

***Paulamys* sp. cf. *P. naso* (Musser, 1981) (Rodentia: Muridae) from Flores Island, Nusa Tenggara, Indonesia — description from a modern specimen and a consideration of its phylogenetic affinities.**

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Abstract

Paulamys naso was described from Holocene and Pleistocene fragments of dentary and lower teeth from western Flores I. by Musser (1981b) and Musser *et al.* (1986).

A single specimen of a distinctive murid live-trapped in 1989 at Kelimutu, central southern Flores, appears to be closely related to *P. naso*. This specimen is described in detail and its phylogenetic relationships are discussed.

Introduction

Musser (1981b) described the genus *Floresomys*, to accommodate a distinctively long-nosed murid (*F. naso*) from fossils represented by dentaries and lower teeth from sediment in Liang Toge cave, near Warukia, 1 km south of Lepa, Menggarai District, West Flores. The deposit was dated at 3550 ± 525 yr BP. The holotype is a "piece of right dentary with a complete molar row and part of the incisor ... from an adult." *Floresomys*, however, is a preoccupied generic name so Musser in Musser *et al.* (1986) proposed the replacement name of *Paulamys* for it. Musser *et al.* (1986) also provide additional observations on fossil dentaries and lower teeth of *P. naso*, younger than 4000 yr BP, collected in two caves in Manggarai District: Liang Soki, 15 km north of Ruteng and Liang Bua, 10-12 km northwest of Ruteng.

In October 1989 an expedition comprising staff from the Western Australian Museum and Museum Zoologicum Bogoriense, trapped a murid rodent with a long snout and short tail at Kelimutu, central south Flores. This specimen has dentaries and lower dentition that are very similar to *P. naso* and is herein tentatively referred to that taxon. It appears to be the first modern representative of the genus *Paulamys*. This paper provides a description of the Kelimutu specimen, and examines its taxonomic status.

Methodology

Measurement and descriptions

External measurements were recorded from the Kelimutu specimen, WAM M32000, following its preservation in 70% ethanol. Weight was taken in the field prior to fixation. Cranial and dental measurements were taken with dial calipers to the nearest one-hundredth millimetre. Measurement points are illustrated in Musser (1970a) and

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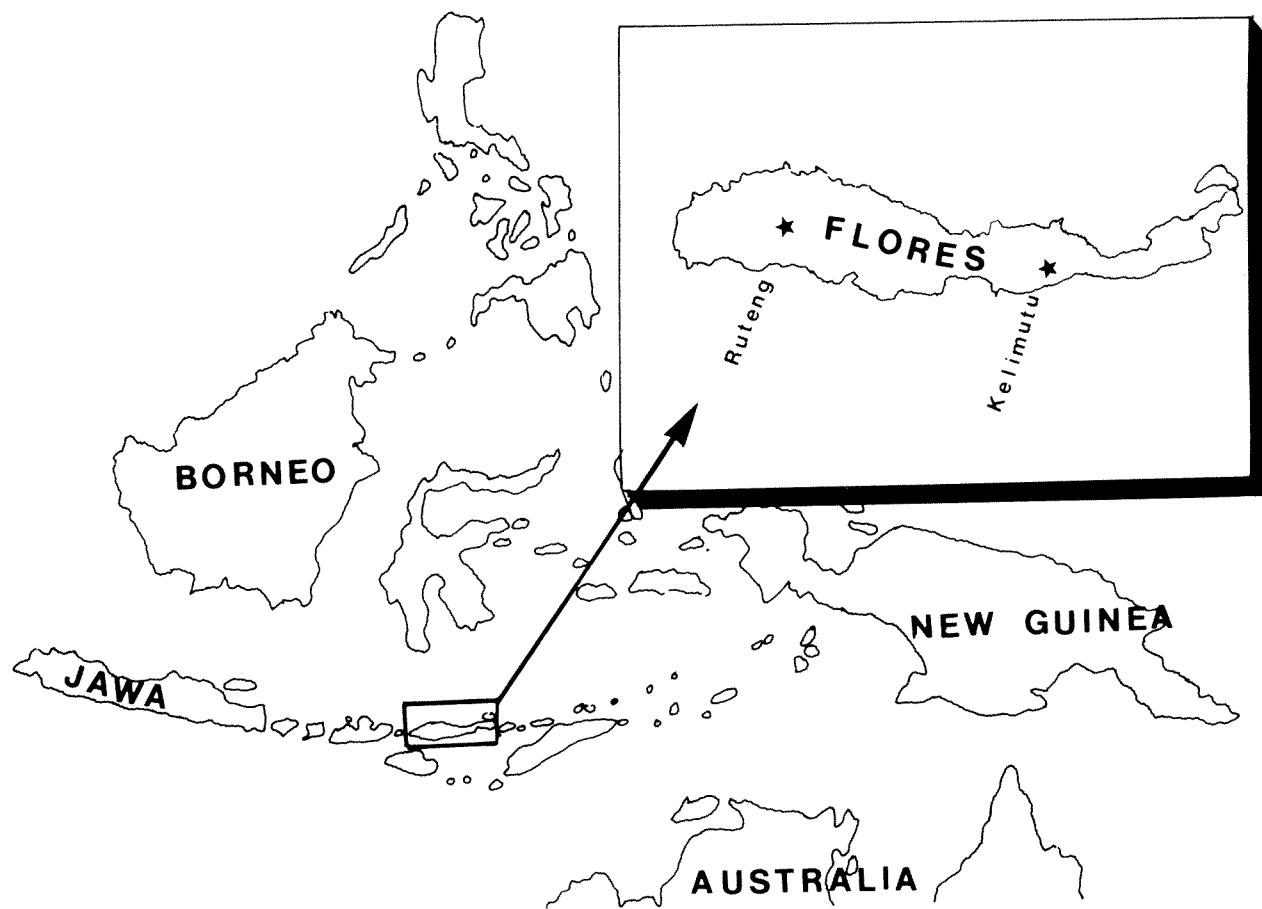


Figure 1. Map of Nusa Tenggara showing the collection locality of WAM M32000.

described in Musser and Newcomb (1983). Description of occlusal structure of teeth follows Musser and Newcomb's (1983: 333) modifications of the numbering system of Miller (1912) for upper molars, and of the nomenclature of Van de Weerd (1976) for lower molars. The terminology of cranial bones and foramina is that employed and illustrated by Musser (1981a, b).

Phylogenetic analysis

Phylogenetic relationships were examined between *Paulamys* sp. cf. *P. naso* and 13 genera — including *Rattus* and some other closely related genera — listed in Table 11 of Musser (1981a: 324), as well as *Bunomys* [described and illustrated in Musser and Newcomb (1983)].

Cladograms were constructed using the tree-building phylogenetic computer package HENNIG 86 (Farris, 1988). The search for the most parsimonious tree was conducted using a branch and bound routine, based on the WAGNER algorithm. The polarity of the 29 character traits used in this analysis for most genera was taken from Musser (1981a, Table 11); character states for *Paulamys* sp. cf. *naso* and *Bunomys* were derived from the descriptions provided in Musser (1981a) to determine polarity of traits, checked against specimens of taxa he too had examined.

The tree was rooted using a hypothetical ancestor that was plesiomorphic for all 29 characters.

Colour: Pelage and skin colour where they follow Ridgway (1912) are capitalised.

Systematics

Paulamys sp. cf. *P. naso* (Musser, 1981)

The Kelimutu specimen

Western Australian Museum No. WAM M32000; juvenile or young adult male, body fixed in 10% formalin, preserved in 70% ethanol; skull and dentaries separate; collected in 'Break Back' commercial rat trap on 25 October 1989.

Collection Locality and Habitat

Near Kampong Woloara, c. 3 km from summit of Gunung Kelimutu, south-central Flores I. (8°42', 121°54'), at c. 1600 m (Figure 1). Collected in dry creek bed (the entrance of which is shown in Figure 2) in dense tall rainforest dominated by large *Ficus* spp., *Zizyphus* sp., *Garuga* sp., *Erythrina*, *Albizia* and *Myristica* sp. to 20-35 m in height. There was a scattered layer of *Rhododendron* sp. shrubs and a dense layer of ferns (one species with fronds up to 7 m long from a base almost at ground level). Vines were abundant throughout. Leaf litter in the dry creek was dense and from 30-50 cm deep. The road to the summit from the forestry department office (c. 7 km from the summit) went through 2-3 km of mixed kebun of coffee, pineapple, banana, and maize; then a narrow zone of c. 1 km of open rough grey barked *Eucalyptus urophylla* to a height of c. 15 m, over a dense low *Lantana*-like vegetation on black soil; before reaching the rainforest zone in which specimen WAM M32000 was collected. Above this zone were patches of *Casuarina junghuhniana* on open stony ground with patches of heath-like vegetation to 0.5 m in height.



Figure 2. Photograph of vegetation close to the place where WAM M32000 was collected.

Diagnosis

Paulamys sp. cf. *naso* is similar to the genus *Rattus* but differs from all other species of *Rattus* (*sensu* Musser and Newcomb (1983)) by having a combination of the following characteristics: body moderately large; tail much shorter than body length; rostrum exceptionally long; dorsolateral margins of braincase without prominent ridges; dorsolateral margin of interorbital region with only a slight beading; incisive foramina terminating posteriorly before anterior alveoli of first upper molar; posterior margin of palatal bridge terminates level with posterior edge of third upper molars and does not extend behind them to form a wide platform; mesopterygoid fossa wide, almost as wide as back of palatal bridge, its walls with moderately large, short, sphenopalatine vacuities; and cusp t_3 absent from second and third upper molars.

Apart from its body size, it may be distinguished readily by any one of the above characters from *Rattus* on Flores (*R. rattus*, *R. argentiventer*, *R. exulans* and *R. norvegicus*). (The skulls of these are illustrated in Musser and Newcomb (1983: 574-575).)

It is readily distinguished from other non-*Rattus* murids on Flores (two genera of which are known only from fossils) which are described and illustrated in detail in Musser (1981b). It differs from *Papagomys* in the following ways: it is much smaller in all measurements; the cranium of WAM M32000 is considerably more inflated; rostrum longer relative to greatest skull length; ridges on dorsolateral sides of braincase and posterorbital region absent; molar cusp morphology considerably simpler — lingual cusps on M^1 and M^2 less discrete; cusp t_3 absent on M^{1-2} ; primary cusps on M_1 and M_2 not a tear-drop shape in cross section and cusps less discrete.

It differs from the fossil taxon *Hooijeromys* spp. (known only from its dentition) in the following ways: it is considerably smaller; cusp t_2 on M^1 is not 'gourd-shaped'; incisive foramina do not extend posterior to anterior margins of M^1 ; zygomatic plate arises from maxilla at a point near the middle of M^1 rather than near posterior edge of M^2 .

It differs from *Spelaeomys florensis* (described from fossil maxillary fragments and mandibles, all with teeth) in having much smaller teeth with a simple rather than elaborate occlusal pattern. In *S. florensis* upper molars are high crowned and individual cusps are discrete and remain separate even after appreciable wear; molars overlap considerably rather than only very slightly.

It differs from *Komodomys rintjanus* in that the dorsal fur is not spinous; the rostrum flattened such that dorsal profile of cranium not strongly arched from nasal tip to occiput; rostrum much longer relative to cranium; top of skull much more inflated (not nearly flat); zygomatic plate narrower, without anterior spines; interparietal wider anteroposteriorly; incisive foramina shorter, terminates posteriorly before M^1 anterior edge; mesopterygoid fossa wider relative to posterior palate width; molar teeth simple, not high coned; labial cusps on second row of M^1 closely applied to adjacent medial cusp and not set apart; M_2 not appreciably wider than M_1 .

Description of *Paulamys* sp. cf. *P. naso* specimen WAM M32000

Measurements (in mm) are as follows

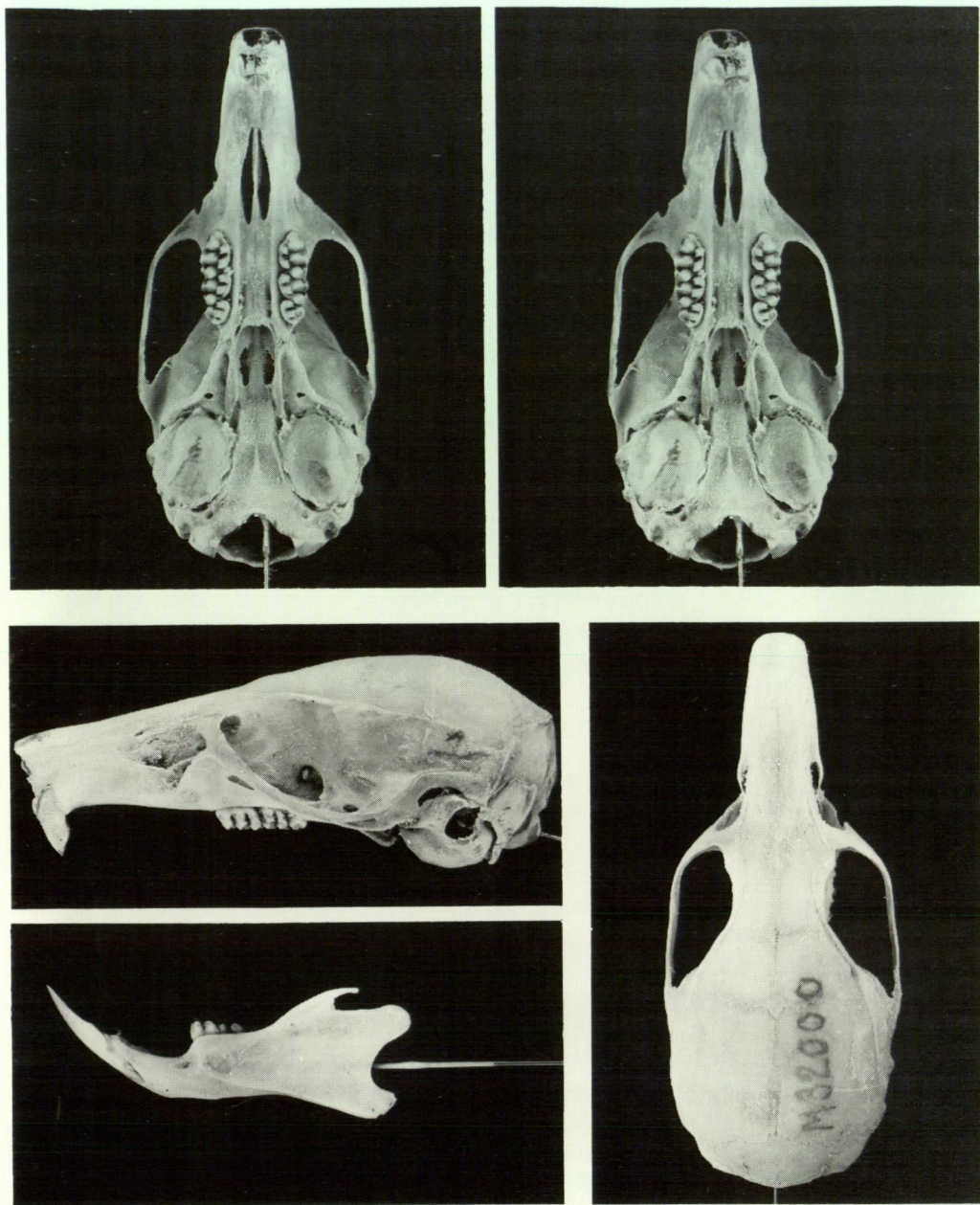


Figure 3. Photographs of skull, dentary and teeth of WAM M32000, ventral aspect of cranium as stereopairs.

Tip of rhinarium to vent length 164; distal tip of tail to vent length 117; hind foot length 39.3; ear length 24.2; greatest skull length 41.88; zygomatic breadth 18.66; interorbital breadth 6.74; braincase breadth 16.74; braincase height 13.03; nasal length 15.94; rostrum length 14.90; rostrum breadth 6.50; rostral tube length anterior to I¹ 1.90; zygomatic plate breadth 3.97; breadth across upper incisor tips 1.85; diastema length 11.77; palatal length 21.46; postpalatal length 14.34; incisive foramen length 7.37; incisive foramina breadth 2.22; incisive foramen posterior to anterior edge M¹ cusp 0.49; palatal bridge length 7.82; palatal bridge breadth at M³ 3.86; mesopterygoid fossa breadth 2.88; bulla length 7.04; bulla height 6.93; M¹⁻³ crown length 7.11; M¹⁻³ alveolar length 7.30; M¹ length 3.58; M¹ breadth 2.35; dentary and incisor length 26.64; dentary length 23.40; dentary height 10.44; M₁₋₃ crown length 7.15; M₁₋₃ alveoli length 7.14; M₁ breadth 1.97; M₂ breadth 2.09; M₃ breadth 1.83; incisor breadth at point emergent from ramus 0.87. Also weight 122 gm, and rows of scales on tail per cm (at one-third tail length from base) 13.

Skull

Cranium of moderate size. Its distinctive features (Figures 3) are: elongate rostrum with dorsal profile in lateral view straight and moderately sharply inflected at interorbital region immediately behind nasal-frontal sutures (where frontal is inflated as two low globose structures); rostrum distal end slightly inflated and elevated dorsally to form narrow rostral tube that extends 1.9 mm anterior to canines; braincase oval; interparietal moderately long anteroposteriorly, anterior margin abuts with slight intrusion between parietals; orbit dorsolateral margins with weak beading but such margins of postorbital region and braincase smooth; braincase lateral surface almost vertical from dorsolateral margin of cranium to squamosal root of zygomatic arch; interorbital region moderately wide; narrow zygomatic plate, slope forward gently from zygomatic arch anterodorsal root, anterior marginal projection absent; incisive foramen moderately long, spindle-shaped, posteriorly terminate 0.49 mm anterior to M¹ anterior cusp; palatal bridge moderately wide, terminating posteriorly at M³ posterior edge; mesopterygoid fossa moderately wide, its walls penetrated by an oval-shaped sphenopalatine vacuity about 3 mm long; pterygoid fossa concave, tilted towards skull midline, penetrated by moderately large interpterygoid foramen; bulla large but because of elongate rostrum only *c.* 17 percent of greatest skull length, eustachian tube short, jagged distally; alisphenoid canal open, not concealed by strut of alisphenoid bone; zygomatic arch squamosal root set halfway down braincase; squamosal root with low horizontal posterior ridge extending about 3mm, but terminating well short of occiput; parietal-squamosal suture strongly sinusoidal-shaped above squamosal root; postglenoid foramen moderately large, lateral margin posterior to foramen ovale with definite ridge.

Dentary

Dentary (Figure 3) with coronoid process slender and low; ramus slender and moderately long; posterior margin between condyloid and angular process concave, shallow; angular process ventral surface tilted to form a moderately wide internal shelf; capsular projection on outside surface at end of incisor smooth; mental foramen

moderately large, immediately anterior to junction of masseteric ridges; dorsal masseteric ridge weak, low; ventral masseteric ridge strong; shelf-like ridge extends from behind M_3 in gentle arc below alveolar line of molars to base of condylar process; large oval mandibular foramen at base of condylar process close but dorsal to above shelf-like ridge.

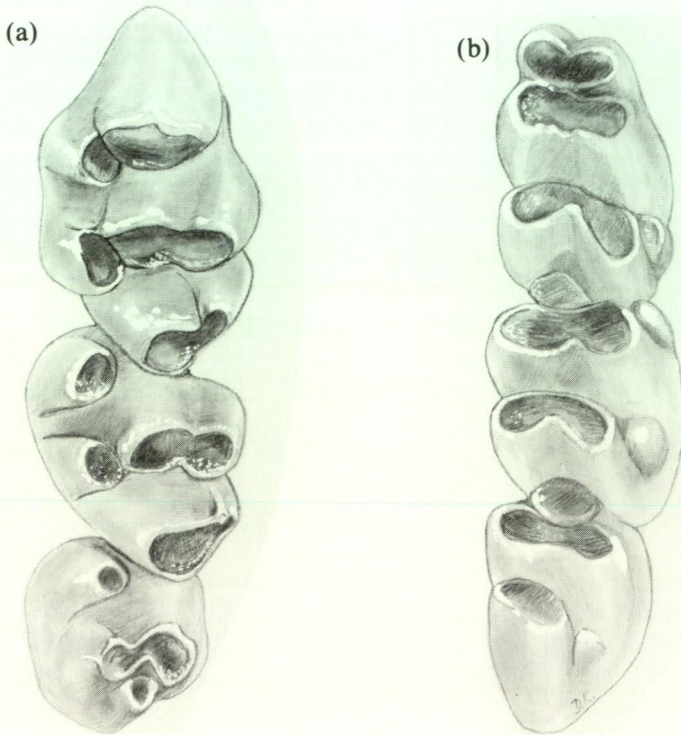


Figure 4. Drawings of occlusal surface of molar rows WAM M32000, (a) upper and (b) lower.

Dentition

WAM M32000 has moderately large brachydont molars, simple occlusal patterns, cusps broadly united to form rows of laminae; laminae gently sloping such that teeth are slightly overlapped by immediate anterior teeth (Figures 3 and 4); M^1 apparently with five roots (anterior, posterior, labial and two lingual); the first three of these roots are obvious externally and through x-ray photographs — the lingual roots are less clear but appear to be separate rather than a single bi-lobed root. M^2 apparently with four roots, the anterior, posterior and labial roots are clear on x-ray photographs; a lingual root is less clear but an alveoli is seen to take this root. M^1 oval-shaped, anterior lamina formed from a small cusp t1 loosely fused with a large cusp t2 (cusp t3 absent); middle lamina weakly chevron-shaped, cusp t4 moderately large and weakly merged to cusp t5, cusp t6

strongly fused to cusp t5 (cusp t7 absent), cusp t8 large and fused with small cusp t9; cusp t9 squarish, with trace of ridge on anterior face. M² broad, consists primarily of large cusp t1 (weakly pressed against M¹ cusp t8) and t8 (merged with very small cusp t9); cusp t9 with small low ridge on anterior face; middle lamina composed of merged cusps t4, t5 and t6, almost straight, cusp t4 more distinct than cusp t6 from central cusp. M³ with cusp t1 moderately large, discrete, loosely against M² cusp t8; middle lamina slightly chevron-shaped; small posterior (cusp t8?). Upper incisors opisthodont, enamel orange.

Occlusal surface of lower molars with oblong outline, surface area decreases evenly from M₁ to M₃. M₁ anterior lamina from fusion of approximately equal sized anterior lingual and labial cusps; broadly adpressed with similar lamina formed from fusion of metaconid and protoconid; posterior lamina more chevron-shaped, formed from fusion of entoconid and hypoconid — the latter cusp with a moderately large posterior labial cusplet; posterior cingulum distinct. M₂ anterior lamina almost straight, formed from metaconid and protoconid, closely adpressed to protoconid is a moderately large anterior labial cusp; second lamina weakly chevron-shaped, has a small posterior labial cusplet; posterior cingulum distinct; M₂ slightly broader than M₁. M₃ anterior lamina straight; small low anterolabial cusp (not visible from occlusal view); and small low posterior labial cusplet on right side only.

Pelage and skin

Fur long and soft; dominant colour of dorsum Brownish Olive flecked with Isabella Color (light brown) and Bister (deep brown); venter, chest and throat a lighter grey. Dorsum hairs with basal two-thirds Pale Quaker Drab (light lilac-grey), middle section Brownish Olive tipped variously with: Isabella Color on back — hairs moderately long (15 mm); Cinnamon on shoulders and head; Chamois on flanks (hairs up to 10 mm long); and Bister on rump. Guard hairs long, particularly on rump where they are Sepia and up to 35 mm long; on flank shorter (up to 20 mm), grey.

On venter, chest and throat, hairs moderately long (up to 13 mm), Pale Quaker Drab. Immediately behind mouth and on cheek light dense hairs of Tilleul-*Buff* (light pink-cream), contrasts sharply with darker hairs of face and head.

Tail with moderately dense hairs, up to 3 mm long, on dorsal surface *Chaetura Drab* (black-brown), on ventral surface *Light Drab* (lilac-grey); scales bicoloured, background *Pale Vinaceous Fawn* (light pink-cream) with central square of *Black*.

Skin of lips, dorsal surface of hands and feet *Vinaceous Buff* (pink-cream); on manus main dorsal surface lightly covered with *Olive Brown* hair but fingers with sparse *White* hair; hair on pes dorsal surface and toes *Olive Brown*; pes plantar surface *Deep Brownish Drab* (dark lilac-brown), ears *Chaetura Drab*.

Pes and manus

Typically *Rattus*-like. Manus claws moderately long (4 mm), pollex with nail, all pads prominent; three interdigital pads: outer and inner kidney-shaped, central pad triangular-shaped, thenar pad approximately one-half area of hypothenar — both moderately large (Figure 5). Pes with moderate pads, all raised, smooth, without lamellae or ridges — although with a lamellae-like pattern to skin pigmentation; inner

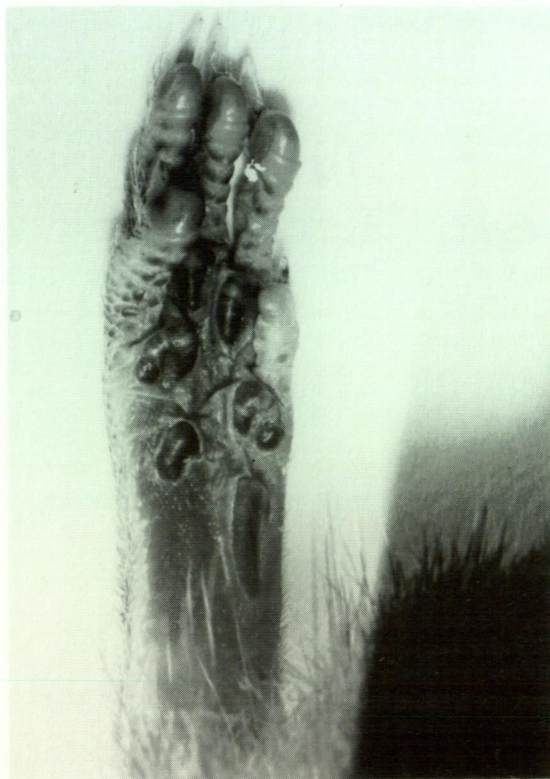


Figure 5. Photograph of plantar surface of pes of WAM M32000.

plantar pad long, 5.5 mm, outer plantar pad 2.4 mm behind nearest interdigital pad and approximately three-quarters size of this front pad; outer interdigital pad broadly kidney-shaped with smaller posterolateral subcircular accessory pad.

Tail

Tail very short (Figure 6), 71 percent of tip of rhinarium to vent length; approximately 13 scale rows per cm and 19 scales around circumference at a position of one-third length of tail from its base; hair length at this position approximately equal to two and one-half times the length of a scale.

Vibrissae

On each side of face approximately 10 very long (up to 60 mm) mystacial vibrissae, dark coloured above lips, lighter closer to lips; three moderately long (up to 40 mm) dark supraciliary vibrissae; two dark genal vibrissae (up to 15 mm long); numerous short (up to 10 mm) white interramal and submental vibrissae; six short (up to 11 mm), white, ulnar carpal vibrissae; four short (up to 11 mm), white, medial antebrachial vibrissae; approximately four short (up to 13 mm), white anconal vibrissae; and two short (c. 4 mm), white calcaneal vibrissae.



Figure 6. Photographs of carcass of WAM M32000.

Diet and Habits

Musser (1981b: 130) speculated that *P. naso* was "likely terrestrial and could have included fungi, insects, snails, earthworms and possibly some fruit in its diet (by analogy with species of *Bunomys*)". The specimen WAM M32000 confirms in part this speculation. It had a full stomach when collected which contained: several oligochaete worms; two insect larva (possibly lepidopteran); a considerable quantity of unidentifiable plant matter (much of which is probably subterranean because it frequently had rootlets and root hairs attached); corms (probably immature) were abundant and may constitute much of the unidentified vegetable matter; several small seeds; several fragments thought to be fungal; and a few fragments of insects (including probable Hymenoptera, a beetle larva and a possible small centipede) the insects were in such small quantity that they may have been ingested incidentally.

The shape of the pads on the pes and manus and the absence of striations on these pads suggest the species is terrestrial. As it was collected in dense rainforest in an area with deep leaf-litter its diet would suggest that *Paulamys* sp. cf. *P. naso* feeds on the ground, using its long snout, and claws, to dig for a variety of food among leaf litter or just beneath the soil.

Identification of WAM M32000

The specimen WAM M32000 appears closely related to the taxon *Paulamys naso*. Its dentary is of a similar shape in that the ramus in front of M_1 is long, there is a prominent lingual shelf-like ridge extending from behind the molar row which slants gradually upwards to the base of the condylar process. Dorsal to this ridge and near the base of the condylar process is a large oval mandibular foramen. Further, the shape of the lower molars and the lamina, particularly the first lamina on M_1 and the slim incisors are all said by Musser (1981b) to be characteristic of *P. naso*.

The specific identity of WAM M32000 is difficult to determine, however, because even with a good series of specimens of modern murid taxa, some species are difficult to distinguish using mandibles alone. Further some diagnostic characters, such as presence or absence of lower molar cusplets are very variable within species (Musser and Newcomb 1983) and within individuals — for example, WAM M32000 has a small posterior labial cusplet on M_3 in the right dentary, but not on the left one. Our comparison is further complicated because we have only a single modern specimen and we are comparing it with fragmentary mandibular material which may be c. 4000 yr old. Altitudinal variation is not thought to be a factor as the earlier specimens from the Menggarai District were collected from a similar altitude as was WAM M32000.

Further, doubt as to whether WAM M32000 represents *P. naso* relates to its slightly smaller teeth. While the breadth of WAM M32000 are similar to values of *P. naso* given by Musser *et al.* (1986, Table 1), its M_{1-3} crown length of 7.15 is less than the range given for *P. naso* (7.3-7.6); its M_{1-3} alveolar length is smaller 7.14 versus 7.5-8.1, and its lower incisors at the point where they are emergent from the dentary sheath is narrower 0.87 versus 1.0-1.2. These lower values of WAM M32000 are unlikely to result from the specimen being younger than the *P. naso* specimens of Musser *et al.* (1986) because the wear on its teeth is approximately intermediate between that figured for two specimens (LB90 and LS9) by Musser *et al.* (1986) which are included in the above range of values for *P. naso*. Finally the dorsal masseteric ridge of WAM M32000 is weak and not "strong" as stated and figured by Musser *et al.* (1986: 4-6) for comparatively aged animals.

Given these uncertainties we hesitate to refer this modern specimen to *P. naso*. Confirmation will probably require discovery of maxillary dentition of *P. naso*.

The generic status of WAM M32000 is discussed later in this paper.

Relationships of *Paulamys*

Musser (1981b) proposed 29 characters which he used for primary analysis of systematic relationships of *Rattus* and other closely related genera. Because both Hooijer (1967)

and Musser (1972b) originally determined the fossil fragments of *Paulamys naso* as *Rattus* we have used these 29 characters for our appraisal of the relationships of WAM M32000. In this analysis we include, in addition to genera considered by Musser (1981a) and Musser *et al.* (1986) to be close to both *Rattus* and *Paulamys*, *Apodemus* and *Arvicanthis*. Both these latter two genera are traditionally recognised as distinct from *Rattus* by Misonne (1969) and Ellerman (1941). While the largely African *Arvicanthis* is considered close to *Rattus* by Jacobs (1978) he places *Apodemus* in a different section of the murid radiation from both *Arvicanthis* and *Rattus*.

The phylogenetic tree constructed using WAM M32000, *Rattus* and 12 other genera was produced (Figure 7). This tree would appear to be reasonably stable: only one tree was produced by the exhaustive branch and bound analyses and the Consistency Index of 0.55 indicates a relatively low level of homoplasy. Characters used to create this tree include the number of roots on M^1 and M_1 . These appear to be 5 and 4 respectively in WAM M32000. However if these two characters are left out or placed in the analysis as unknown characters, the topology of the tree remains as in Figure 7. This tree indicates that of the genera considered, *Paulamys* is closest to *Bunomys* but is also closely related to *Rattus* and *Arvicanthis*.

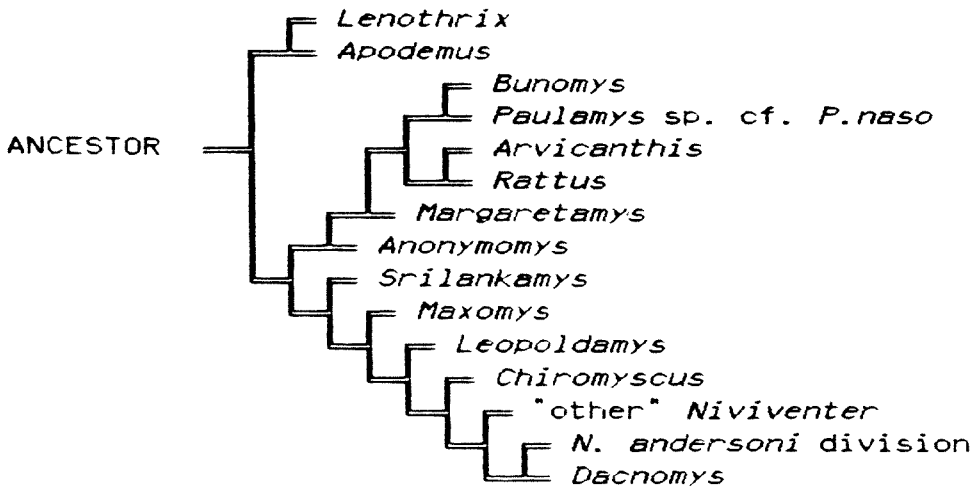


Figure 7. Cladogram of relationships between *Paulamys* sp. cf. *P. naso* and other genera, in part derived from data in Musser (1981a) and Musser and Newcomb (1983).

Paulamys and *Rattus*

The Kelimuta specimen WAM M32000 shares the same polarity for these characters states as *Rattus* for 24 of the 29 listed characters. It differs as follows: *Character 2* (plesiomorphic in WAM M32000) dorsolateral margins of the braincase proper of WAM M32000 is smooth, rather than medium to high ridges or shelves; *Character 8* (plesiomorphic in WAM M32000): incisive foramina are short in WAM M32000,

terminating well before the maxillary toothrows, rather than projecting to the anterior edge of M¹ or posterior to this edge; *Character 9* (plesiomorphic in WAM M32000): posterior rim of the palatal bridge is situated level with the posterior margins of M³ in WAM M32000 rather than projecting way beyond M³ to form a wide platform behind the molar rows; *Character 10* (plesiomorphic in WAM M32000): mesopterygoid fossa is nearly as wide as the back of the palatal bridge and its wall is breached by a moderate, short sphenopalatine vacuity in WAM M32000 rather than having the mesopterygoid fossa one-third to one-half the width of the palatal bridge and the sphenopalatine vacuities huge so as the presphenoid and anterior part of the basisphenoid appear suspended in air; *Character 23* (plesiomorphic in WAM M32000): cusp t3 absent from M² and M³ in WAM M32000 rather than almost always present on M² and often on M³.

It should be noted, however, that the character states given to characters 2, 8, 9, 10 and 23 above for *Rattus* are not unequivocal for they appear to refer only to the Sundaic 'core' taxa. For example, *Character 2*: there are species of *Rattus* (e.g., *niobe* and *verecundus*) where the dorsolateral margins of the braincase proper are smooth; *Character 8*: some species of *Rattus* (e.g. *ceramicus*) have extremely short incise foramen that terminate well in front of anterior edge of M¹; *Character 10*: some species of *Rattus* have sphenopalatine foramen similar to WAM M32000 and *Character 23*: as stated by Musser (1981b) cusp t3 is not always present on M² and M³ in *Rattus*.

It appears that the only robust character separating WAM M32000 from other *Rattus* spp. is *Character 9*, which is the extremely long palatal bridge, such that it does not form a wide platform behind the molar rows. However, it has been pointed out to us (K. Aplin pers. comm.) that this may be a function of the steeply angled aspect of the long rostrum relative to basicranial axis of WAM M32000, which makes an extremely sharp angle and would by necessity create crowding at the posterior palatal region and lead to its shortened state.

Ellerman (1941) and Misonne (1969) made substantial and important attempts to clarify the members of the genus *Rattus*. Musser (1970b) discussed the scope of *Rattus* as proposed by these earlier workers and subsequently, with his co-workers, greatly contracted the membership of *Rattus* by establishing a series of new genera, some of which are only distantly related to *Rattus* (Musser *et al.* 1979; Musser 1981a, b; Musser and Newcomb 1983). In the meantime a number of new species have been described as belonging within *Rattus* and there has been a clarification of the status of a number of putative species of this genus (Musser 1970a, b; 1971; 1972a; 1973a, b; Musser and Boeadi 1980; Musser and Calafia 1982; Taylor, Calaby and Van Deusen 1982; Musser and Heaney 1985; Musser 1986). As a consequence of these studies the number of native species of Indo-Australian *Rattus* was placed at 50 by Musser and Newcomb (1983), although several additional species have been added since that time (Musser and Heaney 1985; Musser 1986).

Despite the considerable attention given to revisionary studies on *Rattus* in recent years, the statement by Musser and Boeadi (1980) that there was no stable definition and diagnosis of *Rattus* still holds. For example, Musser and Newcomb (1983) state that "the monophyly of *Rattus* has yet to be determined. Some groups of species may eventually

be disassociated from *Rattus*, such as the native species in the Australian and New Guinea region."

The zoogeography of *Rattus* in the Indo-Australian region has been discussed by Musser and Newcomb (1983). They draw attention to the absence of known endemic *Rattus* in the Lesser Sunda islands (Nusa Tenggara), an unusual situation given the presence of diverse *Rattus* faunas on the Sunda Shelf to the west and Australia and New Guinea to the east. The species of *Rattus* recorded from Nusa Tenggara are all considered by Musser (1981b) to be introduced to the region (*R. rattus*, *R. norvegicus*, *R. exulans* and *R. argentiventer*). Musser (1981b: 169) raised the possibility that the *Rattus*-like features characterising Australian and New Guinea species may have been independently derived from those that define Asian mainland *Rattus*. Most interestingly, he thought it possible that the Australian and New Guinea *Rattus* "evolved from a *Rattus*-like ancestral stock that was characterised by a suite of derived cranial and dental features similar to those found in some of the *Rattus*-like genera on Flores". If this possibility were correct then he continued by suggesting that native species of *Rattus* may not be found in Nusa Tenggara.

It is of interest that WAM M32000 appears to be closer in some ways to the New Guinea species *R. verecundus* and *R. niobe* and to the Seram species *R. ceramicus*. The species *verecundus* and *niobe* are examples of *Stenomys*, recognised as a genus by Thomas (1910), Tate (1936) and Rümmler (1938) and as a subgenus of *Rattus* by Ellerman (1941, 1949); Tate (1951); Misonne (1969). The distinctive species *ceramicus* was placed in the genus *Nesoromys* by Thomas (1922). *Nesoromys* is included in *Stenomys* by some authors (Rümmler, 1938; Musser, 1981b) but not by others (Tate 1936; Laurie and Hill, 1954; Misonne, 1969). Ellerman (1947-1948) separated the subgenus *Stenomys* from other subgenera of *Rattus* using the key character that their bulla was less than 15 percent of occipitonasal length (WAM M32000 is *c.* 17 percent). *Stenomys* was restricted to species that occur in New Guinea, western and southern Australia, Gaudalcanal, Bougainville and smaller islands in the New Guinea region by Misonne (1969). Musser and Newcomb (1983) would contract Misonne's (1969) concept of *Stenomys* to exclude some species, and would positively place only *Rattus verecundus*, *R. niobe* and *R. richardsoni* in this subgenus — a situation they considered to be supported by Taylor, Calaby and Van Deusen (1982) as a cluster. Musser and Newcomb (1983) would restrict *Stenomys* to Seram and the New Guinea area (and Cape York if *R. leucopus* belongs to *Stenomys*). Ongoing studies by Baverstock, Aplin and others suggest that Australian-New Guinea *Rattus* represent a monophyletic grouping within *Rattus*. Based on a phylogenetic analysis of isozyme electrophoresis and microcomplement fixation of albumin data, Baverstock *et al.* (1986) have shown that *R. leucopus* and other Australian *Rattus* are monophyletic with respect to *R. rattus* and *R. norvegicus* — which are members of the 'core' *Rattus* group of Musser and Newcomb (1983). Furthermore, as yet unpublished electrophoretic data and morphological data (K. Aplin *pers. comm.*) show that *R. leucopus* is very close to members of other New Guinea species including *R. verecundus*, *R. niobe*, *R. steini* etc. The clear implication is that if *Stenomys* is a valid unit, it would have to include all Australian and probably all New Guinea *Rattus*.

The systematic status and relationship of *Paulamys* will be difficult to resolve fully without a clearer definition of the relationship of taxa still placed within *Rattus*, in particular the position of the Australian and New Guinea *Rattus* assemblage.

Paulamys and Bunomys

Musser (1981b: 117) considered that the occlusal configuration of the lower molars in *P. naso* is similar to that in *Bunomys*, a genus of rats, restricted to Sulawesi ranging from lowland to mountain forests including the central part and southwestern peninsula and associated islands. He states that the teeth of *B. fratorum* are most like those of *F. naso* but differ in being "slightly larger ... the laminae are thicker and set closer, so they touch each other; ... anterolabial cusps are usually missing from the second molars ... all the cusplets and anterolabial cusps in *B. fratorum* are low, small, and merge with the laminae at an early stage of wear to lose their definitions quickly, whereas the cusplets and anterolabial cusps remain discrete in *F. (=P.) naso*, the anterolingual and anterolabial cusps forming the anterior lamina of the first molar are dissimilar in size and after little wear coalesce into a high oblong surface that is narrower than the second lamina but flush with its anterior margin, a configuration unlike that in *F. (=P.) naso*".

The new material of *P. naso* described by Musser *et al.* (1986) — and the Kelimutu specimen WAM M32000 — blurs some of these distinctions between *Bunomys* and *Paulamys*. For example, Musser *et al.* (1986: Figure 3) and Figure 4, this paper, indicate that the anterior lamina of M_1 does not always contact the second lamina such that these two lamina are separated by a wide angular space on both the labial and lingual sides of the tooth. Further, the shape of the first lamina on M_1 is not so dissimilar between *P. naso* and species of *Bunomys* [compare Musser and Newcomb (1983: Figure 31D) and Musser *et al.* (1986, Figure 3B)]; the laminae of lower molars of *B. fratorum* are also set further apart.

Musser and Newcomb (1983: 117) also states that *Bunomys* spp. have slender dentaries, with a low ramus and a short segment in front of the tooth row. The illustrations of the dentaries of four species of *Bunomys* in Musser and Newcomb (1983: Figure 29), and our examination of *B. chrysocomus* specimen WAM M27810, indicate that the dentaries are not particularly slender in comparison with WAM M32000, although they have a more erect coronoid process and a relatively shorter dentary ramus anterior to M_1 . Musser and Newcomb (1983: 117) also state that *Bunomys* have a large toothrow set in a small dentary rather than the converse as in *P. naso*. The configuration in WAM M32000 indicates that the relationship of the toothrow to the size of the dentary is not dissimilar to that of *B. chrysocomus* (WAM M27810, Central Sulawesi) and this appears to be also the case in *B. fratorum* which has similar length lower tooth row to WAM M32000 and a slightly larger dentary (see Musser and Newcomb 1983, Table 11 and Figure 29E).

The cusp morphology of the upper tooth row of WAM M32000 is also very similar to that illustrated in Musser and Newcomb (1983: Table 12 Figure 30) for *B. chrysocomus*, *B. andrewsi*, *B. penitus* and *B. fratorum* and there are no consistent differences in cusps or cusplets.

The general configuration of the skull of WAM M32000 is similar to that of *Bunomys* [see description of *Bunomys* in Musser and Newcomb (1983: 393-395)]. For example, the incisive foramen is short, terminating in front of M¹, the palate terminates approximately level with the posterior margin of M³; dorsolateral margin of braincase is without prominent ridges; zygomatic plate, mesopterygoid fossa, interparietal, and sphenopalatine vacuities in the sides of the mesopterygoid fossa are similar in shape. The rostrum of *Bunomys* and WAM M32000 are of similar length [see data in Musser and Newcomb (1983: Table 11)]. For example: the ratio of rostrum length to greatest skull length in WAM M32000 is 0.356 compared to 0.413 (*B. chrysocomus*), 0.360 (*B. andrewsi*), 0.380 (*B. penitus*) and 0.354 (*B. fratrorum*); bulla length to greatest skull length in WAM M32000 is 0.168 compared to 0.193 (*B. c.*), 0.154 (*B. a.*), 0.156 (*B. p.*) and 0.138 (*B. f.*). The rostrum of WAM M32000 is, however, narrower than the rostrum of species of *Bunomys* figured in Musser and Newcomb (1983: Figure 29).

External appearance of WAM M32000 is not dissimilar to *Bunomys* which also have a short-tail (ranging in length from 83 to 87% of body length in *Bunomys chrysocomus*, *B. andrewsi*, *B. penitus*) or tail subequal to body length as in *B. fratrorum*; long hair, and moderately long face.

From Figure 7 it is seen that *Bunomys* and *Paulamys* sp. cf. *P. naso* are very closely related, and in fact share the same polarity for all 29 character states.

Conclusion

The distribution of *Bunomys* which includes the southwestern Peninsula of Sulawesi and offshore islands (Musser and Newcomb 1983) places it in reasonably close geographic proximity to *Paulamys*. On the basis of our rather limited material we can determine no reliable characters that enable us to distinguish *Paulamys* from *Bunomys*. Clearly members of these genera are very closely related as indicated by Musser and Newcomb (1983) and Musser *et al.* (1986). Additional modern specimens are required of *Paulamys* to further examine its systematic status and relationships, particularly with Australian and New Guinea *Rattus*, *Bunomys* and other closely related genera such as the essentially Indo-Chinese genus *Berylmys*.

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References

- Baverstock, P.R., Adams, M., Watts, C.H.S. (1986). Biochemical differentiation among karyotypic forms of Australian *Rattus*. *Genetica*. **71**: 11-22.
- Ellerman, J.R. (1941). *The families and genera of living rodents*. Vol. 2, Family Muridae [British Museum, (Nat. Hist.), London], pp. i-xii, 1-690.
- Ellerman, J.R. (1947-1948). Notes on some Asiatic rodents in the British Museum. *Proc. Zool. Soc. London*. **117**: 259-271.
- Ellerman, J.K. (1949). *The families and genera of living rodents*. Vol. 3, [British Museum, (Nat. Hist.), London], pp. i-v, 1-210.
- Farris, J.S. (1988). "Hennig 86" (version 1.5) — Distributed by J.S. Farris.
- Hooijer, D.A. (1967). Mammalian remains from Liang Toge, Flores. Appendix II. In T. Jacob, Some problems pertaining to the racial history of the Indonesian Region. Doctoral dissertation, Rijksuniversiteit, Utrecht.
- Jacobs, L.L. (1978). Fossil rodents (Rhizomyidae & Muridae) from Neogene Siwalik deposits, Pakistan. *Mus. North. Arizona Press, Bull. Ser.* **52**: 1-103.
- Laurie, E.M.O. and Hill, J.E. (1954). *List of land mammals of New Guinea, Celebes and adjacent islands, 1758-1952*. British Museum (Nat. Hist.). pp. 1-175.
- Miller, Jr. G.S. (1912). *Catalogue of the mammals of western Europe (Europe exclusive of Russia) in the collection of the British Museum*. [British Museum (Nat. Hist.), London] pp. i-xv, 1-1019.
- Misonne, X. (1969). African and Indo-Australian Muridae. Evolutionary trends. *Mus. Roy. L' Afrique Cent. Tervuren. Zool.* **172**: 1-219.
- Musser, G.G. (1970a). Species-limits of *Rattus brahma*, a murid rodent of northeastern India and northern Burma. *Am. Mus. Novit.* **2406**: 1-27.
- Musser, G.G. (1970b). Results of the Archbold Expeditions. No. 93. Reidentification and reallocation of *Mus callitrichus*, and allocations of *Rattus maculipilis*, *R. m. jentinki*, and *R. microbullatus* (Rodentia: Muridae). *Am. Mus. Novit.* **2440**: 1-35.
- Musser, G.G. (1971). Results of the Archbold Expeditions. No. 94. Taxonomic status of *Rattus tatei* and *Rattus frosti*, two taxa of murid rodents known from middle Celebes. *Am. Mus. Novit.* **2454**: 1-19.
- Musser, G.G. (1972a). The species of *Hapalomys* (Rodentia, Muridae). *Am. Mus. Novit.* **2503**: 1-27.
- Musser, G.G. (1972b). Identities of taxa associated with *Rattus rattus* (Rodentia, Muridae) of Sumba Island, Indonesia. *J. Mammal.* **53**: 861-865.
- Musser, G.G. (1973a). Zoogeographic significance of the rice-field rat, *Rattus argentiventer*, on Celebes and New Guinea and the identity of *Rattus pestivulus*. *Am. Mus. Novit.* **2511**: 1-30.
- Musser, G.G. (1973b) Species limits of *Rattus cremoriventer* and *Rattus langbianus*, murid rodents of Southeast Asia and the Greater Sunda Islands. *Am. Mus. Novit.* **2525**: 1-65.
- Musser, G.G. (1981a). Results of the Archbold Expeditions. No. 105. Notes on systematics of Indo-Malayan murid rodents, and descriptions of new genera and species from Ceylon, Sulawesi, and the Philippines. *Bull. Am. Mus. nat. Hist.* **168**: 225-334.
- Musser, G.G. (1981b). The giant rat of Flores and its relatives east of Borneo and Bali. *Bull. Am. Mus. nat. Hist.* **169**: 67-176.
- Musser, G.G. (1986). Sundaic *Rattus*: definitions of *Rattus baluensis* and *Rattus korinchi*. *Am. Mus. Novit.* **2862**: 1-24.
- Musser, G.G. and Boeadi (1980). A new genus of murid rodent from the Komodo Islands in Nusa Tenggara, Indonesia. *J. Mamm.* **61**: 395-413.
- Musser, G.G. and Califia, D. (1982). Results of the Archbold Expeditions. No. 106. Identities of rats from Pulau Maratua and other islands off East Borneo. *Am. Mus. Novit.* **2726**: 1-30.
- Musser, G.G. and Heaney, L.R. (1985). Philippine *Rattus*: a new species from the Sulu Archipelago. *Am. Mus. Novit.* **2818**: 1-32.
- Musser, G.G., Marshall, Jr., J.T. and Boeadi (1979). Definition and contents of the Sundaic genus *Maxomys* (Rodentia, Muridae). *J. Mamm.* **60**: 594-606.

- Musser, G.G. and Newcomb, C. (1983). Malaysian murids and the giant rat of Sumatra. *Bull. Am. Mus. nat. Hist.* **174**: 327-598.
- Musser, G.G., Van de Weerd and Strasser, E. (1986). *Paulamys*, a replacement name for *Floresomys* Musser, 1981 (Muridae), and new material of that taxon from Flores, Indonesia. *Am. Mus. Novit.* **2850**: 1-10.
- Ridgway, R. (1912). 'Color standards and color nomenclature'. (Ridgway, Washington)
- Rümmler, H. (1938). Die systematik und verbreitung der Muriden Neuguineas. *Mitteil. Zool. Mus. Berlin*, **23**: 1-297.
- Tate, G.H.H. (1936). Results of the Archbold Expeditions. No. 13. Some Muridae of the Indo-Australian region. *Bull. Am. Mus. nat. Hist.* **72**: 501-728.
- Tate, G.H.H. (1951). Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. *Bull. Am. Mus. nat. Hist.* **97**: 183-430.
- Taylor, J.M., Calaby, J.H. and Van Deusen, H.M. (1982). A revision of the genus *Rattus* (Rodentia, Muridae) in the New Guinean region. *Bull. Am. Mus. nat. Hist.* **173**: 177-336.
- Thomas, O. (1910). New genera of Australasian Muridae. *Ann. Mag. nat. Hist.* **6**(8): 506-508.
- Thomas, O. (1922). New mammals from New Guinea and neighbouring islands. *Ann. Mag. nat. Hist.* **9**(9): 261-265.
- Van de Weerd, A. (1976). Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alhambra Region, Spain, *Utrecht Micropaleo. Bull. Spec. Publ.* **2**: 1-218.