A New Species of *Melomys* from Manus Island, Papua New Guinea, with Notes on the Systematics of the *M. rufescens* Complex (Muridae: Rodentia)

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Melomys matambuai n. sp. is a large member of the *Melomys rufescens* complex of murid rodents that is endemic to Manus Island, Papua New Guinea. Morphological and biochemical analysis has revealed greater diversity than was previously appreciated within *M. rufescens*. *Melomys matambuai* n. sp. is apparently arboreal, and is known from garden and secondary growth habitats.

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INTRODUCTION

Manus Island is a large, yet isolated, island lying at 1°S 147′E, approximately 290 km north of the Sepik River mouth and 290 km west of New Hanover in the Bismarck Archipelago (Fig. 1). It is still well forested although logging operations are under way in the western part. A diverse bat fauna has been recorded for Manus (Koopman, 1979) but the only non-flying land mammals previously reported are *Rattus exulans* Taylor, Calaby and Van Deusen, 1985, *Spilocuscus kraemeri* Flannery and Calaby, 1987 and *Echymipera kalubu* (Lesson) (as *E. cockrelli* Thomas, 1914). Research currently under way by Tim Flannery, Matthew Spriggs and Corrie Williams indicates that all three of these species have been introduced by humans during the Holocene. Here we report on a fourth species, which is endemic. The holotype was collected during a survey of the mammals of Manus Island undertaken during 1988, which will be reported on elsewhere.

Melomys matambuai n. sp. is a member of the *Melomys rufescens* complex, geographically the most widespread of the *Melomys* species complexes. In addition to the material from Manus described here, it is represented in the Solomon Islands by *Melomys bougainville* Troughton, in the Bismark Archipelago by the nominotypical form and on mainland New Guinea, and islands as far west as Japan and Waigeou, by a complex of taxa which remain poorly resolved. Little recent taxonomic revision has been carried out within the complex, although Flannery and Wickler (1990) have recognised *Melomys bougainville* from the Solomon Islands as being distinct from *Melomys rufescens* (Alston). Our electrophoretic and morphological analyses shed some light on the taxonomy of the remainder of the *M. rufescens* complex, but this is not pursued here for our purpose is primarily to elucidate the systematics and affinities of the Manus animals.

MATERIALS AND METHODS

Electrophoresis was performed on 'Titan III' (Helena Laboratories) 76mm^2 cellulose acetate gels according to standard procedures (Richardson et al., 1986). Gels were run for 60′ with a constant potential drop of 200V between electrodes. Staining protocols were adapted from Harris and Hopkinson (1976) and Richardson et al. (1986).

Fluorescence methods were used for esterase. Stains were applied after quickly mixing with 2 ml of molten 2.5% agarose. Generally, samples were run at least twice for each enzyme. The enzymes stained, abbreviations used herein, E.C. numbers, running buffer and number of presumptive genetic loci are given in Table 1. Samples of liver tissue were ground in 1 volume of tissue to 1 volume of homogenising buffer (Colgan, 1986) in hand-held glass homogenisers. The preparation was centrifuged at 13,500 rpm in an MSE Microcentaur centrifuge and the supernatant divided into three aliquots which were frozen at -80°C awaiting electrophoresis.

TABLE 1

Summary of Electrophoretic Procedures. The columns give, in order, the name of the enzyme, its abbreviation used herein, E.C. number, running buffer and number of presumed genetic loci. Details of running buffers are given in Colgan (1986).

Enzyme	Abbreviation	E.C. No.	Buffer	Loci
Adenosine deaminase	ADA	3.5.4.4	TEM 50	1
Adenylate kinase	AK	2.7.4.3	TEM 50	1
Aspartate aminotransferase	AAT	2.6.1.1	TC 100	2
Esterase	EST	3.1.1.1	TEM 50	2
Fructose diphosphatase	FDP	3.1.3.11	TEM 50	1
Fumarate hydratase	FUM	4.2.1.2	TEM 50	1
Glucose-6-phosphate dehydrogenase	G-6-PDH	1.1.1.49	TC 100	1
Glucosephosphate isomerase	GPI	5.3.1.9	TEM 50	1
Glyceraldehyde phosphate dehydrogenase	GA-3-PDH	1.2.1.12	TEM 50	2
α-Glycerophosphate dehydrogenase	GPD	1.1.1.8	TEM 50	1
Hexokinase	HK	2.7.1.1	TEM 50	1
Isocitrate dehydrogenase	IDH	1.1.1.42	TEM 50	2
Lactate dehydrogenase	LDH	1.1.1.27	TC 100	1
Malate dehydrogenase	MDH	1.1.1.37	TEM 50	2
Malic enzyme	ME	1.1.1.40	TEM 50	1
Mannosephosphate isomerase	MPI	5.3.1.8	TEM 50	1
Phosphoglucomutase	PGM	5.4.2.2	TEM 50	1
6-Phosphogluconate dehydrogenase	6-PGDH	1.1.1.44	TEM 50	1
Pyruvate kinase	PK	2.7.1.40	TEM 50	1

Samples which were electrophoretically processed are indicated in Appendix 1 (see Fig. 1 for localities). Allozymes identified during this study were alphabetically designated in order of their relative anodal mobility. Different loci encoding the same enzyme were numbered in order of anodal mobility. Results were analysed using Swofford's BIOSYS-1 package (Swofford and Selander, 1981). Dendrograms were produced for all available distance metrics and for a variety of distance Wagner procedures. The results of these analyses were all very similar, except where indicated in the 'Results' section below. *Melomys rubex* Thomas, *M. lanosus* Thomas and *M. rattoides* Thomas were included as outgroups.

All measurements are in mm and weights in grams. For the purpose of morphometric analysis eight cranial measurements were made (see Table 3), along with four external measurements and weight. Except for the subadult paratype of *M. matambuai* only adults (determined by the basis of degree of basilar fusion) were used in the morphometric analysis. BZM = Berlin University Museum mammal specimen, LACM = Los Angeles County Museum mammal specimen, M = Australian Museum mammal specimen. Colours, where capitalised, follow Smithe (1974).

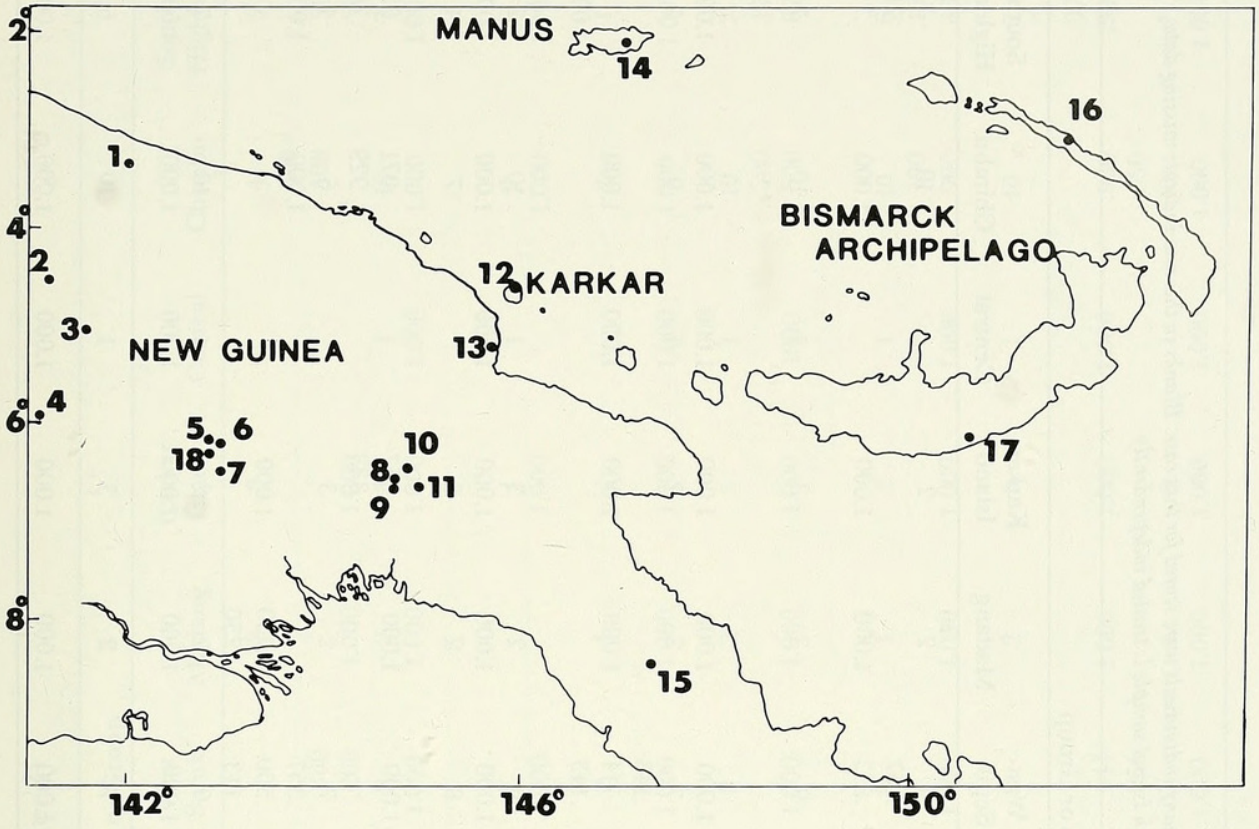

Fig. 1. Map of Papua New Guinea and surrounding islands showing localities of samples used for electrophoresis. Localities 1-4 are in West Sepik Province, 5-7 and 18 are in Southern Highlands Province, 12-13 in Madang Province, 8-11 in Chimbu Province, and 15 in Central Province. 1 = Torricelli Mountains, 2 = Yapsiei area, 3 = Telefomin area, 4 = Munbil area, 5 = Bobole area, 6 = Namosado area, 7 = Waro area, 8 = Noru area, 9 = Doido area, 10 = Yuro area, 11 = Haia area, 12 = Karkar Island, 13 = Siar area, 14 = Polomou area Manus, 15 = Mt Albert Edward, 16 = Madina area New Ireland, 17 = Waipo area New Britain, 18 = Agofia area.

RESULTS

Electrophoresis. A summary of the allozymic frequency data are presented in Table 2. Island samples are presented individually. The mainland samples were pooled within administrative provinces. Four main points are noticeable.

(1) The sample from Manus is genetically distinct from all other *Melomys* in the study, having allozymes of GPI, PGM and FDP which are found nowhere else. It is separated from all *M. rufescens* populations in all phenetic analyses (Figure 2), but is clearly more similar to these than to any other species tested. In distance analyses including all loci (Figure 3), *M. matambuai* is shown as the sister group of New Ireland *M. rufescens*, albeit that they are separated by very long branch lengths.

(2) *M. lanosus* is a poorly known species so that when Flannery (1990) considered, on the grounds of morphological and habitat differences, that it is distinct from *M. rattoides* he suggested that further investigation of the long-footed *Melomys* species was required. The data reported here show that the taxa are genetically distinct. There are 6 fixed allozymic differences (of 19 loci) between the samples.

(3) Some genetic structuring can be seen in *M. rufescens*. Most samples (those from West Sepik, Madang and Central Provinces) cluster together. Samples from Chimbu Province comprise a second group and those from Southern Highlands Province a third. There are genetic differences between the groups. Samples from the Bismarck

TABLE 2

Summary of Allozymic Frequencies. Number in the same row as locus identifications specify how many individuals were scored for that case. Blanks in this row indicate missing data. Populations within a province are pooled, except that each island sample is treated independently

	Species or Group											
Locus	*ratt-oides*	*lanosus*	*rubex*	*matam-buai*	New Ireland	New Britain	West Sepik	Madang	Karkar Island	Central	Chimbu	Southern Highlands
Ada				1	2	1	9	2	2		10	7
A				.500			.167					.286
B				.500	.750	1.000	.833	1.000	1.000		1.000	.714
C					.250							
Ak	2	1	2	1	4	1	9	2	3	1	10	7
A		1.000										
B	1.000											
C			1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Aat-1	2	2	2	1	4	1	7	2	2	1	9	5
A							.143					
B				1.000	1.000	1.000	.714	1.000	1.000	1.000	1.000	
C	1.000	1.000					.143					1.000
D			1.000									
Aat-2	2	2	2	1	4	1	9	2	3	1	10	7
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Est-1	2	2	2	1	4	1	8	2	3		7	4
A		1.000										
B	1.000		1.000	1.000	1.000	1.000	1.000	1.000	.667		.071	.250
C									.333		.929	.750
Est-2	2	2	2	1	4	1	7	2	3		6	4
A				1.000	1.000	1.000	.357				1.000	1.000
B	1.000	1.000	1.000				.500	.750	1.000			
C							.143	.250				
Fdp				1	4		9	2	2	1	10	7
A					1.000		1.000	1.000	1.000	1.000	1.000	1.000
B				1.000								
Fum	2	2	2	1	4	1	7	2	3	1	10	6
A		1.000										
B	1.000		1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

TABLE 2 (continued)

Locus	Species or Group											
	ratt-oides	*lanosus*	*rubex*	*matam-buai*	New Ireland	New Britain	West Sepik	Madang	Karkar Island	Central	Chimbu	Southern Highlands
G-6-pdh	2	1	2	1	4	1	5	2	3		4	5
A	1.000										.500	
B		1.000		1.000	1.000	1.000	.800				.500	.500
C			1.000				.200	1.000	1.000			.500
Gpi	2	2	2	1	4	1	9	2	3	1	10	7
A	1.000	.750	1.000		1.000	.500	1.000	1.000	1.000	1.000	1.000	1.000
B		.250				.500						
C				1.000								
Ga-3-pdh-1	1		2	1	2	1	7		1		9	6
A							1.000		1.000		1.000	1.000
B	1.000		1.000	1.000	1.000	1.000						
Ga-3-pdh-2	1		2	1	1	1	2	1	1		2	1
A						1.000						
B	1.000			1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000
C			1.000									
Gpd	2	2	2	1	4	1	8	2	1	1	10	7
A											.500	.125
B				1.000	1.000		1.000	1.000	1.000	1000	.500	.875
C	1.000	1.000				1.000						
D			1.000									
Hk				1	3		9	1	2	1	10	6
A											.100	.167
B							1.000	1.000	1.000	1.000	.900	.833
C				1.000	1.000							
Idh-1	2	2	2	1	4	1	9	2	3	1	10	7
A		.500										
B	.750			.500								.071
C	.250	.500	1.000	.500	1.000	1.000	.944	1.000	1.000	1.000	.950	.929
D							.056				.050	
Idh-2	2	2	2	1	4	1	7	1	3	1	10	7
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000

TABLE 2 (continued)

Locus	Species or Group											
	ratt-oides	*lanosus*	*rubex*	*matam-buai*	New Ireland	New Britain	West Sepik	Madang	Karkar Island	Central	Chimbu	Southern Highlands
Ldh	2	1	2	1	4	1	8	2	3	1	10	7
A	1.000											
B				1.000							1.000	.143
C		1.000	1.000		1.000	1.000	1.000	1.000	1.000	1.000		.857
Mdh-1	2	1	2	1	4	1	9	2	3	1	10	7
A	1.000	1.000										
B			1.000									
C				1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Mdh-2	2	2	2	1	4	1	9	2	3	1	10	7
A	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
Me	2	1	2	1	4	1	9	2	2	1	10	7
A	1.000	1.000										
B			1.000			.500						
C				1.000	.875	.500	1.000	1.000	1.000	1.000	1.000	.857
D					.125							.143
Mpi	2	2	2	1	4	1	9	2	3	1	8	6
A		1.000	1.000				.278				.125	1.000
B	1.000				.125		.611	1.000		1.000	.313	
C				1.000	.875	.500	.111		1.000		.563	
D						.500						
Pgm	2	2	2	1	4	1	9	2	3	1	10	7
A				1.000								
B	1.000	1.000						.250				
C			1.000		1.000	1.000	1.000	.750	1.000	1.000	1.000	1.000
6-Pgdh	2	2	2	1	4	1	9	2	3	1	10	7
A	1.000	1.000										
B			1.000		.500						.300	
C				1.000	.500	1.000	1.000	1.000	1.000	1.000	.700	1.000
Pk	2	1	2	1	3	1	8	2	2		7	1
A	1.000	1.000	1.000	1.000			.375		1.000		.143	
B					1.000	1.000	.500	1.000			.429	1.000
C							.125				.429	

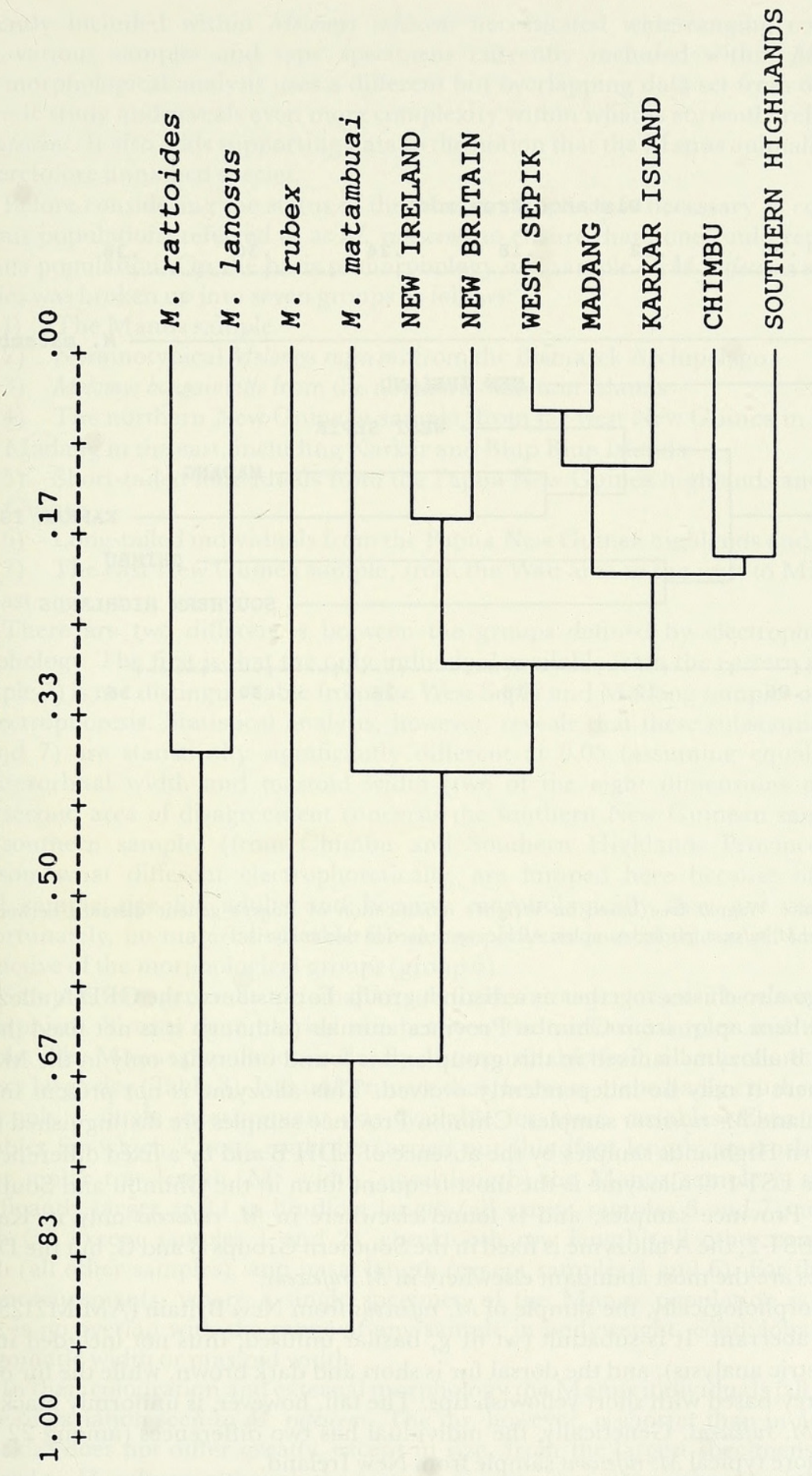

Fig. 2. Phenogram of relationships of *Melomys* populations based on Nei's unbiased genetic distance. Loci with data missing for some populations were not used in this analysis.

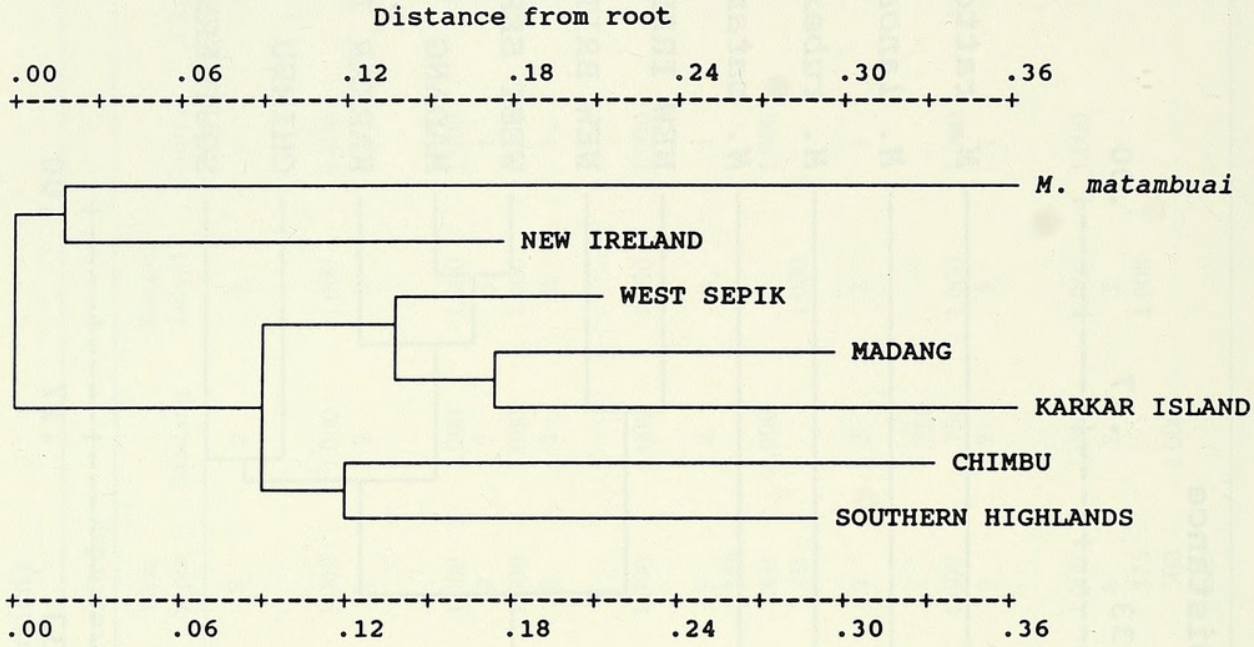

Fig. 3. Distance Wagner tree based on Wright's modification of Roger's genetic distance between *M. matambuai* and *M. rufescens* pooled samples. All loci were used in this analysis.

Archipelago also cluster together as a distinct group. For instance, the GPD A allozyme is seen nowhere apart from Chimbu Province animals (although it is not fixed there). The LDH B allozyme is fixed in this group and is found otherwise only in the Manus sample where it may be independently evolved. This allozyme is not present in any other mainland *M. rufescens* samples. Chimbu Province samples are distinguished from the Southern Highlands samples by the absence of LDH B and by a fixed difference for AAT-1. The EST-1 C allozyme is the most frequent form in the Chimbu and Southern Highlands Province samples, and is found elsewhere in *M. rufescens* only in Karkar Island. At EST-2, the A allozyme is fixed in the Southern Groups B and C, but the D and E allozymes are the most abundant elsewhere in *M. rufescens*.

(4) Morphologically, the sample of *M. rufescens* from New Britain (AM M21234) is somewhat aberrant. It is subadult (wt 61 g, basilar unfused; thus not included in the morphometric analysis), and the dorsal fur is short and dark brown, while the fur of the venter is grey-based with short yellowish tips. The tail, however, is uniformly black and typical of *M. rufescens*. Genetically, the individual has two differences (among 22 loci) from the more typical *M. rufescens* sample from New Ireland.

Morphology. The focus of this study was to determine the status of the *Melomys* sample from Manus Island. Uncertainty as to the status of various named forms

presently included within *Melomys rufescens* necessitated wide-ranging comparisons with various samples and type specimens currently included within *M. rufescens*. Our morphological analysis uses a different but overlapping data set from our electrophoretic study and reveals even more complexity within what is currently referred to as *M. rufescens*. It also adds supporting data to the notion that the Manus animals represent an heretofore unnamed species.

Before considering the status of the Manus sample, it is necessary to consider the various populations referred to as *M. rufescens*, to ensure that none could represent the Manus population. On the basis of morphology our sample of *M. rufescens* and related species was broken up into seven groups as follows:

1) The Manus sample
2) Nominotypical *Melomys rufescens* from the Bismarck Archipelago
3) *Melomys bougainville* from the northern Solomon Islands
4) The northern New Guinean sample, from far west New Guinea in the west to near Madang in the east, including Karkar and Blup Blup Islands
5) Short-tailed individuals from the Papua New Guinea highlands and southern New Guinea
6) Long-tailed individuals from the Papua New Guinea highlands and Mt Sisa
7) The east New Guinea sample, from the Wau area in the west to Milne Bay in the east.

There are two differences between the groups defined by electrophoresis and morphology. The first is that the only individual available from the eastern population (sample 7) is not distinguishable from the West Sepik and Madang samples on the basis of electrophoresis. Statistical analysis, however, reveals that these substantial samples (4 and 7) are statistically significantly different at 0.05 (assuming equal variance) in interorbital width and mastoid width (two of the eight dimensions examined). The second area of disagreement concerns the southern New Guinean samples. The two southern samples (from Chimbu and Southern Highlands Provinces), which are somewhat different electrophoretically, are lumped here because of the very small sample size for adults and because morphologically they are very similar. Unfortunately, no material suitable for electrophoresis is available at all for the most distinctive of the morphological groups (group 6).

Samples were generally too small to subdivide into age classes. There was no sexual dimorphism. 't' tests were carried out between the various samples and the Manus sample. The Manus population is clearly distinguishable from all others on the basis of its very large size (Table 3). It is unfortunate that, because of the badly crushed paratype skull only a single measurement was available for some variables. Even so, for the variables for which 't' tests could be carried out (hindfoot length, interorbital width, upper molar row length, M^1 width, nasal length) the Manus sample is statistically significantly larger at 0.1 in hindfoot length (all except samples 6 and 7), interorbital width (all except samples 1 and 2), cheektooth row length (all other samples), M^1 width (all other samples), and nasal length (except samples 4 and 6). For the remaining measurements, where a single specimen of the Manus population is available, there is no overlap with the range of any sample in bodyweight, condylobasal length, bizygomatic width or mastoid width.

In their colouration and external morphology the Manus individuals fall within the range of variation seen in *M. rufescens*. The fur, however, is shorter than in *M. rufescens*. The skull does not differ greatly, except in size, from the largest specimens currently referred to *M. rufescens* although the rostrum is somewhat more robust and the parietal cresting is less well-developed. Because of its large size and distinctive electrophoretic profile we suggest that the Manus population represents a distinct species.

TABLE 3

External and cranial measurements of the samples of the Melomys rufescens *complex examined during the morphological study. HB = head-body length, TV = tail length, HF = hindfoot length (s.u.), E = ear length (notch), WT = weight, CB = condylobasal length, BZ = bizygomatic width, IO = interorbital width, MA = mastoid width, ML = length of molar row, FM = width across external faces of first upper molar, MW = width of first upper molar, NL = nasal length. 1 =* M. matambuai, *2 =* M. rufescens rufescens *Bismarck Archipelago, 3 =* M. bougainville, *4 = northern New Guinean sample, 5 = short-tailed individuals from the PNG highlands and southern PNG, 6 = long-tailed individuals from the PNG highlands and Mt Sisa, 7 = eastern New Guinea sample*

	1	2	3	4	5	6	7
HB X	151	128	138	132	118	134	135
R		121-137	135-140	92-152	96-130	127-140	134-135
STD	–	7.07	–	13.64	10.08	5.69	–
N	1	4	2	16	15	4	2
TV X	141	147	133	147	143	180	150
R	–	137-158	131-135	131-175	129-163	170-195	149-150
STD	–	8.66	–	14.01	9.47	10.80	–
N	1	4	2	16	15	4	2
HF X	30.7	26.2	25.5	27.4	25.7	29.7	28
R	30.3-31	23.8-29	24-27	24-31	23-28.8	28-31	27-29
STD	–	2.29	–	1.63	1.37	–	–
N	2	4	2	16	15	3	2
E X	18	16.3	12.8	15	15	17.7	17.3
R	–	15.2-17	12.5-13	13.4-17	14-16.1	17.5-18	15.5-19
STD	–	.87	–	1.22	1.03	–	–
N	1	4	2	16	5	3	2
WT X	145	88	86	87	51.7	–	75
R	–	82-95	–	56-121	33-79	–	–
STD	–	5.80	1	22.35	13.47	–	–
N	1	4	1	11	12	0	1
CB X	36.9	32.7	32.9	32.3	29.9	32	32.5
R	–	31.3-33.4	30.8-34.4	22.1-35.8	28.7-31.4	30.1-33	30.2-34.3
STD	–	0.92	1.67	2.51	0.75	1.34	1.36
N	1	5	4	26	9	4	13
BZ X	20.8	18	19.2	17.5	16.5	17.3	17.6
R	–	17.2-18.9	17.8-19.9	16.1-20.3	15.5-17.4	16.4-18.2	16.5-18.8
STD	–	0.67	0.94	0.89	0.52	0.75	0.82
N	1	6	4	23	9	4	13
IO X	6.9	6.1	6.4	5.8	5.5	5.6	5.6
R	6.5-7.2	5.8-6.4	6.0-6.7	5.0-6.7	5.1-5.8	5.1-5.7	5.3-6.2
STD	–	0.23	0.33	0.40	0.27	0.08	0.27
N	2	6	4	26	10	4	13
MA X	15.5	13.5	14.1	13.4	13.0	13.7	13.1
R	–	13-13.9	13.4-14.6	12.8-14.4	12.8-13.4	13.5-13.9	11.9-13.6
STD	–	0.41	0.51	0.39	0.18	0.17	0.49
N	1	5	4	26	9	4	12
ML X	7.1	6.3	6.1	6.2	6.0	6.4	6.2
R	6.9-7.3	5.8-6.6	5.6-6.4	5.6-6.6	5.8-6.2	6.1-6.6	6.0-6.6
STD	–	0.31	0.35	0.25	0.12.	0.26	0.17
N	2	6	4	26	9	4	13
FM X	2.2	1.9	1.8	1.8	1.7	1.9	1.9
R	2.1-2.2	1.8-2.0	1.6-1.9	1.6-2.1	1.7-1.8	1.9-2.0	1.8-2.0
STD	–	0.10	0.13	0.10	0.04	0.05	0.06
N	2	6	4	26	9	4	13
MW X	7.6	7.0	7.2	7.0	6.6	7.2	6.9
R	–	6.7-7.4	6.6-7.6	6.4-8.0	6.4-6.8	7.0-7.5	6.6-7.3
STD	–	0.38	0.45	0.33	0.11	0.21	0.20
N	1	3	4	26	9	4	13
NL X	12.6	11.7	12.1	11.6	10.9	11.6	11.8
R	12.2-12.9	10.9-13.1	11.3-12.7	10-13.2	10.2-11.3	10.2-11.7	10.9-12.8
STD	0.50	0.75	0.64	0.77	0.32	1.11	0.62
N	2	6	4	25	9	4	12

Systematic Description

Melomys Thomas, 1922

Melomys matambuai n.sp.

(Fig. 4, Table 3)

Holotype. AM M19639, adult female study skin, skull, spirit body and frozen liver sample, collected on the 15th of June 1988 at an elevation of 200 m near Polomou DPI Station, south-central Manus (2°08′S 147°05′E), Papua New Guinea.

Paratype. AM M22277 (to be returned to PNG Nature Conservation Section), adult female study skin, fragmented skull and body in spirit, collected by Felix Kinbag of the PNG Nature Conservation Section at the western end of Manus Island.

Diagnosis. Differing from all other species of *Melomys* except some members of the *Melomys rufescens* complex in that the tail is uniformly black, not bicoloured dark above and white underneath. It is the largest member of the *Melomys rufescens* complex, differing from *M. leucogaster* (Jentink) in being larger, in that the bony palate is not thickened, and in that the tail is uniformly black rather than bi-coloured. It differs from all material currently referred to *M. rufescens* as well as *M. bougainville* in being statistically significantly larger at 0.1, assuming equal variance, in molar row length and M^1 width. It is absolutely larger in bodyweight, condylobasal length, bizygomatic width and mastoid width.

Description. The holotype is a mature although not aged female skin and skull, lacking all but the proximal 25 mm of naked tail. It also lacks most of the left ear, and the hands are damaged. The paratype is subadult (the basilar suture is unfused) skin and skull, the skin of which is in good condition, but the skull is badly damaged. The fur is short, and ventrally is pure white to the roots, extending from the chin to the cloaca in a broad swathe. The dorsum is reddish-brown, close to tawny in the holotype, and slightly more brown in the paratype. The underfur of the dorsum of dark grey. The ears and tail are naked, and the tail scales are slightly raised as in *M. rufescens*. There is a single hair per tail scale, and in the holotype the scales on the remaining section of tail are hexagonal. On the paratype the scales are more rectangular. The hands and feet are pale, and are very thinly-furred dorsally.

The holotype skull is entire, while that of the paratype has the rostrum and basicranial regions badly smashed, and lacks the right zygomatic arch. Where preserved the skulls are similar, except that the parietal crests are less-developed in the paratype. The skull of the holotype is largely similar to that of other members of the *M. rufescens* complex, although larger. The molars are moderately worn, and the simple crown patterns are still evident.

Etymology. For Karol Matambuai Kisokau, O.B.E., a Manus man and the first Permanent Secretary of the Papua New Guinea Department of Environment and Conservation, in honour of the enormous contribution that he has made to the development of wildlife management and conservation in his nation.

Discussion

Eight subspecies of *M. rufescens* are recognised by Laurie and Hill (1954). They are as follows:

Melomys rufescens rufescens (Alston) from the islands of the Bismarck Archipelago, and the mountains of northeast New Guinea and eastern Papua

Melomys rufescens stalkeri (Thomas) between Ioma and Morobe, Northern Province, PNG

Melomys rufescens gracilis (Thomas) southeast Papua

Melomys rufescens sexplicatus (Jentink) Jayapura area, Irian Jaya

Melomys rufescens calidor (Thomas) southwestern Irian Jaya

Melomys bougainville Solomon Islands (here recognised as a distinct species)
Melomys rufescens hageni (Troughton) central highlands
Melomys rufescens niviventer (Tate) lower Fly River

Flannery (1990) reduces all except *bougainville* and *stalkeri* to synonyms. This study, however, suggests that at least some of these taxa may represent distinct species. Assignment of the morphologically and electrophoretically-based groups that we recognise here to the various available names is a difficult problem that we cannot fully resolve at present, although a little can be said. The situation regarding the insular taxa is relatively clear. The nominotypical form of *Melomys rufescens* Alston, 1877 (syn. *Mus musavora* Ramsay, 1877) is restricted to the Bismarck archipelago, while *Melomys bougainville* is found only in the northern Solomons. On mainland New Guinea the situation becomes more complex, although it appears probable that *sexplicatus* is the appropriate name for the northern New Guinean and Karkar samples. *Melomys r. gracilis* is distinctive because of its long tail and long, dense fur, there is little doubt that it is the same as our sample 6 (see Tables 3-4). It is highly unlikely however that it is a subspecies, as it occurs in sympatry with a short-tailed *M. rufescens* population (for which the first available name may be *hageni*) in the Mt Hagen and Mt Sisa areas. Unfortunately, we lack tissues from sample 6 animals. The situation to the east and to the south of the Central Cordillera is complex and still unresolved. Electrophoresis suggests some differentiation in the south which is not reflected in our very limited morphological samples, and the names *stalkeri*, *calidor* and *niviventer* are all available. Clearly, all of these are distinct from *M. matambuai* (see Tables 3-4 and Fig. 2).

TABLE 4

Measurements for the holotypes of various named forms of Melomys rufescens *from Tate (1951) and* (bougainville *and* hageni) *from AM M specimens.* Sta = stalkeri, gra = gracilis, sex = sexplicatus, cal = calidor, boug = bougainville, niv = niviventer. *See Table 4 for other abbreviations.*

	rufescens	*sta.*	*grac.*	*sex.*	*cal.*	*boug.*	*hageni*	*niv.*
HB	140	135	140	?150	?153	147	124	121
TV	135	137	180	135	155	140	154	125
HF	28	27	27	24	28	27.5	26.5	26
E	10.5	10	12	–	10	14.3	14	14
CB	–	31.8	31.7	32.8	32.9	34.1	30	31
BZ	17.7	17.1	16.9	17.7	17.4	19.9	16.7	16
IO	5.9	6.0	5.2	5.5	6.2	6.6	5.6	5.6
MA	–	–	–	–	–	14.6	12.8	–
ML	6.5	6.2	6.4	5.9	6.3	6.2	5.9	5.9
FM	2.0	1.8	1.9	1.7	1.9	1.8	1.8	1.8
MW	–	–	–	–	–	–	–	–
NL	11.3	10.0	9.6	11.0	10.5	12.7	10.8	11.1

Both known specimens of *Melomys matambuai* were shot while climbing in trees. The holotype was shot in the evening while it was climbing in low secondary growth approximately 1.5 metres from the ground on the edge of a Cocoa plantation, while the paratype was shot while it was climbing in a sago palm. Despite about 100 trap-nights of effort using Elliott traps on the ground near the type locality, and additional effort where the paratype was taken, no specimens were trapped. These data suggest that *M. matambuai* may be largely arboreal and that it inhabits secondary forest. It may be more arboreal than *M. rufescens* of the Bismarck Archipelago and New Guinea, which are readily trapped on the ground. It is known to the Manus people as *Muserou*.

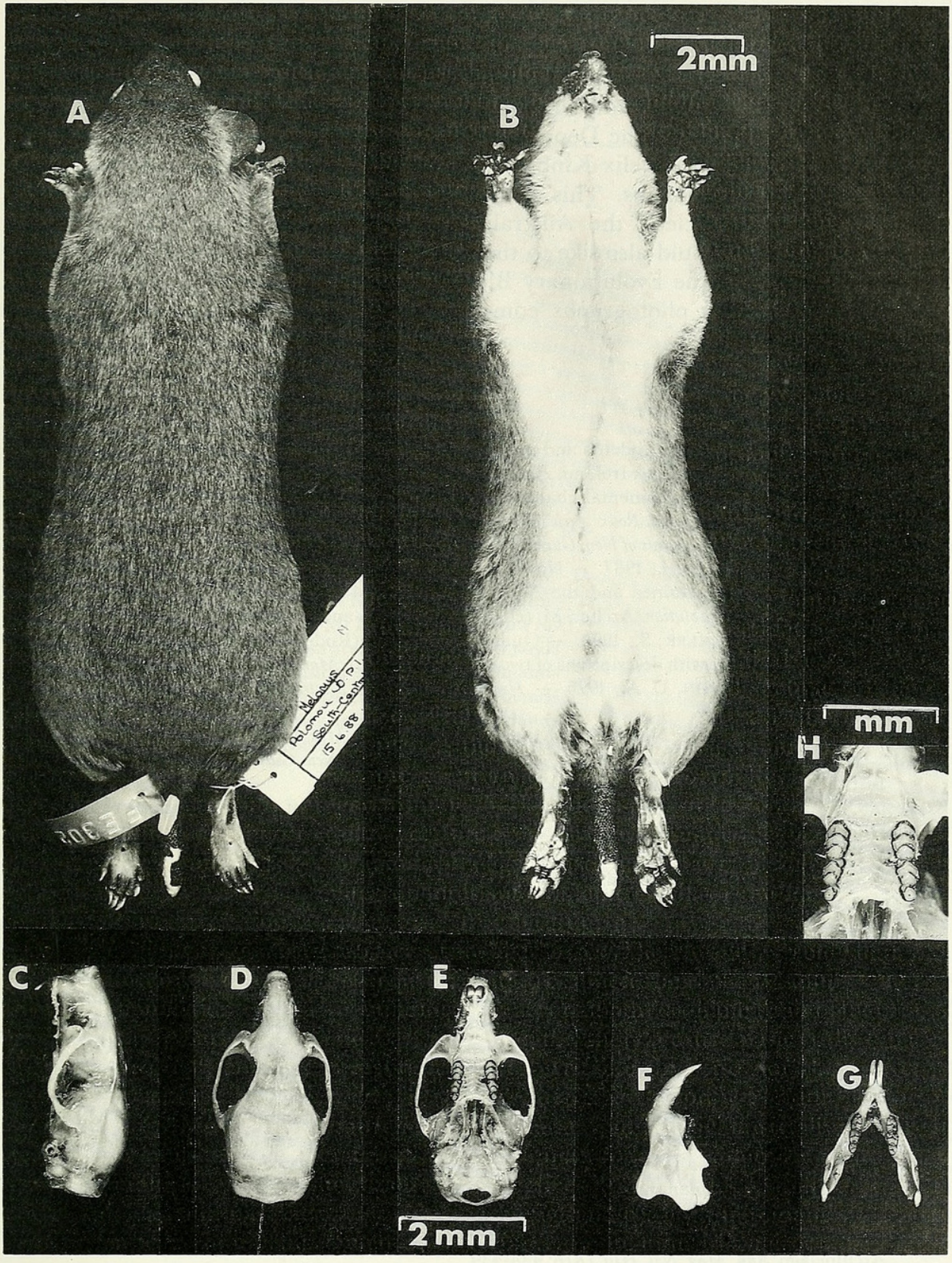

Fig. 4. Holotype of *Melomys matambuai*. Study skin in A, dorsal and B, ventral view. Skull in C, lateral, D, dorsal, E, ventral views, and dentary in F, lateral and G, dorsal views.

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APPENDIX 1

Data for samples used in electrophoresis. Numbers other than M numbers are field numbers. Samples listed by locality under POPULATION are M. rufescens

Population	Location	Samples Scored
M. rattoides	Torricelli Mts, West Sepik	M20919, M20921
M. lanosus	Telefomin area, West Sepik	M18804, M19445
M. rubex	Torricelli Mts, West Sepik	M21552, M21559
M. matambuai	Polomou, Manus Island	M19841
New Ireland	Madina, New Ireland	M20448, M20451, M21262-3
New Britain	Waipo, New Britain	M21234
Tibip	Yapsiei area, West Sepik	M13470, M14867
Yapsiei	Yapsiei, West Sepik	M16768
Bogalmin	Telefomin area, West Sepik	M15955
Wigote	Torricelli Mts, West Sepik	M15956
Fatima	Torricelli Mts, West Sepik	M15866
Munbil	Munbil, Star Mts, West Sepik	M16774, M17704, M17464
Madang	Siar, Madang, Madang Prov.	M21678, A19
Karkar	Karkar Island, Madang Prov.	M19053, M21677, M21679
Kosipe	Mt Albert Edward, Central Prov.	M12651
Yuro	Yuro Mt Karimui Chimbu Prov.	M15163-4, M15161, M15171-2
Haia	Haia, Sth Chimbu, Chimbu Prov.	M13835
Noru	Noru, Mt Karimui, Chimbu Prov.	M14732
Doido	Doido, Mt Karimui, Chimbu Prov.	M15177, M15184, R55
Bobole	Mt Sisa area, Southern Highlands	M16349
Waro swamp	Mt Sisa area, Southern Highlands	M16390
Waro	Mt Sisa area, Southern Highlands	M16386-7, M19859
Namasado	Mt Sisa area, Southern Highlands	M16248
Agofia	Mt Sisa area, Southern Highlands	M16392

APPENDIX 2

Specimens used in the statistical analysis

Sample 1 (Melomys matambuai) M19639, M22277
Sample 2 (*Melomys rufescens*, Bismarck Archipelago) LACM67061-2, BZM60646, M20448, M20451, M2368
Sample 3 (*Melomys bougainville*) M5757, M6493, M19820, M21864
Sample 4 (*Melomys rufescens*, northern New Guinea and Karkar Id) M6217-8, M7130, M7133-4, M7207, M13469, M13470, M13485, M14867, M15886, M17704, M17442-4, M17446-8, M17684, M17686, M19053, M20452, M21677-9, M23767-9
Sample 5 (*Melomys rufescens*, relatively short-tailed southern New Guinea and central highlands individuals) M6166, M9600-1, M9613, M14732, M15175, M15407, M15465-7, M15553, M15555-8, M15608, M16248, M24959
Sample 6 (*Melomys rufescens*, long-tailed individuals from central highlands and Mt Sisa) M9598-9, M15407-8
Sample 7 (*Melomys rufescens*, southeast New Guinea) M4133, M6432, M7136, M7138-9, M7145-7, M7173, M6778, M12651, M14076, M20312.