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Revision of the New Guinean Genus *Mallomys* (Muridae:Rodentia), with Descriptions of Two New Species from Subalpine Habitats

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ABSTRACT. Four species of *Mallomys* are recognised: *M. rothschildi* Thomas, 1898, with the subspecies *M. r. weylandi* Rothschild & Dollman, 1932 (syn. *M. argentata* Rothschild & Dollman, 1932); *M. aroaensis* (De Vis, 1907) with the subspecies *M. a. hercules* Thomas, 1912; *M. istapantap* n.sp., and *M. gunung* n.sp. *Mallomys rothschildi* is the smallest species. It is distinguished from the others by its relatively and often absolutely longer tail, short, diamond-shaped interparietal, and small cranial dimensions. It is found above about 1,500 m along the New Guinean Central Cordillera but is absent in the extreme southeast. It nests primarily in tree hollows. The subspecies *M. r. weylandi* is morphologically much more variable than any other *Mallomys* taxon. This variability may be the result of the absence of congeners within its range. *Mallomys aroaensis* is intermediate in size. Externally it differs from *M. rothschildi* except some individuals of *M. r. weylandi* in its lighter, grey colour, with long white-tipped guard hairs, and an ill-defined dorsal stripe. Cranially, its broad rostrum, inflated frontals, and great bizygomatic width relative to toothrow length distinguish it from all other species of *Mallomys*. It is found only in Papua New Guinea at altitudes from 1,100 m to about 2,450-3,850 m along the Central Cordillera, and to 3,600 m on the Huon Peninsula. It nests primarily in burrows. *Mallomys istapantap* n.sp. is the largest species, and appears to be restricted to subalpine grasslands and the upper montane forest fringe at 2,450-3,850 m in the east-central part of the New Guinean Central Cordillera. It is readily distinguished from all other species of *Mallomys* by its pale ears, and from *M. rothschildi* and *M. aroaensis* by its large size, short tail, large hypsodont molars, and numerous other cranial features (see diagnoses). It also nests in burrows. *Mallomys gunung* n.sp. resembles *M. istapantap* n.sp. externally, but lacks the pale ears of that species and differs markedly in cranial morphology (see diagnosis). Thus far it is known only from the western part of the Central Cordillera, from Mount Carstenz to Mount Wilhelmina, at altitudes of between 3,500 and 4,050 m.

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Species of the genus *Mallomys* are among the very largest of living murids. They are shaggy coated, herbivorous rats found only above 1,000 m along New Guinea's Central Cordillera and Huon Peninsula. Now recognised as part of the New Guinean "old endemic" radiation (Tate, 1951), their precise relationships with other genera remain unclear.

The taxonomy of the species of *Mallomys* has long been contentious. During the late nineteenth and early twentieth centuries a number of species names were proposed, all of which have been regarded more recently as referring to a single variable species. Thomas (1898) based *Mallomys rothschildi* upon a single very dark animal from between Mounts Musgrave and Scratchley in south-eastern New Guinea. In 1912 he proposed a second name, *M. hercules*, for a large, greyish animal from the Huon Peninsula. Unknown to Thomas, Charles De Vis of the Queensland Museum had in 1907 described and named a large grey murid *Dendrosminthus aroaensis*. This specimen came from the head of the Aroa River in south-eastern New Guinea. De Vis clearly had misgivings about naming this animal, as he wrote "...I feel hardly justified in running the risk of perpetrating a synonym, otherwise I should propose for it the name *Dendrosminthus aroaensis*..." (1907, p.11). Although such a "conditional name" would be unavailable were it proposed after 1961, prior to that date this does not prevent availability (see the Code, Art.15). Two additional taxa were described by Lord Walter Rothschild and Guy Dollman in 1932. They recognised both a blackish species (*M. weylandi*) and a grey one (*M. argentata*) from the Weyland Range in western New Guinea.

These matters rested until Rümmler (1938) reviewed the taxonomy of all of the New Guinean murids. He recognised but a single species of *Mallomys*, with three geographical subspecies: *M. r. rothschildi* from south-eastern New Guinea, *M. r. hercules* from the Bismarck Range and Huon Peninsula, and *M. r. weylandi* from the Weyland and Snow Mountains. Tate (1951), in his revision of the New Guinean murids, tentatively maintained Rümmler's three subspecies, but felt that *M. r. weylandi* and *M. r. rothschildi* were very similar, and only doubtfully distinct. He had examined both black and grey furred animals from the Bele River area of Irian Jaya, and had determined that these were simply colour morphs within a single species. Laurie (1952) and Laurie & Hill (1954) also recognised only a single species of *Mallomys* although Laurie (1952) had also noted the existence of both black and grey animals in collections from various parts of Papua New Guinea.

No further revisionary work was undertaken on the genus until this study. However, there were several indications from field workers that Rümmler's solution was not the correct one. Menzies & Dennis (1979), for example, mention that some native peoples from the central highlands of Papua New Guinea recognised two kinds of *Mallomys*. Various social anthropologists and geographers (e.g.

P. Dwyer, D. Hyndman, G. Hope, personal communication) have noticed a similar situation when collecting folk taxonomies and undertaking other work.

Our work on this problem began with the collection by two of us (T.F., K.A.) of *Mallomys* material, including tissues suitable for electrophoresis, from various localities throughout Papua New Guinea during 1981-1986. We had also noted considerable variation within available study material, and had tentatively recognised two species on the basis of cranial and external morphology. Electrophoretic results suggested that three groups could be recognised within our material from Papua New Guinea. This view was substantiated by a thorough examination of all relevant materials, and was extended through the recognition of a fourth species from Irian Jaya based on morphological criteria alone. Armed with this reappraisal of all *Mallomys* material held in Australian institutions, one of us (C.P.G.) travelled to London to examine type and other material held in the British Museum, and sought material in other European museums as well. We afterwards borrowed extensively from the holdings of *Mallomys* in the American Museum of Natural History.

The descriptions of the two new taxa proposed in this work were prepared by Flannery, Aplin and Groves, and only those authors should be cited as authorities for the names.

Materials and Methods

External measurements used in this study were taken from museum labels. In most cases they are known to have been taken on freshly dead individuals. Cranial measurements follow Musser (1970), except for toothrow length, which here has been taken as maximum crown length (rather than alveolar length). Colour nomenclature where capitalised follows Ridgway (1886).

Abbreviations are as follows: B.M. - British Museum (Natural History) mammal specimen. AM M - Australian Museum mammal specimen, AM F - Australian Museum fossil specimen. AMNH - American Museum of Natural History mammal specimen, CM - Australian National Wildlife Collection specimen. RM - Rijksmuseum van Natuurlijke Historie [Leiden] mammal specimen.

Results

Electrophoresis. Specimens of *Mallomys* sampled for electrophoretic analysis are listed in Table 1. Unfortunately, the sample size is small, as many *Mallomys* were received in the field long after death and their tissues had commenced to decay. Elsewhere it has been shown that only a few

animals per population are needed to characterise that population for systematic purposes using allozyme electrophoresis (Richardson *et al.*, 1986, Gorman & Renzi, 1979, Adams *et al.*, 1987).

A total of 39 loci allowed for reliable genetic interpretation in the present study. The enzymes and proteins used are listed in Appendix 1 and Table 2 shows the allelic profiles of the three populations for the 39 loci. A matrix of genetic distances between populations, using both fixed differences (see Richardson *et al.*, 1986) and corrected Nei Distances (Nei Ds, see Nei, 1978) is given in Table 3. The single specimen from Mount Albert Edward (population A, representing *M. istapantap* n.sp.) differed from the other two populations sampled at an average of 33% of its loci (Nei D = 0.38). The Mount Sisa sample (population B, representing *M. aroaensis*) differed from the Telefomin sample (population C, representing *M. rothschildi*), at 15% of loci examined (Nei D = 0.25).

Even in the absence of other data, a good case can be made on the basis of electrophoresis alone that the Mount Albert Edward specimen represents a distinct species. The

level of difference encountered far exceeds that expected for allopatric populations of a single species (typically 0 to 10%, see Richardson *et al.*, 1986). Unfortunately, the *M. rothschildi* and *M. aroaensis* comparison involves two localities 150 km apart. These two allopatric populations exhibit genetic differences greater than are expected for a single species and greater than have been thus far encountered for other species of New Guinean mammals (Adams, unpublished). Nevertheless, the level of difference is by itself not sufficient to characterise two species, as it is not possible to rule out within-species geographic variation. Fortunately, the morphological data indicate extensive sympatry of the two species and the 15% fixed genetic differences encountered here would if found in sympatry, be sufficient to unequivocally characterise the two species.

Morphology. Large samples of *Mallomys rothschildi* (N = 48) and *M. aroaensis*, (N = 72) as well as moderate samples of *M. istapantap* n.sp. (N = 20) and *M. gunung* n.sp. (N = 8) (Appendix 2), were available for this analysis. Several non-metric as well as metric differences in the

Table 1. Details of specimens used in the electrophoretic analysis.

Population	Species	Locality	Specimen no.
A	<i>M. istapantap</i> n.sp.	Mount Albert Edward, Central Province	AM M12875
B	<i>M. aroaensis</i>	Bobole Village Mount Sisa, Southern Highlands Province	AM M16693, AM M17096, AM M17893, AM M17894
C	<i>M. rothschildi</i>	Telefomin area West Sepik Province	AM M13730, AM M15999, AM M17361, AM M17362

Table 2. Allele frequencies at the 39 loci examined. Locus and Allele designation follow Adams *et al.*, 1987. 2N is the number of haploid genomes sampled.

Locus	A (2N)->(2)	B (8)	C (8)	Locus	A (2N)->(2)	B (8)	C (8)
<i>Acon-2</i>	c	b (75) a (25)	b	<i>Gpd</i>	a	b (50) a (50)	b (25) a (75)
<i>Adh-1</i>	a	a	b	<i>Idh-2</i>	b	a	a
<i>Adh-2</i>	-	b	a	<i>Ldh-1</i>	a	b	b
<i>Ak-1</i>	a	a	b (50) a (50)	<i>Mpi</i>	b	a	a
<i>Ak-2</i>	c	b	b (13) a (87)	<i>Pep-A</i>	b	a	b
<i>Dia</i>	b	a	a	<i>Pep-D</i>	b	a	a
<i>Enol</i>	a	a	b	<i>δPgd</i>	a	b	b (25) a (75)
<i>Gapd</i>	-	a	a	<i>Pgm-1</i>	a	b	a
<i>Got-2</i>	a	b	b	<i>Pgm-2</i>	b	a	a
<i>G6pd</i>	b	a	b	<i>Pk-2</i>	a	b (25) a (75)	a

The following loci were invariant: *Acon-1, Acp, Ada, Ca, Fdpase, Got-1, Gpi, Idh-1, Lap, Ldh-2, Mdh-1, Mdh-2, Np, Pep-B, Pep-C, Pkg, Pk-1, Sod, Sordh.*

Table 3. Matrix of genetic differences between the three populations of *Mallomys*. Lower matrix - percentage fixed differences; upper matrix - Nei D's.

	A	B	C
A	-	0.45	0.37
B	35	-	0.23
C	30	14	-

external morphology and cranium were noted between these taxa.

Pelage and external morphology. Pelage and skin differences allow for identification of all four taxa. The overall dorsal colouration of most *M. rothschildi* is black or very dark brown, with a paler underfur. Where the fur is parted to reveal the underfur (e.g. around the ears in study skins) a pale grey or white flash appears to be present. The guard hairs are usually uniformly black. Almost all *M. rothschildi* have some dark fur on the venter, a feature never seen in other species, and in *M. r. rothschildi* the entire venter is grey interspersed with dark guard hairs (unique in the genus). The ears are black, and the tail is long relative to that of other *Mallomys* (Table 4). Within Papua New Guinea, *M. r. rothschildi* is readily distinguished from *M. aroaensis* and *M. istapantap* n.sp. by its dark dorsal colouration, lack of pale tips on the guard hairs and grey venter. *Mallomys rothschildi weylandi*, however, is

polymorphic in colouration. Many individuals are similar in dorsal colouration to *M. r. rothschildi*, but a few are dark grey with light-tipped guard hairs and possess a dark dorsal stripe as in *M. aroaensis*. These differ from all *M. aroaensis* however in having the underfur of the dorsum a darker shade of grey, and (all except one specimen) in having grey patches of fur in the inguinal region.

Mallomys aroaensis, *M. gunung* n.sp. and *M. istapantap* n.sp. differ from most *M. rothschildi* in having an overall greyish rather than black appearance. They also appear "frosted" due to the white tips of the darkish guard hairs. The contrast with the underfur is not as great as in *M. rothschildi*. All have pure white venters, which lack guard hairs. *Mallomys aroaensis* differs from *M. istapantap* n.sp. and *M. gunung* n.sp. in possessing an ill-defined dorsal stripe, which is due to a darkening of the tips of the underfur (but no change in the guard hairs), and a longer tail (Table 4). In some individuals (particularly in the subspecies *M. a. hercules*) the dorsal stripe is broken up into a series of irregular blotches, but some midline darkening is invariably present. Such a feature is never seen in *M. istapantap* n.sp. and *M. gunung* n.sp.

The lighter (flesh coloured) ears of *M. istapantap* n.sp. are of great diagnostic value, the ears of all other species being dark.

Mallomys gunung n.sp. is similar to *M. istapantap* n.sp. in its large size, lack of a dorsal stripe and short tail. It differs however in its darker ears, slightly lighter grey

Table 4. External measurements in mm and gms for the species of *Mallomys*. HB = head body length, TV = tail-vent length, HF = hindfoot length (su), E = ear (notch) length. X = mean, R = range, N = sample size, STD = standard deviation. Samples include all BM, AM and CM specimens (except juveniles) for which measurements taken in the flesh exist.

		HB	TV	HF	E	WT
<i>Mallomys istapantap</i> n.sp.	X	397.1	338	70.3	30.9	1,950
	R	352-477	280-363	60-80	23-37	1,950
	N	12	11	11	12	1
	STD	32.09	24.86	5.93	3.80	-
<i>Mallomys gunung</i> n.sp.	X	418	366	75	35	-
	N	1	1	1	1	-
<i>Mallomys a. aroaensis</i>	X	366	372	69.8	28.8	1,530
	R	292-410	295-420	64.4-76.0	25.3-33.0	1,410-1,710
	N	45	45	44	43	4
	STD	24.5	30.2	2.80	1.84	127.3
<i>Mallomys a. hercules</i>	X	-	-	67.0	25.5	-
	R	-	-	67-67	25-26	-
	N	-	-	2	2	-
<i>Mallomys r. rothschildi</i>	X	366	380.2	69.1	29.3	1,134
	R	306-405	337-423	63.0-80.0	26.0-31.0	925-1,500
	N	27	27	26	26	7
	STD	19.91	22.36	3.83	1.17	203
<i>Mallomys r. weylandi</i>	X	387	402	71.1	26.0	-
	R	350-440	377-440	66-75	17-29	-
	N	9	9	9	9	-
	STD	27.21	19.02	2.76	3.87	-

dorsal colouration which lacks a brownish suffusion, and extremely long claws.

Overall size is also a valuable feature in distinguishing the four taxa. Adult *M. rothschildi* weigh between 925 and 1,500 g, *M. aroaensis* between 1,410 and 1,710 g, and *M. istapantap* n.sp. about 1,950 g. No weights are available for *M. gunung* n.sp., but it is probably slightly smaller than *M. istapantap* n.sp. The values for head plus body length and the skull measurements confirm that *M. rothschildi* is the smallest species, *M. aroaensis* next, and the two high-mountain species largest.

Skull and teeth. We have been able to find no consistent differences in molar cusp patterns between the four *Mallomys* species, although there are differences in size and the degree of hypsodonty. *Mallomys istapantap* n.sp. and *M. gunung* n.sp. have much larger molars (Table 5), which are much more hypsodont than in other species of *Mallomys* (Fig. 1). Major non-metric cranial differences distinguish *M. istapantap* n.sp. from the other species. The premaxillary/maxillary suture of *M. istapantap* n.sp. is more sinuous, with a dorsal and ventral anterior projection of the maxilla (Fig. 2). In the remaining species the ventral projection is absent, the suture running gently posteriorly towards the incisive foramen. The bony palate in both the high-mountain species (*M. gunung* n.sp. and *M. istapantap* n.sp.) is grossly thickened dorsoventrally. That of *M. istapantap* n.sp. slopes gently posteriorly, and unites at an acute angle with the upwardly sloping ventral surface of the mesopterygoid fossa, while in *M. gunung* n.sp. (as in the other species of *Mallomys*) the posterior edge of the bony palate slopes sharply towards the mesopterygoid fossa, intersecting it at a less acute angle (Fig. 2). The mesopterygoid fossa of *M. istapantap* n.sp. differs from that of other taxa in that internally it is strongly elliptical, rather than round (Fig. 2). The orbital region differs from that of the other three species in that the sphenopalatine foramen is slit-like and partly hidden by the maxilla rather than ovoid and readily visible (Fig. 2). In the basicranial region *M. istapantap* n.sp. differs from its congeners in that the alisphenoid makes a much larger contribution to the anterior margin of the postglenoid vacuity than in the remaining species, and that the postglenoid vacuity itself is somewhat different in shape, its anterior edge being less vertically inclined (Fig. 2).

The cranium of *M. aroaensis* differs from that of other *Mallomys* species in having a relatively more inflated rostrum (Fig. 3), as well as inflation of the dorsal part of the maxillary facial lamina.

The cranium of *Mallomys r. rothschildi* differs from that of the other *Mallomys* species in its narrower interorbital region (Table 5), narrower bizygomatic breadth (Table 5), in its anteroposteriorly short, diamond-shaped interparietal (Fig. 4), and in its overall smaller size. *Mallomys rothschildi weylandi* is similar in most cranial dimensions to *M. r. rothschildi*, but the interparietal is more variable in shape, the interorbital width and palatal length are greater, and the molars are smaller (Table 5).

The cranium of *Mallomys gunung* n.sp. differs markedly from that of other *Mallomys* species in the construction of the rostrum. The nasals and dorsal section of the premaxillae are foreshortened, giving the upper incisors the markedly proodont appearance remarked upon by Tate (1951). The incisor enamel is pale yellow, being less strongly pigmented than in all other *Mallomys* species except some high altitude individuals of *M. rothschildi*.

Systematics

Mallomys Thomas, 1898

Type species. *Mallomys rothschildi* Thomas, 1898 (p.2), based upon BM No 97.12.6.6., adult male skin (mounted) and skull from the Owen Stanley Range, between Mount Musgrave (8°55'S, 147°22'E) and Mount Scratchley (8°45'S, 147°29'E), 1,500-1,800 m.

Included species and distributions. *Mallomys rothschildi*: the New Guinean Central Cordillera, from the Weyland Range in the west to the Owen Stanley Range in the east, at altitudes of 1,500 to 3,700 m. Including the subspecies *M. r. rothschildi* (Owen Stanley Range to Telefomin, P.N.G.), and *M. r. weylandi* (Weyland Range to Mount Wilhelmina area, Irian Jaya) (Fig. 5).

Mallomys aroaensis: the eastern part of the New Guinean Central Cordillera, from Mount Sisa in the west to Mount Simpson in the east, at altitudes from 1,100 to 2,450 m; also the Huon Peninsula to 3,600 m (Fig. 6). Including the subspecies *M. a. aroaensis* (Mount Sisa to Owen Stanley Range), and *M. a. hercules* (Huon Peninsula).

Mallomys istapantap n.sp.: the east-central part of the New Guinean Central Cordillera, from Mount Giluwe in the west to Mount Victoria in the east, in subalpine herbfields and forest margins above 2,450 m to at least 3,850 m, and possibly to the limit of vegetation (Fig. 7).

Mallomys gunung n.sp.: from the Snow Mountains to Mount Wilhelmina, Irian Jaya, at altitudes of 3,500 to 4050 m, and possibly to the limit of vegetation (Fig. 7).

Generic diagnosis. Musser (1981) has shown that the species of *Mallomys* lack many derived cranial features seen in large murids with similar molar morphology that are found on islands to the west of New Guinea. He suggests that the species of *Mallomys* are part of a primitive group of murids not closely related to these Asian taxa. His work should be referred to for diagnostic features distinguishing New Guinean from Asian murids. Within New Guinea the species of *Mallomys* can be distinguished from all other murids by possessing the following combination of features: size large (weight between 1 and 2 kg when adult); coat long and dense, somewhat woolly, with long guard hairs projecting from the underfur; mammary formula is 1 + 2 = 6; molars complex, cusps forming "trilobed" pattern on upper molars; palate greatly thickened.



Fig.1. Crania and dentaries of: A, *Mallomys rothschildi rothschildi* AM M15603; B, *Mallomys rothschildi weylandi* AMNH15133; C, *Mallomys aroaensis* holotype QM J2814; D, *Mallomys istapantap* n.sp. holotype AM M7328; and E, *Mallomys gunung* n.sp. holotype AMNH151346.

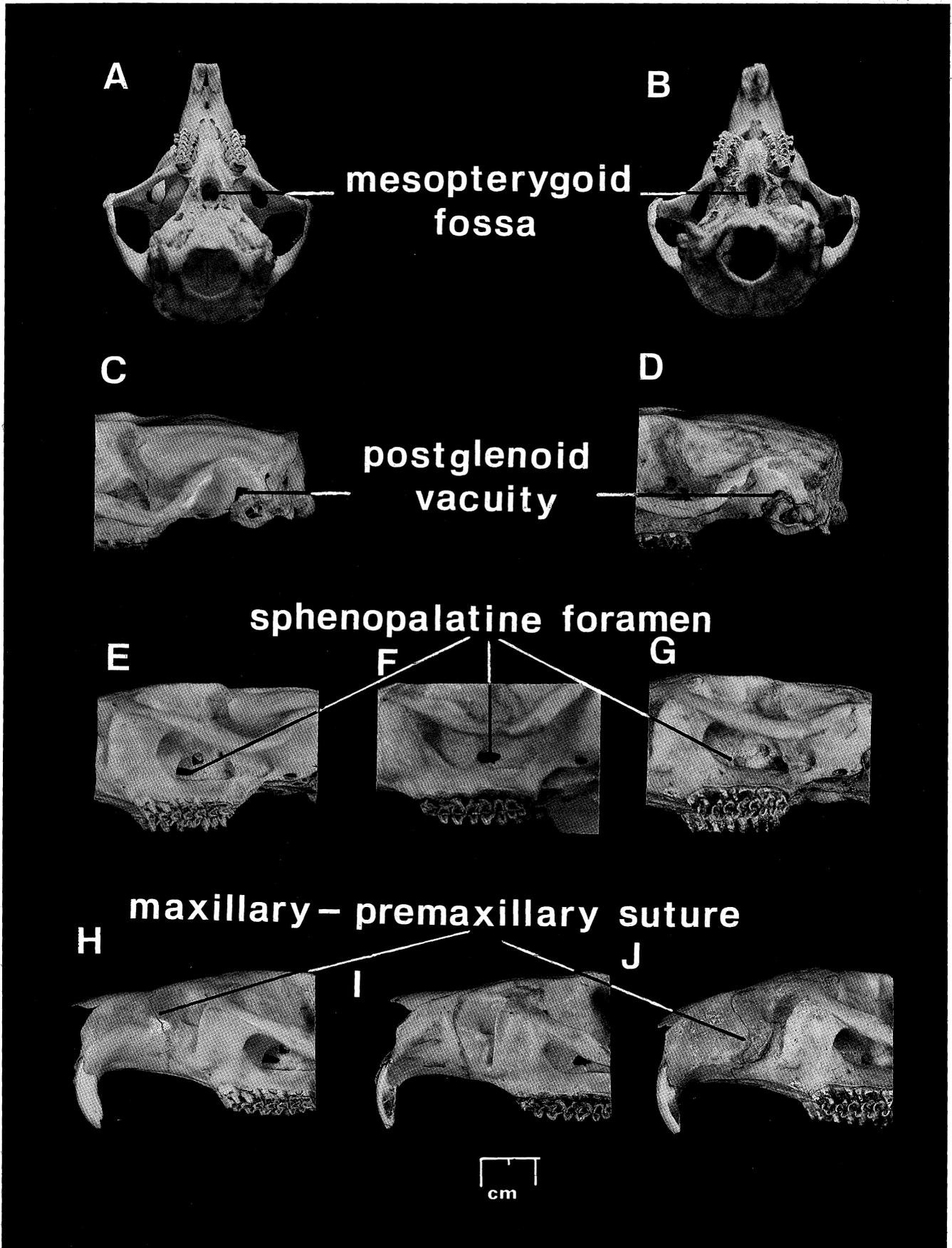


Fig.2. Comparison of the mesopterygoid fossa, postglenoid vacuity, sphenopalatine foramen and maxillary/premaxillary suture, in the holotypes of *Mallomys istapantap* n.sp. (B,D,G,J), *Mallomys gunung* n.sp. (F,I) and *Mallomys aroaensis* (A,C,E,H).

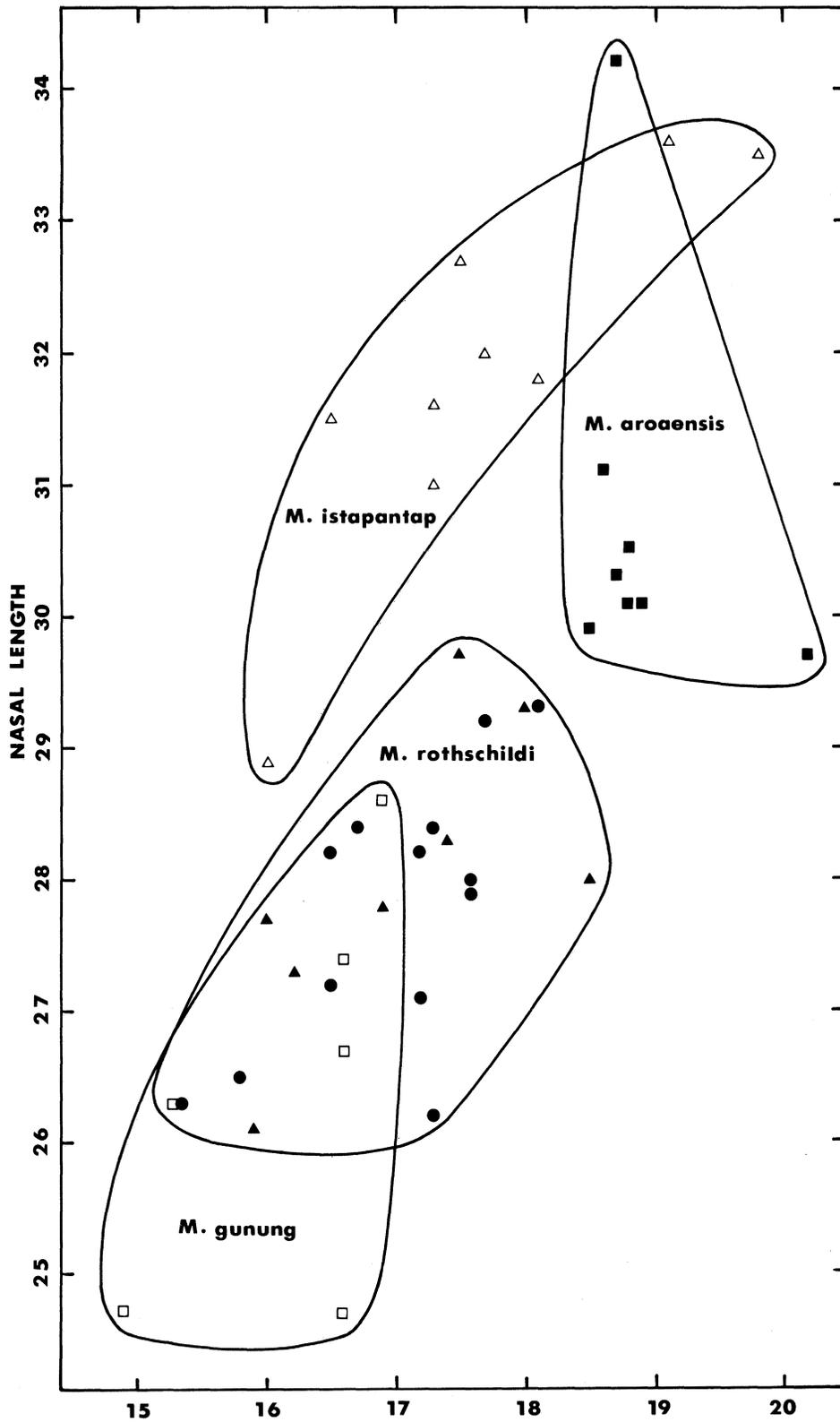


Fig.3. Bivariate plot of nasal length over rostrum width for the four species of *Mallomys* (the dots are *M. r. rothschildi* and the solid triangles are *M. r. weylandi*) (adults only).

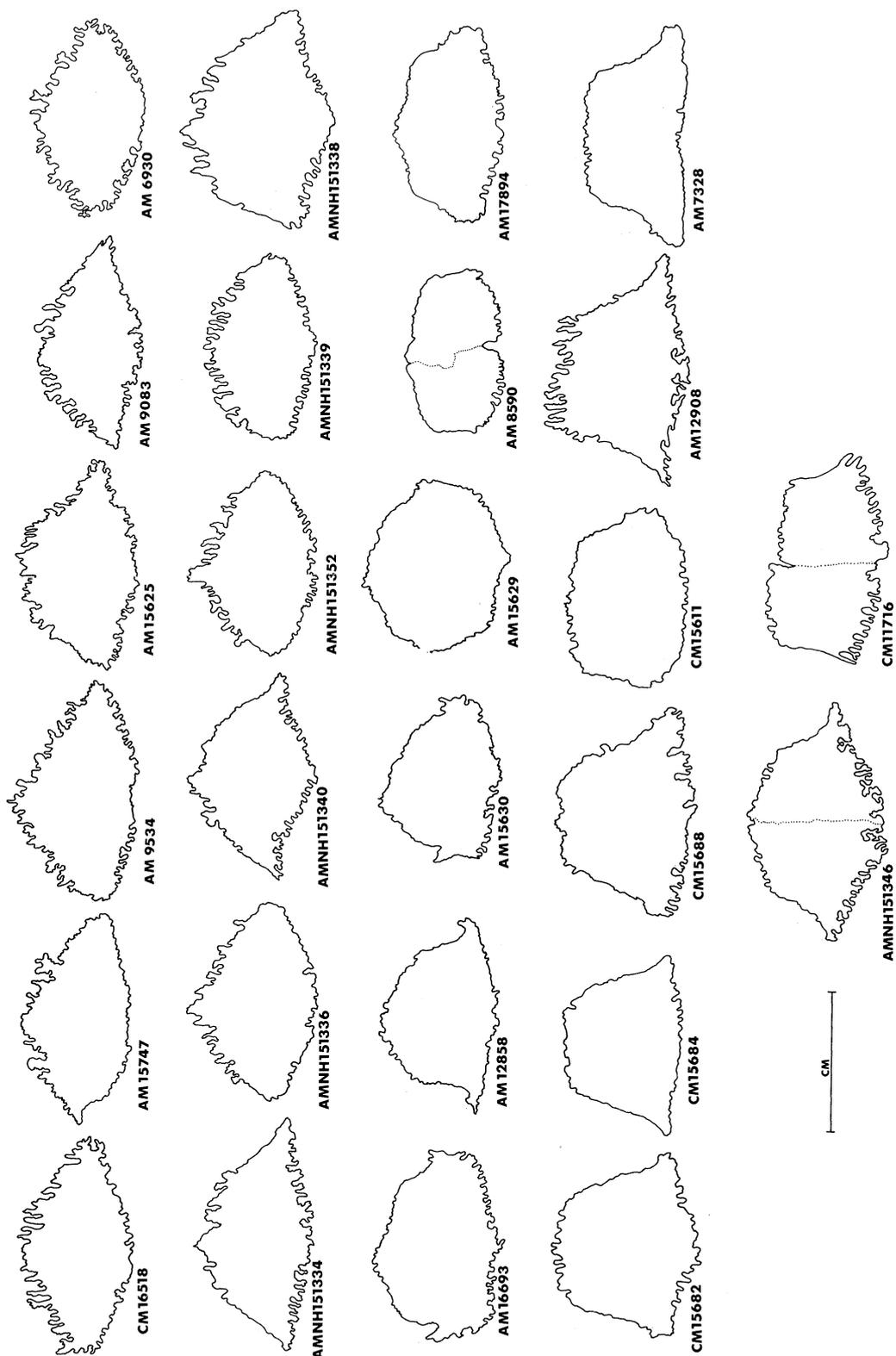


Fig.4. The interparietals of *Mallomys rothschildi rothschildi* (left column), *M. r. weylandi* (second left) column), *Mallomys aroaensis aroaensis* (middle column), *Mallomys istapantap* n.sp. (fourth right) column) and *Mallomys gunung* n.sp. (right column). Except for *M. gunung* n.sp. (where only three complete crania are known), the most common morphologies are towards the bottom of the page, the highly unusual ones at the top.

Table 5. Cranial and dental measurements for the species of *Mallomys* (from specimens held in the AM, QM, RMNH, BM(NH) and CM and borrowed from AMNH. Includes some subadults).

		<i>Mallomys istapantap n.sp.</i>	<i>Mallomys gunung n.sp.</i>	<i>Mallomys aroaensis aroaensis</i>	<i>Mallomys aroaensis hercules</i>	<i>Mallomys rothschildi rothschildi</i>	<i>Mallomys rothschildi weylandi</i>
Condylbasal length	X	76.9	74.9	72.8	74.8	72.1	72.2
	R	75.0-80.6	72.1-77.2	70.2-75.7	74.5-75	68.3-74.6	69.5-75.4
	N	9	3	9	2	13	10
	STD	2.06	2.60	1.89	-	1.85	2.04
Bizygomatic width	X	41.3	40.6	39.3	40.3	38.1	37.5
	R	39.9-42.3	40.2-41.0	36.8-42.4	39-41.3	36.0-39.3	36.0-39.2
	N	9	3	10	4	16	10
	STD	1.03	-	2.23	1.04	1.08	1.11
Palatal length	X	39.9	40.3	36.4	-	35.7	39.7
	R	36.2-42.3	39.3-41.6	34.5-38.6	-	34.0-37.6	35.1-41.9
	N	9	6	10	-	16	8
	STD	1.88	.94	1.43	-	1.05	2.77
Nasal length	X	31.8	26.4	31.0	30.3	27.5	27.9
	R	28.9-33.6	24.7-28.6	26.8-34.2	29-31.5	26.5-29.3	26.1-29.7
	N	9	6	10	4	15	9
	STD	1.42	1.53	2.56	0.87	1.26	1.11
Incisive foramen length	X	15.5	13.7	14.6	15.3	13.7	15.4
	R	14.0-17.2	11.6-14.9	13.6-17.1	14.6-16	12.7-15.0	13.9-15.9
	N	9	6	10	2	17	10
	STD	1.00	1.32	1.15	-	.72	.77
Rostrum breadth at zygomatic plates	X	17.7	16.2	18.8	-	17.0	17.1
	R	16.0-19.8	15.3-16.9	16.5-22.1	-	15.3-18.1	15.9-18.5
	N	9	6	10	-	14	8
	STD	1.18	.83	1.35	-	.77	.96
Maximum nasal width	X	10.3	9.6	9.9	12.4	8.8	9.0
	R	9.4-11.1	9.4-9.8	8.2-10.8	11-13.5	8.0-10.4	8.0-9.6
	N	9	5	10	4	15	10
	STD	.57	.16	.88	1.11	.60	.48
Interorbital width	X	11.2	11.0	10.9	12.2	9.4	10.5
	R	8.8-13.3	10-11.3	9.2-12.3	11-13	8.2-11.1	9.7-11.0
	N	8	5	10	5	16	10
	STD	1.59	.54	1.16	.84	.08	.76
M1-3/ length	X	18.4	18.8	17.0	17.0	17.2	16.5
	R	17.4-19.1	17.4-20	16.3-18.0	16.2-18	15.8-18.2	15.7-17.5
	N	8	5	10	6	18	11
	STD	.57	.96	.67	.57	.64	.21
M1/ length	X	8.9	9.2	8.4	-	8.4	7.9
	R	8.4-9.3	8.1-10.1	7.4-9.9	-	7.7-9.3	7.8-8.7
	N	9	4	10	-	16	9
	STD	.33	.94	.72	-	.39	.42
M1/ width	X	5.4	5.8	5.2	-	5.3	5.2
	R	5.0-6.0	5.6-6.0	4.9-5.4	-	5.2-5.6	5.1-5.4
	N	8	4	10	-	16	9
	STD	.35	.18	.13	-	.12	.11

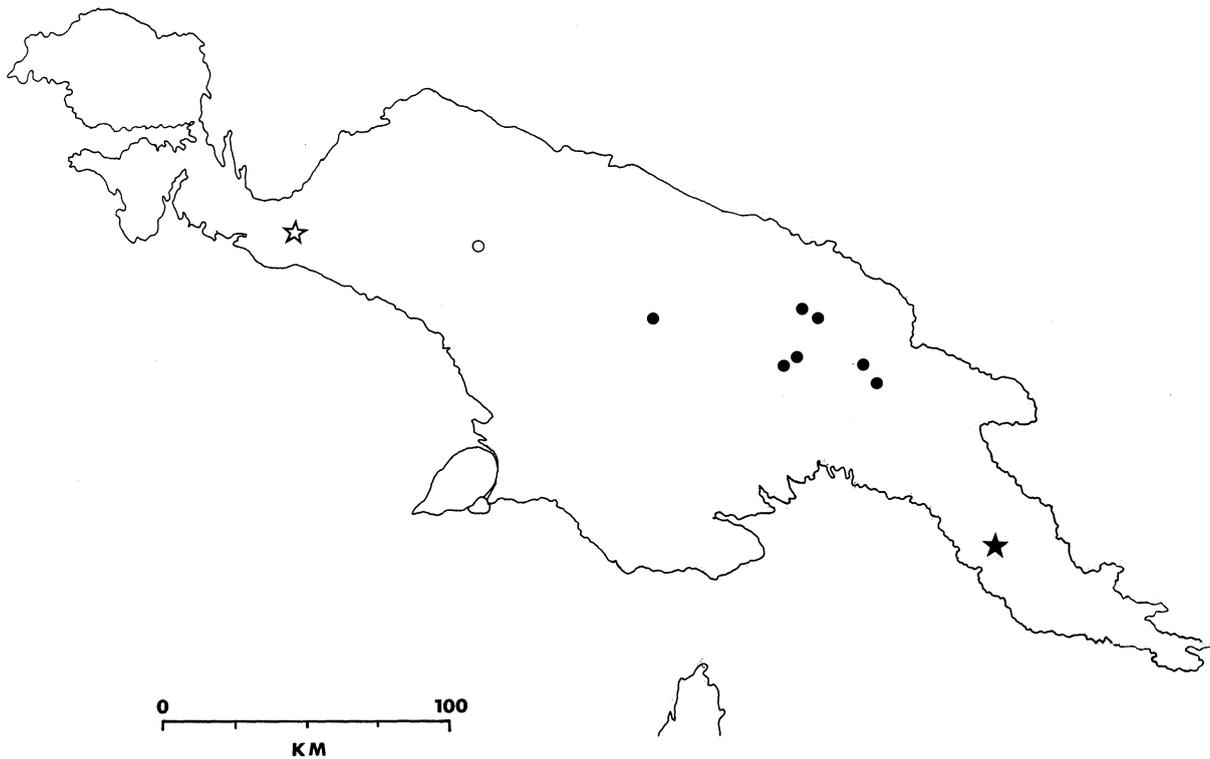


Fig.5. Distribution of *Mallomys rothschildi*. Solid dot and star = *M. r. rothschildi*, open circle and star = *M. r. weylandi*, star = type locality.

***Mallomys rothschildi* Thomas, 1898**

(8°45'S, 147°29'E), 1,500-1,800 m.

Revised diagnosis. All except some individuals of *M. r. weylandi* are distinguishable externally from other species by their much darker dorsal colouration. Contour hairs silvery at base with long black tips; the guard hairs of the midback are uniformly dark (rather than light tipped), and the venter almost always includes some greyish or black hairs. In all *M. rothschildi* the tail is relatively and often absolutely longer than in the other taxa; the depigmented terminal zone extends over two thirds to three quarters of the total tail length; and the tail scales overlap less than in other species, so that the tail surface is smoother, less rasping. In terms of body weight it is the smallest *Mallomys* (Table 4). The cranium can usually be distinguished from that of other species of *Mallomys* by its broad, short and more or less diamond shaped rather than hemidiscoidal interparietal (Fig. 4) and its relatively narrower bizygomatic width (Table 5).

Diagnosis. Invariably blackish dorsally with all black guard hairs. Venter invariably entirely dirty grey with presence of many black guard hairs, rather than largely pure white and lacking guard hairs as in *M. r. weylandi*. Tail scales smaller, usually 9-11 per centimetre of length (in 16 out of 17 skins examined) as opposed to 7-8 in *M. r. weylandi*. Interparietal usually more diamond shaped (Fig. 4), interorbital width usually narrower (Fig. 8), and toothrow length often greater (Table 5).

***Mallomys rothschildi weylandi* Rothschild & Dollman, 1932**

Mallomys weylandi Rothschild & Dollman, 1932: 212.

***Mallomys rothschildi rothschildi* Thomas, 1898**

Type material. Holotype: BM 1939.1943 (previously F.S.M. No 95) adult female skin with skull and dentaries. From The Gebroeders, Weyland Range (3°38'S, 133°55'E), Irian Jaya, 2,100 m.

Mallomys rothschildi Thomas, 1898: 2.

Type material. Holotype: BM 97.12.6.6 adult male skin and skull with dentaries. From between Mounts Musgrave and Scratchley

Synonyms. *Mallomys argentata* Rothschild & Dollman, 1932 (p.212). Based upon the syntypes BM1939.1942 (previously F.S.M. 91) and BM 33.6.1.33, adult female skins and skulls from The Gebroeders, Weyland Range (3°38'S, 133°55'E) Irian Jaya, between 2,150 and 2,450 m.

Diagnosis. Either blackish dorsally with black guard hairs or greyish with pale tipped guard hairs. Ventrally white, but almost always with small patches of greyish fur (often with black guard hairs) in inguinal region. Interorbital width (Fig. 8) and palatal length usually greater than in *M. r. rothschildi*, but toothrow often smaller (Table 5). Only 7-8 scales per cm of tail length as opposed to 9-11 in *M. r. rothschildi*.

Discussion. *Range.* *Mallomys rothschildi* seems to be confined to the western and central sections of the New Guinean Central Cordillera. There are two distinct subspecies. *Mallomys rothschildi weylandi* is found from the Weyland Range in the west to Mount Wilhelmina in the east, while *Mallomys rothschildi rothschildi* occurs from Telefomin in the west to between Mounts Musgrave and Scratchley in the east. The record of the holotype is far to the east of all other records, and it is only to the west of Morobe Province that the species appears to be common. At some localities (e.g. Telefomin, Mount Erimbari) it is caught to the exclusion of other *Mallomys* species. It also seems to be very common in the Mount Hagen area (Laurie, 1952; AMM specimens). At present, a gap of some 330 km (between Mount Wilhelmina and Telefomin) separates the distinctive subspecies *M. r. weylandi* and *M. r. rothschildi*. Investigation of this area should show whether these subspecies abut or intergrade. As presently understood, their morphology gives no indication of any intergradation, so that if this does occur, the intergrade zone is probably a narrow one. The altitudinal range of *M. rothschildi* is poorly known. In the Telefomin area it occurs as low as 1,500 m while on Mount Giluwe it occurs as high as 3,700 m, where it is sympatric with *M. istapantap* n.sp. Throughout the range of *M. r. rothschildi* it is frequently sympatric with *M. aroaensis*, although, as noted above, one or the other species may tend to dominate at any one locality.

Morphological variation. The degree of morphological variability is far greater in *M. r. weylandi* than in *M. r. rothschildi*. Although our sample of *M. r. weylandi* is small it includes remarkable variation in coat colouration and a more limited cranial variability. Overall, this sample shows the greatest variability of any *Mallomys* subspecies. The sample of ten skins studied by us includes five specimens which are indistinguishable in dorsal colouration from *M. r. rothschildi*, and five resembling *M. aroaensis* (Figs 9--10). Ventrally, all except one specimen are almost all white, with small patches of greyish hairs inguinally. The exception lacks the grey inguinal patches. Many individuals have readily visible dark guard hairs in these patches. Two of the blackish and two of the greyish individuals possess a white band encircling the middle of the body. This feature is seen rarely in *M. r. rothschildi*, and never in other species of *Mallomys*. Cranially, *M. r. weylandi* shows considerable variation in the shape of the interparietal. In *M. r. rothschildi* it is almost always diamond shaped and anteroposteriorly short. In *M. r. weylandi* most specimens are like this, but a few are similar to the more arched interparietal common in *M. aroaensis* (see Fig. 4).

We have examined the syntypes of *M. argentata* Rothschild & Dollman, 1932, and cannot distinguish them from any other *M. r. weylandi* on the basis of cranial morphology. In coat colour they are indistinguishable from the lighter coat colour morph present in the *M. r. weylandi* sample from the Bele River. Thus, we are confident that *M. argentata* is a synonym of *M. r. weylandi* Rothschild & Dollman, 1932.

There is little variation within *M. r. rothschildi*. Only two of the 20 British Museum skins and none of the five Australian Museum skins from the central highlands possess a striking white band on either side of the body, reaching from the whitish ventral zone up towards (but not onto) the mid-dorsal region; a third skin has the band on the left side only. However, two of the four Australian Museum specimens from Telefomin possess similar bands. Most specimens have inconspicuous white patches in front of the ears; the types of *M. r. weylandi* and of *M. r. rothschildi* lack them. A specimen (B.M.69.338) from the Schrader Mountains, above Kaironk, at about 1700 m, is larger than other specimens, and is unique in that the tail is shorter than the head plus body. The degree of blackening of the whitish ventral zone varies: in some it is so extensive that the underside looks nearly black, while in others it is pale grey. Finally, some specimens from very high altitudes (e.g. CM 16518 from Mount Wilhelm) have white incisor enamel.

Differences in the degree of morphological variability between subspecies exist in other New Guinean mammals. Flannery & Calaby (1987) discuss the case of *Spilocuscus maculatus*. *Spilocuscus m. goldiei* inhabits southern New Guinea, where it has no congeners. It exhibits great cranial variability. *Spilocuscus m. maculatus* is found in northern New Guinea, where it is sympatric with *Spilocuscus rufoniger*. Cranial variability is much less in *S. m. maculatus* and *S. rufoniger* than in *S. m. goldiei*. Indeed, in some features where two distinct states are found in *S. m. goldiei* (e.g. presence of frontal/maxillary or lachrymal/nasal suture, sometimes on opposite sides of a single skull), one condition (frontal/maxillary suture) is invariably found in *S. rufoniger* and the other (nasal/lachrymal suture) in *S. m. maculatus*. Flannery & Calaby suggest that this loss of variability in the taxa existing sympatrically may be due character displacement owing to interspecific competition, and concomittant changes in skull shape.

The situation seen in the subspecies of *M. rothschildi* and in *M. aroaensis* is strikingly similar to that in the species of *Spilocuscus*. In *M. r. weylandi*, which occurs in the absence of congeners, there is a range of morphological variation that in part encompasses that seen in both *M. r. rothschildi* and *M. aroaensis* which are sympatric in eastern New Guinea. Thus, our findings suggest that sympatry among congeners has the potential to reduce the range of morphological variation present in a taxon. Although the ecology of the species of *Spilocuscus* and *Mallomys* remains entirely unstudied, we consider it possible that this is due to character displacement owing to competitive interaction.

Reproduction and nest sites. A lactating female was

taken on 25 July 1972 on Mount Erimbari, and a suckling young (WT = 148 g) on 10 July 1985 in the Telefomin area. Almost all specimens of this species for which data exist were taken from tree hollows, or were shot at night in the canopy. The only exception that we know of is AMM15999, a young animal that was taken from deep in a limestone cave at 1,500 m in the Telefomin area. Interestingly, other *Mallomys* species have not been recorded for the Telefomin area.

Mallomys aroaensis (De Vis, 1907)

Dendrosminthus aroaensis De Vis, 1907: 11.

Type material. Holotype: QM J2814, male study skin and skull with dentaries collected at the head of the Aroa River (9°05'S, 146°48'E), Papua New Guinea.

Diagnosis. *Mallomys aroaensis* differs from all other *Mallomys* species in possessing the following combination of characters: usually relatively broader rostrum and more inflated frontal region; depigmented region of tail extending over only one half to two thirds length of tail (usually longer in other species), usually 7 or 8 scales per cm of tail length (only 1 skin in 33 studied did not, having 9), as opposed to 9 or more in *M. gunung* n.sp. and *M. r. rothschildi*, and 8-9 in *M. istapantap* n.sp. Differs from *M. rothschildi* in longer nasals (Fig. 3), shorter tail, pure white venter (rare in *M. rothschildi*) and lighter

coloured dorsal underfur. Differs from *M. istapantap* n.sp. and *M. gunung* n.sp. in considerably smaller size, in possessing poorly-defined, dark dorsal stripe, has longer tail, smaller molars and thinner bony palate. Differs from *M. istapantap* n.sp. in darker ears, shape of posterior of bony palate, mesopterygoid fossa and postglenoid vacuity (Fig. 2). Differs from *M. gunung* n.sp. in darker incisor enamel, and unretracted nasals and premaxillae.

Mallomys aroaensis aroaensis De Vis, 1907

Diagnosis. Lacking extreme inflation of frontals and rostrum seen in *M. a. hercules*; dorsal colour greyer, with more marked frosting (due to better expressed banding on hairs); mid-dorsal darkening better expressed.

Mallomys aroaensis hercules (Thomas, 1912)

Mallomys hercules Thomas, 1912: 19.

Type material. Holotype: BM 12.1.31.1, adult male skin and skull with dentaries from the Rawlinson Mountains, Huon Peninsula (6°43'S, 147°06'E), Papua New Guinea.

Diagnosis. Frontals and rostrum showing extreme inflation; dorsal grey tone with less frosting as white bands are less sharply expressed; little mid-dorsal darkening; white ventral

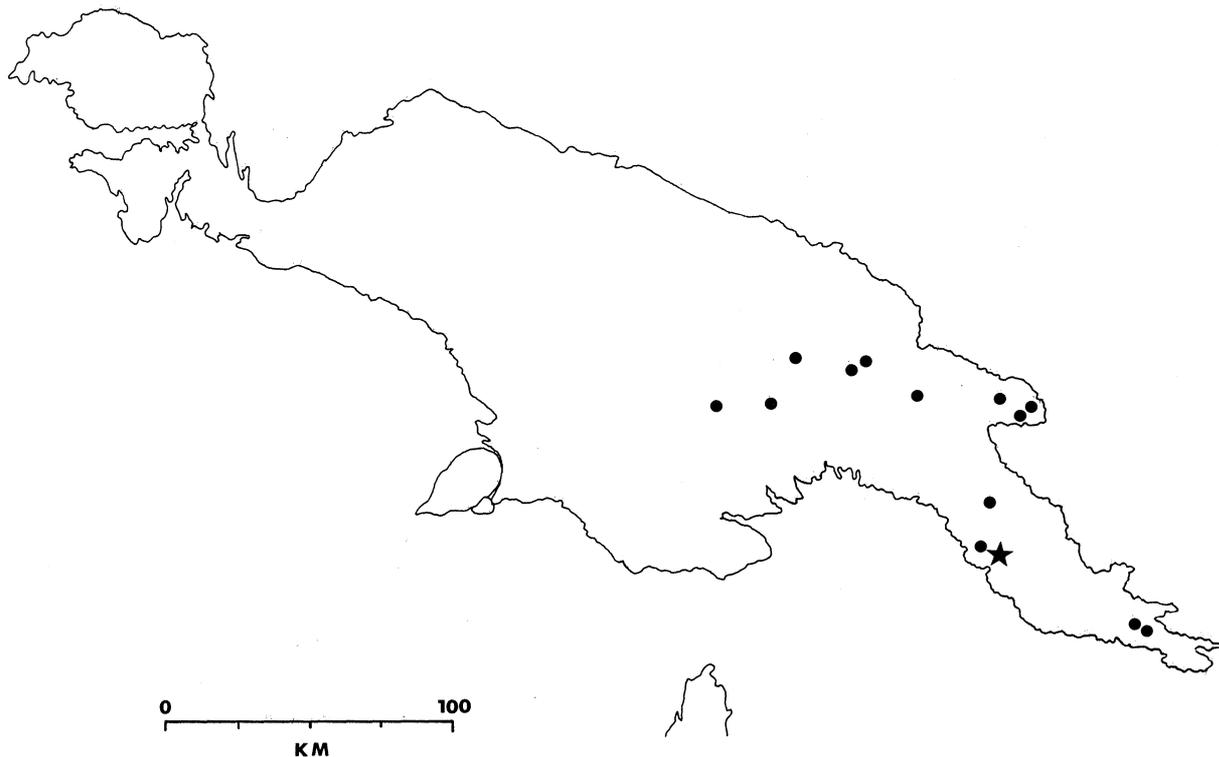


Fig.6. Distribution of *Mallomys aroaensis*. Star = type locality.

zone narrower than in *M. a. aroaensis*; tail has 8 or 9 scales per cm of length, on upper end of range for species.

Discussion. *Type specimen.* Although De Vis' description of *Dendrosminthus aroaensis* was somewhat unconventional (see introduction), it is nonetheless sufficient according to the Code of Zoological Nomenclature to allow the name to stand as valid. Soon after De Vis' description, the type specimen sank into obscurity. Longman (1916) reports that the skin had been lost, but that the skull remained. The identity of the skull, however may have been confused. Tate (1951:275) notes that only the front half of the skull was preserved, but on p.373 he gives a condylo-incisive length. In both places he notes the specimen number as "Queensland Museum No. 2814", but on p.275 he records it as male, and on p.373 as female. Although De Vis (1907) gives no specimen number, he does note that the type is a male. A search by one of us (K.A.) of the Queensland Museum collections revealed that only one *Mallomys* specimen is presently held in that institution. It is represented by a complete skull (QM J2814), which is listed in the register as the type of *M. aroaensis*. There is no mention of a skin, and at first no trace of the skin of the holotype could be found. However, a search of a drawer labelled "Foreign Mounts" revealed a study skin of a *Mallomys* specimen in poor condition, lacking the right pes and with brittle skin (see Figs 11-12). The skin is clearly male as it has a large epididymal sack. A wooden label attached to the specimen reads "*Dendrosminthus aroaensis* de Vis Aroa R. B N Guinea E28 Type". There can be no doubt that this specimen is the previously lost study skin of the holotype of *Dendrosminthus aroaensis*.

There is also no doubt that *M. aroaensis* constitutes the first valid name for the lower altitude grey-furred species of *Mallomys*. In all ways it is consistent in morphology with specimens referred to this taxon here, showing the characteristic inflated rostrum, round mesopterygoid fossa, grey dorsal (with an ill-defined dark dorsal stripe) and white ventral colouration.

Range. This species as presently interpreted is restricted to Papua New Guinea. Specimens of the subspecies *M. a. aroaensis* are recorded from Mount Sisa (190 km east of the Irian Jayan border) to Mount Simpson in far eastern Papua New Guinea. *Mallomys a. hercules* is restricted to the Huon Peninsula, and represents the only occurrence of *Mallomys* off the Central Cordillera. There they extend to 3,600 m in altitude. At some locations (e.g. Mount Sisa), *M. aroaensis* is far more common than other species, while throughout the eastern end of its range (from Mount Scratchley to Mount Simpson), it is the only *Mallomys* species to be found. It has been recorded from as low as 1,100 m on Mount Sisa, Southern Highlands Province (e.g. AMM16693), to 2,000 m on Mount Albert Edward (AM M12858), and 2,450 m at Baiyanka (BM 47.1339-40) and on Lamende Range, northwest of Mount Giluwe (BM 53.349-50). At this latter locality the species is sympatric with (or perhaps stratified just below) *M. istapantap* n.sp.

Variation. Because of the variability present in *M. r. weylandi*, the possibility needs to be discussed that *M. aroaensis* and *M. rothschildi* in Papua New Guinea

represent a single, highly variable taxon. We have carefully considered this possibility, and feel that the overwhelming evidence indicates that the material includes two distinct species. Distinct and consistent differences in pelage, relative tail length, number of tail scales, and somewhat less constant differences in nasal length rostrum width and interorbital width all support the division into two taxa. The range of morphological and external variation present in this sample from Papua New Guinea is far greater than that seen in *M. r. weylandi* from Irian Jaya. Furthermore, the two groups behave as species in the field. They occupy different nesting sites, and some factor or factors, including competitive exclusion, often ensures that one or the other species is dominant at any one locality.

There is little doubt but that the Huon Peninsula *Mallomys* is correctly referred to *M. aroaensis*, of which it is however a distinctive subspecies. There remains one problem: whether all other Papua New Guinean populations are consubspecific. In general, skins here referred to nominotypical *M. aroaensis* are greyish, with grey bases to the hairs, followed by clear but not sharply marked alternating black and white bands, usually two pairs, the tips being white; long guard hairs, with blackish bases and long white tips, protrude through the coat of contour hairs. Younger specimens are more distinctly frosted; the white tips of the guard hairs wear down with age. The midback has always some degree of darkening, and the shoulders and thighs tend to be lighter. There is clearly expressed geographic variation in details of this pattern. Specimens from the Mount Simpson area, of the far south-eastern Papua New Guinea mainland, are rather uniform, light grey, with most prominent mid-dorsal darkening; those from the Aroa and Angabunga Rivers are rather more yellow tinged; and skins from more westerly localities are medium to dark grey. The ventral zone is creamy to yellow toned in the Mount Simpson skins, and this sort of tone is found as far west as the Hagen Range; west of Mount Hagen, however, the tone is more purely creamy. This variability makes it seem possible that future research will result in the subdivision of our taxon *M. a. aroaensis*.

Reproduction and nest sites. Reproduction and diet in the species are poorly known. Two of us (TF, KA) collected a female from a burrow near Kosipe, altitude 2,000 m, on Mount Albert Edward on 27 Dec. 1981. She was carrying a late term naked foetus with a head body length of c.80 mm, but it was lost to dogs before further measurements could be obtained. A second female pregnant with a single foetus was taken by K.A. on Mount Sisa on 14 Oct. 1985.

Substantial data suggests that this taxon usually nests in burrows. Two of the authors' (T.F., K.A.) personal experience in Central and Southern Highlands Province, and the testimony of many Papuan informants supports this. We know of no records of animals being found in tree hollows.

Mallomys istapantap n.sp.

Figs 1-2, 11-12, Tables 4-5

Type material. HOLOTYPE: AM M7328, female study skin and skull with dentaries collected at Korelum, Mount Hagen district

(5°52'S, 144°14'E) on 17 July 1945 by Captain Neptune B. Blood.

PARATYPES: AM M12908, female skull with dentaries and hand and foot in alcohol, collected on the margin of the Neon Basin, 2,900--3,000 m, Mount Albert Edward (8°28'S, 147°20'E) on 20 Dec. 1981 by K. Aplin; AM M12875, juvenile female, flat skin with skull and dentaries (young of M12908, locality as for M12908); CM 15611, male study skin and skull with dentaries and partial skeleton. Collected at Kilenbokingl 3,650 m, Mount Wilhelm (5°49'S, 144°57'E) on 30 July 1970 by J. Hope; CM 15612, female study skin and skull with partial skeleton. Data as for CM 15611; CM 15682, female study skin and skull with partial skeleton. Collected on Mount Wilhelm, on 14 Aug. 1969 by J. Hope; CM 15684, male study skin and skull with dentaries and partial skeleton. Collected at Lake Koromonk, 3,850 m (6°06'S 143°18'E) Mount Wilhelm on 6th Aug. 1969 by J. Hope; CM 15681, male study skin and skull with dentaries and partial skeleton. Collected at Mondia, Mount Wilhelm (2,900-3,000 m) on 3 Oct. 1969 by J. Hope.

Etymology. Pronounced "ee-stap-an-tap", from "I stap antap", a Melanesian pidgin term meaning literally "it is above", frequently used in conjunction with animals and plants found only on mountaintops. Thus, "*Mallomys* from the mountaintops".

Diagnosis. *Mallomys istapantap* n.sp. differs from all other *Mallomys* species in having paler ears, in the shape of the maxillary-premaxillary suture (Fig. 2), the greater extent of the alisphenoid contribution to the edge of the postglenoid vacuity (Fig. 2), the elongate and dorsoventrally flattened sphenopalatine foramen (Fig. 2), the elliptical shape of the mesopterygoid fossa (Fig. 2), and the gentle

(rather than steep) way in which the posterior edge of the palate slopes towards the mesopterygoid fossa (Fig. 2). Its large size, hypsodont molars, excessively thickened palate, short tail and long thick underfur further distinguish it from all species except *M. gunung* n. sp. It has a very long depigmented zone on the tail (often some three quarters of the total length as in *M. rothschildi*) It differs from *M. aroaensis* in that there is no dorsal stripe, and the body contour hairs are unbanded, dark, but the plentiful thick underfur gives it an overall grey tone. Furthermore, more of the masseteric foramen is hidden behind the zygomatic plate when the skull is viewed from the side than in other species of *Mallomys* (Fig. 1), and the parietal crests are generally less well developed.

Description. *Skull.* The skull of the holotype is in good condition, but the left bulla is missing and the pterygoids are damaged. It is from a relatively young but clearly adult animal. The incisive foramina are slightly asymmetrical, the left one being longer than the right. The bony palate is greatly thickened, and its surface is ornamented by a median crest and two lateral crests that run close to the molar alveolar margin. These ridges coalesce at the posterior margin of the bony palate. Posteriorly, the palate slopes gently upwards and backwards to intersect the sloping ventral wall of the mesopterygoid fossa. These surfaces meet in the middle of the rear face of the bony palate. The nasals terminate abruptly posteriorly, there being almost no wedging into the frontals. The nasals maintain an even width for their posterior half, but widen rapidly anteriorly. The nasal tips do not overhang the premaxillae. The premaxillary/maxillary suture has the "S" shape

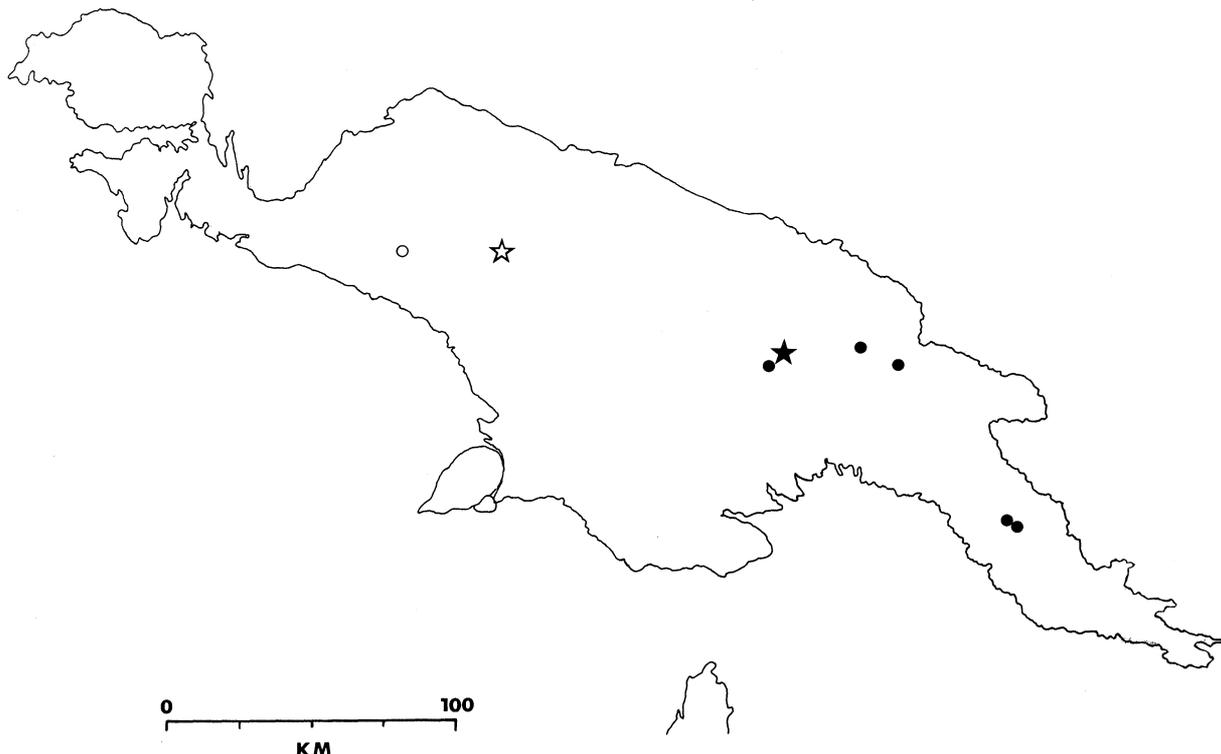


Fig.7. Distribution of *Mallomys istapantap* n.sp. (closed circles and star), and *M. gunung* n.sp.(open circles and star). Star = type locality.

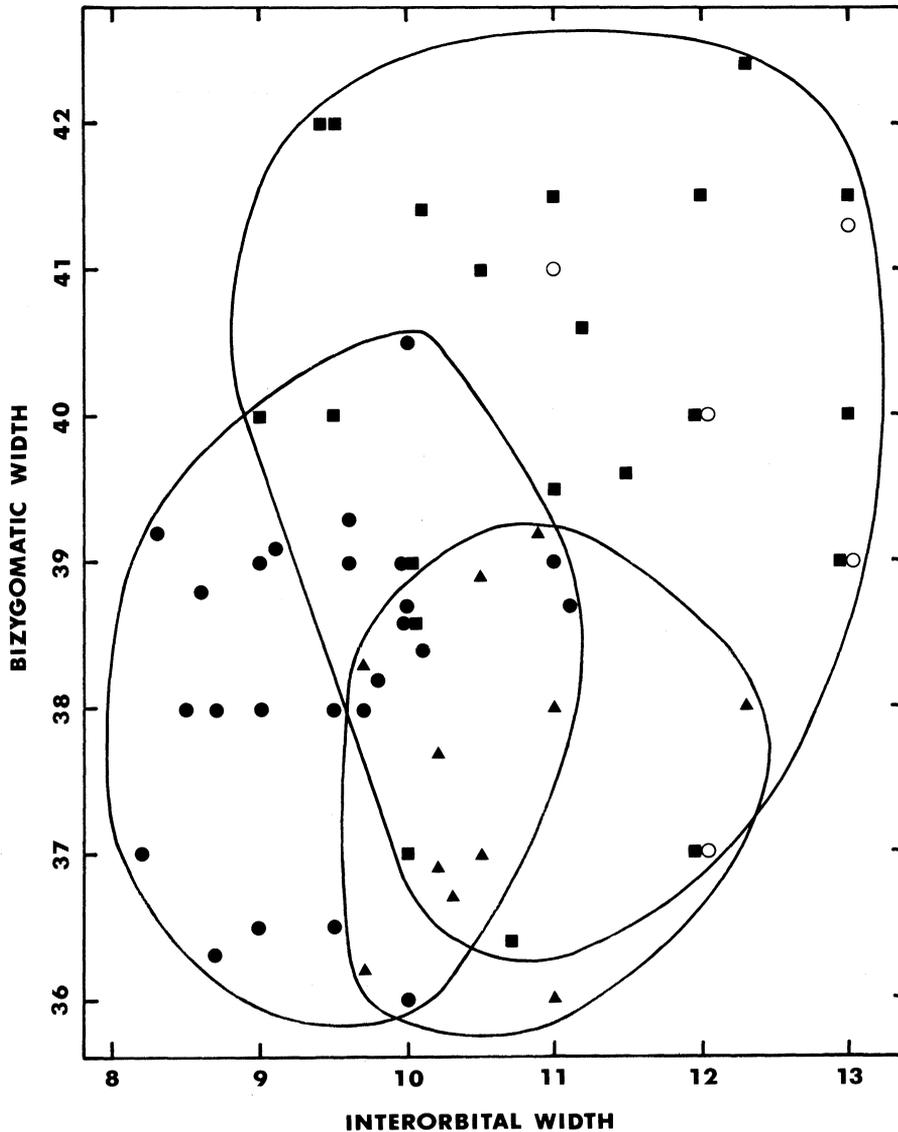


Fig.8. Bivariate plot of bizygomatic width over interorbital width for *Mallomys aroaensis aroaensis* (squares), *M. a. hercules* (open circles), *Mallomys rothschildi rothschildi* (solid dots) and *M. r. weylandi* (triangles).

characteristic of this species (Fig. 2). The premaxillae project posteriorly alongside the nasals, but terminate 3 mm anterior to the nasal/frontal suture. When viewed from above, the rostrum has a distinctly step-shaped form. Anteriorly, the lateral surfaces of the premaxillae are parallel sided until they approach the maxillary suture, when they expand rapidly. Just posterior to this suture, the lateral walls of the maxillae again assume a parallel orientation. The frontals are only slightly inflated, while the maxillary portion of the dorsal surface of the cranium is uninflated. The zygomatic plate is broad, and half to one third the length of the masseteric foramen is hidden behind it. The zygomatic arches are broad and sturdy, and the interorbital region is broad. Two poorly-defined supraorbital crests are present. Posteriorly, they diverge and weaken, to become very poorly-defined parietal crests. The mesopterygoid fossa is clearly elliptical with its long axis

oriented dorsoventrally. The pterygoids are damaged thereby obscuring much of their morphology. The bulla is as in other species of *Mallomys*.

The incisor morphology is as in other species of *Mallomys*. The incisor enamel is pigmented orange, and is a deeper hue on the uppers than the lowers. The molars are very large and only lightly worn. The right M1/ has a small aberrant cusplule positioned just anteromedial to T2. Both M2/s have small T3's developed, a feature that we have not seen in other individuals of a species of *Mallomys*. The molars are also extremely high crowned. This is difficult to quantify as the molars wear rapidly, and even when lightly worn part of the crown base is still hidden in the alveoli. However, the height of the anterior of the crown of the M/1 of the holotype is c.5 mm. Apart from these differences, the crown patterns of the molars do not differ from those of other species of *Mallomys*. The dentary is similar to that of

other *Mallomys*.

Skin. The study skin of the holotype is in good condition. The mammae number is $1 + 2 = 6$, and the nipples are small, possibly indicating that the animal was nulliparous. The dorsal surface is covered with dense, dark grey fur. The underfur of the midback is c.23 mm long, but numerous contour hairs project up to 10 mm beyond this, and the guard hairs extend a further 25-30 mm. The contour hairs are dark brown to black; because of the thickness of the underfur they make little contribution to the overall dorsal colour. Over most of the back the guard hairs have a short white tip (8-10 mm long). Over the shoulders and head, however, the white tips are very short or absent. The base of the underfur is dark grey, but has pale and dark tipping. The overall dorsal colouration is difficult to quantify owing to the intermixing of white, grey, brownish and black elements. It falls close, however, to Clove Brown or Blackish Slate. This colour persists onto the dorsal surface of the forelimbs. On the rump and dorsal surface of the hindlimbs, however, the colour is paler, being close to Slate Grey. There is an abrupt colour change to the ventral surface where the dark fur gives way to pure white with no guard hairs intermixed. Along the midline of the venter there are some hairs with an orange/yellow discolouration. This may be an artefact as the hairs are concentrated along the slit made into the body cavity, probably during preparation. Anterior to the forelimbs, the pure white of the venter gives

way to short, grey underfur. This extends to within 10-15 mm of the lower lip, where very short brownish hairs are present.

The ears, hands and feet are clothed in short brown hairs on their dorsal surfaces. The flesh of the ears is pale, there is no dark eye ring, and the vibrissae are black. The pads of the hand and hindfoot are as in other species of *Mallomys*. The proximalmost 125 mm of the tail is dark, close to black. The distalmost 155 mm is white (in other specimens there is generally a much higher proportion of white). There are three hairs per tail scale, and 8 to 9 scales per cm in the middle of the tail. Most scales are rectangular, and approximately twice as broad as long.

Discussion. *Range.* *Mallomys istapantap* n.sp. is morphologically and electrophoretically (though *M. gunung* n.sp. is unknown in this latter respect) the most distinctive of the *Mallomys* species. Its large hypsodont molars and associated cranial adaptations make it easily recognisable, even as a partial trophy skull or skeletal pick up.

The distribution of *M. istapantap* n.sp. is intriguing. It appears to be restricted to subalpine herbfields and grassland, and bordering upper montane forest along the east-central portion of the New Guinean Central Cordillera. Within this area it seems to favour the upper montane forest/alpine grassland ecotone. Geoff Hope (personal communication) has commented that many of the C.M. specimens reported upon here come from this habitat, and we (T.F., K.A.) have

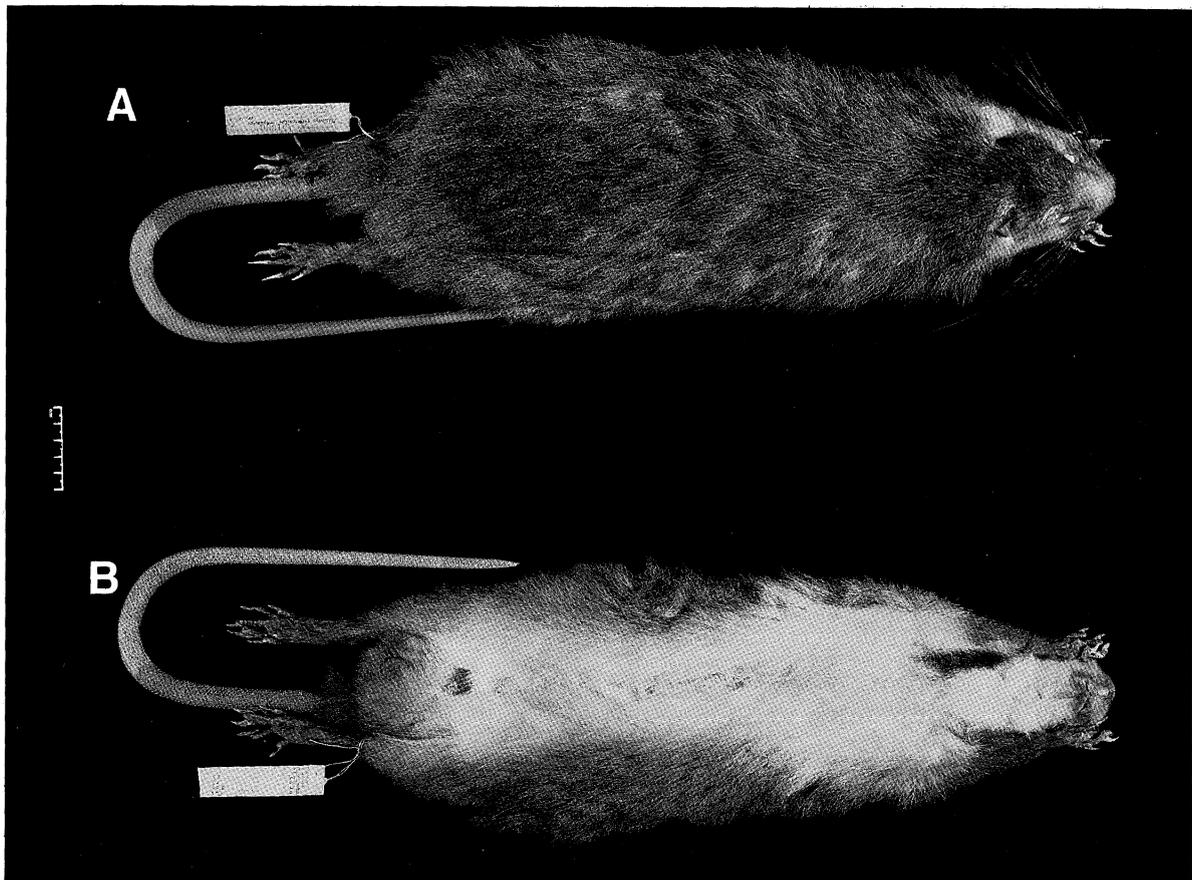


Fig.9. Skin of AMNH151336, *Mallomys rothschildi weylandi* (light phase) in A, dorsal and B, ventral views. Bele River, Irian Jaya.

also obtained specimens in this area. Altitude varies from "8,000 to 9,000 feet" (= 2,540 to 2,750 m) (BM 53.344 to 53.346 and 53.348) and "9,000 feet" (= 2,750 m) (BM 53.343 to 53.347 and 53.349) and 2,900 to 3,000 m (e.g. AM M12908, CM 15681) to 3,850 m (CM 15684) but the species may occur higher. The westernmost records for the taxon are from Mount Giluwe (Southern Highlands Province) but based on continuous high topography it seems likely that it occurs at least as far west as the Yuma Range to the east of Lake Kapiago. In the east, it is found as far as Mount Victoria (there is a partial pick up skull, AM M8209, from this locality) in the Owen Stanley Ranges. Its distribution in this region is doubtless disjunct, being limited to the higher peaks. It is fairly certain that this taxon is absent from the high ranges to west of the Strickland River in Irian Jaya. This is because moderate-sized collections of *Mallomys* skulls, which do not contain *M. istapantap* n.sp., are known from the Snow Mountains, Irian Jaya, where it seems to be replaced by *M. gunung* n.sp. On Mount Giluwe *M. istapantap* n.sp. is sympatric with *M. r. rothschildi*, while on the Lamende Range north-east of Mount Giluwe a specimen of *M. aroaensis* (BM 53.349) was collected at 2,450 m at the same time as some *M. istapantap* n.sp. at 2,540 to 2,750 m. However, it is unclear whether these two species exist sympatrically, or replace each other altitudinally in this area, as the altitude is near the known limit for both taxa.

Diet, reproduction and nest sites. Diet and reproduction

in *M. istapantap* n.sp. are poorly known. The only data regarding reproduction known is that two of us (T.F., K.A.) collected a female (AM M12908) and a fully-furred young (AM M12875) from a burrow in a moss mound at 2,900 to 3,000 m on Mount Albert Edward on 20 Dec. 1981.

Biology. The large, hypsodont molars of *Mallomys istapantap* n.sp. suggest that it must cope with an abrasive vegetable diet. The teeth of other *Mallomys* species from high altitude areas sometimes suffer extreme wear (e.g. CM 11716), so high molar crowns may significantly increase the reproductive lifespan of an individual. Many alpine herbfields in montane New Guinea contain little grass, but hard and presumably abrasive ferns are common. These and other abrasive leaves may form a significant part of the diet of *M. istapantap* n.sp. Equally interesting from a dietary point of view is the degree of orange (iron) pigmentation in the incisor enamel. As noted previously, specimens of *M. rothschildi* and *M. gunung* n.sp. from high altitudes possess white incisor enamel, while those from lower altitudes have the normal orange colouration. However, even the highest altitude *M. istapantap* n.sp. that we have examined have orange incisor enamel. The widespread occurrence of species with pale incisor enamel in upper montane habitats (e.g. *Rattus richardsoni*, *Melomys albidens*, *Melomys fellowsi*) suggests that the ability to fix iron into the enamel matrix of the incisors may be affected by altitude. If this ability is greater in *M. istapantap* n.sp.



Fig.10. Skin of AMNH151352, *Mallomys rothschildi weylandi* (dark phase) in A, dorsal and B, ventral views. Bele River, Irian Jaya.

than *M. rothschildi* and *M. gunung* n.sp. this may well be a further adaptation to high-altitude living.

***Mallomys gunung* n.sp.**

Figs 1-2, 11-12, Tables 4-5

Type material. HOLOTYPE: AMNH 151346, adult male study skin and skull with dentaries, collected at 3,800 m, 2 km east of Mount Wilhelmina (4°15'S, 138°45'E), Irian Jaya, Indonesia on 19 Sept. 1938 during the 3rd Archbold Expedition.

PARATYPES: AMNH 151437, adult male study skin and skull with dentaries collected at 3,650 m, 7km north-east of Wilhelmina Top (4°15'S, 138°45'E), Irian Jaya, Indonesia on 11 Sept. 1938 during the 3rd Archbold Expedition; AM M19029, sex unknown, anterior half of skull and dentaries only collected at 3,760 m, Moraine Camp, Meren Valley, Mount Carstenz (4°05'S, 137°11'E) on 9 Dec. 1983 by R.G. Peters; AM M19028, sex unknown, anterior part of skull only collected at 3,780 m, Moraine Camp, Mount Carstenz (4°05'S, 137°11'E) on 9 Dec. 1983 by R.G. Peters; AM M19030, sex unknown anterior part of skull collected at 3,500 m, Ertzberg Meadow, Mount Carstenz (4°05'S, 137°11'E)

on 9 Dec. 1983 by R.G. Peters; CM 11716, sex unknown, partial skeleton with skull and dentaries collected at 4,050 m on Mount Carstenz (4°05'S, 137°11'E) by G.S. Hope.

Etymology. *Gunung* is Bahasa Indonesia for mountain, signifying its montane and Irian Jayan distribution. The name is thereby intended as an Indonesian equivalent of the Papua New Guinean *istapantap*.

Diagnosis. This species differs from all other *Mallomys* species in the retraction of the premaxillaries and nasals (Figs 2-3), a difference reflected in the short distance between the premaxillary/maxillary and nasal/premaxillary sutures, as well as the very short nasals relative to molar size (Table 5). It is also unique in the genus in its long, slender claws. It further differs from *M. aroaensis* and *M. rothschildi* in its larger molars, extensive palatal thickening, relatively shorter tail and lack of a dorsal stripe, and in the abundant, thick underfur. It differs from *M. istapantap* n.sp. in the shape of the premaxillary/maxillary suture, posterior bony palate morphology (both of which are as in *M. aroaensis*) and in having a round rather than sharply



Fig.11. Dorsal views of study skins of the holotypes of A, QM J2814, *Mallomys aroaensis* (holotype); B, AMNH151346, *Mallomys gunung* n.sp. (holotype); and C, AM M7328, *Mallomys istapantap* n.sp. (holotype).

elliptical mesopterygoid fossa, and a pale (yellowish white) incisor enamel. Furthermore, the ears are darker than in *M. istapantap* n.sp, and the dorsum has more greyish rather than slightly brownish tones; the tail scales are more numerous (at least 9 per cm of length), but the depigmented zone is much shorter, only two thirds of the tail length at the most.

Description. *Skull.* The skull of the holotype is in good condition although the left zygomatic arch has been broken then glued back into place, and the left pterygoid is broken. It is from an adult with well worn molars. As in other species of *Mallomys*, especially *M. istapantap* n.sp., the bony palate is greatly thickened, with its surface ornamented by a sharp median crest. The posterior face of the bony palate slopes sharply to meet the gently sloping ventral floor of the mesopterygoid fossa. The incisor enamel is very pale yellow. The part of the premaxillae supporting the incisors projects markedly anteriorly, such that when viewed from the dorsal aspect, the incisors can be seen projecting well clear of the nasals. The dorsal part of the premaxillae and the nasals are short relative to other *Mallomys* species. The maxillary/premaxillary suture is almost vertically oriented. The rostrum is narrow as in

M. rothschildi, and the interorbital region is very deeply dished. The sphenopalatine foramen is large, oval shaped and clearly visible as in *M. rothschildi*. The interparietal is divided into left and right parts by a suture in two of the three available crania. This is a rare feature otherwise in the genus. The interparietal is squarer than in *M. rothschildi*. The zygomatic arches flare broadly, and the parietal crests are well developed and subparallel. They are best developed anteriorly, becoming poorly defined in the region of the interparietal. The mesopterygoid foramen is round and the bulla as in other species of *Mallomys*. The basisphenoid possesses a sharp medial ridge.

The incisors, although similar in morphology to those of other species of *Mallomys*, are much paler in colour than all except some high altitude *M. rothschildi* from Papua New Guinea. The uppers and lowers are similarly coloured, being a pale yellow. The molars are very large and hypsodont, closely resembling those of *M. istapantap* n.sp. in morphology. The dentary is as in other *Mallomys*.

The study skin of the holotype is in good condition. The dorsal surface is clothed in dense, grey fur, slightly lighter than and lacking the brownish tinge of *M. istapantap* n.sp.; blackish contour hairs protrude through it. The guard hairs

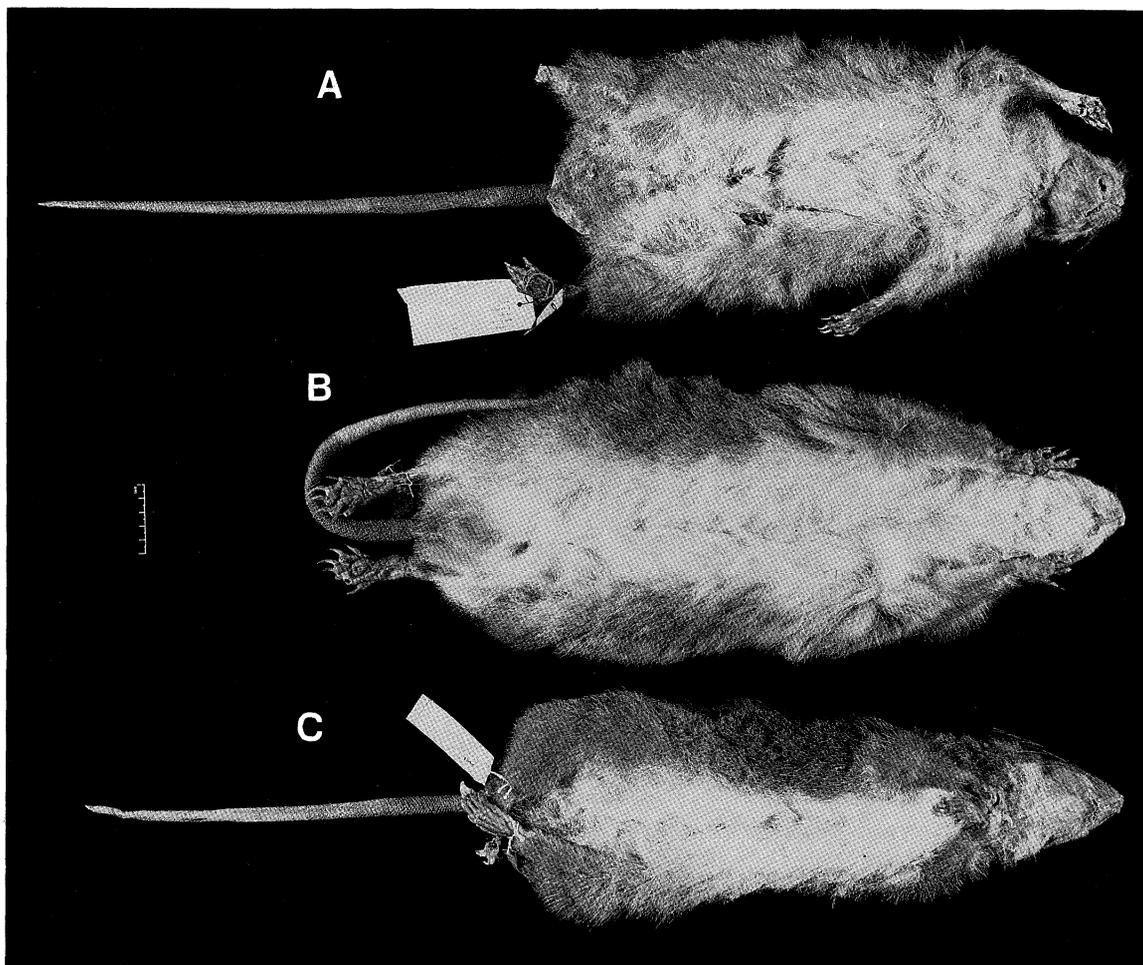


Fig.12. Ventral views of study skins of the holotypes of A, QM J2814, *Mallomys aroensis* (holotype); B, AMNH151346, *Mallomys gunung* n.sp. (holotype); and C, AM M7328, *Mallomys istapantap* n.sp. (holotype).

all possess long (about 20 mm) white tips. The underfur is approximately 35 mm deep on the back, with the guard hairs extending a further 35 mm beyond that. As in *M. istapantap* n.sp. the guard hairs of the shoulders and head lack white tips. The ventral surface is covered in long, yellowish white fur, with no dark guard hairs intermixed. This pale fur extends anteriorly to the lower lip.

The ears are blackish and have a very fine covering of dark hairs. The hands and feet are clothed in long, coarse mixed dark and light hairs, with pale hairs predominating on the digits. The claws are unusually long and gracile, differing markedly from the more robust, shorter claws of other *Mallomys* species. A distinct dark eye ring is present and the vibrissae are black. The proximal most 125 mm of the tail is black, the distal portion (190 mm) being yellowish. There are three hairs per tail scale, and nine scales per cm in the middle of the tail. Most scales are roughly rectangular, and approximately twice as broad as long.

Discussion. *Range.* The cranial morphology of *Mallomys gunung* n.sp. is so distinctive that the species can be recognised quite easily on the basis of cranial fragments such as are often found as pick ups or in archaeological sites. Indeed, the majority of records of this taxon at present are from such material. Hope (1976) reported upon archaeological material that she assigned to *Mallomys rothschildi* from Mapala rockshelter, located at 3,996 m on Mount Carstenz. These specimens (AMF54828 and F54829) clearly represent *M. gunung* n.sp. The AM and CM paratypes of this species are all pick ups, found in the alpine meadows of the Carstenz area. The only specimens collected as whole animals thus far known are the holotype, collected 2 km east of Mount Wilhelmina, and the AMNH paratype, collected 7 km north-east of Mount Wilhelmina. This limited information indicates that *M. gunung* n.sp. has a restricted distribution centred on the alpine meadows of the Snow Mountains. The lowest elevations recorded are 3,500 m at Ertzberg Meadow, and the highest 4,050 m. However, the species may extend to higher elevations, as Hope (1976) notes "...There seems to be no doubt that on Mount Jaya this species [most probably *M. gunung* n.sp.] inhabits not only the grassland of the Kembang Plateau, but the most barren and inhospitable areas of the mountain as well..." (Hope, 1976:218). Nothing is known of the life history of this species.

Discussion

Phylogenetic relationships. Because we can identify no close outgroup for the species of *Mallomys*, and because of the nature of character distribution within the genus, it is difficult to interpret relationships at present. *Mallomys istapantap* n.sp. and *M. gunung* n.sp. share a number of similarities; it is unclear in most cases if the condition exhibited by these taxa is plesiomorphic or derived. The lack of a dorsal stripe, short tail, large molars and overall large size are of uncertain polarity, although we think they are probably derived; the hypsodont condition of the molars

seen in both of these taxa is clearly highly derived, but may well be due to convergence, as both species are restricted to a similar environment (alpine meadows) and thus may have similar diets. These similarities aside, we can find no compelling evidence to suggest that they are close relatives. Both species possess a number of unique morphological adaptations within the genus. In *Mallomys istapantap* n.sp. these are centered in the bony palate, mesopterygoid fossa and rostrum whereas *Mallomys gunung* n.sp. has unique incisors and rostral morphology. The electrophoretic distinctiveness of *M. istapantap* n.sp. is suggestive of an early derivation within the evolution of the genus. However, because *M. gunung* n.sp. is unknown electrophoretically, this does not help in determining the relationship between the two high altitude taxa.

Considerable evidence suggests that the two lower altitude species, *Mallomys rothschildi* and *M. aroaensis*, are close relatives. They are closer to each other electrophoretically than either is to *M. istapantap* n.sp. and furthermore display a great degree of phenetic similarity. Unfortunately, due in part to lack of a suitable outgroup, we have been unable to identify any synapomorphies uniting these two species. The principle of metachromism (Hershkovitz, 1968) indicates that the agouti-banded hair type of *M. aroaensis* is more primitive than the saturated black of *M. rothschildi*; but the inflated rostrum and frontals of the former are presumably the more derived condition. Thus neither can be regarded as wholly primitive. It can be noted that the two high altitude species both have saturated-patterned contour hairs, so presumably relate in this respect to *M. rothschildi*.

Zoogeography. The distribution of the species of *Mallomys* poses some interesting questions. With the exception of *M. aroaensis*, which occurs on the Huon Peninsula, all *Mallomys* are restricted in distribution to the New Guinean Central Cordillera. *Mallomys rothschildi* is a widespread species, being present from the Weyland Range in the west to the Aroa River in the east. Interestingly, the Huon Peninsula form, *M. a. hercules*, resembles *M. rothschildi* to some degree. This latter species is absent from the high Huon Peninsula. *Mallomys istapantap* n.sp. and *M. gunung* n.sp. have the most restricted range, probably occupying disjunct alpine and subalpine habitats only.

The degree of sympatry between the species of *Mallomys* is difficult to establish. It is evident that in some areas where extensive sampling has been undertaken, only a single species is present; examples include the presence of only *M. aroaensis* on the Huon Peninsula and in the far southeast, as already pointed out, and of *Mallomys gunung* n.sp. high in the Snow Mountains. In other locations we have specimen-backed evidence for two species sympatry: *M. rothschildi* and *M. aroaensis* on Mount Elimbari and the Schrader Range, and *M. rothschildi* and *M. istapantap* n.sp. on Mount Giluwe. Furthermore, collections in the Australian Museum show that three species (*M. istapantap* n.sp., *M. rothschildi*, *M. aroaensis*) exist in close proximity if not in sympatry in the Mount Hagen area. At some well documented locations, one species seems to predominate, with a second being much rarer (e.g. *M. rothschildi* at

Telefomin, Baiyanka, Yanka, and Mount Elimbari; and *M. aroaensis* at Mount Sisa). Such patterns of distribution may become more easily understood when more is known about the ecology of these taxa.

Many upper montane species are spread throughout the Central Cordillera (e.g. *Phalanger sericeus*, *Pogonomelomys ruemmleri*). Although populations of these taxa may be disjunct today, it is probable that continuous suitable habitat (and thus populations) were found along the entire Central Cordillera during Pleistocene glacial maxima. The fact that some species were clearly able to occupy all of this range, while others were unable to spread, may be related to precise habitat needs. In the instance of the *Mallomys* species it seems possible that *M. istapantap* n.sp. and *M. gunung* n.sp. are more strictly tied to subalpine grassland than the other mammalian taxa that occur within and around this vegetation type. Tracts of upper montane forest thus may have acted as a barrier to these giant rats, but not less ecologically restricted species.

Summary

Electrophoretic and morphological evidence concur as to the presence of three species of the genus *Mallomys* in Papua New Guinea. Additional morphological analysis indicates the presence of a fourth species, in the high mountains of central Irian Jaya. Examination of all type material indicates that only two of the four species are previously named. The correct names for these taxa are *Mallomys rothschildi* Thomas, 1895 and *Mallomys aroaensis* (De Vis, 1907). The remaining species are described as new: *Mallomys gunung* n.sp. and *Mallomys istapantap* n.sp. Two distinct subspecies of *M. rothschildi*, *M. r. weylandi* (western New Guinea), and *M. r. rothschildi* (eastern New Guinea) can be recognised. Two subspecies of *M. aroaensis*, *M. a. aroaensis* (from the Central Cordillera in Papua New Guinea) and *M. a. hercules* (from the Huon Peninsula) can also be discerned. *Mallomys gunung* n.sp. is restricted to subalpine and alpine habitats in the Snow Mountains, while *M. istapantap* n.sp. is restricted to subalpine grassland and upper montane forest in the eastern and central parts of the Central Cordillera. The three Papua New Guinean species may exist in sympatry in parts of eastern New Guinea.

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APPENDIX I

Enzymes and proteins examined during electrophoresis: Aconitate hydratase (ACON, E.C. 4.2.1.3), acid phosphatase (ACP, E.C. 3.1.3.2), adenosine deaminase (ADA, E.C. 3.5.4.4), alcohol dehydrogenase (ADH, E.C. 1.1.1.1), adenylate kinase (AK, E.C. 2.7.4.3), carbonate dehydratase (CA, E.C. 4.2.1.1), diaphorase (DIA, E.C. 1.8.1.4), enolase (ENOL, E.C. 4.2.1.11), fructose-diphosphatase (FDPASE, E.C. 3.1.3.11), glyceraldehyde-phosphate dehydrogenase (GAPD, E.C. 1.2.1.12), aspartate aminotransferase (GOT, E.C. 2.6.1.1), glucose-6-phosphate dehydrogenase (G6PD, E.C. 1.1.1.49), glycerol-3-phosphate dehydrogenase (GPD, E.C. 1.1.1.8), glucose-phosphate isomerase (GPI, E.C. 5.3.1.9), isocitrate dehydrogenase (IDH, E.C. 1.1.1.42), leucine aminopeptidase (LAP, E.C. 3.4.11.1), lactate dehydrogenase (LDH, E.C. 1.1.1.27), malate dehydrogenase (MDH, E.C. 1.1.1.37), mannose-phosphate isomerase (MPI, E.C. 5.3.1.8), purine nucleoside phosphorylase (NP, E.C. 2.4.2.1), peptidases (PEP, E.C. 3.4.11? or 13.4.13?), 6-phosphogluconate dehydrogenase (6PGD, E.C. 1.1.1.44), phosphoglycerate kinase (PGK, E.C. 2.7.2.3), phosphoglucomutase (PGM, E.C. 5.2.4.2.), pyruvate kinase (PK, E.C. 2.7.1.40), superoxide dismutase (SOD, E.C. 1.15.1.1), and L-iditol dehydrogenase (SORDH, E.C. 1.1.1.14).

APPENDIX II

Specimens Examined (excluding types)

Mallomys r. rothschildi CM3958 Mount Giluwe; CM16518, 15683, 12687 Mount Wilhelm; AM M15603, AM M15745-15748, M15625-15626, M15627, M15628, Mount Elimbari; AM M9083 Schrader Range, AM M6930 Mount Hagen area; AM M9534 Tomba, Hagen Range; AM M13730, AM M17361-17362, AM M15999 Telefomin; BM69-338 Schrader Range; BM53.340-2 Hagen-Giluwe area; BM53.345, Mount Giluwe; BM50.1784-7,9,90,92 Hagen Range; BM50.1780 Mount Wilhelm, BM47.1334-8 Bismarck Range; BM 39.3974 between Mounts Musgrave and Scratchley (type of *M. rothschildi*).

Mallomys r. weylandi AMNH103261, 101949 Weyland Range, AMNH151333-151334, 6, 8-40, 51-2, Bele River-Mount Wilhelmina area, Irian Jaya.

Mallomys a. aroaensis AM M6931 Hagen area; AM M16693, 15629-15630, 17096, 17893-17894 Mount Sisa, Southern Highlands; M9583 north slopes Wahgi Divide, Jimi Valley; AM M8590

Wonenara, eastern highlands; BM47.1242-3 Ramu River; BM50.1191 Kratke Mountains.; BM50.1781 Mount Wilhelm; BM47.1339 Purari-Ramu Divide; BM53.363-7 Mount Giluwe; BM53.337-9 BM50.1783,8, 91-7, Hagen Range; BM50.1193-8 Bubu River district; BM1939.1945, Aroa River; BM1939-1944 Angabunga River; BM47.1341,44-55, Mount Simpson.

Mallomys a. hercules RMNH 29251, 292 Huon Gulf; RMNH 29292, 230 Rawlinson Mountains.

Mallomys istapantap n.sp. AM M8209 Mount Victoria; RMNH10446 north of Lake Aunde, Mount Wilhelm; AMNH192178 Mount Otto (near summit). BM 53.343,-4,-6,-7, and -8 Mount Giluwe". BM 53.349 Lamende Range, north-west of Mount Giluwe. CM16730-1 Lake Bendenumbum Mount Giluwe, CM15688 Mount Giluwe.

Mallomys gunung n.sp. AM F54828-9 Mapala rockshelter, Mount Carstenz, Irian Jaya.