad with prominent plantar (interdigital and metatarsal) pads (but not as prominent as in *R. andamanensis*) and usually with obvious ridges/lamellae (in contrast to *R. argentiventer,* the pads of which are characteristically smooth). The ears are thinly furred, rounded and relatively large. The tail is shorter, equal to or rather longer than head and body (Table 22); it is uniformly dark/black throughout, covered with numerous short stiff black hairs; very occasionally there is a short, white tip. There are five or six pairs of mammae; one pectoral pair, one or two postaxillary pairs and three inguinal pairs. The skull is medium-sized. Medway & Lim (1966) and Musser & Califia (1982) suggest that *R. tanezumi* (= *R. r. diardii*) has longer incisive formina, longer maxillary toothrows and more strongly developed and more angular supraorbital ridges in comparison to *R. tiomanicus* (= *tiomanicus* and *jalorensis* in Medway & Lim 1966). This latter character is illustrated in Fig. 43. Additional photographs of the skull are included in Musser & Califia (1982, Figure 2), Marshall (1988, page 477) and Musser & Newcomb (1983, Figure 110 = *R. rattus* from Thailand).

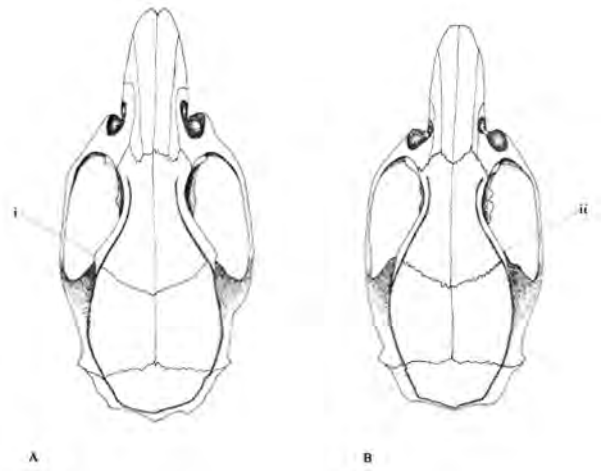

Fig. 43. Crania of adult *Rattus*: (A): *R. tanezumi*, Sabah (USNM 292689, male); (B): *R. tiomanicus*, Sabah (USNM 292672, male) modified from Musser & Califia (1982, Figure 2). i: the angular supraorbital ridge of *R. tanezumi*; ii: the smooth, curved supraorbital ridge of *R. tiomanicus.*

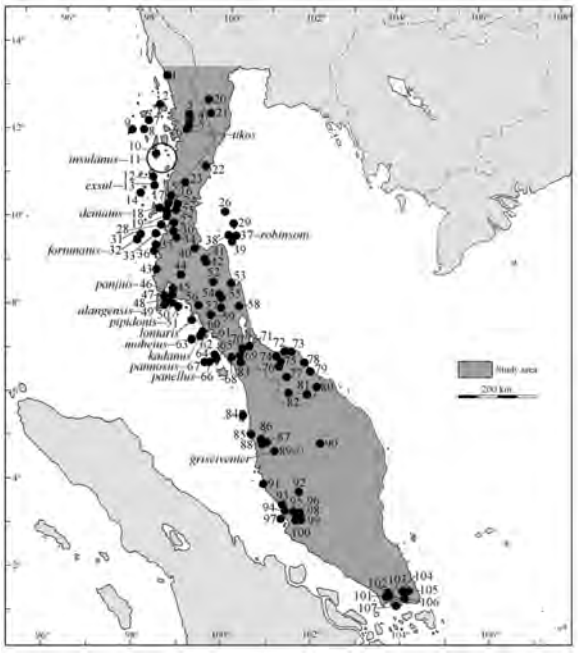

Fig. 44. Distribution of *Rattus tanezumi* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Nathé Mine; 2. King's Island; 3. Tagoot; 4. Thaget; 5. Banlaw; 6. Tenasserim Town; 7. Ross Island; 8. Criddles Island; 9. Sir John Hayes Island; 10. Malcolm Island; 11. Helfer Island (exact location not determined); 12. Sullivan Island (Lampi Island); 13. James Island; 14. Loughborough Island; 15. Maliwun; 16. Bankachon; 17. Victoria Point; 18. Hastings Island; 19. Victoria Island. **Thailand:** 20. Kaeng Kra Chan National Park; 21. Pa La U; 22. Bang Saphan; 23. Pak Chan; 24. Ban Bang Bane; 25. Ban Bang Non; 26. Koh Tao; 27. Pa Toh Watershed Management; 28. De Lisle Island; 29. Ban Tai; 30. Ban Kam Phuan; 31. Koh Surin Nua; 32. Chance Island; 33. Koh Yam Yai; 34. Phato Watershed Conservation and Management Unit; 35. Koh Rah; 36. Koh Prah Tung; 37. Koh Samui; 38. Ban Bang Khla, Koh Samui; 39. Khao Phlu (base of), Koh Samui; 40. Ao Ko; 41. Khao Sai; 42. Ban Plai Num; 43. Khao Lak; 44. Klong Phraya Wildlife Sanctuary; 45. Koh Boi Yah; 46. North Panjang Island (Koh Yao Noi); 47. Koh Naka Yai; 48. Koh Maprau; 49. Koh Alan Yai; 50. Panjang Island (Koh Yao Yai); 51. Pipidon Island; 52. Ban Tha–Phae; 53. Banna; 54. Tham Nam; 55. Khao Phu Khao Ya National Park; 56. Ban Khuan Dang; 57. Pak Jam; 58. Khuan Khi Sian; 59. Trang; 60. Lontar Island; 61. Pulau Muntia (Koh Muk); 62. Kadan Island; 63. Pulau Mohea; 64. Bulon Island; 65. Tarutao Island; 66. Koh Rawi; 67. Adang Island; 68.Wang Bla Chan; 69. Khao Rup Chang; 70. Kuan Khao Wang Forest Park; 71. Prince of Songkla University; 72. Pak Num; 73. Ban Nai Tan Yong; 74. Nam Tok Sai Khao; 75. Ban Lam Mai; 76. Sam Yak A–Sen; 77. Ban Chok; 78. Ban Thon; 79. Ban Ya Kan; 80. Pa Phru; 81. Hala Bala Wildlife Research Station; 82. Biserat. **Malaysia:** 83. Pelarit; 84. Penang (Island); 85. Krian Road; 86. Kledang Hill; 87. Larut Hills; 88. Taiping; 89. Perak (State); 90. Aring; 91. Bagan Datoh; 92. Semangko Pass; 93. Tanjong Karang; 94. Kuala Selangor; 95. Rawang; 96. Gombak Forest Reserve; 97. Pulau Angsa; 98. Klang Gates; 99. Ampang; 100. Kuala Lumpur; 101. Pelepak; 102. Pulai; 103. Johore Bahru; 104. Kangka Senibong; 105. Pasir Gudang; 106. Tanjong Surat. **Singapore:** 107. Singapore Island. For full locality details, see Gazetteer and Appendix I.

Karyology (based on specimens from Thailand, Musser and Newcomb 1983 = *R. rattus*). 2N= 42, FN= 54; there are seven pairs of metacentric chromosomes; 13 pairs of telocentrics; the X and Y sex chromosomes are telocentrics (Musser & Newcomb 1983).

Fossil history. There are four localities in Thailand including two in the peninsular, from which fossil specimens dating back to the middle Pleistocene have been recovered (Pearch et al. 2013). These were referred to *R. rattus* by Chaimanee (1998) but are included here in *R. tanezumi.*

Taxonomic notes. Previously specimens here referred to *tanezumi* from Southeast Asia were included in *R. rattus* (see Corbet & Hill 1992) with those from Singapore, Malaysia and peninsular Thailand frequently referred to *R. rattus diardii* Jentink, which was described from western Java (see Musser & Califia 1982). However, Baverstock et al. (1983) showed differences in the karyology between true *R. rattus* (2N= 38/40) and the Southeast Asian form, *R. tanezumi* (2N= 42) and Musser & Carleton (2005) treated the two taxa as distinct species and included all '*R. rattus'* from Southeast Asia in *R. tanezumi.* Subsequently, Aplin et al. (2011) have cautioned that this 'bipartite separation' over-simplifies a more complex evolutionary history, the details of which have yet to be resolved. Meanwhile, Latinne et al. (2013b) suggest that the taxon *tanezumi* may itself include a complex of discrete genetic lingeages and possibly species.

Distribution and conservation status. *Rattus tanezumi* has a range that extends from Afghanistan through north India, Nepal, Bhutan to southern China, and Korea to Taiwan and Japan (although it may be introduced to the latter two countries) (Musser & Carleton 2005). Within the study area, it is recorded from Myanmar, Thailand and Malaysia and Singapore (Fig. 44).

Its conservation status is listed by IUCN as 'Least Concern' "due to its wide distribution and tolerance of a wide variety of habitat types" (Heaney & Molur 2008).

Ecology and reproduction. In Thailand, *R. tanezumi* is found in a wide-range of habitats including buildings and human habitation, where it is common. However, it has been collected in primary forest in Phatthalung and Phang Nga Provinces, tropical rain forest in Naratiwat Province, evergreen forest in Songkhla and Chumphon Provinces, and secondary forest in Trang, Surat Thani and Phetchaburi Provinces. In Tarutao National Park, Satun Province, it was found in primary forest on the islands of Tarutao, Adang, and Rawi, and in secondary forest on Bulon Island (UP unpublished data). In mainland Malaysia, *R. tanezumi* is generally associated with houses, outhouses and stores in urban areas, where it is the dominant species (Medway 1969, = *R. rattus*) and can be a significant pest, responsible for major post-harvest losses (Aplin et al. 2003, = *R. rattus* Complex). However in Singapore, it occupies not only houses but also field and fringe habitats (Medway & Lim 1966, = *diardii*) and in Lao PDR it is known from field and forest habitats. Where it also occurs in rural habitats, *R. tanezumi* may cause extensive damage to cereal, vegetable and fruit crops, including coconuts (Aplin et al. 2003). Its diet also includes refuse, slugs and snails (Medway 1969). It builds loose spherical nests of shredded vegetation, cloth or other material. These are placed in a confined space, including in a burrow, in roof thatch, in a wall cavity or inside a mud-brick wall, in a pile of cut wood, in a straw pile, among stored sacks of grain, among rocks, in a tree hollow or a fallen log or other natural sites, such as the fork of a tree (Aplin et al. 2003). In Kuala Lumpur, pregnant females were collected in all months, without significant seasonal variation (Medway 1969). However, in rural areas pregnancy is synchronised with cycles of crop maturation (Aplin et al. 2003). Average gestation period is 21 days and mean litter size is 5.7 (one to 11). Young reach sexual maturity at about 80 days (Medway 1969).

Rattus tiomanicus

Malaysian wood rat, Malaysian field rat

Mus tiomanicus Miller 1900a: 209; Tioman Island, Malaysia.
Mus jalorensis Bonhote 1903a: 29; Nong Chik, Pattani, peninsular Thailand.
Mus jarak Bonhote 1905: 69; Jarak Island, Straits of Malacca.
Mus rattus rumpia Robinson & Kloss 1911a:169; Rembia Island, Sembilan Islands, west of Malaysia.
Epimys tingius Miller 1913: 9; Tinggi Island, eastern Malaysia.
Epimys roa Miller 1913: 10; Maratua Island, eastern Malaysia.
Epimys rattus viclana Miller 1913: 13; Langkawi Island, western Malaysia.
Rattus rattus payanus Chasen & Kloss 1931: 79: Paya Island, Straits of Malacca, Malaysia.
Rattus rattus perhentianus Chasen 1940: 155; East Perhentian Island, eastern Malaysia.
Rattus rattus pemanggis Chasen 1940: 156; Pemanggil Island, eastern Malaysia.
Rattus rattus pharus Hill 1960: 75; Pisang Island, Straits of Malacca, Malaysia.
Rattus rattus sribuatensis Hill 1960: 76; Sribuat Island, Pahang, Malaysia.
Rattus rattus kabanicus Hill 1960: 77; Kaban Island, Johore Islands, Malaysia.
Rattus rattus terutavensis Hill, 1960: 79; Telok Udang, Terutau Island, Southwest Thailand.
Rattus tiomanicus tenggolensis Yong 1971: 89; Tenggol Island, off eastern Malaysia.

Description (based on personal observation and Miller 1900a, Bonhote 1903a, Chasen 1940, Medway & Lim 1966, Medway 1969, Musser & Califia 1982, Marshall 1988, Corbet & Hill 1992, Aplin et al. 2003, Francis 2008). This is a medium-large rat (Tables 20 and 23) with a mass of 55–152 g (Medway 1969). The dorsal pelage is sleek, moderately long and soft; the proportion of slender spine-like hairs seems to vary geographically and between individuals; the guard hairs are black, short and inconspicuous, barely extending beyond the overhairs. The general colour is a warm yellowish-brown, grizzled with blackish-brown. The flanks and cheeks are slightly paler than the back and much less profusely sprinkled with dark hairs. Each hair is ashy-grey at the base with a broad, brownish tip. The spine-like hairs are whitish with a black tip. The underparts tend to be white in mainland populations in Malaysia but are variably coloured in island populations, including white suffused with grey to buffy grey (Musser & Califia 1982). Throughout the ventral pelage, except on the chin and throat, the hairs are a light slate-grey at the base. The line of demarcation between the upper and lower surfaces is usually well defined. The tail is unicoloured, dark above and below. The plantar (interdigital and metatarsal) pads on the hind feet are less well-developed than those of *R. andamanensis* and are more ridged than those of *R. argentiventer.* According to Medway & Lim (1966), where *R. tiomanicus* and *R. tanezumi* co-exist, the upper toothrow is shorter in *R. tiomanicus* (= *tiomanicus* and *jalorensis* in Medway & Lim 1966) than in *R. tanezumi* (= *diardii* in Medway & Lim 1966). In addition, the supraorbital ridges of *R. tiomanicus* flow backwards on either side of the skull in smooth, vase-shaped curves (Fig. 43). This is in contrast to *R. tanezumi,* where the supraorbital ridges are high and wide and form a conspicuous angular shelf just behind the interorbital area (Musser & Califia 1982). Photographs of the skull of *R. tiomanicus* are included in Musser & Newcomb (1983, Figures 110 and 111).

Sperm morphology. Information on the sperm morphology of two specimens from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. There are no recorded fossil specimens of *R. tiomanicus* from Thailand (Pearch et al. 2013).

Taxonomic notes. Previously many specimens here referred to *tiomanicus* were included in *R. rattus jalorensis*. However, Medway & Lim (1966) explored the rela-

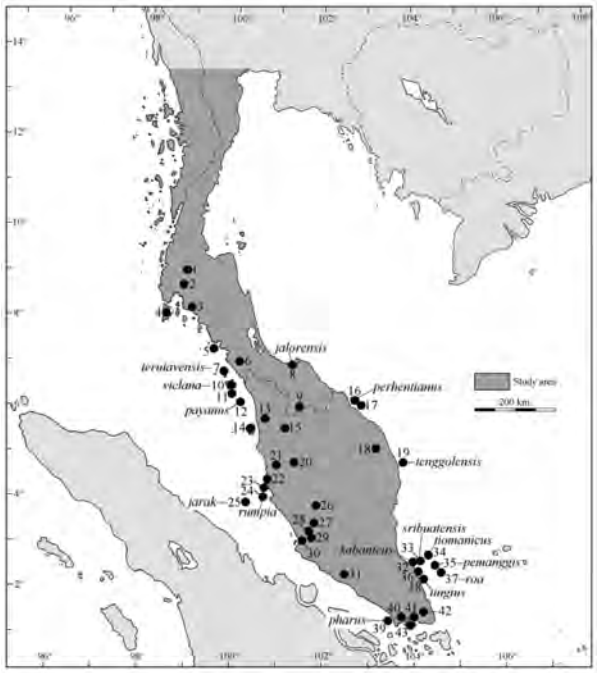

Fig. 45. Distribution of *Rattus tiomanicus* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Thailand:** 1. Rajjaprabha Dam; 2. Klong Phraya Wildlife Sanctuary; 3. Ghirbi; 4. Junk Seylon (= Phuket); 5. Pulau Telibon; 6. Khuan Kalong; 7. Talok Udang, Terutau Island; 8. Nong Chik; 9. Biserat. **Malaysia:** 10. Langkawi Island; 11. Pulau Dayang Bunting; 12. Paya Island; 13. Kedah Peak; 14. Penang Island; 15. Temengoh; 16. E. Perhentian Island; 17. Great Redang Island; 18. Bukit Jong; 19. Tenggol Island; 20. Telom; 21. Taiping Hill (near); 22. Tanjong Huntu; 23. Pangkor Besar Island; 24. Pulau Rumpia; 25. Jarak Island; 26. Bukit Fraser; 27. Bukit Lanjang Forest Reserve; 28. Subang Forest Reserve; 29. Kuala Lumpur; 30. Cheras; 31. Gunong Tampin; 32. Kaban Island; 33. Sribuat Island; 34. Tioman Island; 35. Pemanggil Island; 36. Pulau Babi; 37. Aur Island; 38. Tinggi Island; 39. Pisang Island; 40. Pelepak; 41. Kangka; 42. Pasir Gudang. **Singapore:** 43. "Various localities". For full locality details, see Gazetteer and Appendix I.

tionships between *tiomanicus, jalorensis,* and *diardii* Jentink (which was described from western Java). They concluded that *tiomanicus* was the prior name for *jalorensis* and that these taxa were separate from *diardii*. This view was supported by the chromosomal characters (Yong et al. 1972) and also by an analysis of red cell proteins (Chan 1977). Musser & Califia (1982) followed this view, referring *diardii* to *R. rattus* (now considered to be *R. tanezumi* in Southeast Asia, Musser & Carleton 2005) and treating *jalorensis* as a synonym of *R. tiomanicus*. They included a list of synonyms of *tiomanicus* from throughout its range and outlined its geographically variable characters. Previously, Hill (1960) provided descriptions of the pelage colour and measurements (see also Table 23) for most of the taxa currently referred to *R. tiomanicus* from peninsular Thailand and Malaysia.

Distribution and conservation status. *Rattus tiomanicus* is a Sundaic species with a range extending from peninsular Thailand to Sumatra, Java, Bali, Borneo and Palawan (Musser & Carleton 2005). Within the study area, it is recorded from southern peninsular Thailand and Malaysia and Singapore (Fig. 45).

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, presumed large population, tolerance of a broad range of habitats, and because its population is likely to be increasing. It is considered a pest in parts of its range" (Aplin & Frost 2008).

Ecology and reproduction. In southern peninsular Thailand, *R. tiomanicus* was collected in secondary evergreen forest and in an oil palm plantation in Surat Thani Province at approximately 400 metres a.s.l. (UP unpublished data). In mainland Malaysia, this species was found in gardens, plantations, scrub, secondary forest, mangrove and disturbed or regenerating woodland. It tends to avoid primary forest, although some island populations are found in high forest. It enters houses freely (Medway 1969). Although frequently trapped on the ground, it is also an accomplished climber. In oil palm plantations, where it can be a major pest species (reducing yields by up to 5 %), it often shelters in piles of cut fronds and less frequently in cut stumps or fallen logs. Very occasionally, it is found in terrestrial burrows. Its nests are thought to be off the ground and presumably in crowns of palms and in hollow stumps and logs. Litter size ranges from 2 to 7 with a mean size of 4.4. Average female pregnancy rates were 17.6 % (27.9 % if restricted to sexually mature individuals) on an annual basis (Aplin et al. 2003). Oestrus occurs every 5–8 days and the gestation period is 21–22 days. Young reach sexual maturity after about 85 days (Medway 1969).

Genus *Sundamys*

Sundamys rats

Sundamys Musser & Newcomb 1983: 401; type species *Mus muelleri* Jentink.

Remarks. This genus is endemic to the Malaysian peninsula and islands on the Sunda Shelf. There are three species. Two are extralimital. *Sundamys infraluteus* (Thomas) is restricted to northern Borneo and western Sumatra. *Sundamys maxi* (Sody) is only known from western Java. *Sundamys muelleri* is the most widespread. Described from western Sumatra, its range extends to peninsular Myanmar, Thailand and Malaysia, Borneo to the Philippines and numerous Sundaic islands (Musser & Newcomb 1983).

Description. The generic description is omitted since there is only one species of this genus in the study area.

Sundamys muelleri

Müller's Sundamys

Mus mülleri Jentink 1880: 16; Batang Singgalang, Pada Highlands, western Sumatra.

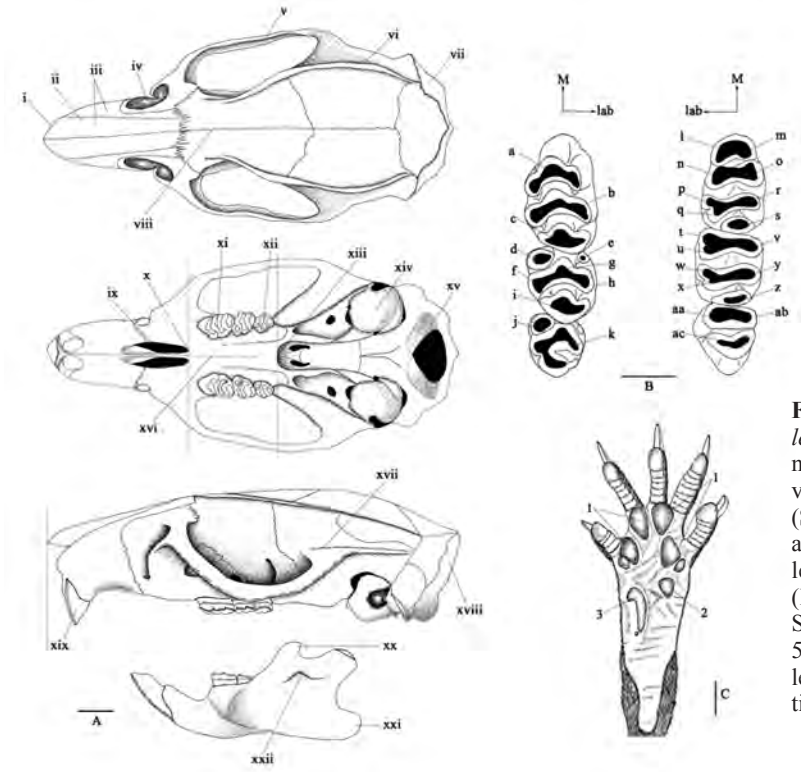

Fig. 46. Skull and dentition of *Sundamys muelleri* (54–4392 CTNCR), Mueang District, Ranong Province, peninsular Thailand. (A): dorsal, ventral and lateral view of skull and mandible (Scale = 5 mm); (B): occlusal view of upper (left) and lower (right) left molars (Scale = 2 mm); (C): left hind foot of *S. muelleri* (PSUZC–MM2012.205), Na Thawi District, Songkhla Province, peninsular Thailand (Scale = 5 mm). Indicative numbers (i–xxii) and (1–3) and letters (a–ac) are explained in the text 'Description' for *S. muelleri*. M: mouth; lab: labial.

M. validus Miller 1900d: 141; Khow Sai Dow, Trang, peninsular Thailand.
Mus muelleri foederis Robinson & Kloss 1911b: 245; Ulu Temengor, Perak, Malaysia.
Rattus victor Miller 1913: 16; near mouth of Rompin River, Pahang, Malaysia.

Description (based on personal observation and Musser & Newcomb 1983). The body size ranges from large to very large (Table 24) with a body weight according to Rudd (1965) for males ranging from 210–412 g and for females from 206–441 g and according to Lim (1970) a mean for 30 males of 335 g and 30 females of 292 g. The tail is longer than the head and body and unicoloured, dark brown above and below. Tail scales are large with 9–12 rows of scales/cm. The fur on the upper parts of the body is thick, shaggy and slightly 'harsh' to touch but is without spines (Fig. 51G). There are over-hairs on the rump (12–18 mm in length) and black guard hairs on the back and rump (8–15 mm). The colour is dark tawny brown, darkest in the midline of the back and paler on the flanks. The under parts have soft, dense and short (6–8 mm) fur. The colour varies between individuals and geographically. According to Musser & Newcomb (1983), specimens from peninsular Malaysia have under parts that are white, cream, grey or buffy-grey; sometimes the chin and throat are paler than the rest of the under parts. There is usually a clear line of demarcation between the dorsal and ventral pelage along the flanks. The ears are small, round, and dark brown. The hind feet (Fig. 46C) are broad, moderately long, and brown, above and below; they have large interdigital pads (1), a conspicuous outer metarsal pad (2) and an inner metarsal pad (3), which is elongated and kidney-shaped; the claws are unpigmented. Females have eight mammae: one pair pectoral, one postaxillary and two inguinal.

The skull is medium to large and robust. The rostrum (Fig. 46Aiii) is long and wide, sufficiently broad almost to enclose the nasolacrimal capsules (iv). The nasals (ii) slightly exceed the length of the rostrum and incisors (xix); their tips (i) are pointed or rounded. The braincase is long, broadest between the squamosal roots (xvii), which are set high on the side of the braincase; it narrows towards the interorbital area (viii). The supraorbital ridges (vi) are well-developed; they continue on the lateral margins of the braincase and terminate at the supraoccipital (xvii). The zygomata (v) are robust, parallel with each other or slightly narrowed anteriorly. The incisive foramina (ix) are wide but short relative to the length of the diastema; their posterior margins (x) are variable in position, being in front of, in line with, or posterior to the anterior surfaces of the first molars (M^1) (xi). The palate (xvi) is long and broad; its posterior border (xiii) extends beyond the last upper molars (M^3) (xii). The distance from the back edge of the palate to the ventral margin of the foramen magnum (xv) (postpalatal length) is shorter than the palatal length. The tympanic bullae (xiv) are very small relative to the size of the skull. In each half mandible, the coronoid process (xx) is prominent; the angular process (xxi) is well-developed but thin; the incisor root (xxii) forms a

moderately defined process. Numerous photographs of the skull are included in Musser & Newcomb (1983, including Figures 33, 42 and 60) and in Marshall (1988, page 480).

The incisors are large and sturdy; the enamel layers are smooth and deep orange. The upper incisors are orthodont/opisthodont (xix). The molars are slightly cuspidate in young individuals but become laminate with age (Fig. 5G/H and O/P). The first upper molar (M^1) is long and wide and slightly overlaps the second (M^2), which in turn overlaps the third (M^3). In M^1, cusps t1, t2, and t3 (Fig. 46Ba) are fused in older individuals (t1 is separate in younger individuals, Fig. 5G); cusps t4, t5, t6 (b) are also fused; the third row comprises one large medial cusp, which is representative of both t8 and t9 (c); cusp t7 is absent; in some individuals there is a small, wedge-shaped posterior cingulum (illustrated in Figure 40 in Musser & Newcomb 1983). In the second upper molar (M^2), there is a large t1 (d) and a smaller t3 (e); in the second row, cusps t4 (f), t5 (g) and t6 (h) appear fused in some individuals and less so in others (Fig. 5G and H); in the third row, cusp t7 is absent; cusps t8 and t9 (i) are fused. In the third upper molar (M^3), cusp t1 (j) is large and prominent; cusp t3 is usually present but smaller than t1 (absent in Figs 5G and 46B); cusps t4, t5, t6 are fused; the last row comprises cusp t8 and possibly cusp t9; sometimes cusps t4, t5, t6, t8 and t9 (k) are fused (as illustrated in Fig. 46B) as a result of tooth wear.

In the mandibular toothrow, the first lower molar (M_1) has an anterocentral cusp in approximately half of individuals (according to Musser & Newcomb 1983), it is absent in the specimens illustrated in Figs. 5O, 5P and 46B; the anterolabial (l) and anterolingual (m) cusps are fused; the protoconid (n) is fused with the metaconid cusp (o); a small posterior labial cusplet (p) may or may not be present, it is fused with the hypoconid (q) and entoconid cusps (r) in Fig. 46B but is separate in the younger individual in Fig. 5O; a well-developed posterior cingulum (s) is present. In the second lower molar (M_2), a large anterior labial cusp (t) is fused with the protoconid (u) and metaconid cusps (v) (the anterior labial cusp is not seen in Fig. 5O); a posterior labial cusplet (w) is always present, it is fused, in older individuals, with the hyconid (x) and entoconid cusps (y); the posterior cingulum (z) is well-developed. In the third lower molar (M_3), the protoconid (aa) is fused with the metaconid cusp (ab); the posterior lamina is constituted only by the entoconid cusp (ac).

Karyology. 2N= 42, FN= 59 (male), FN= 58 (female); there are six pairs of small metacentric chromosomes; one pair of large subtelocentric chromosomes, one pair of small subtelocentric chromosomes, 12 pairs of telocentric chromosomes; the X sex chromosome is a large submetacentric; the Y sex chromosome is a small telocentric (Musser & Newcomb 1983).

Sperm morphology. Information on the sperm morphology of a specimen from peninsular Malaysia is included in Breed & Yong (1986).

Fossil history. There are no recorded fossil specimens of *S. muelleri* from Thailand (Pearch et al. 2013).

Taxonomic notes. Specimens from peninsular Myanmar-Thailand-Malaysia are referred to *S. m. validus*. The external, cranial and dental dimensions are much larger than those from elsewhere in the species' range. Musser & Newcomb (1983) suggested that the differences were so great as to indicate possibly a specific difference. It should be noted that the smaller size of the holotype of *foederis* (BM.21.11.8.41) (Table 24) reflects the fact that it is a very young adult-juvenile (Guy Musser pers. comm.). Latinne et al. (2013b) suggested that there were two genetic lineages of *Sundamys* in Thailand but that the genetic distance was low (less than 2.5 %).

Distribution and conservation status. *Sundamys muelleri* has a range that extends from peninsular Myanmar, Thailand and Malaysia to Sumatra, Borneo, the Philippines and numerous Sundaic islands (Musser & Newcomb 1983). Its distribution is illustrated in Fig. 47.

Its conservation status is listed by IUCN as 'Least Concern' "in view of its wide distribution, presumed large population, it occurs in a number of protected areas, and because it is unlikely to be declining at nearly the rate required to qualify for listing in a threatened category" (Ruedas et al. 2008d).

Ecology and reproduction. *Sundamys muelleri* is essentially a nocturnal, terrestrial rodent although it can climb the branches of trees. It nests on the ground, usually near streams and is a good swimmer. In Malaysia, it favours low-lying land and valley bottoms in primary and tall secondary forest. It normally spends the day in one or more regularly used dens, under logs, in holes in the ground or under the roots of trees. It emerges in late afternoon or early evening, although occasionally it may be active in the middle of the day (Harrison 1957a, Medway 1969, Musser & Newcomb 1983). According Lim 1970, it is rarely found in lowland primary forest but is abundant in lowland disturbed primary and secondary forests and mangrove forests.

In peninsular Thailand, it was collected in primary forest at approximately 95 metres a.s.l. in Phatthalung Province; in evergreen forest at approximately 190 m. a.s.l. in Chumphon Province and at approximately 50 m. a.s.l. in Songkhla Provinc; and in secondary evergreen forest in Phetchaburi Province (UP unpublished data).

In general, it is a species of lowland forest that has rarely been encountered above 925 metres (3000 feet), although Yong (1969c) reports it from 985 metres (3200 feet) on Kedah Peak and Musser & Newcomb (1983) from 1075 metres (3500 feet) from Maxwell's Hill and Telom in Perak, Malaysia. Its diet consists of insects, fruits, leaves, shoots and other vegetable matter; also crabs, land snails,

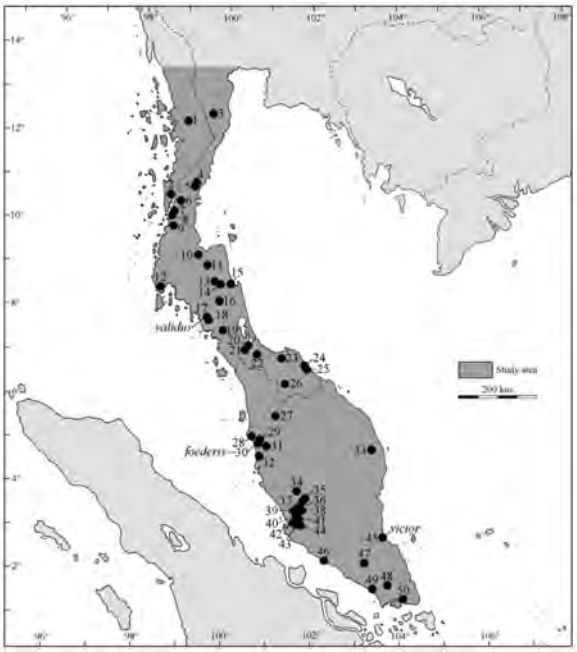

Fig. 47. Distribution of *Sundamys muelleri* in the Myanmar-Thai-Malaysian peninsula and Singapore. **Myanmar:** 1. Thagyet; 2. Maliwun. **Thailand:** 3. Pa La U; 4. Klong Bang Jai; 5. Ban Tha San; 6. Tasan; 7. Ban Bang Non; 8. Ranong; 9. Pa Toh Watershed Management; 10. Khao Nong; 11. Ban Plai Num; 12. Tang Pran; 13. Khao Luang; 14. Nam Tok Tha–Phae; 15. Nakhon Si Thammarat; 16. Khao Phu Khao Ya National Park; 17. Trang; 18. Ban Khao Chong; 19. Khow Sai Dow; 20. Nga Chang Waterfall; 21. Kuan Khao Wang Forest Park; 22. Khao Num Kang National Park; 23. Na Pra Du; 24. Ban Ya Kan; 25. Narathiwat; 26. Tonto Waterfall. **Malaysia:** 27. Temengoh; 28. Kuala Longnai; 29. Maxwell's Hill; 30. Ulu Temengor; 31. Telom; 32. Changkat Mentri; 33. Bukit Besi; 34. Semangko Pass; 35. Ulu Cemperoh; 36. Ginting Bidei; 37. Ulu Gombak; 38. Kampong Janda Baik; 39. Bukit Lanjang Forest Reserve; 40. Bukit Lagong; 41. Kepong; 42. Subang; 43. Kuala Lumpur; 44. Ulu Langat; 45. Rumpin River (near mouth of); 46. Malacca; 47. Sembrong / Sembrong River; 48. Kangka Kuli; 49. Tamok; 50. Kudong. Not located: Ka Kuli (poss. = 48). For full locality details, see Gazetteer and Appendix I.

and even a partially digested caecilian was found in the stomach of one specimen (Musser & Newcomb 1983). The young are born in nests built in sheltered positions. In Malaysia, pregnant females were recorded in all months but most frequently in the period July to September. Mean litter size was 3.8, with a range of 1 to 9) (Medway 1969).

GENERIC KEYS

In order to facilitate the correct identification of specimens to generic level, a range of characters, external, cranial, and dental has been incorporated into a matrix key (Tables 25A, B & C). Each character, where possible has been linked to a drawing or a photograph to help explain the feature being described. For external characters, a summary is provided in Figs 48, 49 and 50, with an additional set of colour photographs of the most common murine genera in the region included in Fig. 51. For the cranial and dental characters, reference is made to particular features illustrated in figures included in the main body of the paper. For measurements, the reader is guided to the relevant Tables.

The grouping of the genera corresponds to a group of four genera that are arboreal specialists, with complex dentition, which includes cusp t7 on the first upper molar (M^1) and feet adapted to climbing, most especially large plantar and digitial pads (Table 25A). The second group includes one mouse genus, *Mus,* and three of the generally smaller rats, although it is appreciated that some species (and/or individuals) of these 'smaller' rats, especially in the genus *Rattus* and to a lesser extent *Maxomys* can be large. The final grouping includes the large rats, *Leopoldamys, Berylmys, Bandicota* and *Sundamys.*

RECOMMENDATIONS

One of the primary objectives of the current study is to provide a summary of existing knowledge of murine rodents in the Myanmar-Thai-Malaysian peninsula and to highlight priorities, which would particularly benefit from further studies.

As is apparent from the paper, much previous taxonomic research of rodents in the study area was morphometric, whereas that conducted most recently is primarily genetics-based. As noted by a number of previous authors (Musser & Carleton 2005, Pagès et al. 2010, Chaval et al. 2010, Latinne et al. 2013b), it would be of considerable benefit to combine the two approaches to maximise the potential to determine phylogenies and resolve difficult taxonomic problems. In the broadest terms, priority genera for further taxonomic research include *Rattus*, *Niviventer* and *Maxomys.* Particular priorities within these taxa include:

Maxomys surifer, which as currently understood is considered to include 4 highly divergent genetic lineages (Latinne et al. 2013b) and is most probably a complex of cryptic species (Gorog et al. 2004, Aplin et al. 2008c, Achmadi et al. 2013);

Niviventer fulvescens, the taxonomy of which is still open to discussion (Musser & Carleton 2005, Pagès et al. 2010). Some authors recognise the peninsular form *bukit* as a discrete species (Corbet & Hill 1992, Balakirev et al. 2011) whilst others include this taxon in *fulvescens* (Abe 1983, Musser & Carleton 2005);

Rattus tanezumi and *R. tiomanicus*, which are probably complexes of morphologically cryptic species. Latinne et al. (2013b) recognised at least four distinct genetic lineages of *Rattus* in peninsular Thailand, the identifi-

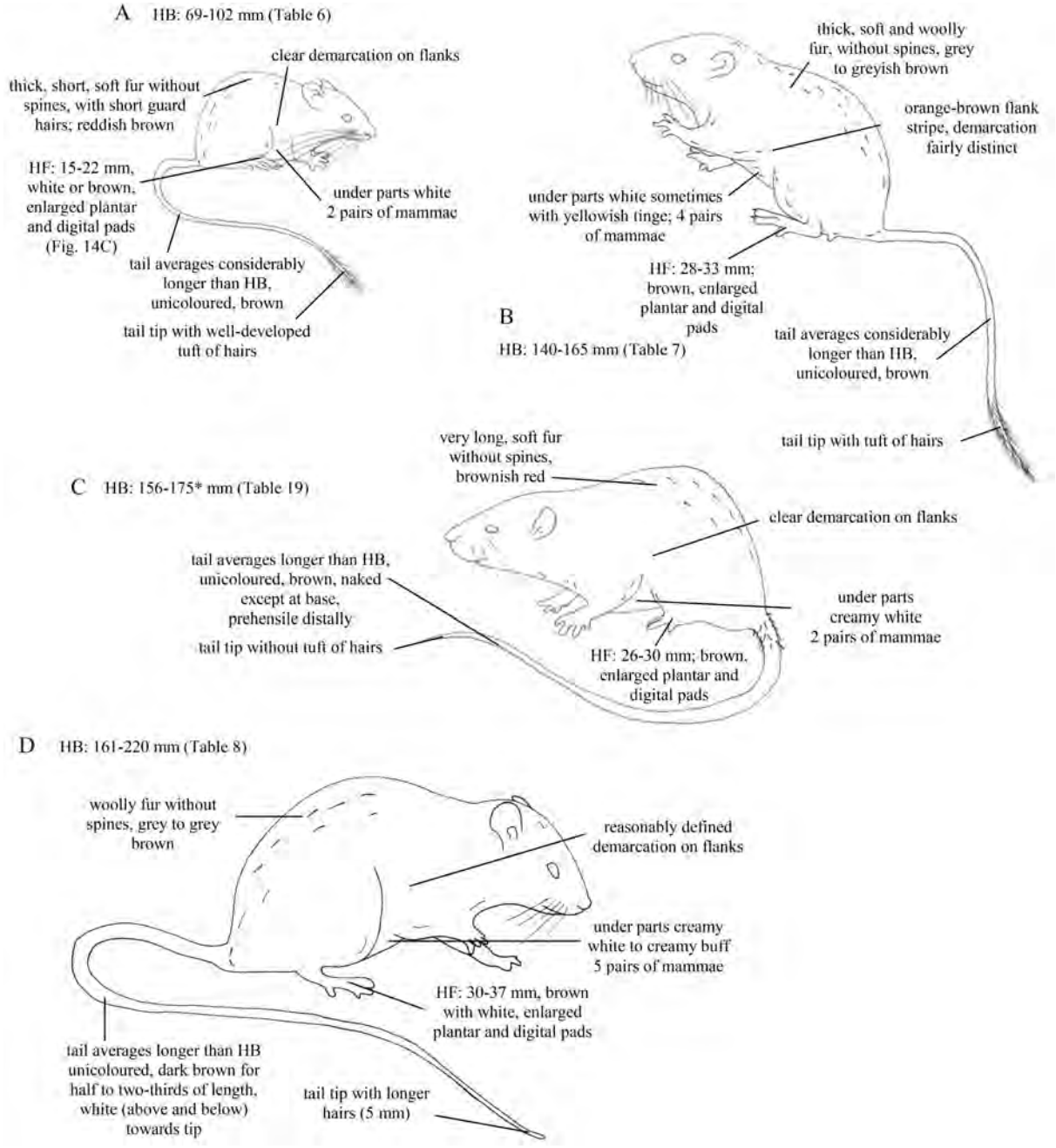

Fig. 48. External characters of four genera of murine rodents (A): *Chiropodomys*; (B): *Hapalomys*; (C): *Pithecheir*; (D): *Lenothrix.* Drawings based on Francis (2008). Size approximately proportional to all genera illustrated in Figs 48, 49, and 50. To be used in conjunction with the character matrix in Table 25A.

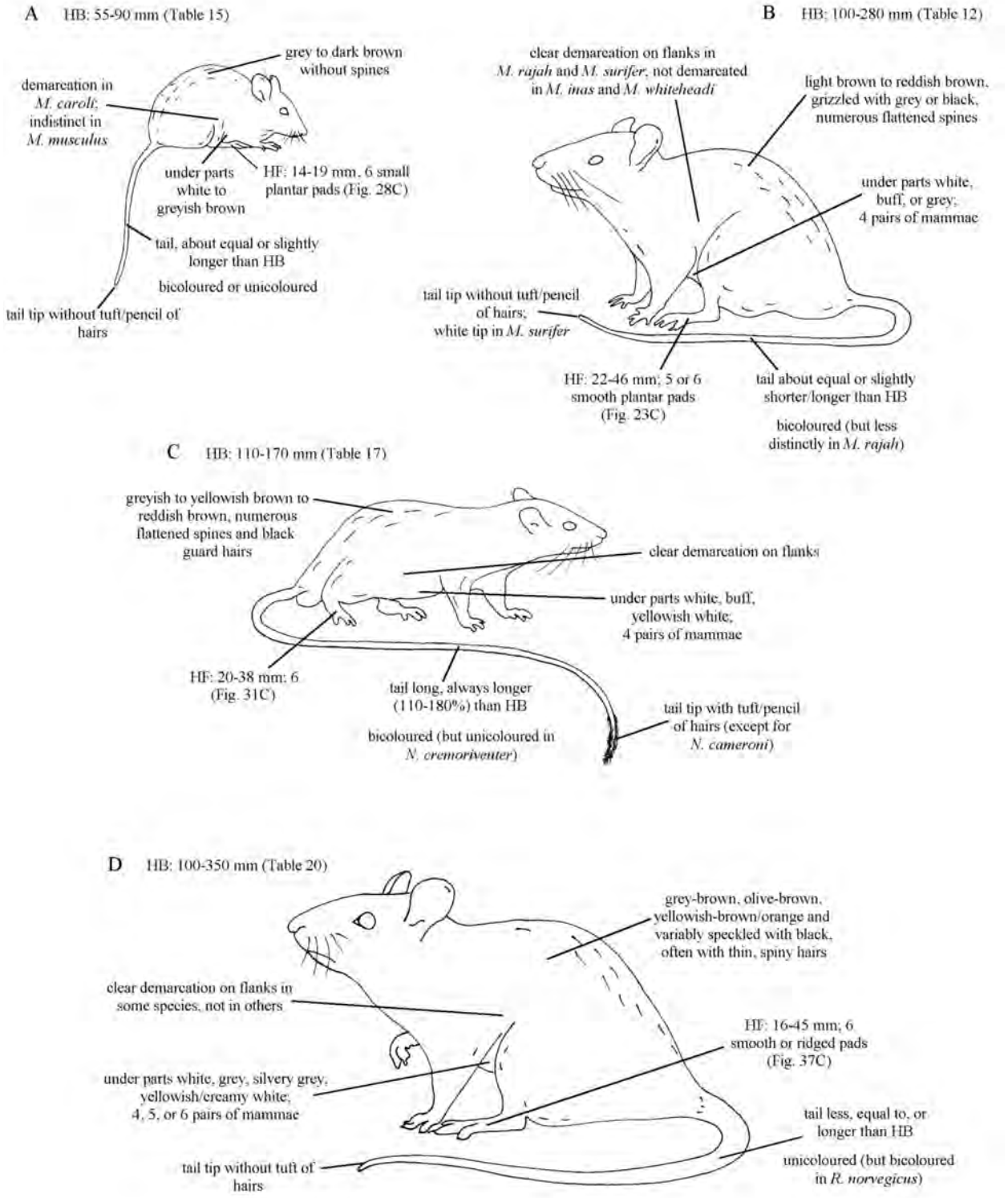

Fig. 49. External characters of four genera of murine rodents (A): Mus; (B); *Maxomys*; (C): *Niviventer*; (D): *Rattus*. Drawings based on Francis (2008). Size approximately proportional to all genera illustrated in Figs 48, 49, and 50. However, it should be noted that there is considerable variation in size between species, especially in *Rattus* and *Maxomys*. To be used in conjunction with the character matrix in Table 25B.

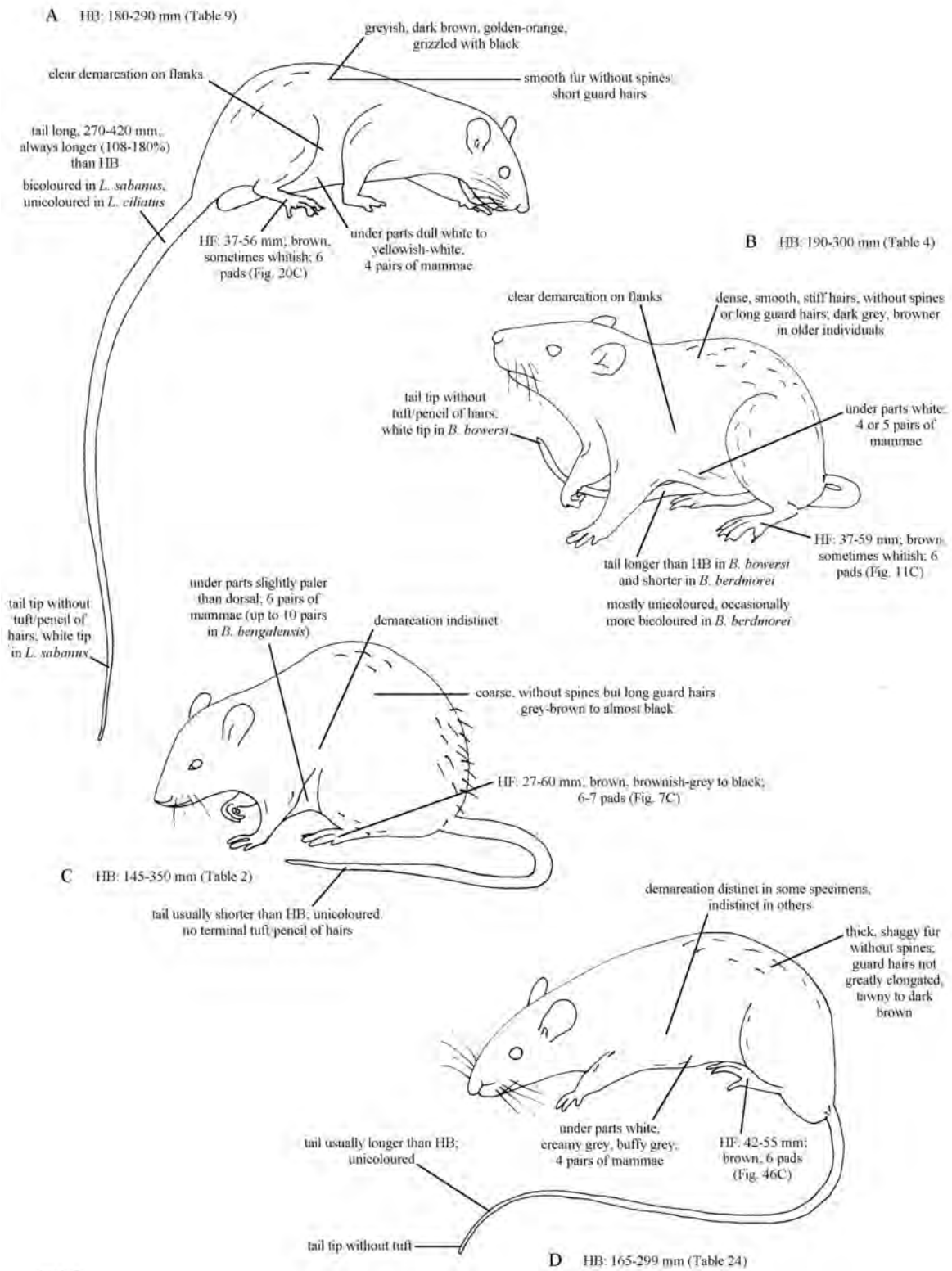

Fig. 50. External characters of four genera of murine rodents (A): *Leopoldamys*; (B): *Berylmys*; (C): *Bandicota*; (D): *Sundamys*. Drawings based on Francis (2008). Size approximately proportional to all genera illustrated in Figs 48, 49, and 50. However, it should be noted that there is considerable variation in size between species, especially in *Bandicota* and *Berylmys*. To be used in conjunction with the character matrix in Table 25C.

cation of which were not determined. Pagès et al. (2010) suggested further research incorporating molecular data from the holotypes of the different *Rattus* taxa, especially the numerous synonyms, would be the most suitable way to determine accurately the taxonomy of this genus in Southeast Asia. Aplin et al. (2011) noted that more research was required to determine the true phylogeny of the *R. rattus-R. tanezumi* species complex.

Outside these 'problem genera', there are also other interesting, unresolved taxonomic ambiguities:

Berylmys berdmorei and especially its relationship to the taxon *mullulus*. In general, the geographical variation of *B. berdmorei* from throughout its range is little understood (Musser & Newcomb 1983);

Berylmys bowersi; Musser & Newcomb (1983) noted differences in cranial morphology between Indochinese and Sundaic populations. This observation was supported by both Pagès et al. (2010) and Latinne et al. (2013b) who recognised two distinct genetic lineages, one from northern Thailand and one from Kanchanaburi Province and peninsular Thailand;

Leopoldamys sabanus, which may be a species complex. Musser (1981) and Musser & Carleton (2005) remarked on the considerable morphological variation between populations of *L. sabanus* from the Indochinese and Sundaic subregions and among insular populations from the Sundaic subregion. Subsequently, Latinne et al. (2013b) suggested that *L. sabanus (*sensu stricto) is essentially confined to the Sundaic subregion whilst Balakirev et al. (2013) restricted *L. sabanus* to Borneo and referred specimens from peninsular Thailand-Malaysia to *L. vociferans*.

In terms of conservation, there are a number of taxa that require extensive further research. Much of this is ecological, determining the reliance of a particular species on a particular habitat type. Other studies need to focus on population status and determine existing and potential threats. Species of special interest include:

Hapalomys longicaudatus, which is listed as 'Endangered' by IUCN and is thought to be possibly extinct in Thailand and Myanmar (Aplin & Lunde 2008a). A high priority is to determine its distribution and population status in the remaining areas of undisturbed bamboo habitat within evergreen lowland forest;

Maxomys rajah and *M. whiteheadi*, both of which are listed as 'Vulnerable' by IUCN. Both are thought to be at risk because of the extensive loss and degradation of lowland forest, which is believed to be their favoured habitat (Aplin et al. 2008e). Currently, data on their ecology and behaviour are very limited and much further study is required;

Niviventer cameroni is a montane species, endemic to the Cameron Highlands of peninsular Malaysia. Listed as 'Vulnerable' by IUCN, it is thought to be threatened by habitat loss but currently very little known about its ecology (Musser & Ruedas 2008);

Niviventer cremoriventer is another 'Vulnerable' species, whose ecology, population status and behaviour has been little researched (Ruedas et al. 2008e);

Pithecheir parvus is listed as 'Data Deficient' by IUCN (Aplin et al. 2008h). Further study is needed to determine the habitat preferences of this species in order to support the findings of Muul & Lim (1971) that this species is found in both secondary and pristine forest.

In terms of ecology and reproductive biology, little is known about *Bandicota savilei, Berylmys berdmorei*, or *Lenothrix canus* in the study area. In addition, studies focusing on zoogeography and phylogeography would be of considerable interest.

Finally, rodents are frequently regarded by man in a negative context. It would therefore be of great value to undertake some detailed research of the ecosystem services provided by this diverse, adaptable and often abundant group of small mammals.

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Fig. 51. Seven common murine genera in peninsular Myanmar-Thai-Malaysia. (A): *Maxomys* (*M. surifer*); (B): *Niviventer* (*N. cremoriventer*); (C): *Rattus* (*R. tanezumi*); (D): *Leopoldamys* (*L. sabanus*); (E): *Berylmys* (*B. bowersi*); (F): *Bandicota* (*B. indica*); (G): *Sundamys* (*S. muelleri*). Not to scale.

Table 1. A list, in chronological order, of the 95 taxa of murine rodent described from the Myanmar-Thai-Malaysian peninsula and Singapore. Taxa in bold are currently recognised as distinct species (Musser & Carleton 2005).

	Year	Author, date	Taxon	Current species (Musser & Carleton 2005)	Country of type locality	Type locality on map
1	1851	Blyth 1851	***Mus berdmorei***	***Berylmys berdmorei***	Myanmar	Fig. 12, loc. 2
2	1865	Cantor in Blyth 1865	*Mus rama*	*Mus musculus*	Malaysia	Fig. 30, loc. 2
3	1868	Peters 1868	*Chiropodomys penicillatus*	*Chiropodomys gliroides*	Malaysia	Fig. 15, loc. 8
4	1900	Miller 1900a	***Mus tiomanicus***	***Rattus tiomanicus***	Malaysia	Fig. 45, loc. 34
5	1900	Miller 1900a	*Mus obscurus* = *M. pullus* Miller 1901	*Rattus exulans*	Malaysia	Fig. 41, loc. 24
6	1900	Miller 1900b	***Mus cremoriventer***	***Niviventer cremoriventer***	Thailand	Fig. 33, loc. 8
7	1900	Miller 1900b	***Mus surifer***	***Maxomys surifer***	Thailand	Fig. 23, loc. 50
8	1900	Miller 1900b	*Mus vociferans*	*Leopoldamys sabanus*	Thailand	Fig. 22, loc. 34
9	1900	Miller 1900b	*Mus ferreocanus*	*Berylmys bowersii*	Thailand	Fig. 13, loc. 6
10	1900	Miller 1900b	*Mus validus*	*Sundamys muelleri*	Thailand	Fig. 47, loc. 17
11	1900	Miller 1900b	*Mus asper*	*Maxomys whiteheadi*	Thailand	Fig. 27, loc. 5
12	1900	Miller 1900b	*Mus pellax*	*Maxomys rajah*	Thailand	Fig. 25, loc. 4
13	1900	Miller 1900c	*Mus vociferans lancavensis*	*Leopoldamys sabanus*	Malaysia	Fig. 22, loc. 40
14	1900	Miller 1900c	*Mus surifer flavidulus*	*Maxomys surifer*	Malaysia	Fig. 23, loc. 69
15	1900	Miller 1900c	*Mus surifer butangensis*	*Maxomys surifer*	Thailand	Fig. 23, loc. 61
16	1900	Miller 1900c	*Mus pannosus*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 67
17	1900	Bonhote 1900	***Mus ciliata***	***Leopoldamys ciliatus***	Malaysia	Fig. 21, loc. 2
18	1903	Miller 1903a	*Mus stridens*	*Leopoldamys sabanus*	Malaysia	Fig. 22, loc. 71
19	1903	Miller 1903a	*Mus matthaeus*	*Leopoldamys sabanus*	Myanmar	Fig. 22, loc. 14
20	1903	Miller 1903a	*Mus stridulus*	*Leopoldamys sabanus*	Myanmar	Fig. 22, loc. 4
21	1903	Miller 1903a	*Mus lucas*	*Leopoldamys sabanus*	Myanmar	Fig. 22, loc. 12
22	1903	Miller 1903a	*Mus gilbiventer*	*Niviventer cremoriventer*	Myanmar	Fig. 33, loc. 1
23	1903	Miller 1903a	*Mus luteolus*	*Maxomys surifer*	Myanmar	Fig. 23, loc. 17
24	1903	Miller 1903a	*Mus umbridorsum*	*Maxomys surifer*	Myanmar	Fig. 23, loc. 12
25	1903	Miller 1903a	*Mus casensis*	*Maxomys surifer*	Myanmar	Fig. 23, loc. 29
26	1903	Miller 1903a	*Mus bentincanus*	*Maxomys surifer*	Myanmar	Fig. 23, loc. 7
27	1903	Miller 1903a	*Mus domelicus*	*Maxomys surifer*	Myanmar	Fig. 23, loc. 9
28	1903	Bonhote 1903b	*Mus bukit*	*Niviventer fulvescens*	Malaysia	Fig. 34, loc. 28
29	1903	Bonhote 1903a	***Mus annandalei***	***Rattus annandalei***	Malaysia	Fig. 39, loc. 4
30	1903	Bonhote 1903a	*Mus jalorensis*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 8
31	1903	Bonhote 1903a	*Mus griseiventer*	*Rattus tanezumi*	Malaysia	Fig. 44, loc. 89
32	1905	Bonhote 1905	*Mus jarak*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 25
33	1906	Bonhote 1906	***Mus inas***	***Maxomys inas***	Malaysia	Fig. 24, loc. 1
34	1906	Bonhote 1906	*Mus klossi*	*Maxomys whiteheadi*	Malaysia	Fig. 27, loc. 36
35	1907	Thomas 1907	*Gunomys varillus*	*Bandicota bengalensis*	Malaysia	Fig. 8, loc. 2
36	1907	Thomas 1907	*Gunomys varius*	*Bandicota bengalensis*	Malaysia	Fig. 8, loc. 2
37	1908	Kloss 1908a	*Mus villosus*	*Rattus annandalei*	Singapore	Fig. 39, loc. 16
38	1908	Kloss 1908a	*Mus surifer microdon* = *Epimys s. binominatus* Kloss 1915	*Maxomys surifer*	Malaysia	Fig. 23, loc. 94
39	1909	Thomas & Wroughton 1909	*Mus vociferans tersus*	*Leopoldamys sabanus*	Thailand	Fig. 22, loc. 36
40	1911	Kloss 1911a	*Mus surifer flavigrandis*	*Maxomys surifer*	Malaysia	Fig. 23, loc. 73
41	1911	Kloss 1911a	*Mus surifer grandis*	*Maxomys surifer*	Malaysia	Fig. 23, loc. 74
42	1911	Robinson & Kloss 1911a	*Mus rattus rumpia*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 24
43	1911	Robinson & Kloss 1911a	*Mus surifer leonis*	*Maxomys surifer*	Singapore	Fig. 23, loc. 105
44	1911	Robinson & Kloss 1911b	*Mus muelleri foederis*	*Sundamys muelleri*	Malaysia	Fig. 47, loc. 30
45	1912	Robinson 1912	*Epimys surifer pemangilis*	*Maxomys surifer*	Malaysia	Fig. 23, loc. 95
46	1912	Robinson 1912	*Epimys surifer aoris*	*Maxomys surifer*	Malaysia	Fig. 23, loc. 97
47	1913	Miller 1913	*Epimys stentor*	*Leopoldamys sabanus*	Myanmar	Fig. 22, loc. 10
48	1913	Miller 1913	*Epimys vociferans insularum*	*Leopoldamys sabanus*	Myanmar	Fig. 22, loc. 6
49	1913	Miller 1913	*Epimys vociferans clarae*	*Leopoldamys sabanus*	Myanmar	Fig. 22, loc. 8
50	1913	Miller 1913	*Rattus rattus fortunatus*	*Rattus tanezumi*	Myanmar	Fig. 44, loc. 32
51	1913	Miller 1913	*Rattus rattus exsul*	*Rattus tanezumi*	Myanmar	Fig. 44, loc. 13
52	1913	Miller 1913	*Rattus rattus insulanus*	*Rattus tanezumi*	Myanmar	Fig. 44, loc. 11
53	1913	Miller 1913	*Rattus rattus dentatus*	*Rattus tanezumi*	Myanmar	Fig. 44, loc. 18
54	1913	Miller 1913	*Epimys lepidus*	*Niviventer fulvescens*	Myanmar	Fig. 34, loc. 1
55	1913	Miller 1913	*Epimys solus*	*Niviventer cremoriventer*	Thailand	Fig. 33, loc. 14
56	1913	Miller 1913	*Epimys pannellus*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 66
57	1913	Miller 1913	*Epimy rattus viclana*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 10
58	1913	Miller 1913	*Epimys roa*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 37
59	1913	Miller 1913	*Epimys tingius*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 38
60	1913	Miller 1913	*Rattus victor*	*Sundamys muelleri*	Malaysia	Fig. 47, loc. 45
61	1914	Robinson & Kloss 1914	*Epimys jerdoni pan*	*Niviventer fulvescens*	Thailand	Fig. 34, loc. 7
62	1914	Robinson & Kloss 1914	*Epimys surifer manicalis*	*Maxomys surifer*	Thailand	Fig. 23, loc. 27
63	1914	Robinson & Kloss 1914	*Epimys surifer spurcus*	*Maxomys surifer*	Thailand	Fig. 23, loc. 31
64	1914	Robinson & Kloss 1914	*Epimys remotus*	*Rattus andamanensis*	Thailand	Fig. 38, loc. 5
65	1914	Robinson & Kloss 1914	*Epimys orbus*	*Niviventer fulvescens*	Malaysia	Fig. 34, loc. 9
66	1916	Kloss 1916b	***Pithecheirus melanurus parvus***	***Pithecheir parvus***	Malaysia	Fig. 36, loc. 2

	Year	Author, date	Taxon	Current species (Musser & Carleton 2005)	Country of type locality	Type locality on map
67	1916	Kloss 1916c	*Epimys surifer eclipsis*	*Maxomys surifer*	Thailand	Fig. 23, loc. 42
68	1919	Hinton 1919	*Rattus rattus tikos*	*Rattus tanezumi*	Myanmar	Fig. 44, loc. 6
69	1931	Chasen & Kloss 1931	*Rattus rattus payanus*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 12
70	1931	Kloss 1931	*Rattus canus malaisia*	*Lenothrix canus*	Malaysia	Fig. 19, loc. 13
71	1937	Chasen 1937	*Rattus rattus panjius*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 46
72	1937	Chasen 1937	*Rattus rattus alangensis*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 49
73	1937	Chasen 1937	*Rattus rattus lontaris*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 60
74	1937	Chasen 1937	*Rattus rattus kadanus*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 62
75	1937	Chasen 1937	*Rattus rattus moheius*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 63
76	1937	Chasen 1937	*Rattus rattus pipidonis*	*Rattus tanezumi*	Thailand	Fig. 44, loc. 51
77	1940	Chasen 1940	***Rattus rapit cameroni***	***Niviventer cameroni***	Malaysia	Fig. 32, loc. 1
78	1940	Chasen 1940	*Rattus rattus robinsoni*	*Rattus tanezumi*	Malaysia	Fig. 44, loc. 37
79	1940	Chasen 1940	*Rattus rattus perhentianus*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 16
80	1940	Chasen 1940	*Rattus rattus pemanggis*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 35
81	1940	Chasen 1940	*Rattus sabanus dictatorius*	*Leopoldamys sabanus*	Malaysia	Fig. 22, loc. 43
82	1940	Chasen 1940	*Rattus sabanus salanga*	*Leopoldamys sabanus*	Thailand	Fig. 22, loc. 28
83	1940	Chasen 1940	*Rattus surifer puket*	*Maxomys surifer*	Thailand	Fig. 23, loc. 45
84	1940	Chasen 1940	*Rattus surifer telibon*	*Maxomys surifer*	Thailand	Fig. 23, loc. 54
85	1940	Chasen 1940	*Rattus surifer muntia*	*Maxomys surifer*	Thailand	Fig. 23, loc. 52
86	1940	Chasen 1940	*Rattus surifer pidonis*	*Maxomys surifer*	Thailand	Fig. 23, loc. 48
87	1941	Sody 1941	*Rattus rattus chaseni*	*Rattus argentiventer*	Malaysia	Fig. 40, loc. 19
88	1960	Hill 1960	*Rattus rattus pharus*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 39
89	1960	Hill 1960	*Rattus rattus sribuatensis*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 33
90	1960	Hill 1960	*Rattus rattus kabanicus*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 32
91	1960	Hill 1960	*Rattus rattus terutavensis*	*Rattus tiomanicus*	Thailand	Fig. 45, loc. 7
92	1971	Yong 1971	*Rattus tiomanicus tenggolensis*	*Rattus tiomanicus*	Malaysia	Fig. 45, loc. 19
93	1989	Boonsong & Felten 1989	*Bandicota bangchakensis*	*Bandicota savilei*	Thailand	Fig. 10, loc. 4

Table 2. External, cranial and dental measurements of *Bandicota*. Measurements sourced from: [i] Musser & Brothers (1994); [ii] Chasen (1936: Chasen selected the 'five largest specimens' available to him) and [iii] Pimsai (2012).

HB	Tail	(Tail/HB)%	HF	GLS	ONL	ZB	LN	LD	LIF	BBPM^3	LB	ALM^1-M^3
						B. bengalensis **(West Bengal, India) [i]**						
185.1 ± 9.70 (161-208) 39	143.3 ± 9.70 (112-163) 35	77%	33.3 ± 1.80 (27-38) 39	39.8 ± 1.59 (36.0-43.9) 37	37.8 ± 1.56 (33.4-41.3) 37	22.4 ± 0.90 (20.6-25.2) 37	11.8 ± 0.70 (9.8-13.3) 38	12.2 ± 0.81 (10.5-13.8) 38	8.1 ± 0.46 (7.0-9.3) 29	3.9 ± 0.31 (3.3-4.8) 40	8.1 ± 0.44 (7.3-9.0) 38	7.2 ± 0.39 (6.6-8.3) 39
						(Penang, Malaysia) [ii]						
222.0 ± 12.63 (210-243) 5	173.2 ± 10.45 (160-188) 5	78.0% ± 3.16 (73-81) 5	35.6 ± 1.34 (34-37) 5	47.2 ± 1.10 (46.0-48.5) 5	*	26.3 ± 0.88 (25.2-27.2) 5	*	14.9 ± 0.33 (14.5-15.3) 5	8.7 ± 0.39 (8.1-9.1) 5	*	*	8.1 ± 0.24 (7.9-8.5) 5
						B. indica **(Thailand & Vietnam) [i]**						
255.8 ± 30.6 (188-328) 32	229.7 ± 21.8 (190-280) 32	90%	53.0 ± 3.6 (46-60) 34	56.8 ± 3.1 (49.0-64.2) 30	56.6 ± 3.3 (49.0-64.2) 30	30.2 ± 2.1 (26.1-33.6) 32	20.5 ± 2.0 (17.0-24.3) 32	17.1 ± 1.5 (14.6-20.1) 35	10.3 ± 0.7 (8.8-11.5) 35	5.8 ± 0.6 (4.2-6.9) 35	10.4 ± 0.6 (9.3-12.2) 34	11.5 ± 0.4 (10.7-12.4) 36
						(Thailand) [iii]						
266.1 ± 28.5 (230-350) 17	232.4 ± 29.3 (146-275) 17	87.3% (56-109%) 17	53.4 ± 4.7 (42-60) 17	58.0 ± 2.59 (54.1-63.4) 19	*	30.7 ± 1.57 (27.3-32.9) 20	21.3 ± 1.51 (18.6-24.2) 20	18.0 ± 1.26 (15.3-21.2) 20	10.1 ± 0.53 (9.4-11.2) 20	*	10.0 ± 0.60 (8.6-11.0) 19	11.1 ± 0.54 (10.2-12.1) 20
						B. savilei **Thailand) [i]**						
194.8 ± 16.60 (145-225) 33	156.4 ± 18.75 (75-178) 32	80%	37.4 ± 1.70 (33-40) 33	44.9 ± 1.96 (41.8-50.1) 29	44.9 ± 1.88 (42.0-47.8) 32	24.6 ± 1.04 (22.4-26.5) 31	15.5 ± 0.98 (13.8-17.6) 32	13.1 ± 1.04 (11.5-15.5) 33	8.1 ± 0.53 (7.3-9.5) 33	4.7 ± 0.35 (4.0-5.4) 33	8.9 ± 0.34 (8.1-9.5) 33	9.2 ± 0.29 (8.6-9.7) 33
						(holotype of *bangchakensis*) [i]						
*	*	*	*	49.2	49.2	27.1	17.5	15.6	9.2	4.3	10.2	8.7

Table 3. Matrix key to the three species of *Bandicota* currently known from the Myanmar-Thai-Malaysian peninsula.

Size (Table 2)	Tail/ Dorsal pelage	Mammae	Skull	Teeth
		Bandicota bengalensis		
Extralimitally the smallest species. However, specimens from Penang can be quite large. Hind foot: 27-38 mm	Tail shorter, 112-188 mm, averages 78% of head and body length; 10-12 rows of scales/cm. Dorsal pelage coarse, admixture black and cream-buff, without brown tints in specimens from Penang (browner elsewhere)	10-20 (most frequently between 14-17)	Skull medium (36.0-48.5 mm). Nasals short, when viewed from above do not cover incisors; posterolateral surface of the supraoccipital (Fig. 7Axvi) is greatly reduced	Upper toothrow: 6.6-8.5 mm. Upper incisors procumbent (Fig. 7Dxxiv). Posterior cingulum absent on M_1 and M_2
		Bandicota indica		
Largest species (external and cranial); hind feet long: 42-60 mm	Tail relatively long, 146-280 mm, averages 88% of head and body length; 8 rows of scales/cm. Dorsal pelage coarse, dark, blackish-brown	12 (6 pairs)	Skull large (49.0-64.2 mm). Nasals long, when viewed from above they cover incisors; posterolateral surface of the supraoccipital (Fig. 7Axvi) not greatly reduced	Upper toothrow: 10.2-12.4 mm. Upper incisors opisthodont (Fig. 7Axv). Posterior cingulum (Fig. 6Bq & v) present on M_1 and M_2
		Bandicota savilei		
Extralimitally intermediate in size between *B. bengalensis* and *B. indica;* hind feet: 33-40 mm	Tail shorter, 75-178 mm, averages 80% of head and body length; 10-12 rows of scales/cm. Dorsal pelage softer, paler, brownish	12 (6 pairs)	Skull medium (41.8-50.1 mm). Nasals long, when viewed from above they cover incisors; posterolateral surface of the supraoccipital (Fig. 7Axvi) not greatly reduced	Upper toothrow: 8.6-9.7 mm. Upper incisors opisthodont. Posterior cingulum present on M_1 and M_2

Table 4. External, cranial and dental measurements of *Berylmys*. Measurements sourced from: [i] Musser & Newcomb (1983), [ii] Pimsai (2012) and [iii] Miller (1900b).

HB	Tail	(Tail/HB)%	HF	GLS	ZB	LN	LD	LIF	BBPM^3	LB	ALM^1-M^3
					Berylmys berdmorei (SE Thailand) [i]						
216.6 ± 22.9 (190-225) 9	170.9 ± 13.2 (149-192)	79%	39.8 ± 2.8 (37-46) 9	44.5 ± 3.4 (38.0-50.3) 9	23.6 ± 1.1 (21.8-25.8) 10	18.7 ± 1.3 (16.4-20.8) 9	14.8 ± 1.0 (13.5-16.8) 10	8.4 ± 0.7 (7.2-9.7) 10	4.9 ± 0.4 (4.5-5.8) 10	9.0 ± 0.4 (8.4-9.6) 10	7.2 ± 0.3 (6.9-7.8) 10
					(holotype of *mullulus*) [i]						
*	*	*	*	39.0	21.3	*	12.6	7.7	4.5	7.1	6.6
					Berylmys bowersi (peninsular Thailand & Malaysia) [i]						
264.2 ± 18.6 (230-300) 24	283.3 ± 11.5 (262-300) 24	107%	55.0 ± 1.80 (52-59) 24	57.7 ± 2.5 (52.0-63.1) 27	27.0 ± 1.2 (24.4-28.4) 27	24.9 ± 1.4 (22.0-28.7) 27	17.6 ± 1.1 (15.4-19.9) 27	10.4 ± 0.5 (9.6-11.3) 27	5.9 ± 0.4 (5.1-6.6) 27	7.0 ± 0.3 (6.2-7.3) 27	9.8 ± 0.4 (9.1-10.5) 27
					(Thailand) [ii]						
256.2 ± 18.4 (235-269) 3	270.7 ± 14.3 (255-283) 3	106% (96-117%) 3	55.5 ± 0.6 (55-56) 4	55.1 ± 3.5 (50.0-57.5) 4	27.82 ± 1.8 (25.4-29.8) 4	22.3 ± 2.0 (19.5-23.8) 4	16.5 ± 1.6 (14.1-17.5) 4	9.9 ± 1.2 (8.3-11.2) 4	*	7.3 ± 0.2 (7.1-7.6) 4	9.3 ± 0.6 (8.7-10.0) 4
					(holotype of *ferreocanus* with one additional specimens from type locality for external measurements) [iii]						
238, 241	251, 260	106%	53, 53	53.6	25.4	22.6	15.8	9.4	*	*	9.4

Table 5. Matrix key to the two species of *Berylmys* currently known from the Myanmar-Thai-Malaysian peninsula.

Size (Table 4)/ Dorsal pelage	Tail	Mammae	Skull	Upper incisors
		Berylmys berdmorei		
Smaller: HB: 190-255 mm. HF: 37-46 mm. Steel-grey fur	149-192 mm always shorter (mean = 79%) than head and body length; tail without white tip	5 pairs	Smaller: GLS: 38.0-50.3 mm Upper toothrow: 6.6-7.8 mm	Slightly procumbent
		Berylmys bowersi		
Larger: HB: 230-300 mm. HF: 52-59 mm. Brownish grey to dull-tan fur	251-300 mm averages longer (mean = 107%) than head and body length; well developed white tip	4 pairs	Larger: GLS: 50.0-63.1 mm Upper toothrow: 8.7-10.5 mm	Orthodont

Table 6. External, cranial and dental measurements of *Chiropodomys gliroides*. Measurements sourced from: [i] Musser (1979) and [ii] Pimsai (2012).

HB	Tail	(Tail/HB)%	HF	ONL	ZB	LN	LD	LIF	BBPM³	LB	ALM¹-M³
					Chiropodomys gliroides from peninsular Malaysia [i]						
86.2 ± 7.4 (69-102) 57	116.0 ± 10.1 (94-143) 57	135%	18.8 ± 1.6 (15-22) 57	25.4 ± 0.8 (24.0-26.7) 23	14.6 ± 0.8 (13.7-15.5) 23	8.2 ± 0.6 (7.0-9.4) 23	6.9 ± 0.3 (6.4-7.4) 23	3.6 ± 0.3 (3.0-4.2) 23	3.1 ± 0.2 (2.8-3.4) 10	3.4 ± 0.2 (2.6-3.3) 23	3.8 ± 0.2 (3.3-4.2) 23
					Thailand [ii]						
81.0 (77, 85) 2	111.0 (105, 117) 2	137%	19.0 (18, 20) 2	24.5 ± 0.3 (24.2-24.9) 3	14.4 ± 0.3 (14.1-14.6) 3	7.3 ± 0.3 (7.0-7.5) 3	6.6 ± 0.2 (6.5-6.8) 3	3.9 ± 0.2 (3.8-4.1) 3	*	3.9 ± 0.4 (3.6-4.3) 3	3.9 ± 0.1 (3.9-4.0) 3

Table 7. External, cranial and dental measurements of *Hapalomys longicaudatus*. Measurements sourced from: [i] Musser (1972) and [ii] Musser & Newcomb (1983).

HB	Tail	(Tail/HB)%	HF	GLS/ONL	ZB	LN	LD	LIF	BBPM¹	LB	ALM¹-M³
					Hapalomys longicaudatus from peninsular Malaysia [i and ii]						
156.6 ± 9.7 (140-165) 7	195.3 ± 9.3 (176-203) 7	125%	30.0 ± 1.9 (28-33) 7	39.3 ± 1.5 (37.9-41.5) 7	21.0 (20.0-22.0) 5	12.2 (11.5-12.6) 6	10.1 (9.1-10.9) 6	6.4 (6.2-6.8) 5	2.2 (2.2-2.3) 10	8.3 ± 0.3 (7.8-8.6) 7	7.8 ± 0.2 (7.6-8.0) 9

Table 8. External, cranial and dental measurements of *Lenothrix canus*. Measurements sourced from: [i] Musser & Newcomb (1983), [ii] Kloss (1931) and [iii] Muul & Lim (1971).

HB	Tail	(Tail/HB)%	HF	GLS/ONL	ZB	LN	LIF	LB	ALM¹-M³
				Lenothrix canus [i]					
200.2 ± 13.6 (161-215) 19	241.2 ± 20.7 (190-270) 17	120%	35.2 ± 1.4 (33-37) 19	45.9 ± 1.1 (43.8-48.4) 19	*	*	*	6.0 ± 0.3 (5.5-6.4) 18	8.8 ± 0.3 (8.4-9.3) 19
				(holotype of *malaisia*) [ii]					
190	215	113%	35	43.9	23.5	15.0	6.0	*	8.1
				(Malaysia) [iii]					
(165-220)	(200-265)	*	(30-37)	*	*	*	*	*	*

Table 9. External, cranial and dental measurements of *Leopoldamys*. Measurements sourced from: [i] Yong (1970), [ii] Medway (1969), [iii] Bonhote (1900), [iv] Pimsai (2012) and [v] Miller (1900b).

HB	Tail	(Tail/HB)%	HF	GLS/ONL	ZB	LN	LIF	LB	ALM¹-M³
				Leopoldamys ciliatus from peninsular Malaysia [i]					
251.2 ± 2.3 (200-275) 22	334.6 ± 4.5 (310-355) 22	134.2% ± 1.6 (124-144%) 22	53.2 ± 0.4 (51-56) 22	58.3 ± 0.6 (54.3-62.6) 17	*	*	*	5.4 ± 0.1 (5.0-5.6) 17	10.2 ± 0.1 (9.6-10.7) 17
				(peninsular Malaysia) [i]					
251.2 ± 2.8 (200-275) 22	334.6 ± 4.5 (310-355) 22	133%	53.2 ± 0.4 (51-56) 22	58.3 ± 0.6 (54.3-62.6) 17	*	*	*	5.4 ± 0.1 (5.0-5.6) 17	10.2 ± 0.1 (9.6-10.7) 17
				(peninsular Malaysia) [ii]					
215-256	300-390	120-165%	45-55	*	*	*	*	*	*
				(holotype of *ciliatus*) [iii]					
290	315	108%	47	57.0	*	21.5	*	*	*
				Leopoldamys sabanus from Thailand [iv]					
224.6 ± 16.1 (190-252) 14	328.5 ± 19.5 (295-362) 14	146%	44.2 ± 3.8 (37-51) 14	55.6 ± 2.5 (51.0-61.3) 16	24.5 ± 0.9 (22.8-26.3) 16	21.7 ± 1.1 (19.8-23.6) 17	7.5 ± 0.6 (6.2-8.6) 16	5.6 ± 0.3 (5.2-6.2) 14	9.7 ± 0.6 (8.7-10.8) 16
				(specimens from Trang, Thailand referred to *vociferans* including the holotype) [v]					
224 (216-229) 7	342 (323-380) 7	153%	43 (40-46)	56.0	25.8	21.4	8.0	*	11.8
				(peninsular Malaysia) [i]					
240.4 ± 1.8 (210-260) 50	369.1 ± 3.1 (315-420) 50	154%	47.8 ± 0.3 (44-52) 50	55.5 ± 0.6 (51.4-60.3) 21	*	*	*	5.1 ± 0.1 (4.7-5.6) 21	9.6 ± 0.1 (8.7-10.3) 21
				(peninsular Malaysia) [ii]					
180-255	270-415	122-182%	42-50	*	*	*	*	*	*

Table 10. Matrix key to the two species of *Leopoldamys* (sensu Musser & Carleton 2005) currently known from the Myanmar-Thai-Malaysian peninsula.

Size (Tables 9 and 11) / Colour of pelage on flanks & underparts	Tail	Supraorbital bristles	Hind feet	Skull
		Leopoldamys ciliatus		
Large: HB: 200-290 mm. Flanks are fawn (light yellowish-brown) to dull brown; underparts are yellowish-white, often with a dark median patch	Usually unicoloured, brown above and below	>70 mm in length	Average longer: 45-56 mm	GLS: 54.3-62.6 mm Upper toothrow: 9.6-10.7 mm
		Leopoldamys sabanus		
Large: HB: 190-290 mm. Flanks are chestnut (reddish brown); underparts are yellowish-white without a dark median patch	Usually bicoloured, darker above and paler below and with a pale (white) tip	about 40 mm in length	Average shorter: 37-52 mm	GLS: 51.0-61.3 mm Upper toothrow: 8.7-11.8 mm

Table 11. External, cranial and dental measurements of *Leopoldamys sabanus* (sensu Musser & Carleton 2005) from a range of localities (see Fig. 22) in Myanmar, Thailand and Malaysia. Measurements sourced from [i] Miller (1903a), [ii] Hill (1960), [iii] Miller (1913), and [iv] Chasen (1940).

	HB	Tail	(Tail/HB)%	GLS	CBL	ALM^1-M^3
stridulus (Bentinck Island, Myanmar) [i]	222	292	132%	52.0	*	*
insularum (Domel Island, Myanmar) [ii]	248	330	133%	53.7	50.1	9.7
clarae (Clara Island, Myanmar) [ii]	235	316	135%	52.1	48.1	9.6
stentor (James Island, Myanmar) [ii]	262	323	123%	56.8	53.6	9.7
lucas (St Luke Island, Myanmar) [i]	215	309	144%	52.4	*	*
matthaeus (De Lisle Island/Koh Priam, Myanmar) [i]	245	332	136%	55.4	50.9	10.7
salanga (Junk Seylon, Pulau Panjang, Telibon, Lontar, Thail.) [iii]	217 (200-230) 10	320 (303-350) 10	148%	*	49.6 (47.5-52.6) 9	10.0 (9.7-10.5) 10
vociferans (peninsular Thailand) [iii]	239 (208-290) 53	358 (270-414) 53	150%	*	51.9 (46.7-54.0) 51	10.1 (9.5-10.9) 51
tersus (Terutao Island, Thailand) [iii]	217 (198-235) 18	322 (290-342) 17	148%	*	48.5 (45.7-50.5) 16	9.8 (9.2-10.2) 17
lancavensis (Pulau Langkawi, Malaysia) [iii]	231 (210-250) 17	335 (310-375) 16	145%	*	50.0 (47.3-52.2) 16	9.9 (9.7-10.3) 17
dictarorius (Penang Island, Malaysia) [iv]	219	305	139%	53.5	*	9.8
stridens (Pulau Tioman, Malaysia) [iii]	233 (220-256) 6	330 (316-347) 6	142%	*	51.5 (49.0-53.3) 6	10.1 (9.9-10.3) 6

Table 13. Matrix key to the four species of *Maxomys* (sensu Musser & Carleton 2005) currently known from the Myanmar-Thai-Malaysian peninsula.

Size (Tables 11 and 13)	Tail	Dorsal pelage colour	Ventral pelage	Skull
		Maxomys inas		
Medium. HB: 124-165 mm. HF: 30-33 mm	Medium, 131-167 mm. Bicoloured, dark above, pale below, nearly naked and without a white tip	Rich, yellowish, reddish brown, variably grizzled with black	Yellowish-brown to grey-chestnut or pinkish buff; not clearly demarcated from flanks	Medium. GLS: 36.1-40.3 mm Upper toothrow: 6.2-6.7 mm
		Maxomys rajah		
Larger. HB: 140-280 mm. HF: 34-46	Longer, 140-287 mm. Bicoloured but not sharply, dark above and pale below, colours indefinite towards tip	Light brown to dull buff brown without any reddish tinge, relatively few black hairs	White, clearly demarcated from flanks	Larger. GLS: 40.9-48.6 mm Upper toothrow: 6.6-8.1 mm
		Maxomys surifer		
Larger. HB: 144-224 mm. HF: 30-41 mm	Longer, 140-225 mm. Bicoloured, dark above, pale below, usually with white tip	Yellowish-orange to bright reddish brown, variably grizzled with black	White to creamy white, clearly demarcated from flanks	Larger. GLS: 39.9-49.0 mm Upper toothrow: 5.9-7.5 mm
		Maxomys whiteheadi		
Smaller. HB: 100-141 mm. HF: 22-30 mm	Short, 88-118 mm, shorter than head and body. Bicoloured, dark above, pale below, without a white tip	Reddish-brown, grizzled with dark brown in some specimens	Belly grey or dull buff fading to buffy grey on chin; not clearly demarcated from flanks	Smaller. GLS: 29.2-34.8 mm Upper toothrow 5.1-6.2 mm

Table 12. External, cranial and dental measurements of *Maxomys*. Measurements sourced from: [i] Musser et al. (1979), [ii] Hill (1960), [iii] Medway (1969) and [iv] Pimsai (2012).

HB	Tail	(Tail/HB)%	HF	GLS	CBL	ZB	LN	LD	LIF	LB	ALM¹-M³
						Maxomys inas (Malaysia) [i]					
147.5 ± 11.3 (124-162) 10	149.2 ± 9.5 (135-167) 10	101%	32.0 ± 0.8 (31-33) 10	37.7 ± 1.6 (36.1-40.3) 6	*	16.6 ± 0.7 (16.0-17.8) 5	12.7 ± 0.9 (11.9-14.4) 6	8.9 ± 0.6 (8.5-9.8) 6	5.7 ± 0.5 (5.2-6.4) 6	5.2 ± 0.1 (5.1-5.3) 6	6.4 ± 0.2 (6.2-6.7) 6
						(Malaysia) [ii]					
143 (125-165) 17	147 (130-166)	103%	*	*	*	*	*	*	*	*	6.3 (6.0-6.6)
						(Malaysia) [iii]					
125-160	131-158	91-115%	30-33	*	*	*	*	*	*	*	*
						Maxomys rajah (Thailand) [iv]					
186.3 ± 41.9 (162-280) 7	197.4 ± 40.3 (170-287) 7	106%	38.3 ± 2.4 (34-40) 7	43.6 ± 2.4 (41.5-47.0) 4	*	19.3 ± 1.3 (18.0-20.9) 4	*	13.2 ± 2.3 (10.9-17.4) 6	6.2 ± 0.6 (5.2-6.8) 6	4.9 ± 0.3 (4.4-5.3) 5	6.7 ± 0.2 (6.6-7.0) 6
						(geographical origin not stated) [i]					
192.9 ± 18.4 (166-226) 13	184.1 ± 14.6 (162-210) 12	95%	38.5 ± 2.4 (35-43) 13	45.1 ± 2.6 (40.9-48.6) 13	*	20.1 ± 1.2 (18.5-22.1) 13	17.6 ± 1.5 (15.6-19.4) 13	12.3 ± 0.9 (10.4-13.3) 13	6.7 ± 0.5 (5.8-7.5) 13	4.6 ± 0.3 (4.3-5.3) 13	7.3 ± 0.3 (6.9-8.1) 13
						(Malaysia) [ii]					
197 (162-220) 17	201 (173-215) 17	102%	*	*	*	*	*	*	*	*	7.1 (6.8-7.4) 18
						(Malaysia) [iii]					
140-235	140-217	84-115%	35-46	*	*	*	*	*	*	*	*
						Maxomys surifer (Thailand) [iv]					
180.5 ± 12.6 (144-203.0) 23	177.4 ± 12.0 (158-206) 21	98%	36.1 ± 2.6 (30-41) 23	44.8 ± 2.6 (39.9-47.9) 23	*	20.4 ± 1.0 (18.6-22.1) 18	*	12.6 ± 0.86 (11.0-13.7) 23	6.1 ± 0.5 (4.9-6.9) 23	4.8 ± 0.2 (4.2-5.2) 22	6.5 ± 0.3 (5.9-7.0) 23
						('Tenasserim' Myanmar) [ii]					
187 (162-207) 32	197 (178-216) 29	105%	*	*	40.5 (38.2-44.3) 32	*	*	*	*	*	6.7 (6.0-7.3) 33
						(South peninsular Thailand) [ii]					
185 (165-214) 23	193 (167-217) 23	104%	*	*	41.3 (39.6-44.8) 17	*	*	*	*	*	6.8 (6.3-7.3) 17
						(Peninsular Malaysia) [ii]					
193 (164-220) 41	199 (171-199) 39	103%	*	*	42.3 (39.0-45.3) 40	*	*	*	*	*	6.9 (6.2-7.4) 39
						(Malaysia) [iii]					
170-220	167-225	90-126%	32-40	*	*	*	*	*	*	*	*
						Maxomys whiteheadi (Thailand) [iv]					
127.4 ± 14.8 (103-141) 5	101.7 ± 15.4 (84-112) 3	80%	*	32.8 ± 2.1 (30.5-34.8) 3	*	15.0 ± 0.7 (14.3-15.6) 3	*	8.0	5.3	4.3	5.2
						(geographical origin not stated) [i]					
110.8 ± 8.5 (100-126) 22	96.7 ± 4.5 (88-108) 21	87%	25.8 ± 0.9 (24-28) 22	31.2 ± 1.3 (29.2-33.7) 21	*	14.1 ± 0.6 (12.6-14.8) 16	11.0 ± 0.7 (9.8-12.5) 21	7.7 ± 0.5 (6.9-8.5) 22	4.7 ± 0.4 (4.0-5.4) 21	4.2 ± 0.2 (3.9-4.7) 21	5.5 ± 0.3 (5.1-6.2) 21
						(Malaysia) [iii]					
110-135	90-118	83-100%	22-30	*	*	*	*	*	*	*	*

Table 14. External, cranial and dental measurements of *Maxomys surifer* (sensu Musser & Carleton 2005) from a range of localities (see Fig. 25) in Myanmar, Thailand and Malaysia. Measurements sourced from [i] Miller (1903a), [ii] Hill (1960), [iii] Kloss (1916c) and [iv] Kloss (1911a).

	HB	Tail	(Tail/HB)%	GLS	CBL	ALM^1-M^3
bentincanus (Bentinck Island, Myanmar) [i]	205	180	88%	47.0	*	*
domelicus (Domel Island, Myanmar) [i]	200	150	75%	49.0	*	*
umbridorsum (Loughborough Island, Myanmar) [i]	180	170	94%	42.0	*	*
luteolus (De Lisle Island/ Koh Piam, Myanmar) [ii]	183 (171-195) 5	176 (168-183) 5	96%	45 [i]	39.3 (37.8-41.4) 5	7.2 (6.9-7.4) 5
luteolus (Sugar Loaves/ Koh Yam Yai, Myanmar/Thailand) [ii]	184 (168-199) 5	169 (154-182) 5	92%	*	39.8 (36.7-42.0) 5	6.7 (6.5-6.8) 5
casensis (Koh Rah, Thailand) [ii]	189 (169-206) 10	193 (180-222) 10	102%	47 [i]	40.9 (39.5-42.6) 9	7.1 (6.6-7.4) 10
manicalis (Koh Pennan, Thailand) [ii]	176 (170-180) 3	178 (172-187) 3	101%	*	38.5 (37.5-39.2) 4	6.6 (6.5-6.6) 4
spurcus (Koh Samui, Thailand) [ii]	178 (165-192) 5	182 (170-193) 5	102%	*	37.9 (37.6-38.3) 3	6.6 (6.2-6.9) 5
puket (Junk Seylon, Thailand) [ii]	159 (145-180) 13	169 (148-195) 13	106%	*	38.7 (36.8-40.2) 12	6.6 (6.2-6.8) 12
puket (Junk SeylonPulau Sireh, Thailand) [ii]	162, 172	178, 188	110%	*	38.5, 39.9	6.3, 6.8
puket (Koh Boi, Thailand) [ii]	167 (160-170) 4	167 (155-173) 4	100%	*	39.3 (38.1-40.1) 3	6.5 (6.4-6.7) 4
puket (Pulau Lontar, Thailand) [ii]	160 (150-175) 12	169 (150-203) 12	106%	*	38.6 (37.1-40.7) 12	6.7 (6.2-6.9) 12
puket (Pulau Panjang, Thailand) [ii]	162 (151-183) 9	172 (161-186) 9	106%	*	37.4 (36.2-40.0) 7	6.6 (6.0-6.9) 7
pidonis (Koh Pipidon, Thailand) [ii]	198 (183-208) 9	186 (178-196) 9	94%	*	41.0 (39.3-43.0) 9	6.9 (6.7-7.2) 9
eclipsis (Koh Kra, Thailand) [iii]	197 (191-201) 3	183 (171-197) 3	93% (90-98%) 3	45.6 (45.1-46.0) 4	39.0 (38.6-39.3) 3	7.0 (6.9-7.2) 3
muntia (Koh Muk, Thailand) [ii]	188 (174-202) 13	180 (169-200) 13	96%	*	40.9 (38.9-43.7) 13	7.1 (6.9-7.5) 13
telibon (Telibon Island, Thailand) [ii]	172 (159-188) 7	181 (175-188) 7	105%	*	39.3 (38.0-41.4) 8	7.1 (6.9-7.3) 8
butangensis (Adang Island, Thailand) [ii]	200 (194-209) 4	171 (164-175) 4	86%	*	42.7 (42.2-43.2) 3	7.2 (7.0-7.4) 3
flavidulus (Pulau Langkawi, Malaysia) [ii]	180 (160-195) 32	163 (140-190) 32	91%	*	39.9 (38.0-42.8) 27	6.8 (6.4-7.3) 29
flavigrandis (East Perhentian Island, Malaysia) [iv]	208	180	87%	48.0, 48.8	*	7.4, 7.9
grandis (Great Redang Island, Malaysia) [iv]	204	188	92%	49.0	*	7.5
binominatus (Pulau Tioman, Malaysia) [ii]	195 (183-208) 7	180 (155-193) 6	92%	*	42.5 (41.3-44.1) 7	6.9 (6.7-7.1) 7
pemangilis (Pulau Pemanggil, Malaysia) [ii]	209 (192-224) 7	164 (148-179) 7	79%	*	42.0 (40.5-44.3) 6	7.1 (6.8-7.3) 6
aoris (Pulau Aur, Malaysia) [ii]	202 (193-210) 3	187 (184-191) 3	93%	*	43.1 (40.5-44.5) 4	7.2 (7.0-7.5) 4
leonis (Singapore) [ii]	177 (161-192) 7	176 (153-185) 7	99%	*	39.6 (37.1-41.8) 10	6.6 (6.2-6.8) 10

Table 15. External, cranial and dental measurements of *Mus*. Measurements sourced from: [i] Aplin et al. (2003), [ii] Marshall 1977a, [iii] Francis (2008), [iv] Bonhote (1902), [v] Kloss (1921), [vi] Pimsai (2012), and [vii] Medway (1969).

HB	Tail	(Tail/HB)%	HF	GLS/ONL	ZB	LN	LB	ALM^1-M^3
				Mus caroli (Thailand) [i]				
76	78	102%	18	*	*	*	*	*
				(Malaysia) [i]				
79	84	106%	18	*	*	*	*	*
				(Malaysia) [ii]				
75.3 ± 4.4 33	74.6 ± 4.5 34	99%	17.8 ± 0.7 33	20.6 ± 0.6 33	*	6.8 ± 0.4 33	3.6 ± 0.2 33	3.3 ± 0.1 33
				(origin not specified) [iii]				
65-85	65-95	100%	16.5-19.2	19-22	*	*	*	3.1-3.5
				(holotype of *caroli* from Okinawa, Japan [iv]				
75	86	115%	18	22.0	*	8.0	4.0	*
				(holotype of *ouwensi* from Java [v]				
55	62	113%	15	21.0	11.0	*	*	3.3
				Mus musculus (Thailand) [vi]				
80	75	94%	15	22.7 ± 1.6 (21.0-24.2) 3	12.2 ± 0.3 (11.9-12.4) 3	8.3 ± 0.9 (7.4-9.1) 3	3.7 ± 0.2 (3.5-3.9) 3	3.6 ± 0.2 (3.3-3.7) 3
				(Thailand) [i]				
76	79	104%	16.5	*	*	*	*	*
				(origin not specified) [iii]				
65-90	67-92	105%	14.5-18.5	18.5-22.0	*	*	*	2.9-3.5
				(Malaysia) [vii]				
60-90	*	90-120%	14-17	*	*	*	*	*
				(origin not specified) [ii]				
75.9 ± 5.9 47	79.4 ± 6.4 49	105%	16.5 ± 1.0 54	20.3 ± 0.8 49	*	7.2 ± 0.5 35	3.5 ± 0.1 34	3.2 ± 0.2 37

Table 16. Matrix key to the two species of *Mus* currently known from the Myanmar-Thai-Malaysian peninsula.

Size (Table 15)	Tail	Pelage colour	Upper incisors	Skull
		Mus caroli		
Small. HB: 55-85 mm	Bicoloured, dark (black) above, pale below	Upperparts, brownish-yellow to brownish-grey; ventral surface, white	Dark orange enamel and procumbent	Nasal bones do not hide incisors when viewed from above; incisive foramina shorter
		Mus musculus		
Small. HB: 65-90 mm	Unicoloured, brown above and below (occasionally slighter paler below)	Upperparts, dark greyish-brown to brown; ventral surface, slightly paler greyish-brown (in the study region; extralimitally often white)	Orange enamel and opisthodont	Nasal bones hide incisors when viewed from above; incisive foramina longer

Table 17. External, cranial and dental measurements of *Niviventer*. Measurements sourced from: [i] Chasen (1940), [iia] Medway (1969, = *R. fulvescens*), [iib] Medway (1969), [iii] Francis (2008), [iv] Musser (1973a); [v] Miller (1903a), [vi] Miller (1913), [vii] Pimsai (2012), [viii] Abe (1983), [ix] Robinson & Kloss (1914) and [x] Bonhote (1903b).

HB	Tail	(Tail/HB)%	HF	GLS	ZB	LN	LD	LIF	BBPM³	LB	ALM¹-M³
					Niviventer cameroni (holotype of *cameroni*, with one additional specimen) [i]						
152, 154	241, 263	165%	32, 37	41.0, 41.5	17.3, 17.8	15.2, 16.0	*	*	*	*	7.2, 7.2
					(Malaysia) [iia]						
130-167	205-270	132-180%	30-38	*	*	*	*	*	*	*	*
					(Malaysia) [iii]						
130-170	205-270	132-180%	30-38	40-43	*	*	*	*	*	*	6.3-7.2
					Niviventer cremoriventer (Thailand) [iv]						
136.0 ± 8.5 (128-146) 4	171.0 ± 8.3 (160-180) 4	126%	24.0 ± 3.6 (20-25) 3	33.7 ± 6.2 (33.2-34.4) 3	15.2, 16.1	11.7 ± 0.3 (11.5-12.0) 3	8.5 ± 0.4 (7.7-8.6) 4	5.4 ± 0.2 (5.3-5.6) 4	3.8 ± 0.1 (3.7-3.9) 4	4.3 ± 0.2 (4.2-4.5) 3	6.1 ± 0.2 (5.8-6.3) 4
					(Malaysia) [iv]						
147.5 ± 7.8 (137-165) 15	175.4 ± 17.0 (140-200) 14	119%	27.5 ± 1.0 (26-29) 15	36.1 ± 1.15 (34.1-37.9) 15	16.9 ± 0.8 (15.5-18.2) 15	12.8 ± 0.5 11.9-13.5) 15	9.1 ± 0.4 (8.3-10.0) 15	6.1 ± 0.3 (5.7-6.6) 15	*	4.6 ± 0.2 (4.2-4.8) 15	6.1 ± 0.3 (5.5-6.4) 15
					(Malaysia) [iib]						
110-152	120-200	110-142%	24-27	*	*	*	*	*	*	*	*
					(holotype of *gilbiventer*) [v]						
125	185	148%	27	35.0	16.0	13.0	*	6.4	*	*	*
					(holotype of *solus*) [vi]						
160	220	138%	30	36.5	17.1	13.0	8.7	*	*	*	6.3
					Niviventer fulvescens (Thailand) [vii]						
137.9 ± 11.2 (115-154) 10	181.9 ± 18.6 (160-219) 9	132%	27.8 ± 2.7 (22-32) 10	35.9 ± 1.71 (33.2-39.6) 11	16.4 ± 0.9 (15.3-17.9) 10	13.2 ± 0.9 (11.8-15.0) 12	8.8 ± 0.5 (8.1-9.4) 10	6.1 ± 0.4 (5.3-6.6) 9	*	4.4 ± 0.2 (4.1-4.6) 8	6.1 ± 0.3 (5.7-6.6) 10
					(Thailand) [viii]						
146.6 ± 10.6 (118-160) 20	180.7 ± 15.3 (156-215) 20	123.7% ± 7.4 (115.1-142.4%) 20	28.3 ± 1.3 (26-31) 20	36.5 ± 1.6 (32.7-38.7) 20	16.5 ± 0.5 (15.4-17.5) 20	*	9.0 ± 0.7 (7.7-9.9) 20	*	*	*	*
					(holotype of *lepidus*) [vi]						
140	159	114%	26	CBL: 31.4	*	*	8.3	*	*	*	6.0
					(holotype of *pan*) [ix]						
149	174	117%	27.5	37.7	17.0	14.7	10.0	*	*	*	*
					(holotype of *orbus*) [ix]						
153	235	154%	32	38.1	17.0	13.9	9.8	6.3	*	*	6.3
					(holotype of *bukit*) [x]						
121	148	122%	24.5	37.0	18.0	15.0	9.5	*	*	*	*

Table 18. Matrix key to the three species of *Niviventer* (sensu Musser & Carleton 2005) currently known from the Myanmar-Thai-Malaysian peninsula.

Size (Table 17). Dorsal/ ventral pelage	Tail	Hind foot	Skull
	Niviventer cameroni		
Medium. HB: 130-170 mm. Bright reddish-brown with black guard hairs; underparts white	Long. 205-270 mm; 132-180% of head and body length. Bicoloured without a conspicuous tuft at tip	Longer. 30-38 mm	Larger. GLS: 40-43 mm Upper toothrow: 6.3-7.2 mm
	Niviventer cremoriventer		
Medium. HB: 110-165 mm. Bright orange to reddish brown with black guard hairs; underparts white to cream buff	Medium-long. 120-220 mm; 110-142% of head and body length. Unicoloured, dark above and below with a conspicuous tuft/pencil of hairs at tip	Medium. 20-30 mm broad for climbing	Medium. GLS: 33.2-37.9 mm Upper toothrow: 5.5-6.4 mm
	Niviventer fulvescens		
Medium. HB: 115-160 mm. Yellowish-brown to orange-brown with black guard hairs; underparts are white to yellowish-white	Medium-long. 148-219 mm; 114-154% of head and body length. Bicoloured (but not always markedly) dark above and pale below with tuft/pencil of hairs at tip	Medium. 22-32 mm	Medium. GLS: 32.7-39.6 mm Upper toothrow: 5.7-6.6 mm

Table 19. External, cranial and dental measurements of *Pithecheir*. Measurements sourced from: [i] Musser & Newcomb (1983) and [ii] Kloss (1916b).

HB	Tail	(Tail/HB)%	HF	GLS	ZB	LN	LIF	LB	ALM^{1}-M^{3}
				Pithecheir parvus [i]					
165.8 ± 6.5 (156-175) 11	186.7 ± 7.0 (179-205) 11	112.6%	27.6 ± 1.2 (26-30) 11	42.3 ± 1.5 (39.0-44.0) 11	*	*	*	10.6 ± 0.5 (9.6-11.5) 11	7.9 ± 0.2 (7.5-8.2) 11
				Pithecheir parvus (holotype) [ii]					
122	140	114.8%	26	34.7	17.4	7.5	6.0	8.8	7.3

Table 20. External, cranial and dental measurements of *Rattus*. Measurements sourced from: [i] Robinson & Kloss 1914, [ii] Hill (1960), [iii] Marshall (1988), [iv] Corbet & Hill 1992, [v] Harrison Institute collection, [vi] Medway (1969); [vii]: Bonhote (1903a), [viii] Kloss 1908a, [ix] Pimsai 2012, [x] Sody (1941), [xi] Miller (1900a) and [xii] Medway & Lim (1966).

Tail	(Tail/HB)%	HF	GLS/ONL	CBL	ZB	LN	LD	LIF	LB	ALM¹-M³
				Rattus andamanensis (holotype of *remotus* from Thailand) [i]						
273	121%	39	49.1	*	22.0	18.9	13.3	9.4	*	8.2
				(Koh Samui, Thailand) [ii]						
288	122%	*	*	46.0, 47.6	*	*	*	9.0, 9.4	7.1, 8.0	8.2, 8.9
				(from Thailand) [iii]						
242	116%	40	*	*	*	*	*	*	*	*
				(Asia) [iv]						
*	115-125%	(33-40)	*	*	*	*	*	*	*	*
				(Cambodia) [v]						
*	*	31, 33	44.2, 46.8	41.8, 43.1	21.4, 21.5	17.8, 17.9	12.1, 12.3	8.4, 8.9	7.1, 7.9	7.5, 7.8
				Rattus annandalei (Malaysia) [ii]						
238 (215-250) 4	125%	*	*	46.5 (43.7-49.2) 4	*	*	*	7.9 (7.6-8.3) 4	7.8 (7.4-8.0) 4	8.3 (8.0-8.5) 4
				(referred to *bullatus* (Lyon), specimens from Malaysia and Singapore) [ii]						
233 (207-257) 14	119%	*	*	44.1 (40.5-48.1) 14	*	*	*	7.4 (6.6-8.2) 14	8.0 (7.6-8.6) 14	8.3 (7.9-9.0) 14
				(Malaysia) [vi]						
(156-270) 39	(101-147%) 39	(35-40) 39	*	*	*	*	*	*	*	(7.5-8.0) 39
				(Asia) [iv]						
*	(100-150%)	(35-40)	43, 51	*	*	*	*	6.4, 8.0	*	(7.0-8.0)
				(holot. of *annandalei* f. Malaysia) [vii]						
196	130%	35	44.0	*	19.5	16.0	11.0	7.5	8.0	7.5
				(holot. of *villosus* from Singapore) [viii]						
251	113%	41	52.0	*	24.0	20.0	15.0	8.3	8.5	9.0
				Rattus argentiventer (Thailand) [ix]						
168.7 ± 5.5 (165-175) 3	91%	35.6 ± 2.2 (33.7-38.0) 3	44.0 ± 1.2 (42.8-45.2) 3	*	21.7 ± 0.8 (21.2-22.3) 3	16.0 ± 1.2 (14.7-17.1) 3	12.6 ± 0.8 (11.7-13.3) 3	8.9 ± 0.7 (8.2-9.5) 3	7.4 ± 0.3 (7.1-7.6) 3	7.3 ± 0.5 (6.9-7.9) 3
				(Malaysia) [vi]						
(130-192) 47	(81-125%) 47	(32-35) 47	*	*	*	*	*	*	*	*
				(Malaysia) [ii]						
172, 175	90%	*	40.8, 43.7	*	*	*	*	*	*	7.6, 7.8
				(holotype of *chaseni*) [x]						
200	103%	41	44.6	39.1	20.8	15.1	12.0	8.5	*	*
				Rattus exulans (Thailand) [ix]						
131.8 ± 15.1 (110-180) 19	109%	22.6 ± 3.3 (16-31) 20	30.8 ± 1.2 (28.2-32.4) 22	*	14.4 ± 0.8 (13.3-16.7) 20	11.0 ± 0.7 (9.7-12.3) 21	8.0 ± 0.5 (7.0-8.7) 22	5.6 ± 0.2 (5.3-6.0) 20	5.6 ± 0.3 (5.1-6.1) 20	5.0 ± 0.2 (4.6-5.5) 19
				(Malaysia) [vi]						
(108-147) 48	(100-125%) 48	(20-25) 48	*	*	*	*	*	*	*	*
				(holot. of *obscurus* from Malaysia) [xi]						
133	110%	22.6	30.0	*	13.6	11.0	8.0	5.4	*	4.6
				Rattus norvegicus (Thailand) [ix]						
196.2 ± 24.5 (125-240) 16	77%	42.1 ± 2.1 (38-45) 16	51.1 ± 2.9 (47.3-59.1) 18	*	25.1 ± 1.5 (22.9-27.9) 18	19.5 ± 1.3 (17.2-22.0) 18	14.6 ± 0.7 (13.7-15.7) 18	8.6 ± 0.4 (8.0-9.2) 17	7.9 ± 0.5 (6.7-8.7) 17	7.7 ± 0.4 (7.3-8.4) 18
				(Malaysia) [vi]						
(170-230) 7	(79-97%) 7	(40-45) 7	*	*	*	*	*	*	*	*
				Rattus tanezumi (Thailand) [ix]						
186.1 ± 24.2 (142-258) 20	107%	31.6 ± 4.0 (20-40) 21	41.8 ± 1.6 (39.2-44.7) 21	*	20.0 ± 1.1 (18.3-22.5) 21	15.3 ± 1.0 (13.7-17.9) 21	11.2 ± 0.5 (10.3-12.3) 22	7.7 ± 0.4 (7.0-8.6) 22	7.5 ± 0.6 (6.6-8.6) 22	7.1 ± 0.3 (6.5-7.6) 22
				(Malaysia) [vi]						
*	(90-120%)	(31-39)	*	*	*	*	*	*	*	*
				(Malaysia) [xii]						
180.5 ± 4.2	106%	35.0 ± 0.4	41.6 ± 0.3	*	*	*	*	7.7 ± 0.1	*	7.1 ± 0.0
				(Malaysia) [xii]						
186.9 ± 1.9	101%	35.2 ± 0.2	41.5 ± 0.2	*	*	*	*	7.7 ± 0.1	*	7.1 ± 0.1
				Rattus tiomanicus (Thailand) [ix]						
169, 170	103%	31.1, 35.8	41.0, 42.5	*	19.4, 19.4	13.4, 16.6	11.4, 11.5	7.3, 7.8	6.4, 7.7	6.9, 7.00
				(Malaysia) [ii]						
173 (160-198) 19	109%	*	39.8 (37.1-43.9) 23	*	*	*	*	*	*	6.7 (6.1-7.1) 23
				(Malaysia) [vi]						
(125-198)	(85-124%)	(28-32)	*	*	*	*	*	*	*	*
				(Malaysia) [xii]						
160.6 ± 1.3	96%	31.7 ± 0.2	40.2 ± 0.4	*	*	*	*	6.8 ± 0.1	*	6.8 ± 0.0
				(Singapore) [xii]						
158.8 ± 4.3	90%	32.7 ± 0.3	40.6 ± 0.9	*	*	*	*	7.1 ± 0.1	*	6.7 ± 0.1

Table 21. Matrix key to the seven species of *Rattus* currently known from the Myanmar-Thai-Malaysian peninsula.

Size/dorsal pelage	Tail/ventral pelage	Mammae	Skull	Teeth
		Rattus andamenensis		
Large (Table 20) hind feet with large, prominent, finely ridged pads. Pelage long and shaggy with thin flexible spiny-hairs; yellow-orange to sooty brown with black. Long vibrissae on head up to 60 mm in length.	Tail exceeding head and body length (115-125% of head and body length), blackish brown above and below. Ventral pelage creamy white	12 (1 pair pectoral, 2 pairs postaxillary 3 pairs inguinal)	Skull large (44-49 mm), strongly ridged with short broad rostrum and long incisive foramina; sides of braincase slanted	Upper toothrow long (7.5-8.9 mm)
		Rattus annandalei		
Moderately large (Table 20). Pelage is soft and shaggy but includes thin spiny hairs; grizzled yellowish-buff-brown, darker on the rump	Tail usually exceeding head and body length (100-150%), it is blackish above and below. Ventral pelage white tinged with yellow	8, 10 or 12 (2 or 3 pairs pectoral and 2 or 3 pairs inguinal)	Skull large (43-52 mm), elongated and large tympanic bullae	Upper toothrow long (7.0-9.0 mm)
		Rattus argentiventer		
Moderate size (Table 20). Hind feet with smooth plantar pads. Pelage includes thin, spiny-hairs; colour is yellowish-orange brown speckled with black ('salt and pepper' effect), tuft of orange hairs in front of each ear (most visible in young individuals)	Tail usually shorter than head and body length (81-125%), it is blackish-brown above and below. Ventral pelage silvery grey (never creamy) with white hair tips and grey bases	12 (1 pair pectoral, 2 pairs postaxillary and 3 pairs inguinal)	Skull medium-large (40.8-45.2 mm), with short, broad rostrum which curves conspicuously downwards, interorbital region narrow, tympanic bullae moderately large	Upper toothrow medium-long (6.9-7.8 mm)
		Rattus exulans		
Small (Table 20). Superficially similar to a large mouse. Pelage is short and includes spine-like hairs; colour is grey-brown to brown, with some yellowish-red buff	Tail usually exceeds head and body length (100-125%), uniformly dark brown above and below. Ventral pelage pale, sometimes with a yellow tinge	8 (2 pairs pectoral and 2 pairs inguinal)	Skull small (28.2-32.4 mm)	Upper toothrow short (4.6-5.5 mm)
		Rattus norvegicus		
Large (Table 20). Pelage is short but with long guard hairs that give a shaggy appearance; it is without prominent spine-like hairs; colour is grey brown to plain brown	Tail short, usually shorter than head and body length (79-97%) and weakly bicoloured, dark above and paler below, sometimes with a mottled appearance. Ventral pelage is pale brown or grey, often with a white patch on the chest	12 (3 pairs pectoral and 3 pairs inguinal)	Skull large (47.3-59.1 mm), with long incisive foramina	Upper toothrow medium-long (7.3-8.4 mm)
		Rattus tanezumi		
Medium-sized (Tables 20 and 22). Hind feet with ridged interdigital and metatarsal pads. Pelage includes slender spine-like hairs; colour is olive-brown grizzled with grey or orange-red, with long black guard hairs	Tail is shorter, equal to, or longer than head and body length (85-132%) and uniformly dark throughout, very occasionally there is a short white tip. Ventral pelage is usually brownish grey to creamy white, sometimes with a yellowish tinge	10 to 12 (1 pair pectoral, 1 or 2 pairs postaxillary and 3 pairs inguinal)	Skull medium-sized (39.2-44.7 mm), with angular supraorbital ridges (Fig. 43) and longer incisive foramina (in comparison to *R. tiomanicus*) sides of braincase vertical	Upper toothrow medium (6.5-7.6 mm)
		Rattus tiomanicus		
Medium-large (Tables 20 and 23). Hind feet with ridged interdigital and metatarsal pads. Pelage is sleek, moderately long and soft with some thin, spine-like hairs; colour is warm yellowish-brown grizzled with blackish-brown, with some short black guard hairs	Tail is shorter, equal to, or longer than head and body length (85-124%) and uniformly dark throughout. Ventral pelage is usually white in mainland populations but whitish-grey to buffy grey in island populations	10 (2 pairs pectoral and 3 pairs inguinal)	Skull medium-sized (37.1-47.4 mm), with shorter incisive foramina (in comparison to *R. tanezumi*)	Upper toothrow medium (6.1-7.1 mm)

Table 22. External, cranial and dental measurements of *Rattus tanezumi* from a range of localities (see Fig. 42) in Myanmar, Thailand and Malaysia. Sourced from [i] Hinton (1919), [ii] Miller (1913), [iii] Hill (1960), [iv] Chasen (1937), [v] Miller (1900c) and [vi] Bonhote (1903a).

	HB	Tail	(Tail/HB)%	GLS/ONL	CBL	ALM^{1}-M^{3}
tikos (Tenasserim, Myanmar) [i]	169.8 ± 9.9 (156-189) 17	185.0 ± 13.3 (161-216) 15	109.6 ± 5.6 (93.6-116.0) 15	*	*	*
insulanus (Helfer Island, Myanmar) [ii]	185	185	100%	*	40.6	7.6
exsul (James Island, Myanmar) [ii]	175	183	105%	*	37.4	6.9
dentatus (Hastings Island, Myanmar) [ii]	180	190	106%	*	39.0	7.0
fortunatus (Chance Island, Myanmar) [ii]	205	215	105%	*	41.5	7.2
robinsoni (Koh Pennan, Thailand) [iii]	176 (159-193) 20	194 (177-213) 20	110%	43.3 (39.5-44.4) 19	39.6 (37.7-41.7) 19	7.5 (7.0-7.8) 20
panjius (North Panjang Island, peninsular Thailand) [iv]	170	195	115%	43.5	40.8	7.6
alangensis (Alang Yai Island, peninsular Thailand) [iv]	160.2 ± 5.4 (150-170) 12	190.8 ± 11.0 (165-205) 9	119.6 ± 5.6 (106.5-127.1) 9	41.8 ± 1.5 (38.8-44.3) 12	39.3 ± 1.1 (37.3-41.0) 12	6.7 ± 0.3 (6.2-7.1) 12
pipidonis (Pipidon Island, peninsular Thailand) [iv]	193.6 ± 14.4 (180-218) 5	202.8 ± 10.4 (195-218) 4	103.5 ± 4.8 (100.0-111.1) 4	45.7 ± 0.9 (44.7-46.8) 4	42.9 ± 0.7 (42.0-43.6) 4	7.3 ± 0.2 (7.1-7.5) 5
lontaris (Lontar Island, peninsular Thailand) [iv]	145.1 ± 10.7 (130-156) 7	173.7 ± 11.0 (160-189) 7	119.9 ± 5.3 (111.1-126.2) 7	38.6 ± 1.0 (37.5-39.7) 6	36.1 ± 1.1 (35.0-37.4) 7	6.6 ± 0.2 (6.4-6.9) 7
moheius (Pipidon Island, peninsular Thailand) [iv]	187.8 ± 8.4 (173-196) 8	208.3 ± 7.7 (198-217) 8	111 ± 3.2 (105.8-114.5) 8	43.6 ± 1.3 (42.1-45.2) 8	41.0 ± 1.1 (39.4-42.6) 8	7.5 ± 0.2 (7.1-7.9) 8
kadanus (Kadan and Muntia Islands, peninsular Thailand) [iv]	187.6 ± 10.3 (175-206) 11	216.4 ± 12.1 (201-240) 11	115.5 ± 6.8 (101.9-127.1) 11	44.0 ± 1.1 (42.4-45.7) 11	42.3 ± 1.2 (40.5-44.2) 11	7.2 ± 0.2 (6.6-7.4) 11
pannosus (Adang Island, peninsular Thailand) [v]	203	203	100%	*	*	*
panellus (Rawi Island, peninsular Thailand) [ii]	205	175	85%	*	42.3	8.0
griseiventer (peninsular Malaysia) [vi]	161	212	132%	42.0	*	7.0

Table 23. External, cranial and dental measurements of *Rattus tiomanicus* from a range of localities (see Fig. 43) in Myanmar, Thailand and Malaysia. Based on [i] Hill (1960), [ii] Chasen & Kloss (1931) and [iii] Yong (1971).

	HB	Tail	(Tail/HB)%	GLS/ONL	CBL	ALM^1-M^3
terutavensis (Tarutao Islands, Thailand)[i]	164 (140-180) 18	178 (152-195) 18	109%	38.1 (37.5-40.5) 16	39.2	6.8 (6.5-7.1) 16
jalorensis (Malaysia) [i]	158 (143-170) 19	173 (160-198) 19	109%	39.8 (37.1-43.9) 23	37.9 (35.2-41.4) 23	6.7 (6.1-7.1) 23
viclana (Pulau Lankawi, Malaysia) [i]	166 (152-177) 16	182 (165-201) 16	110%	40.4 (38.4-43.2) 15	38.1 (36.3-39.9) 15	7.2 (7.0-7.6) 15
payanus (Paya Island, Malaysia) [ii]	188	198	105%	46.2	*	7.3
perhentianus (East Perhentian Island, Malaysia) [i]	181 (170-197) 13	202 (183-225) 13	112%	42.8 (39.9-45.3) 11	40.3 (38.1-42.8) 11	7.4 (6.9-7.6) 12
tenggolensis (Tenggol Island, Malaysia) [iii]	174.0 ± 2.5 (150-200)	174.9 ± 2.0 (146-189)	101%	41.7	*	7.0
rumpia (Pulau Rumpia/ Sembilan Islands, Malaysia) [i]	187 (169-201) 15	220 (199-233) 14	118%	45.0 (43.0-46.6) 15	43.2 (41.0-45.7) 15	7.5 (7.2-7.9) 15
jarak (Jarak Island, Malaysia) [i]	168 (155-185) 20	177 (160-193) 20	105%	40.6 (38.5-42.1) 17	38.8 (37.2-39.9) 17	6.6 (6.1-6.8) 17
tiomanicus (Pulau Tioman, Malaysia) [i]	169 (150-184) 5	188 (173-197) 5	111%	41.3 (39.1-42.8) 5	38.8 (36.9-40.3) 5	7.1 (6.8-7.2) 5
sribuatensis (Sribuat Island, Malaysia) [i]	185 (182-195) 5	199 (191-207) 4	108%	43.4 (42.4-44.3) 4	41.3 (39.5-42.4) 5	6.9 (6.8-7.0) 5
kabanicus (Kaban Island, Malaysia) [i]	185 (180-194) 5	190 (180-194) 5	103%	43.5 (43.0-44.2) 5	41.2 (40.5-41.8) 5	6.9 (6.5-7.2) 5
pemanggis (Pulau Pemanggil, Malaysia) [i]	178 (172-186) 6	202 (185-211) 6	113%	42.4 (39.7-44.5) 4	39.8 (37.1-42.0) 4	7.2 (7.1-7.4) 4
roa (Aur Island, Malaysia) [i]	180 (167-195) 3	223 (221-226) 3	124%	42.3 (41.9-42.5) 3	40.6 (40.3-41.1) 3	7.1 (7.1-7.3) 3
tingius (Tinggi Island, Malaysia) [i]	190 (185-199) 6	210 (192-227) 6	111%	44.8 (43.1-47.4) 7	42.2 (41.5-42.8) 6	7.5 (7.2-7.8) 7
pharus (Pisang Island, Malaysia) [i]	178 (170-184) 6	193 (185-204) 6	108%	41.9 (40.8-43.4) 5	39.9 (38.6-40.7) 5	6.9 (6.7-7.0) 5

Table 24. External, cranial and dental measurements of *Sundamys*. Measurements sourced from: [i] Pimsai (2012), [ii] Miller (1900d), [iii] Musser & Newcomb (1983), [iv] Medway (1969), [v] Miller (1913) and [vi] Robinson & Kloss (1911b).

HB	Tail	(Tail/HB)%	HF	GLS	ZB	LN	LD	LIF	BBPM3	LB	ALM1-M3
					Sundamys muelleri (Thailand) [i]						
222.5 ± 11.9 (215-240) 4	270.0 ± 20.0 (250-290) 4	122%	48.0 ± 0.8 (47-49) 4	54.8 ± 2.0 (52.2-56.7) 5	27.4 ± 1.6 (24.9-29.0) 5	21.6 ± 1.3 (20.2-23.0) 6	14.2 ± 0.8 (13.0-15.0) 5	8.8 ± 0.3 (8.2-9.3) 6	*	7.6 ± 0.4 (7.0-8.0) 6	10.1 ± 1.6 (9.8-10.3) 5
					(holotype of *validus*, Thailand) [ii]						
254	267	105%	46	55.0	28.0	22.6	14.6	9.0	*	*	11.0
					(peninsular Malaysia) [iii]						
243.1 ± 17.7 (209-299) 58	285.6 ± 19.6 (248-370) 58	116%	51.5 ± 1.9 (47-55) 62	57.2 ± 2.1 (53.3-62.2) 54	27.5 ± 1.1 (25.6-30.2) 48	23.1 ± 1.2 (21.0-25.5) 54	15.3 ± 0.8 (13.7-17.1) 54	9.6 ± 0.5 (8.6-11.1) 54	5.9 ± 0.4 (5.0-6.9) 54	6.5 ± 0.3 (5.2-7.3) 54	10.3 ± 0.4 (9.4-11.6) 54
					(peninsular Malaysia) [iv]						
165-245	195-300	105-143%	42-52	*	*	*	*	*	*	*	9.2-10.2
					(holotype of *victor*, Malaysia) [v]						
265	291	110%	49	59.6	29.2	23.7	17.0	9.0	*	*	10.4
					(holotype of *foederis*, Malaysia) [vi]						
182	239	131%	45	48.0	22.5	18.6	12.2	8.1	*	*	10.0

Table 25A. Character matrix of four murine genera: *Chiropodomys, Hapalomys, Pithecheir* and *Lenothrix*. *: measurements of the holotype of *Pithecheir parvus* are omitted (see Table 19).

Genus	Size/ Hind feet	Pelage	Skull	Tympanic bulla	Incisive foramina	Bony palate	Upper cheekteeth
Chiropodomys	Small: HB: 69-102 mm HF: 15-22 mm Tail: 94-143 mm (Table 6). Hind feet with enlarged plantar and digital pads (Fig. 14C)	Dorsal: reddish-brown. Ventral: white (Fig. 48A)	ONL: 24.0-26.7 mm. Broad and short. (Fig. 14A, Table 6)	Medium, TB ≈ 15% of GLS (Fig. 14Aix)	Short. Posterior margins in line with, or slightly pass, anterior margins of first molars (Fig. 14Avi)	Posterior border extends just beyond third molars (Fig. 14Aviii)	3.3-4.2 mm. Complex cusps, t7 on M^1 (Fig. 14Bf)
Hapalomys	Medium: HB: 140-165 mm HF: 28-33 mm Tail: 176-203 mm (Table 7). Hind feet with enlarged plantar and digital pads	Dorsal: greyish-brown. Ventral: white, yellowish tinge (Fig. 48B)	GLS: 37.9-41.5 mm. Short rostrum. (Fig. 16A, Table 7)	Large and globular, TB ≈ 21% of GLS (Fig. 16Axi)	Short. Posterior margins in front of anterior margins of first molars (Fig. 16Avii)	Posterior border in line with posterior borders of third molars (Fig. 16Ax)	7.6-8.0 mm. Complex cusps, t7 on M^1 (Fig. 16Bi)
Pithecheir	Medium: HB: 156-175* mm HF: 26-30 mm Tail: 179-205 mm (Table 19). Hind feet with enlarged plantar and digital pads	Dorsal: brownish-red. Ventral: creamy white (Fig. 48C)	GLS: 39.0-44.0* mm. Short rostrum. (Fig. 35A, Table 19)	Very large, TB ≈ 25% of GLS (Fig. 35Axi)	Short. Posterior margins in front of anterior margins of first molars (Fig. 35Avii)	Posterior border ends before, or in line with, the posterior borders of third molars (Fig. 35Ax)	7.5-8.2* mm. Complex cusps, t7 on M^1 (Fig. 35Bg)
Lenothrix	Medium: HB: 161-220 mm HF: 30-37 mm Tail: 190-270 mm (Table 8). Hind feet with enlarged plantar and digital pads	Dorsal: grey, grey-brown. Ventral: white, creamy buff (Fig. 48D)	GLS: 43.8-48.4 mm. Long rostrum. (Fig. 18A, Table 8)	Medium, TB ≈ 17% of GLS (Fig. 18Ax)	Short. Posterior margins in front of anterior margins of first molars (Fig. 18Avii)	Posterior border ends before, or in line with, the posterior borders of third molars (Fig. 18Aix)	8.4-9.3 mm. Complex cusps, t7 on M^1 (Figs 4 & 18Bd)

Table 25B. Character matrix of four murine genera: *Mus, Maxomys, Niviventer* and *Rattus*.

Genus	Size/ Hind foot	Tail	Pelage	Skull	Tympanic bulla/ lachymals	Incisive foramina	Palatal bridge	Upper cheekteeth
Mus	Small: HB: 55-90 mm HF: 14-19 mm. Hind feet elongated, small plantar pads (Fig. 28C, Table 15)	Tail: 62-95 mm. Uniform brown or bicoloured. About equal, slightly shorter/longer than HB (90-120% of HB) (Table 15)	Dorsal: grey to dark brown. Ventral: white to greyish-brown (Fig. 49A)	Small. GLS: 18.5-24.2 mm (Table 15). Coronoid process is hooked backwards; emargination on mandible well-developed (Fig. 28Axiii & xv respectively)	Tympanic bullae medium (TB ≈ 18% of GLS) (Fig. 28Aix, Table 15); lachrymals small (Fig. 28Aiii)	Long, posterior margins extend to, or pass well beyond, the anterior margins of first molars (Fig. 28Avi)	Posterior border extends beyond third molars (Fig. 28Aviii)	2.9-3.7 mm. Unlike *Maxomys, Rattus, Niviventer*, length of M^1 considerably exceeds M^2 and M^3 combined (Fig. 28B)
Maxomys (Figs. 2A, 3E, 51A)	Small to large HB: 100-280 mm, HF: 22-46 mm. Hind feet elongated, 5 or 6 medium-small plantar pads (Fig. 23C, Tables 12 & 14)	Tail: 84-287 mm. Bicoloured but less distinctly in *M. rajah*. About equal, slightly shorter/longer than HB (83-126% of HB) (Tables 12 & 14)	Dorsal: light brown to reddish-brown, grizzled with black, numerous flat spines (Fig. 3B). Ventral: white, buff, or grey (Fig. 49B)	Small to large, GLS: 29.2-49.0 mm (Tables 12 & 14). Coronoid process small; emargination on mandible weak (Fig. 23Axiv & xvi respectively)	Tympanic bullae small to medium (TB ≈ 10-16% of GLS) (Fig. 23Ax, Table 12); lachrymals large (Fig. 23Aiii)	Short and wide, posterior margins terminate well in front of anterior margins of first molars (Fig. 23Aviii)	Posterior border in line with, or slightly anterior to, posterior borders of third molars (Fig. 23Aix)	5.1-8.1 mm. M^1 and M^2 broader, more cuspidate (Fig. 23Ba,b,c,d, h,i); cusp t3 on M^2 (Fig. 23Bg) present
Niviventer (Fig. 51B)	Small to medium: HB: 110-170 mm, HF: 20-38 mm. Hind feet elongated or broad, 6 medium plantar pads (Fig. 31C, Table 17)	Tail long: 120-270 mm. Bicoloured but unicoloured in *N. cremoriventer*. Always longer than HB (110-180% of HB) (Table 17)	Dorsal: greyish, yellowish/reddish-brown, numerous flattened spines. Ventral: white, buff, yellowish white (Fig. 49C)	Medium, GLS: 32.7-43.0 mm (Table 17). Coronoid process small; emargination on mandible weak (Fig. 31Axix & xxi respectively)	Tympanic bullae small (TB ≈ 12.5% of GLS) (Fig. 31Axiii, Table 17); lachrymals small (Fig. 31Aiii)	Long and narrow, posterior margins extend to, or slightly pass, the anterior margins of first molars (Fig. 31Aix)	Posterior border in line with, or slightly before or after the posterior borders of third molars (Fig. 31Axii)	5.5-7.2 mm. M^1 and M^2 narrow and laminate (Fig. 31Ba,b,e); cusp t3 on M^2 absent
Rattus (Fig. 51C)	Small to large: HB: 100-350 mm, HF: 16-45 mm. Hind feet with 6 medium plantar pads (Fig. 37C, Tables 20, 22 & 23), pads enlarged in arboreal species, eg. *R. andamanensis*	Tail variable: 108-288 mm. Unicoloured but bicoloured in *R. norvegicus*. Shorter, about equal or considerably longer than HB (80-150% of HB) (Tables 20, 22 & 23)	Dorsal: grey/olive-brown, yellowish/orange-brown, often with thin spines (Fig. 3A). Ventral: white, grey, creamy-yellowish white (Fig. 49D)	Small to large, GLS: 28.2-59.1 mm (Tables 20, 22 & 23). Coronoid process strong; emargination on mandible well-developed (Fig. 37Axvii & xix respectively)	Tympanic bullae medium to large (TB ≈ 15-22% of GLS) (Fig. 37Axii, Table 20); lachrymals small (Fig. 37Aiii)	Long and narrow, posterior margins extend to, or slightly pass, the anterior margins of first molars (Fig. 37Aviii)	Posterior border extends beyond third molars (Fig. 37Axi)	4.6-9.0 mm. M^1 and M^2 broader, more cuspidate (Fig. 37Ba,b,c, d,i); cusp t3 on M^2 (Fig. 37Bh) present

Table 25C. Character matrix of four murine genera: *Leopoldamys, Berylmys, Bandicota* and *Sundamys*.

Genus	Size/ Hind foot	Tail	Pelage	Skull	Tympanic bulla/ lachymals	Incisive foramina	Palatal bridge	Upper cheekteeth
Leopoldamys (Fig. 51D)	Medium to large: HB: 180-290 mm. HF: 37-56 mm. Hind feet elongated, 6 plantar pads (Fig. 20C, Tables 9 & 11)	Very long: 270-420 mm. Unicoloured/ bicoloured. Always longer than HB (108-182% of HB) (Table 9 &11)	Dorsal: greyish-brown to golden-orange, short guard hairs. Ventral: dull white to yellowish-white (Fig. 50A)	Large, elongated and narrow, GLS: 51.0-62.6 mm (Tables 9 & 11 Fig. 20A). Zygomatic arches parallel/slightly convergent anteriorly (Fig. 20Aiv)	Tympanic bullae small (TB ≈ 9-11% of GLS) (Fig. 20Axi, Table 9)	Short and broad, posterior margins terminate well in front of anterior margins of first molars (Fig. 20Aviii)	Posterior border in line with, or slightly anterior to, posterior borders of third molars (Fig. 20Ax)	8.7-11.8 mm, molars laminate; t3 on M^2 mostly absent (Fig. 20B)
Berylmys (Fig. 51E)	Medium to large: HB: 190-300 mm, HF: 37-59 mm. Hind feet elongated, 6 medium plantar pads (Fig. 11C, Table 4)	Tail variable: 149-300 mm. Uni-/bicoloured, white tip in *B. bowersi*. Shorter than HB in *B. berdmorei*, longer in *B. bowersi* (Table 4)	Dorsal: dark grey, browner in old individuals, without long guard hairs. Ventral: white (Fig. 50B)	Medium to large, GLS: 38.0-63.1 mm (Table 4). Zygomatic arches strongly convergent anteriorly (Fig. 11Aiv)	Tympanic bullae variable (Fig. 11Aix, Table 4) (TB ≈ 12-13% of GLS in *B. bowersi* possibly much larger in *B. berdmorei* (18-20%)	Long, posterior margins mostly terminate in front of the anterior margins of first molars but some in line with, or beyond (Fig. 11Avi)	Posterior border in line with, or slightly anterior to posterior borders of third molars (Fig. 11Aviii)	6.6-10.5 mm, molars more cuspidate in young individuals, laminate in older; t3 on M^2 mostly absent (Figs 5A,B & 11B)
Bandicota (Fig. 51F)	Medium to large: HB: 145-350 mm, HF: 27-60 mm. Hind feet elongated, 6 to 7 plantar pads (Fig. 7C, Table 2)	Tail relatively short: 75-280 mm. Unicoloured. Usually shorter than HB (56-109% of HB) (Table 2)	Dorsal: grey brown to almost black, numerous long guard hairs (Fig. 3C). Ventral: slightly paler than dorsal (Fig. 50C)	Medium to large, GLS: 36.0-64.2 mm (Table 4). Zygomatic arches slightly convergent anteriorly (Fig. 7v)	Tympanic bullae large (TB ≈ 18-20.5% of GLS) (Fig. 7Axi, Table 2)	Long and narrow, posterior margins terminate just before, extend to, or slightly pass, the anterior margins of first molars (Fig. 7Aviii)	Posterior border extends beyond third molars (Fig. 37Ax)	6.6-12.4 mm, molars laminate, except in the youngest of individuals; cusp t3 on M^2 absent (Fig. 7B)
Sundamys (Fig. 51G)	Medium to large: HB: 165-299 mm, HF: 42-55 mm. Hind feet with 6 plantar pads (Fig. 46C, Table 24)	Tail: 195-370 mm. Unicoloured. Usually longer than HB (105-143% of HB) (Table 24)	Dorsal: tawny to dark brown, guard hairs not elongated (Fig. 3A). Ventral: white, creamy/buffy-grey (Fig. 50D)	Large, GLS: 48.0-62.2 mm (Table 24). Zygomatic arches parallel/slightly convergent anteriorly (Fig. 46Av)	Tympanic bullae small to medium (TB ≈ 11-14% of GLS) (Fig. 46Axiv, Table 24)	Usually short and broad, posterior margins before, in line with, or slightly pass the anterior margins of first molars (Fig. 46Ax)	Posterior border extends beyond third molars (Fig. 46Axiii)	9.4-11.6 mm, molars laminate, except in younger individuals; cusp t3 on M^2 present (Figs. 5G,H & 46Be)

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Appendix I. A list of sources for the localities included in each of the 28 distribution maps for the murine rodents in the study area.

MALAYSIA

Locality	Species	Fig. no.	No. on map	Reference	Page no.
16th. mile of Pahang Road, Ulu Gombok, Kuala Lumpur	*Chiropodomys gliroides*	15	14	Musser (1979)	408
	Leopoldamys sabanus	22	56	N.H.M., London	
27 km. north-east of Kuala Lumpur	*Niviventer cremoriventer*	33	45	Musser (1973)	11
Ampang Selangor	*Rattus tanezumi*	44	99	Hill (1960)	70
Aring	*Rattus exulans*	41	16	Bonhote (1900d)	879
	Rattus tanezumi	44	90	Bonhote (1900d)	878
Aur Island	*Rattus exulans*	41	27	Medway (1969)	75
	Rattus tiomanicus	45	37	Miller (1913b)	10
Ayer Bangi	*Pithecheir parvus*	36	8	Lim and Muul (1975)	182
Ayer Kring	*Maxomys surifer*	26	92	N.H.M., London	
Bagan Datoh	*Rattus argentiventer*	40	27	Chasen (1933)	20
	Rattus tanezumi	44	91	Chasen (1933)	16
Bagan Serai	*Rattus argentiventer*	40	22	Chasen (1933)	19
Bagan Triang	*Rattus argentiventer*	40	15	Chasen (1933)	19
Bakok	*Chiropodomys gliroides*	15	26	Musser (1979)	408
Bekok	*Maxomys rajah*	25	24	A.M.N.H.	
Belatop	*Hapalomys longicaudatus*	17	3	N.H.M., London	
Bentong	*Maxomys surifer*	26	87	N.H.M., London	
	Maxomys whiteheadi	27	21	N.H.M., London	
Bentong Forest	*Chiropodomys gliroides*	15	13	Musser (1979)	408
Binting Bidai	*Leopoldamys sabanus*	22	52	N.H.M., London	
Briah	*Rattus argentiventer*	40	18	Chasen (1933)	19
Brinchang Peak	*Niviventer cremoriventer*	33	29	N.H.M., London (BM62.746)	
Bruas	*Rattus annandalei*	39	2	Muul and Lim (1971)	435
Bukit Bangkong	*Maxomys rajah*	25	15	N.H.M., London	
Bukit Besar	*Maxomys surifer*	26	98	Bonhote (1903a)	26
	Niviventer cremoriventer	33	18	Bonhote (1903b)	26
	Niviventer fulvescens	34	28	Bonhote (1903b)	125
Bukit Besi	*Niviventer cremoriventer*	33	33	Musser (1973)	11
	Sundamys muelleri	47	33	Musser & Newcomb (1983)	406
Bukit Cherakah	*Rattus annandalei*	39	7	Muul & Lim (1971)	435
Bukit Dantai	*Maxomys rajah*	25	23	Sody (1941)	292
Bukit Fraser	*Rattus tiomanicus*	45	26	Hill (1960)	71
	Maxomys inas	24	6	N.H.M., London	
Bukit Fraser (above Semangko Pass)	*Leopoldamys ciliatus*	21	7	N.H.M., London	
Bukit Gantang	*Maxomys surifer*	26	82	N.H.M., London	
	Maxomys whiteheadi	27	19	N.H.M., London	
Bukit Jong	*Rattus exulans*	41	15	Hill (1960)	83
	Rattus tiomanicus	45	18	Hill (1960)	71
Bukit Kutu	*Chiropodomys gliroides*	15	11	Hill (1960)	105
	Lenothrix canus	19	5	Muul & Lim (1971)	435
	Leopoldamys ciliatus	21	5	Muul & Lim (1971)	435
	Maxomys inas	24	7	N.H.M., London	
	Pithecheir parvus	36	2	Kloss (1916e)	250
Bukit Lagong	*Chiropodomys gliroides*	15	16	Musser (1979)	408
	Lenothrix canus	19	7	N.H.M., London	
	Maxomys rajah	25	18	N.H.M., London	
	Maxomys surifer	26	91	N.H.M., London	
	Maxomys whiteheadi	27	24	N.H.M., London	
	Niviventer cremoriventer	33	42	Musser (1973)	11
	Rattus annandalei	39	8	Muul & Lim (1971)	435
	Sundamys muelleri	47	40	Musser & Newcomb (1983)	406
Bukit Lagong Forest Reserve	*Leopoldamys sabanus*	22	63	N.H.M., London	
	Niviventer cremoriventer	33	43	Musser (1973)	11
Bukit Lanjang	*Leopoldamys sabanus*	22	64	N.H.M., London	
	Rattus annandalei	39	9	Muul & Lim (1971)	435
Bukit Lanjang Forest Reserve	*Lenothrix canus*	19	9	N.H.M., London	
	Maxomys rajah	25	16	Fain et al. (1980)	111

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Maxomys whiteheadi	27	25	N.H.M., London	
	Rattus tiomanicus	45	27	Fain et al. (1980)	109
	Sundamys muelleri	47	39	N.H.M., Thailand	
Bukit Lantar	*Leopoldamys sabanus*	22	69	N.H.M., London	
Bukit Mandol	*Chiropodomys gliroides*	15	24	Musser (1979)	408
	Lenothrix canus	19	14	Muul & Lim (1971)	435
	Niviventer cremoriventer	33	47	Musser (1973)	11
	Rattus annandalei	39	15	Muul & Lim (1971)	435
Bukit Perangoh	*Pithecheir parvus*	36	6	N.H.M., London	
Bukit Tampin	*Maxomys surifer*	26	96	N.H.M., London	
Bukit Tangga	*Leopoldamys sabanus*	22	70	N.H.M., London	
	Maxomys whiteheadi	27	31	N.H.M., London	
Cameron Highlands	*Niviventer cameroni*	32	1	Chasen (1940a)	176
Changkat Mentri	*Sundamys muelleri*	47	32	Musser & Newcomb (1983)	406
Cheras	*Maxomys rajah*	25	21	N.H.M., London	
	Maxomys surifer	26	93	N.H.M., London	
	Maxomys whiteheadi	27	30	N.H.M., London	
	Rattus annandalei	39	12	Hill (1960)	85
	Rattus argentiventer	40	31	Chasen (1933)	20
	Rattus tiomanicus	45	30	Hill (1960)	71
	Leopoldamys sabanus	22	67	N.H.M., London	
Dayang Bunting	*Maxomys surifer*	26	72	Medway (1969)	79
E. Perhentian Island	*Maxomys surifer*	26	73	Kloss (1911)	119
	Maxomys whiteheadi	27	11	Yong (1971)	87
	Rattus tiomanicus	45	16	Chasen (1940a)	155
Fraser's Hill	*Berylmys bowersii*	13	12	Yong & Dhaliwal (1970)	155
	Leopoldamys sabanus	22	57	Yong (1970)	360
Genting	*Leopoldamys sabanus*	22	50	N.H.M., London	
	Niviventer cremoriventer	33	36	Musser (1973)	11
Genting Sempat	*Niviventer cremoriventer*	33	39	Musser (1973)	11
Genting Simpah	*Leopoldamys sabanus*	22	59	Yong (1970)	360
Georgetown, Penang Island	*Bandicota bengalensis*	8	2	Thomas (1907d)	204
	Rattus norvegicus	42	4	Flower (1900)	362
Ginting Bidai	*Leopoldamys sabanus*	22	55	N.H.M., London	
	Maxomys surifer	26	88	N.H.M., London	
	Maxomys whiteheadi	27	22	N.H.M., London	
	Sundamys muelleri	47	36	Robinson & Kloss (1911b)	246
Gombak	*Maxomys whiteheadi*	27	27	N.H.M., London	
Gombak Forest Reserve	*Chiropodomys gliroides*	15	17	Fain et al. (1980)	117
	Rattus tanezumi	44	96	Fain et al. (1980)	109
Gomok (Johore State) (Malaysia)	*Rattus exulans*	41	Not located	Hill (1960)	83
Great Redang Island	*Maxomys surifer*	26	74	Kloss (1911)	119
	Rattus tiomanicus	45	17	Hill (1960)	82
Gunong Benom	*Chiropodomys gliroides*	15	10	Musser (1979)	408
	Lenothrix canus	19	4	Muul & Lim (1971)	435
	Leopoldamys ciliatus	21	4	Yong (1970)	360
	Leopoldamys sabanus	22	51	Yong (1970)	360
	Maxomys inas	24	5	N.H.M., London	
	Pithecheir parvus	36	1	Muul & Lim (1971)	436
Gunong Bunga Buah	*Leopoldamys ciliatus*	21	9	Yong (1968)	174
Gunong Ijan	*Leopoldamys sabanus*	22	48	N.H.M., London	
	Maxomys surifer	26	83	N.H.M., London	
Gunong Ijau	*Niviventer cremoriventer*	33	25	Musser (1973)/N.H.M., London	11
	Rattus norvegicus	42	5	Hill (1960)	105
Gunong Kutu	*Chiropodomys gliroides*	15	5	Musser (1979)	408
Gunong Mengkuang	*Chiropodomys gliroides*	15	9	Hill (1960)	105
	Leopoldamys ciliatus	21	6	N.H.M., London	
	Maxomys inas	24	8	N.H.M., London	
Gunong Semanggul	*Maxomys whiteheadi*	27	18	N.H.M., London	
	Niviventer cremoriventer	33	24	Musser (1973)	11
	Rattus argentiventer	40	23	Chasen (1933)	19
Gunong Tahan	*Chiropodomys gliroides*	15	6	Musser (1979)	
	Leopoldamys ciliatus	21	3	N.H.M., London	
	Maxomys inas	24	4	N.H.M., London	

Locality	Species	Fig. no.	No. on map	Reference	Page no.
Gunong Tampin	*Rattus tiomanicus*	45	31	Hill (1960)	71
Gunong Ulu Kali	*Leopoldamys ciliatus*	21	8	Yong (1970)	360
Gunung Kerbau	*Niviventer cremoriventer*	33	27	Musser (1973)	11
Gunung Sinyom	*Niviventer cremoriventer*	33	37	Musser (1973)	11
Gurun	*Maxomys surifer*	26	75	N.H.M., London	
	Rattus norvegicus	42	3	Hill (1960)	105
Jarak Island	*Rattus tiomanicus*	45	25	Bonhote (1905b)	69
Jaram	*Chiropodomys gliroides*	15	15	Flower (1900)	361
Jelebu District	*Leopoldamys ciliatus*	21	12	Medway (1969)	82
	Maxomys inas	24	9	Medway (1969)	80
Jenka	*Leopoldamys sabanus*	22	53	N.H.M., London	
	Maxomys rajah	25	11	Fain *et al*. (1980)/N.H.M., London	111
Jeram Kawan	*Maxomys rajah*	25	9	N.H.M., London	
	Maxomys surifer	26	84	Bonhote (1903a)	26
Johor Bahru	*Maxomys surifer*	26	103	Bonhote (1903a)	8
	Mus musculus	30	3	Bonhote (1906b)	11
	Rattus exulans	41	31	Bonhote (1906b)	11
	Rattus norvegicus	42	7	Bonhote (1906b)	11
	Rattus tanezumi	44	103	Bonhote (1906b)	11
Ka Kuli (poss. Kangka Kuli?)	*Sundamys muelleri*	47	Not located	Miller (1913b)	16
Kaban Island	*Rattus tiomanicus*	45	32	Hill (1960)	77
Kaki Bukit	*Leopoldamys sabanus*	22	39	Yong (1970)	360
Kampong Awak	*Maxomys rajah*	25	13	Fain et al. (1980)	113
Kampong Janda Baik	*Berylmys bowersii*	13	13	Yong (1968)	174
	Leopoldamys sabanus	22	61	Yong (1968)	174
	Sundamys muelleri	47	38	Yong (1968)	174
Kampong Janda Buah	*Leopoldamys sabanus*	22	65	Yong (1968)	174
Kampong Perigi	*Mus caroli*	29	4	Langham and Ming (1976)	147
Kampong Pulau Betong	*Rattus argentiventer*	40	14	Liat et al. (1971)	71
Kangka	*Rattus tiomanicus*	45	41	Bonhote (1906b)	10
	Rattus exulans	41	32	Bonhote (1906b)	11
Kangka Ketcho	*Maxomys surifer*	26	101	Bonhote (1903a)	8
Kangka Kuli	*Maxomys surifer*	26	100	Bonhote (1903a)	8
	Sundamys muelleri	47	48	Bonhote (1906b)	10
Kangka Senibong	*Rattus tanezumi*	44	104	Bonhote (1906b)	11
Karang	*Leopoldamys sabanus*	22	72	N.H.M., London	
Kedah Peak	*Chiropodomys gliroides*	15	4	Musser (1979)	408
	Leopoldamys ciliatus	21	1	Medway (1969)	82
	Leopoldamys sabanus	22	42	Robinson & Kloss (1916)	223
	Maxomys surifer	26	76	Robinson & Kloss (1916)	223
	Maxomys whiteheadi	27	12	N.H.M., London	
	Niviventer cremoriventer	33	19	Musser (1973)	11
	Rattus argentiventer	40	13	Chasen (1933)	20
	Rattus tiomanicus	45	13	Robinson & Kloss (1916)	223
Kedah State	*Berylmys bowersii*	13	9	Musser & Newcomb (1983)	379
Kelanta	*Hapalomys longicaudatus*	17	5	Musser (1972)	14
Kemidak	*Lenothrix canus*	19	15	Muul & Lim (1971)	435
Kepong	*Berylmys bowersii*	13	15	A.M.N.H.	
	Maxomys whiteheadi	27	26	A.M.N.H.	
	Niviventer cremoriventer	33	46	Musser (1973)	11
	Sundamys muelleri	47	41	Musser & Newcomb (1983)	406
Kepong Forest Reserve	*Chiropodomys gliroides*	15	18	Musser (1979)	408
Kepong, 8 miles N.W.of Kuala Lumpur	*Lenothrix canus*	19	12	N.H.M., London	
Klang	*Rattus annandalei*	39	14	A.M.N.H.	
Klang Gates	*Leopoldamys sabanus*	22	54	N.H.M., London	
	Maxomys rajah	25	17	N.H.M., London	
	Rattus exulans	41	20	Hill (1960)	83
	Rattus tanezumi	44	98	Chasen (1933)	16
Kledang Hill	*Rattus tanezumi*	44	86	Chasen (1933)	16
Kota Bharu	*Niviventer fulvescens*	34	22	Medway (1969)	79
	Rattus norvegicus	42	2	Bonhote (1900d)	879
Kota Tongkat	*Maxomys surifer*	26	86	N.H.M., London	
Krian	*Rattus argentiventer*	40	19	Sody (1941a)	269
Krian Road	*Maxomys rajah*	25	7	N.H.M., London	

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Rattus tanezumi	44	85	Chasen (1933)	16
Kuala Berang	*Lenothrix canus*	19	3	Muul & Lim (1971)	435
	Niviventer cremoriventer	33	28	Musser (1973)	11
Kuala Jerlun	*Bandicota indica*	9	10	Musser and Brothers (1994)	55
Kuala Kubu	*Leopoldamys sabanus*	22	58	A.M.N.H.	
Kuala Kurau	*Rattus argentiventer*	40	20	Chasen (1933)	19
Kuala Longnai	*Sundamys muelleri*	47	28	Musser & Newcomb (1983)	406
Kuala Lumpur	*Berylmys bowersii*	13	16	Harrison (1956)	6
	Chiropodomys gliroides	15	20	Harrison (1956)	6
	Lenothrix canus	19	10	Harrison (1956)	6
	Leopoldamys sabanus	22	66	Harrison (1956)	6
	Maxomys rajah	25	20	Harrison (1956)	6
	Maxomys whiteheadi	27	29	F.M.N.H.	
	Niviventer cremoriventer	33	44	Lim et al. (1965)	610
	Rattus annandalei	39	13	Lim et al. (1965)	610
	Rattus argentiventer	40	30	Harrison (1956)	6
	Rattus exulans	41	21	U.S.N.M.	
	Rattus norvegicus	42	6	Lim et al. (1965)	610
	Rattus tanezumi	44	100	Chasen (1933)	16
	Rattus tiomanicus	45	29	Harrison (1956)	6
	Sundamys muelleri	47	43	Harrison (1956)	6
Kuala Lumpur (near)	*Hapalomys longicaudatus*	17	7	Musser (1972)	15
Kuala Selangor	*Rattus annandalei*	39	6	A.M.N.H.	
	Rattus tanezumi	44	94	Chasen (1933)	16
Kuala Tahan	*Niviventer cremoriventer*	33	34	Musser (1973)	11
Kudong	*Lenothrix canus*	19	17	Muul & Lim (1971)	435
	Sundamys muelleri	47	50	Musser & Newcomb (1983)	406
Labis Forest Reserve	*Pithecheir parvus*	36	9	Lim & Muul (1975)	182
Labong Edan	*Maxomys whiteheadi*	27	20	N.H.M., London	
Langkawi Island	*Leopoldamys sabanus*	22	40	Miller (1900c)	188
	Rattus exulans	41	12	Medway (1969)	75
	Rattus tiomanicus	45	10	Miller (1913b)	13
Larut Hills	*Rattus tanezumi*	44	87	Chasen (1933)	16
Lenggong	*Maxomys surifer*	26	80	N.H.M., London	
	Maxomys whiteheadi	27	15	N.H.M., London	
	Niviventer cremoriventer	33	23	Musser (1973)	11
	Niviventer fulvescens	34	24	Medway (1969)	79
Lerek	*Lenothrix canus*	19	2	Muul & Lim (1971)	435
Lubok Tamang	*Niviventer cremoriventer*	33	31	N.H.M., London	
	Niviventer cremoriventer	33	41	Musser (1973)	11
Malacca	*Rattus exulans*	41	25	Flower (1900)	361
	Sundamys muelleri	47	46	N.H.M., London	
Malaysian peninsular (no exact locality)	*Chiropodomys gliroides*	15	8	Peters (1868)	448
Maxwell's Hill	*Berylmys bowersii*	13	10	N.H.M., London	
	Leopoldamys sabanus	22	46	N.H.M., London	
	Maxomys inas	24	2	Medway (1969)	80
	Maxomys surifer	26	81	N.H.M., London	
	Niviventer cremoriventer	33	26	Musser (1973)	11
	Niviventer fulvescens	34	25	N.H.M., London	
	Rattus argentiventer	40	24	Hill (1960)	71
	Rattus exulans	41	14	Hill (1960)	83
	Sundamys muelleri	47	29	Musser & Newcomb (1983)	406
Meru	*Rattus annandalei*	39	10	Muul & Lim (1971)	435
Meru Forest Reserve	*Pithecheir parvus*	36	5	Muul & Lim (1971)	436
Mount Lun Chun	*Maxomys whiteheadi*	27	35	Bonhote (1906b)	10
Mount Pulai	*Leopoldamys sabanus*	22	73	N.H.M., London	
	Maxomys whiteheadi	27	36	Bonhote (1906b)	10
Mt. Brinchang	*Maxomys inas*	24	3	Fain et al. (1980)	114
	Niviventer fulvescens	34	27	N.H.M., London	
Mt. Inas	*Leopoldamys ciliatus*	21	2	Bonhote (1900d)	879
	Maxomys inas	24	1	Bonhote (1906b)	9
Muka Head Forest Reserve, Penang Island	*Lenothrix canus*	19	1	Lim et al. (1971)	72

Locality	Species	Fig. no.	No. on map	Reference	Page no.
Nyalas	*Maxomys whiteheadi*	27	32	N.H.M., London	
Padang Sireh	*Maxomys surifer*	26	68	N.H.M., London	
Padang Tuan	*Maxomys whiteheadi*	27	33	N.H.M., London	
Pahang (State)	*Rattus argentiventer*	40	28	A.M.N.H.	
	Rattus exulans	41	18	U.M.M.Z.	
Pahang Road, 16 miles north-east of Kuala Lumpur	*Lenothrix canus*	19	11	N.H.M., London	
	Niviventer cremoriventer	33	49	N.H.M., London	
Pangkor Besar Island	*Leopoldamys sabanus*	22	49	N.H.M., London	
	Maxomys rajah	25	10	N.H.M., London	
	Rattus tiomanicus	45	23	Chasen (1933)	8
Parit Buntar	*Rattus argentiventer*	40	16	Chasen (1933)	19
Pasir Gudang	*Rattus exulans*	41	33	Bonhote (1906b)	11
	Rattus tanezumi	44	105	Bonhote (1906b)	11
	Rattus tiomanicus	45	42	Bonhote (1906b)	10
Paya Island	*Rattus tiomanicus*	45	12	Chasen & Kloss (1931)	79
Pelarit	*Maxomys surifer*	26	67	N.H.M., London	
	Maxomys whiteheadi	27	10	N.H.M., London	
	Niviventer fulvescens	34	21	N.H.M., London	
	Rattus tanezumi	44	83	Chasen (1933)	16
Pelepak	*Maxomys surifer*	26	104	Bonhote (1903a)	8
	Maxomys whiteheadi	27	37	Bonhote (1906b)	10
	Rattus exulans	41	30	Bonhote (1906b)	11
	Rattus tanezumi	44	101	Bonhote (1906b)	11
	Rattus tiomanicus	45	40	Bonhote (1906b)	10
Pemanggil Island	*Maxomys surifer*	26	95	Robinson (1912)	593
	Rattus tiomanicus	45	35	Chasen (1940a)	156
Penang Island	*Rattus tanezumi*	44	84	Flower (1900)	361
	Mus musculus	30	2	Cantor (in Blyth, 1865)	194
	Leopoldamys sabanus	22	43	Chasen (1940a)	165
	Niviventer cremoriventer	33	20	Musser (1973)	11
	Rattus exulans	41	13	Medway (1969)	75
	Rattus tiomanicus	45	14	Chasen (1933)	8
Perak (State)	*Rattus tanezumi*	44	89	Bonhote (1903a)	30
Perlis	*Bandicota indica*	9	9	Harrison (1956)	27
Pisang Island	*Rattus tiomanicus*	45	39	Hill (1960)	75
Pulai	*Maxomys rajah*	25	25	N.H.M., London	
	Maxomys surifer	26	102	Bonhote (1903a)	8
	Rattus tanezumi	44	102	Bonhote (1906b)	11
Pulau Angsa	*Rattus tanezumi*	44	97	Chasen (1933)	16
Pulau Aur	*Maxomys surifer*	26	97	Robinson (1912)	594
Pulau Babi	*Rattus tiomanicus*	45	36	Hill (1960)	77
Pulau Dayang Bunting	*Rattus tiomanicus*	45	11	Hill (1960)	76
Pulau Rumpia	*Rattus tiomanicus*	45	24	Robinson & Kloss (1911a)	169
Pulo Langkawi	*Maxomys surifer*	26	69	Miller (1900e)	189
	Niviventer cremoriventer	33	17	Miller (1900e)	191
Rawang	*Maxomys rajah*	25	12	N.H.M., London	
	Maxomys surifer	26	89	N.H.M., London	
	Rattus tanezumi	44	95	Chasen (1933)	16
Rumpin River (near mouth of)	*Sundamys muelleri*	47	45	Miller (1913b)	16
Runuk Tanjong	*Maxomys rajah*	25	8	N.H.M., London	
Sap Patchung	*Maxomys whiteheadi*	27	Not located	N.H.M., London	
Segamat	*Rattus exulans*	41	26	Hill (1960)	83
Selensing	*Rattus argentiventer*	40	25	Chasen (1933)	19
Semangko Pass	*Hapalomys longicaudatus*	17	6	Musser (1972)	15
	Rattus exulans	41	19	Hill (1960)	83
	Rattus tanezumi	44	92	Hill (1960)	70
	Sundamys muelleri	47	34	Musser & Newcomb (1983)	406
	Chiropodomys gliroides	15	12	Musser (1979)	408
Semangoh [Semangko]	*Maxomys whiteheadi*	27	17	N.H.M., London	
Sembrong / Sembrong River	*Sundamys muelleri*	47	47	Miller (1913b)	16
Si Karang	*Maxomys surifer*	26	99	N.H.M., London	
Sribuat Island	*Rattus tiomanicus*	45	33	Hill (1960)	76
Subang	*Lenothrix canus*	19	8	Muul & Lim (1971)	435

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Niviventer cremoriventer	33	48	Musser (1973)	11
	Sundamys muelleri	47	42	Musser & Newcomb (1983)	406
Subang Forest Reserve	*Maxomys rajah*	25	19	Fain et al. (1980)/A.M.N.H.	117
	Maxomys whiteheadi	27	28	A.M.N.H.	
	Pithecheir parvus	36	4	Muul & Lim (1971)	436
	Rattus annandalei	39	11	A.M.N.H.	
	Rattus tiomanicus	45	28	Fain *et al*. (1980)	109
Sungei Buloh	*Lenothrix canus*	19	13	Kloss (1931b)	105
Sungei Jengka Forest Reserve	*Pithecheir parvus*	36	3	Lim & Muul (1975)	182
Sungei Kilim, Pulau Langkawi	*Leopoldamys sabanus*	22	41	N.H.M., London	
	Maxomys surifer	26	70	N.H.M., London	
Sungei Kubong, Pulau Langkawi	*Maxomys surifer*	26	71	N.H.M., London	
Sungei Tua	*Rattus argentiventer*	40	29	Musser (1973)	7
Sungkai	*Rattus annandalei*	39	4	Bonhote (1903a)	30
Tahan	*Niviventer cremoriventer*	33	35	Musser (1973)	11
Taiping	*Berylmys bowersii*	13	11	N.H.M., London	
	Leopoldamys sabanus	22	47	N.H.M., London	
	Niviventer fulvescens	34	26	Medway (1969)	79
	Rattus annandalei	39	1	Hill (1960)	84
	Rattus argentiventer	40	26	Chasen (1933)	19
	Rattus tanezumi	44	88	Chasen (1933)	16
Taiping Hill (near)	*Rattus tiomanicus*	45	21	Hill (1960)	71
Tamok	*Chiropodomys gliroides*	15	25	Musser (1979)	408
	Lenothrix canus	19	16	Muul & Lim (1971)	435
	Sundamys muelleri	47	49	Musser & Newcomb (1983)	406
Tamok Forest Reserve	*Maxomys whiteheadi*	27	34	A.M.N.H.	
Tanah Wat Forest	*Pithecheir parvus*	36	7	N.H.M., London	
Tanjong Dungan	*Niviventer cremoriventer*	33	32	Musser (1973)	11
Tanjong Hantu (Tanjong Tuan)	*Maxomys surifer*	26	85	N.H.M., London	
	Niviventer cremoriventer	33	30	N.H.M., London	
	Rattus annandalei	39	3	N.H.M., London	
	Rattus exulans	41	17	Hill (1960)	83
	Rattus tiomanicus	45	22	Hill (1960)	71
Tanjong Karang	*Rattus tanezumi*	44	93	Hill (1960)	70
Tanjong Malim	*Niviventer cremoriventer*	33	38	Musser (1973)	11
	Rattus annandalei	39	5	Muul & Lim (1971)	435
Tanjong Piandang	*Rattus argentiventer*	40	17	Chasen (1933)	19
Tanjong Rabok	*Chiropodomys gliroides*	15	21	Musser (1979)	408
Tanjong Surat	*Rattus tanezumi*	44	106	Hill (1960)	70
Tebraun	*Rattus exulans*	41	29	Bonhote (1906b)	11
Telok Anson	*Rattus argentiventer*	40	21	Chasen (1933)	19
Telok Bahang, Penang Island	*Niviventer cremoriventer*	33	21	Musser (1973)	11
	Maxomys surifer	26	78	N.H.M., London	
Telom	*Rattus tiomanicus*	45	20	Bonhote (1903a)	29
	Sundamys muelleri	47	31	Musser & Newcomb (1983)	406
Telom River	*Chiropodomys gliroides*	15	7	Musser (1979)	408
Temengoh	*Maxomys surifer*	26	77	N.H.M., London	
	Maxomys whiteheadi	27	13	N.H.M., London	
	Niviventer cremoriventer	33	22	Musser (1973)	11
	Niviventer fulvescens	34	23	Medway (1969)	79
	Rattus tiomanicus	45	15	Hill (1960)	71
	Sundamys muelleri	47	27	N.H.M., London	
Templer Park	*Leopoldamys sabanus*	22	60	Fain et al. (1980)	110
Tenggol Island	*Rattus tiomanicus*	45	19	Yong (1971)	89
Teroi Tua	*Mus caroli*	29	3	Langham & Ming (1976)	147
Tinggi Island	*Rattus exulans*	41	28	Medway (1969)	75
	Rattus tiomanicus	45	38	Miller (1913b)	9
Tioman Island	*Leopoldamys sabanus*	22	71	Miller (1903a)	28
	Maxomys surifer	26	94	Kloss (1908)	145
	Niviventer cremoriventer	33	50	Musser (1973)	11
	Rattus exulans	41	24	Miller (1900a)	178/213
	Rattus tiomanicus	45	34	Miller (1900a)	209
Titi Batu	*Mus caroli*	29	2	Langham & Ming (1976)	147
Tredoh Peak	*Maxomys whiteheadi*	27	16	N.H.M., London	

Locality	Species	Fig. no.	No. on map	Reference	Page no.
Tulai Island	*Rattus exulans*	41	23	Medway (1969)	75
Ulu Cemperoh	*Sundamys muelleri*	47	35	Musser & Newcomb (1983)	406
Ulu Gombak	*Chiropodomys gliroides*	15	19	Musser (1979)	408
	Lenothrix canus	19	6	Muul & Lim (1971)	435
	Sundamys muelleri	47	37	Musser & Newcomb (1983)	406
Ulu Gombak, 20th. mile [of] Pahang Road	*Leopoldamys sabanus*	22	62	Rudd (1965)	589
	Leopoldamys ciliatus	21	10	Rudd (1965)	589
	Maxomys rajah	25	14	Rudd (1965)	589
	Maxomys surifer	26	90	Rudd (1965)	589
	Maxomys whiteheadi	27	23	Rudd (1965)	590
	Berylmys bowersii	13	14	Rudd (1965)	590
Ulu Gombok	*Niviventer cremoriventer*	33	40	Musser (1973)	11
Ulu Kelantan	*Hapalomys longicaudatus*	17	4	Musser (1972)	14
Ulu Langat	*Berylmys bowersii*	13	17	N.H.M., London	
	Chiropodomys gliroides	15	22	Musser (1979)	408
	Leopoldamys sabanus	22	68	N.H.M., London	
	Rattus exulans	41	22	U.S.N.M.	
	Sundamys muelleri	47	44	Musser & Newcomb (1983)	406
Ulu Langat Forest Reserve	*Chiropodomys gliroides*	15	23	Musser (1979)	408
	Leopoldamys ciliatus	21	11	N.H.M., London	
	Maxomys rajah	25	22	N.H.M., London	
Ulu Selama	*Leopoldamys sabanus*	22	44	N.H.M., London	
	Maxomys rajah	25	6	N.H.M., London	
	Maxomys surifer	26	79	N.H.M., London	
	Maxomys whiteheadi	27	14	N.H.M., London	
Ulu Temengor	*Sundamys muelleri*	47	30	Robinson & Kloss (1911b)	245
Ulu Trengganu	*Leopoldamys sabanus*	22	45	Yong (1970)	360
Yunong Jang	*Berylmys bowersii*	13	Not located	N.H.M., London	
MYANMAR					
5 miles south of Karathuri	*Chiropodomys gliroides*	15	1	Musser (1979)	406
Bankachon	*Chiropodomys gliroides*	15	2	Musser (1979)	406
	Hapalomys longicaudatus	17	1	Musser (1972)	13
	Leopoldamys sabanus	22	11	Wroughton (1915)	715
	Maxomys surifer	26	14	Kloss (1919b)	376
	Niviventer fulvescens	34	2	Wroughton (1915)	714
	Rattus tanezumi	44	16	Hinton (1919)	400
Banlaw	*Rattus tanezumi*	44	5	Hinton (1919)	400
Bentinck Island	*Leopoldamys sabanus*	22	4	Miller (1903a)	29
	Maxomys surifer	26	7	Miller (1903a)	38
Bokpyin	*Niviventer fulvescens*	34	1	Miller (1913b)	20
Clara Island	*Leopoldamys sabanus*	22	8	Miller (1913b)	20
Criddles Island	*Rattus tanezumi*	44	8	Lindsay (1926)	48
Domel Island	*Leopoldamys sabanus*	22	6	Miller (1913b)	19
	Maxomys surifer	26	9	Miller (1903a)	38
Hastings Island	*Leopoldamys sabanus*	22	13	Miller (1913b)	20
	Maxomys surifer	26	15	Lindsay (1926)	48
	Rattus tanezumi	44	18	Miller (1913b)	14
Helfer Island	*Leopoldamys sabanus*	22	Not located	Miller (1913b)	20
	Rattus tanezumi	44		Miller (1913b)	14
James Island	*Leopoldamys sabanus*	22	10	Miller (1913b)	19
	Rattus tanezumi	44	13	Miller (1913b)	15
King's Island	*Leopoldamys sabanus*	22	2	Lindsay (1926)	48
	Maxomys surifer	26	2	Lindsay (1926)	48
	Rattus argentiventer	40	2	Lindsay (1926)	47
	Rattus tanezumi	44	2	Lindsay (1926)	48
Kisseraing Island	*Leopoldamys sabanus*	22	5	Miller (1913b)	20
	Maxomys surifer	26	8	Lindsay (1926)	48
Lampi Island	*Maxomys surifer*	26	11	Lindsay (1926)	48
Loughborough Island	*Maxomys surifer*	26	12	Miller (1903a)	38
	Rattus tanezumi	44	14	Miller (1913b)	15
Malcolm Island	*Leopoldamys sabanus*	22	7	Lindsay (1926)	48

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Maxomys surifer	26	10	Lindsay (1926)	48
	Rattus tanezumi	44	10	Lindsay (1926)	48
Maliwun	*Maxomys surifer*	26	13	N.H.M., London	
	Rattus argentiventer	40	5	Wroughton (1915)	715
	Rattus tanezumi	44	15	Hinton (1919)	400
	Sundamys muelleri	47	2	Musser & Newcomb (1983)	405
Mergui (Myeik)	*Bandicota bengalensis*	8	1	Musser & Brothers (1994)	55
Mergui [Myeik] (no exact location)	*Berylmys berdmorei*	12	2	Blyth (1851a)	173
Nathé Mine	*Berylmys berdmorei*	12	1	Lindsay (1926)	47
	Rattus tanezumi	44	1	Lindsay (1926)	48
Ross Island	*Leopoldamys sabanus*	22	3	Lindsay (1926)	48
	Maxomys surifer	26	5	Lindsay (1926)	48
	Rattus argentiventer	40	3	Lindsay (1926)	47
	Rattus tanezumi	44	7	Lindsay (1926)	48
Sir John Hayes Island	*Maxomys surifer*	26	6	Lindsay (1926)	48
	Rattus tanezumi	44	9	Lindsay (1926)	48
St. Luke Island	*Leopoldamys sabanus*	22	12	Miller (1903a)	30
St. Matthew Island	*Leopoldamys sabanus*	22	14	Miller (1903a)	29
	Maxomys surifer	26	17	Miller (1903a)	38
Sullivan Island (Lampi Island)	*Leopoldamys sabanus*	22	9	Miller (1913b)	20
	Niviventer cremoriventer	33	1	Miller (1903a)	35
	Rattus tanezumi	44	12	Miller (1913b)	15
Tagoot	*Rattus tanezumi*	44	3	Hinton (1919)	400
Taok Plateau	*Maxomys surifer*	26	Not located	N.H.M., London	
Tavoy Island	*Leopoldamys sabanus*	22	1	N.H.M., London	
	Maxomys surifer	26	1	Lindsay (1926)	48
	Rattus argentiventer	40	1	Lindsay (1926)	47
Tenasserim River	*Maxomys surifer*	26	3	N.H.M., London	
Tenasserim Town	*Rattus argentiventer*	40	4	Wroughton (1915)	715
	Rattus tanezumi	44	6	Hinton (1919)	400
Thaget	*Maxomys surifer*	26	4	Wroughton (1915)	714
	Rattus tanezumi	44	4	Hinton (1919)	400
	Sundamys muelleri	47	1	Musser & Newcomb (1983)	405
Victoria Island	*Leopoldamys sabanus*	22	15	Wroughton (1915)	715
	Maxomys surifer	26	18	N.H.M., London	
	Rattus tanezumi	44	19	Hinton (1919)	400
Victoria Point	*Maxomys surifer*	26	16	N.H.M., London	
	Niviventer fulvescens	34	3	Wroughton (1915)	714
	Rattus argentiventer	40	6	Wroughton (1915)	715
	Rattus tanezumi	44	17	Hinton (1919)	400
SINGAPORE					
Botanical Gardens	*Rattus annandalei*	39	16	Kloss (1908)	146
Changi	*Maxomys surifer*	26	105	Robinson & Kloss (1911a)	170
Singapore (Island)	*Mus musculus*	30	4	Flower (1900)	362
	Rattus norvegicus	42	8	Dhaliwal (1961)	351
	Rattus tanezumi	44	107	Chasen (1933)	16
	Maxomys rajah	25	26	Hill (1960)	90
	Rattus tiomanicus	45	43	Dhaliwal (1961)	351
Tanglin	*Rattus exulans*	41	34	Flower (1900)	362
THAILAND					
30 km. west of Chumphon	*Niviventer fulvescens*	34	5	Abe (1983)	151
Adang Island	*Rattus tanezumi*	44	67	Miller (1900e)	190
Ao Ko	*Niviventer fulvescens*	34	8	N.H.M., Thailand	
	Rattus tanezumi	44	40	N.H.M., Thailand	
Ban Bang Bane	*Rattus tanezumi*	44	24	N.H.M., Thailand	
Ban Bang Khla, Kho Samui	*Rattus exulans*	41	3	N.H.M., Thailand	
	Rattus tanezumi	44	38	N.H.M., Thailand	
Ban Bang Nawn	*Niviventer cremoriventer*	33	4	Musser (1973)	11
Ban Bang Non	*Maxomys surifer*	26	25	N.H.M., Thailand	
	Niviventer cremoriventer	33	5	N.H.M., Thailand	

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Rattus tanezumi	44	25	N.H.M., Thailand	
	Sundamys muelleri	47	7	N.H.M., Thailand	
Ban Chok	*Rattus tanezumi*	44	77	N.H.M., Thailand	
Ban Kam Phuan	*Rattus argentiventer*	40	7	N.H.M., Thailand	
	Rattus tanezumi	44	30	N.H.M., Thailand	
Ban Khao Chong	*Maxomys whiteheadi*	27	4	N.H.M., Thailand	
	Sundamys muelleri	47	18	N.H.M., Thailand	
Ban Khuan Dang	*Rattus tanezumi*	44	56	N.H.M., Thailand	
Ban Kok Klap	*Maxomys surifer*	26	36	N.H.M., London	
Ban Lam Mai	*Maxomys whiteheadi*	27	7	N.H.M., Thailand	
	Rattus tanezumi	44	75	N.H.M., Thailand	
Ban Na	*Maxomys surifer*	26	22	This paper	
Ban Na Pum	*Bandicota indica*	9	2	Musser & Brothers (1994)	55
	Bandicota savilei	10	3	Musser & Brothers (1994)	53
Ban Nai Tan Yong	*Rattus tanezumi*	44	73	N.H.M., Thailand	
Ban Pa Lau	*Rattus andamanensis*	38	1	N.H.M., Thailand	
Ban Phi Tham	*Niviventer fulvescens*	34	11	N.H.M., Thailand	
Ban Plai Nam	*Leopoldamys sabanus*	22	23	N.H.M., Thailand	
	Maxomys rajah	25	2	N.H.M., Thailand	
	Maxomys whiteheadi	27	2	N.H.M., Thailand	
	Rattus tanezumi	44	42	N.H.M., Thailand	
	Sundamys muelleri	47	11	N.H.M., Thailand	
Ban Tai	*Rattus exulans*	41	2	N.H.M., Thailand	
	Rattus tanezumi	44	29	N.H.M., Thailand	
Ban Tha San	*Sundamys muelleri*	47	5	Musser & Newcomb (1983)	405
Ban Tha-Phae	*Rattus tanezumi*	44	52	N.H.M., Thailand	
Ban Thon	*Leopoldamys sabanus*	22	37	N.H.M., Thailand	
	Maxomys surifer	26	64	N.H.M., Thailand	
	Rattus exulans	41	9	N.H.M., Thailand	
	Rattus tanezumi	44	78	N.H.M., Thailand	
Ban Ya Kan	*Leopoldamys sabanus*	22	38	N.H.M., Thailand	
	Rattus tanezumi	44	79	N.H.M., Thailand	
	Sundamys muelleri	47	24	N.H.M., Thailand	
Bang Chak	*Bandicota indica*	9	6	Musser & Brothers (1994)	55
	Bandicota savilei	10	4	Lekagul & Felten (1989)	53
Bang Lang Dam	*Maxomys whiteheadi*	27	8	N.H.M., Thailand	
Bang Saphan	*Rattus tanezumi*	44	22	N.H.M., Thailand	
Bangnara	*Rattus argentiventer*	40	11	Chasen (1933)	20
Banna	*Rattus tanezumi*	44	53	N.H.M., Thailand	
Biserat	*Rattus exulans*	41	10	Bonhote (1900d)	879
	Rattus tanezumi	44	82	Bonhote (1903a)	28
	Rattus tiomanicus	45	9	Bonhote (1903a)	29
Bulon Island	*Rattus tanezumi*	44	64	This paper	
Chance Island (Koh Surin Tai)	*Maxomys surifer*	26	29	Miller (1903a)	38
	Rattus tanezumi	44	32	Miller (1913b)	15
Chong	*Maxomys surifer*	26	44	N.H.M., London	
	Niviventer cremoriventer	33	9	Musser (1973)	11
Chumpann	*Leopoldamys sabanus*	22	17	N.H.M., London	
De Lisle Island	*Rattus tanezumi*	44	28	Chasen (1937)	82
	Maxomys surifer	26	26	N.H.M., London	
Gap	*Maxomys surifer*	26	51	N.H.M., London	
Ghirbi	*Rattus tiomanicus*	45	3	Chasen (1933)	6
Goah Tanah	*Maxomys surifer*	26	65	Bonhote (1903a)	26
Hala Bala Wildlife Research Station	*Maxomys rajah*	25	5	This paper	
	Maxomys surifer	26	66	This paper	
	Maxomys whiteheadi	27	9	This paper	
	Rattus exulans	41	11	This paper	
	Rattus tanezumi	44	81	This paper	
Junk Seylon [Phuket Island]	*Leopoldamys sabanus*	22	28	Chasen (1940a)	166
	Maxomys surifer	26	45	Chasen (1940a)	169
	Rattus tiomanicus	45	4	Chasen (1937)	84
Kadan Island	*Rattus tanezumi*	44	62	Chasen (1937b)	89
Kaeng Kra Chan NationalPark	*Rattus tanezumi*	44	20	This paper	
Kam Phaeng Phet	*Bandicota indica*	9	8	Musser & Brothers (1994)	55

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Bandicota savilei	10	5	Musser & Brothers (1994)	53
Khao Lak	*Maxomys surifer*	26	39	Kloss (1919b)	376
	Rattus tanezumi	44	43	Kloss (1919b)	337
	Rattus exulans	41	5	Gyldenstolpe (1917)	45
Khao Luang	*Leopoldamys sabanus*	22	26	N.H.M., London	
	Maxomys rajah	25	3	N.H.M., Thailand	
	Maxomys surifer	26	40	N.H.M., London	
	Niviventer cremoriventer	33	7	Musser (1973)	11
	Niviventer fulvescens	34	12	N.H.M., London	
	Sundamys muelleri	47	13	N.H.M., Thailand	
Khao Mon	*Niviventer fulvescens*	34	4	N.H.M., Thailand	
Khao Nong	*Niviventer fulvescens*	34	9	Robinson & Kloss (1914a)	228
	Leopoldamys sabanus	22	21	N.H.M., London	
	Maxomys surifer	26	37	N.H.M., London	
	Sundamys muelleri	47	10	Musser & Newcomb (1983)	405
Khao Num Kang National Park	*Maxomys surifer*	26	57	This paper	
	Niviventer cremoriventer	33	11	P.S.U. Museum	
	Sundamys muelleri	47	22	P.S.U. Museum	
Khao Phlu (base of), Koh Samui	*Rattus argentiventer*	40	8	N.H.M., Thailand	
	Rattus tanezumi	44	39	N.H.M., Thailand	
Khao Phu Khao Ya National Park	*Leopoldamys sabanus*	22	31	This paper	
	Maxomys whiteheadi	27	3	This paper	
	Rattus tanezumi	44	55	This paper	
	Sundamys muelleri	47	16	This paper	
Khao Rai	*Bandicota savilei*	10	2	Musser & Brothers (1994)	53
Khao Ram	*Maxomys whiteheadi*	27	6	N.H.M., London	
	Niviventer fulvescens	34	18	N.H.M., London	
Khao Rup Chang	*Rattus tanezumi*	44	69	U.S.N.M.	
Khao Sai	*Rattus tanezumi*	44	41	N.H.M., Thailand	
Khao Tha-Phet	*Leopoldamys sabanus*	22	22	N.H.M., Thailand	
	Maxomys rajah	25	1	N.H.M., Thailand	
	Maxomys whiteheadi	27	1	N.H.M., Thailand	
Khao Ying Mee	*Bandicota indica*	9	5	N.H.M., Thailand	
Khlong Saeng	*Niviventer cremoriventer*	33	6	N.H.M., Thailand	
	Niviventer fulvescens	34	10	N.H.M., Thailand	
Khlong Wan [Tapli]	*Niviventer cremoriventer*	33	2	Musser (1973)	11
Khow Sai Dow	*Sundamys muelleri*	47	19	Musser & Newcomb (1983)	405
Khuan Kalong	*Rattus tiomanicus*	45	6	N.H.M., Thailand	
Khuan Khi Sian	*Rattus tanezumi*	44	58	N.H.M., Thailand	
Klong Bang Jai	*Sundamys muelleri*	47	4	N.H.M., London	
Klong Phraya Wildlife Sanctuary	*Bandicota indica*	9	4	N.H.M., Thailand	
	Berylmys bowersii	13	3	N.H.M., Thailand	
	Leopoldamys sabanus	22	24	N.H.M., Thailand	
	Rattus tanezumi	44	44	N.H.M., Thailand	
	Rattus tiomanicus	45	2	N.H.M., Thailand	
	Rattus argentiventer	40	10	N.H.M., Thailand	
Klong Tun Sai	*Leopoldamys sabanus*	22	30	Hill (1960)	87
Koh Alan Yai	*Rattus tanezumi*	44	49	Chasen (1937b)	88
Koh Boi Yah	*Rattus tanezumi*	44	45	Chasen (1937b)	85
Koh Kra	*Maxomys surifer*	26	42	Kloss (1916)	53
	Rattus andamanensis	38	2	Musser & Carleton (2005)	1464
Koh Maprau	*Rattus tanezumi*	44	48	Chasen (1937b)	88
Koh Muk	*Maxomys surifer*	26	52	Chasen (1940a)	170
Koh Naka Yai	*Rattus tanezumi*	44	47	Chasen (1937b)	88
Koh Pennan	*Maxomys surifer*	26	27	Robinson & Kloss (1914a)	230
Koh Pha-ngan	*Rattus andamanensis*	38	4	Musser & Carleton (2005)	1464
Koh Prah Tung	*Rattus tanezumi*	44	36	Chasen (1937)	
Koh Rah	*Maxomys surifer*	26	33	N.H.M., London	
	Rattus tanezumi	44	35	Chasen (1937)	84
Koh Rawi	*Niviventer cremoriventer*	33	15	Musser (1973)	11
	Rattus tanezumi	44	66	Miller (1913b)	8
Koh Samui	*Niviventer fulvescens*	34	7	Robinson & Kloss (1914a)	229
	Rattus andamanensis	38	5	Robinson & Kloss (1914a)	231
	Rattus norvegicus	42	1	Marshall & Nongngork (1970)	502

Locality	Species	Fig. no.	No. on map	Reference	Page no.
	Rattus tanezumi	44	37	Chasen (1940b)	154
	Maxomys surifer	26	31	Robinson & Kloss (1914a)	230
Koh Surin Nua	*Maxomys surifer*	26	28	N.H.M., Thailand	
	Rattus tanezumi	44	31	N.H.M., Thailand	
Koh Tao	*Rattus exulans*	41	1	N.H.M., Thailand	
	Rattus tanezumi	44	26	N.H.M., Thailand	
Koh Tarutao	*Maxomys surifer*	26	55	N.H.M., London/N.H.M., Thailand	
Koh Tau	*Rattus andamanensis*	38	3	Musser & Carleton (2005)	1464
Koh Yam Yai	*Rattus tanezumi*	44	33	Chasen (1937)	83
	Maxomys surifer	26	30	N.H.M., London	
Koh Yao Noi [North Panjang Island]	*Rattus tanezumi*	44	46	Chasen (1937b)	85
Koh Yao Yai [Panjang Island]	*Maxomys surifer*	26	46	N.H.M., Thailand	
	Rattus exulans	41	6	N.H.M., Thailand	
	Rattus tanezumi	44	50	N.H.M., Thailand	
Krung Ching	*Leopoldamys sabanus*	22	25	N.H.M., Thailand	
Kuan Khao Wang Forest Park	*Maxomys surifer*	26	56	This paper	
	Rattus tanezumi	44	70	This paper	
	Sundamys muelleri	47	21	This paper	
Lam Nam Kra Buri National Park	*Maxomys surifer*	26	24	This paper	
Lam-ra	*Leopoldamys sabanus*	22	32	N.H.M., London	
	Maxomys surifer	26	47	N.H.M., London	
Lontar Island	*Rattus tanezumi*	44	60	Chasen (1937b)	88
Mae Wad	*Niviventer fulvescens*	34	20	N.H.M., Thailand	
Maprit	*Berylmys bowersii*	13	1	Kloss (1916a)	27
	Leopoldamys sabanus	22	16	N.H.M., London	
	Maxomys surifer	26	20	Kloss (1919b)	377
Marmok	*Maxomys surifer*	26	21	N.H.M., London	
Muang	*Niviventer cremoriventer*	33	10	Musser (1973)	11
Muang Yala	*Rattus exulans*	41	8	U.S.N.M.	
Na Pra Du	*Maxomys surifer*	26	59	N.H.M., Thailand	
	Sundamys muelleri	47	23	N.H.M., Thailand	
Nakhon Si Thammarat	*Sundamys muelleri*	47	15	Musser & Newcomb (1983)	405
Nakhon Si Thammarat Province	*Berylmys bowersii*	13	4	Musser & Newcomb (1983)	378
Nam Tok Sai Khao	*Maxomys surifer*	26	58	N.H.M., Thailand	
	Niviventer cremoriventer	33	13	N.H.M., Thailand	
	Niviventer fulvescens	34	19	N.H.M., Thailand	
	Rattus tanezumi	44	74	N.H.M., Thailand	
Nam Tok Tamot	*Niviventer fulvescens*	34	17	N.H.M., Thailand	
Nam Tok Tha-Phae	*Sundamys muelleri*	47	14	N.H.M., Thailand	
Nam Tok Ton Te	*Maxomys surifer*	26	53	N.H.M., Thailand	
Narathiwat	*Sundamys muelleri*	47	25	Musser & Newcomb (1983)	405
Narathiwat Province	*Berylmys bowersii*	13	8	Musser & Newcomb (1983)	379
Nga Chang Waterfall	*Sundamys muelleri*	47	20	Musser & Newcomb (1983)	405
Nong Chik	*Rattus tiomanicus*	45	8	Bonhote (1903a)	29
Nongkok	*Leopoldamys sabanus*	22	27	N.H.M., London	
	Maxomys surifer	26	41	N.H.M., London	
	Niviventer fulvescens	34	14	N.H.M., London	
Pa La U	*Bandicota indica*	9	1	This paper	
	Rattus tanezumi	44	21	This paper	
	Sundamys muelleri	47	3	This paper	
Pa Phru	*Rattus tanezumi*	44	80	N.H.M., Thailand	
Pa Toh Watershed Management	*Rattus tanezumi*	44	27	This paper	
	Sundamys muelleri	47	9	This paper	
Pak Chan	*Rattus tanezumi*	44	23	This paper	
Pak Jam	*Berylmys bowersii*	13	5	P.S.U. Museum	
	Maxomys surifer	26	49	This paper	
	Rattus tanezumi	44	57	This paper	
Pak Num	*Rattus tanezumi*	44	72	N.H.M., Thailand	
Pak Tho Khao Jeen	*Bandicota savilei*	10	1	Musser & Brothers (1993)	53
Pasir Raja, Pulau Lontar	*Leopoldamys sabanus*	22	33	Hill (1960)	87
Pattani	*Hapalomys longicaudatus*	17	2	Musser (1972)	14
	Niviventer cremoriventer	33	12	Musser (1973)	11

Locality	Species	Fig. no.	No. on map	Reference	Page no.
Phato Watershed Conservation and Management Unit	*Rattus tanezumi*	44	34	P.S.U. Museum	
	Bandicota indica	9	3	P.S.U. Museum	
	Leopoldamys sabanus	22	18	P.S.U. Museum	
	Maxomys surifer	26	32	P.S.U. Museum	
Phetchaburi	*Berylmys berdmorei*	12	3	Markvong et al. (1973)	26
Pipidon Island	*Maxomys surifer*	26	48	Chasen (1940a)	171
	Rattus tanezumi	44	51	Chasen (1937b)	92
Plai Nam	*Maxomys surifer*	26	38	N.H.M., Thailand	
Prachuapkhirikhan	*Mus caroli*	29	1	Marshall (1977)	198
Prince of Songkla University	*Rattus exulans*	41	7	This paper	
	Rattus tanezumi	44	71	This paper	
Pulau Mohea	*Rattus tanezumi*	44	63	Chasen (1937b)	91
Pulau Muntia [Koh Muk]	*Rattus tanezumi*	44	61	Chasen (1937b)	90
Pulau Telibon	*Leopoldamys sabanus*	22	35	Hill (1960)	87
	Rattus tiomanicus	45	5	Chasen (1937b)	90
Pulo Adang	*Maxomys surifer*	26	61	Miller (1900e)	190
	Niviventer cremoriventer	33	16	Miller (1900e)	191
Pulo Rawi	*Maxomys surifer*	26	60	Miller (1900e)	190
Rajjaprabha Dam	*Berylmys bowersii*	13	2	This paper	
	Leopoldamys sabanus	22	20	This paper	
	Rattus argentiventer	40	9	This paper	
	Rattus exulans	41	4	This paper	
	Rattus tiomanicus	45	1	This paper	
Rangae	*Rattus argentiventer*	40	12	N.H.M., Thailand	
Ranong	*Sundamys muelleri*	47	8	Musser & Newcomb (1983)	405
Sam Yak A-Sen	*Maxomys surifer*	26	63	N.H.M., Thailand	
	Rattus tanezumi	44	76	N.H.M., Thailand	
Song Hong	*Maxomys surifer*	26	43	N.H.M., London	
Talok Udang, Terutau Island	*Rattus tiomanicus*	45	7	Hill (1960)	79
Tan Ta Ya Phi Rom Temple	*Bandicota indica*	9	7	This paper	
Tang Pran	*Niviventer fulvescens*	34	13	N.H.M., London	
	Sundamys muelleri	47	12	Musser & Newcomb (1983)	405
Tap-Li	*Niviventer fulvescens*	34	6	N.H.M., London	
	Maxomys surifer	26	19	N.H.M., London	
Tarutao Island	*Rattus tanezumi*	44	65	N.H.M., Thailand	
	Niviventer cremoriventer	33	14	Miller (1913b)	22
Tasan	*Maxomys surifer*	26	23	N.H.M., London	
	Niviventer cremoriventer	33	3	Musser (1973)	11
	Sundamys muelleri	47	6	N.H.M., London	
Telibon Island	*Maxomys surifer*	26	54	Chasen (1940a)	170
Telok Poh, Pulau Panjang [Koh Yao Yai]	*Leopoldamys sabanus*	22	29	Hill (1960)	87
Teratau Island	*Leopoldamys sabanus*	22	36	Thomas & Wroughton (1909b)	535
Tha Chang	*Leopoldamys sabanus*	22	19	T.T.U.	
	Maxomys surifer	26	34	T.T.U.	
Tham Nam	*Rattus tanezumi*	44	54	N.H.M., Thailand	
Thung Chalee Wildlife Sanctuary	*Maxomys surifer*	26	35	N.H.M., Thailand	
Tone Sai Waterfall National Park	*Niviventer fulvescens*	34	15	Abe (1983)	151
Tonto Waterfall	*Sundamys muelleri*	47	26	Musser & Newcomb (1983)	405
Trang	*Berylmys bowersii*	13	6	Miller (1900d)	140
	Leopoldamys sabanus	22	34	Miller (1900d)	138
	Maxomys rajah	25	4	Miller (1900d)	147
	Maxomys surifer	26	50	Miller (1900d)	148
	Maxomys whiteheadi	27	5	Miller (1900d)	145
	Niviventer cremoriventer	33	8	Miller (1900d)	144
	Niviventer fulvescens	34	16	N.H.M., London	
	Rattus tanezumi	44	59	U.S.N.M.	
	Sundamys muelleri	47	17	Miller (1900d)	141
Trang Province	*Chiropodomys gliroides*	15	3	Musser (1979)	408
	Mus musculus	30	1	Marshall (1977)	208
Wang Bla Chan	*Maxomys surifer*	26	62	N.H.M., Thailand	
	Rattus tanezumi	44	68	N.H.M., Thailand	
Yala Province	*Berylmys bowersii*	13	7	Musser & Newcomb (1983)	378

