# AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

# A Revision of the Genus *Uromys* Peters, 1867 (Muridae: Mammalia) with Descriptions of Two New Species

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ABSTRACT. *Uromys* Peters, 1867 is re-defined so that it is monophyletic. The clade includes nine species placed in two monophyletic subgenera: *U. (Cyromys)* includes the species *porculus, rex* and *imperator*; *U. (Uromys)* includes the species *anak, neobritannicus, hadrourus, caudimaculatus, emmae* n.sp. and *boeadii* n.sp. *Uromys (Cyromys)* includes more plesiomorphic species, which are all restricted to Guadalcanal in the Solomon Islands. Species of *U. (Uromys)* are more derived, as in their possession of greatly simplified molars, and in having the number of interdental ridges of the soft palate greatly multiplied. The genus is widespread in Melanesia and northern Australia. Three distinct subspecies of *U. caudimaculatus*, and three of *U. anak* (one new) are recognised. *Uromys boeadii* n.sp., from Biak Island, and *Uromys emmae* n.sp., from Owi Island, both in Geelvinck Bay, are newly described.

The generic name *Uromys* was proposed by Peters, 1867 for *Mus macropus* Gray, 1866. *Mus macropus* is a primary homonym (*nec* Hodgson), and thus the first available name for the species is *Hapalotis caudimaculatus* Krefft, 1867. Until 1922 all mosaic-tailed rats from Australasia were referred to the genera *Uromys* or *Mus*. In 1922, however, Thomas divided the species previously assigned to *Uromys* between three genera: *Uromys*, *Melomys* and *Solomys*. He defined the members of his newly restricted genus *Uromys* as follows: size large (hindfoot length greater than 52 mm,

skull longer than 70 mm), tail long, incisive foramina short, bony palate extends to behind M³, incisors deep, and ridges of the soft palate duplicated and up to 12 in number. He included in *Uromys* only taxa currently recognised as belonging within the species *caudimaculatus* and *anak*.

Rümmler (1938) was the next major reviser to deal with the genus as a whole. He differentiated the species of *Uromys* from other New Guinean murids by their possession of a high infraorbital canal which narrows to a slit-like base, wide maxillary plate, simple molars and

a practically hairless tail whose scales have a raised hump. He further noted that the species of *Uromys* were larger than the species of *Melomys*, and that the bony palate extended further posteriorly in *Uromys*. He included the species *anak*, *salamonis*, *imperator*, *caudimaculatus* and *neobritannicus* within the genus.

Tate (1951) was the most recent comprehensive reviewer of the genus *Uromys*. Synonymising *Solomys* with it, he defined it as follows: tail with one hair per tail scale, tail long and feet scansorial; more or less pronounced postorbital ridging, incisive foramina short, palate short (an error for long?), bulla small, incisors massive, molars simple, skull massive with uninflated braincase. He included the species *anak*, *caudimaculatus*, *sapientis*, *salebrosus*, *rex*, *imperator*, *porculus*, *salamonis* and *ponceleti* within *Uromys*. As part of their checklist of the mammals of the New Guinean and Sulawesian regions, Laurie & Hill (1954) included only the species *caudimaculatus*, *anak*, *neobritannicus*, *rex*, *imperator* and *salamonis* within *Uromys*, referring *porculus* to *Melomys*, and *sapientis*, *salebrosus* and *ponceleti* to *Solomys*.

The concept of *Uromys* has thus been highly unstable over the last century. The principal reviewers have, however, always included a core of two species, *caudimaculatus* and *anak* within it; other large murid species from Melanesia have been variously included and excluded with little apparent attempt at determining phylogenetic relationships.

Quite apart from problems of defining the genus, there has been a wide diversity of opinion among workers regarding species limits and subspecies concepts for some of the included taxa. Without doubt, that with the least stable taxonomic history is *Uromys caudimaculatus* and its various named races. As previously constituted, this species has a wide range (Fig. 1) and great degree of morphological diversity. Thomas (1922) recognised seven distinct species (*aruensis*, *macropus*, *multiplicatus*, *nero*, *papuanus*, *scaphax* and *validus*) which later workers have regarded as belonging within *U. caudimaculatus*. Rümmler (1938) recognised six subspecies of *caudimaculatus*: *caudimaculatus* and *sherrini* from Queensland, *seibersi* from the Kei Islands, *aruensis* from the Aru Islands, *validus* from New Guinea and nearby Islands, and *barbatus* from montane New Guinea. Tate (1951) showed that the last of these taxa in fact belongs within a monotypic genus (*Xenuromys*), which is not closely related to the *Uromys/Melomys* complex, and recognised only the subspecies *caudimaculatus*, *aruensis* and *multiplicatus*, in which he was followed by Laurie & Hill (1954).

Our concept of *Uromys* differs from that of all previous workers. We recognise a group of nine species that on the basis of a suite of shared derived characters forms a monophyletic group, here recognised as the genus *Uromys*. We further recognise two monophyletic subgenera: the more plesiomorphic *Cyromys* and the more derived *Uromys*. We divide specimens previously allocated to *U. caudimaculatus* between three subspecies, and describe a new, related species based upon hitherto unexamined material; we divide *U. anak*
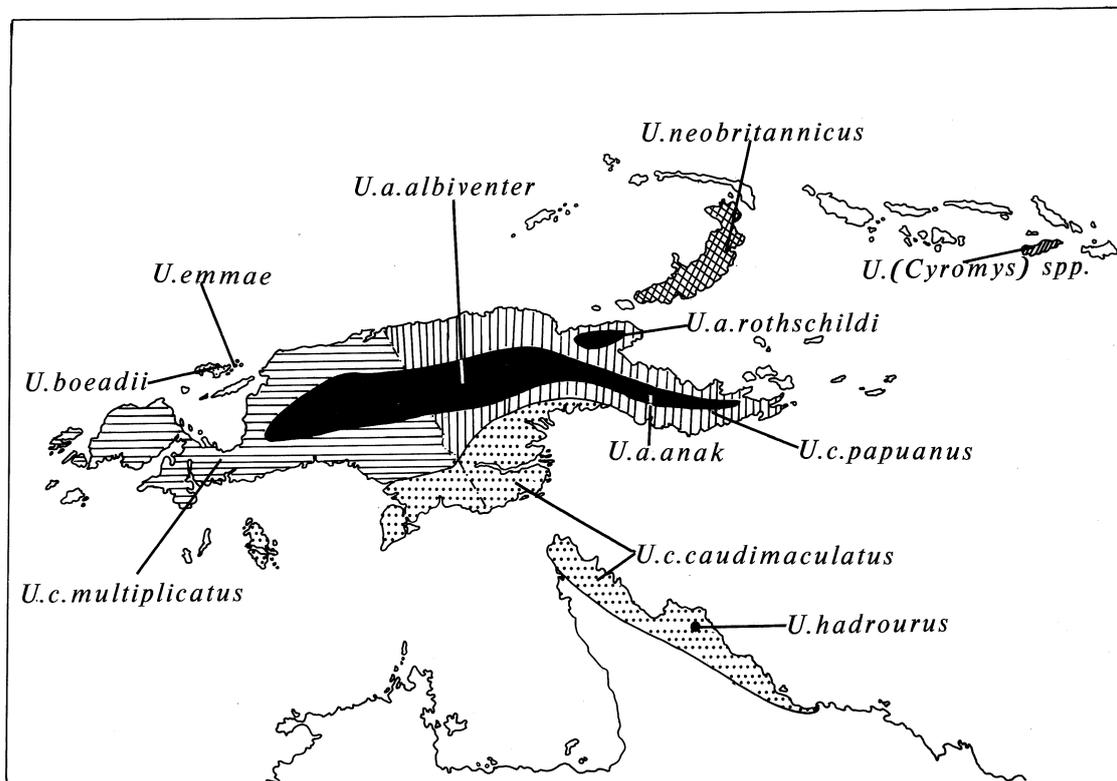


**Fig. 1.** Map of the New Guinean region showing the approximate distribution of the species and subspecies of *Uromys*.

into three subspecies (one of them new); and we describe a new species of uncertain affinities.

## Materials and Methods

During the course of this study we have examined all material referable to the species of *Uromys* held in the Natural History Museum (London), the Bishop Museum (Hawaii), the Rijksmuseum van Natuurlijke Historie (Leiden), the Australian National Wildlife Collection (Canberra), the Queensland Museum (Brisbane), the Museum of Victoria (Melbourne) and the Australian Museum (Sydney) (for list of localities for *U. caudimaculatus* and *U. anak* see Table 1 [Appendix]). In particular we have examined the holotypes or syntypes of all named taxa except *Uromys papuensis* Ramsay (which cannot be located among the collections of either the Australian or Macleay Museums, where it can reasonably be expected to have been lodged), *Uromys neobrittanicus* Tate & Archbold, and *Uromys waigeouensis* Frechkop. One of us (TFF) also briefly examined material in the American Museum of Natural History, New York; more detailed examination at a later time will enable our conclusions to be more extensively documented, but as it is clear that this material does not affect the conclusions, we do not think it advisable to hold up this revision.

The following abbreviations are used: AM M and AM S – Australian Museum mammal specimen; BM – Natural History Museum mammal specimen; BBM – Bishop Museum; CM – National Wildlife Collection mammal specimen; NMV – Museum of Victoria Mammal Specimen. All tables in this paper are listed in the Appendix.

We took a number of measurements on each specimen; unfortunately, time precluded taking our full list on every single specimen, but in all cases greatest skull length (maximum: nuchal surface to anterior edge of premaxillae or nasals), condylobasal length, bizygomatic breadth and maxillary tooth row length were measured, and any flesh measurements recorded on the specimen label were noted. As well as normal univariate comparisons, we calculated certain simple indices (tail as percent of head + body; ear as percent of condylobasal length). We also performed a number of multivariate analyses, using SPSS-X Discriminant Functions programs. We used Direct method for all analyses, and for comparative purposes both Mahalanobis and Rao methods in one case; the results for all three methods are very close. We performed three analyses. (i) All species of *Uromys* except for *U. emmae* n.sp. and *U. boeadii* n.sp., using the following variables: greatest skull length, condylobasal length, anterior skull height (perpendicular to posterior margin of palate), anterior zygomatic width (between most convex points on zygomatic process of malar bones), posterior zygomatic width (maximal bizygomatic width), rostral height (perpendicular to premaxillary/maxillary

suture on palate), braincase breadth, rostral length (anterior orbit margin to prosthion), rostral breadth (across rostrum on premaxillary/maxillary suture). (ii) *Uromys caudimaculatus* and *U. emmae*, using the following variables: greatest skull length, condylobasal length, posterior zygomatic width, head + body length, tail length, hindfoot length, ear length (samples are listed in Tables 1-2). (iii) *Uromys anak* and *U. boeadii*, using the same variables as listed in analysis 2 (samples are listed in Tables 1-2). Note that only variables subject to ontogenetic change were included, ie, toothrow length was not incorporated as being liable to distort the results. In order to exclude, or at any rate minimise, discrimination by size alone, subadults as well as adults were included in each sample; this at the same time avoids discrimination on the basis of chance differences in age or sex composition between samples. In all but these cases, we ensured that the number of specimens in each sample was greater than the number of discriminating variables. The three exceptions were *U. boeadii* and *U. emmae*, for which there was but a single specimen each, and *U. hadrourus*, for which there were two adult skulls. The composition of our samples in the analyses was determined by prior inspection, ie, we were concerned to test the validity of our taxonomic assessments in a morphometric analysis.

We finally performed a cladistic analysis using (i) Hennig86 (using, out of the 49 characters found to be distinctive of species within the genus [Table 3], those 41 in which more than one taxon showed the derived condition), and (ii) MacClade (Wayne & David Maddison), using all 49 characters. Hennig86 is a basic cladistic program which finds all the most parsimonious trees; MacClade is a tree manipulation program; when the basic outlines of *Uromys* phylogeny were clear, we wished to examine the effect of different placements of certain key taxa, especially *U. boeadii*. The default parameters were used for these computer programs, including ordered variables for Hennig 86. *Melomys rufescens* was used as an outgroup.

## Systematics

### *Uromys* Peters, 1867

**Type species.** *Hapalotis caudimaculatus* Krefft, 1867.

**Revised generic diagnosis.** The species of *Uromys* can be differentiated from all other murids in possessing the following combination of features: i) soft palate has between six and 12 irregular ridges in region between molar rows (Fig. 2); ii) palate extends posteriorly beyond posterior margin of M3; iii) lower incisors much deeper than wide; iv) anterolateral spine of bulla greatly expanded.

**Notes.** McAllen & Bruce (1989) suggest that *Melanomys* is a new generic name proposed by

Winter (1983) for the species *hadrourus*. This name results from a typographical error in a reference, and in any case is preoccupied by *Melanomys* Thomas, 1902.

The generic diagnosis differentiates *Uromys* from all other Muridae, including its close relatives *Solomys* and *Melomys*, with which it agrees in possessing a so-called mosaic tail (described, for example in Tate, 1951). Species of *Uromys* differ additionally from species of *Melomys* in their larger size, and from species of *Solomys* in lacking the latter's greatly thickened palate, and by the relatively larger, thicker incisors, more elongate basoccipital, and the posteriorly broadened palate. We transfer to *Uromys* two species previously referred to *Melomys* (*M. porculus* and *M. hadrourus*), and transfer *salamonis*, previously placed within *Uromys*, to *Solomys*.

The Discriminant Analysis (Fig. 3) discriminated the quasi-specific samples on the basis of (first function, accounting for 42.5% of total variance) greatest skull length and snout length, and (second function, 35.9% of variance) overall size except for braincase breadth. A third function accounted for 12.3% of variance, but was an absolute size discriminator, distinguishing only *U. hadrourus* effectively. The two subgenera are not sharply distinguished by the analysis: *U. caudimaculatus*,
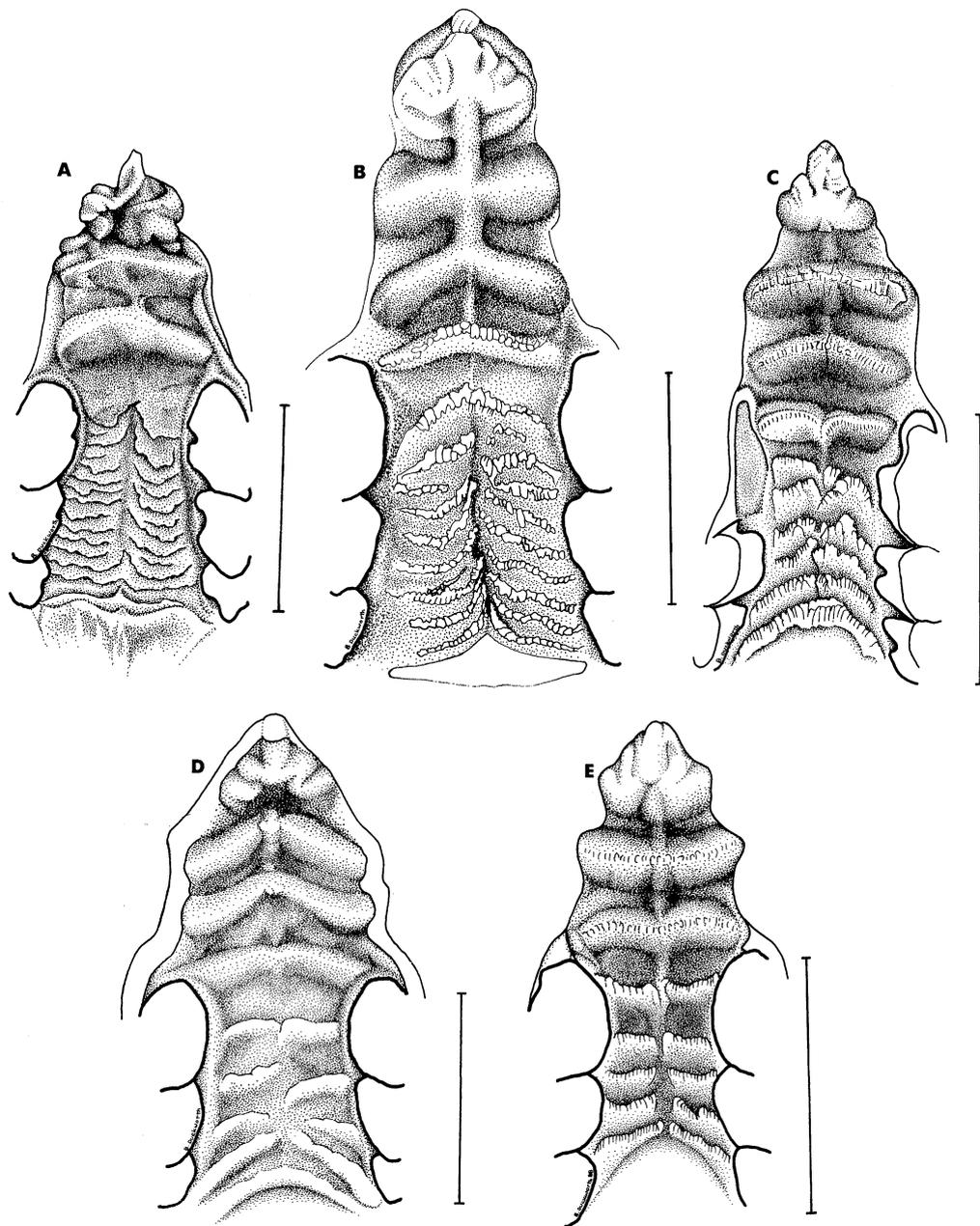


**Fig. 2.** The soft palate of (A) *Uromys caudimaculatus*, (B) *U. anak*, (C) *U. rex*, (D) *Xenuromys barbatus* and (E) *Solomys sapientis*.
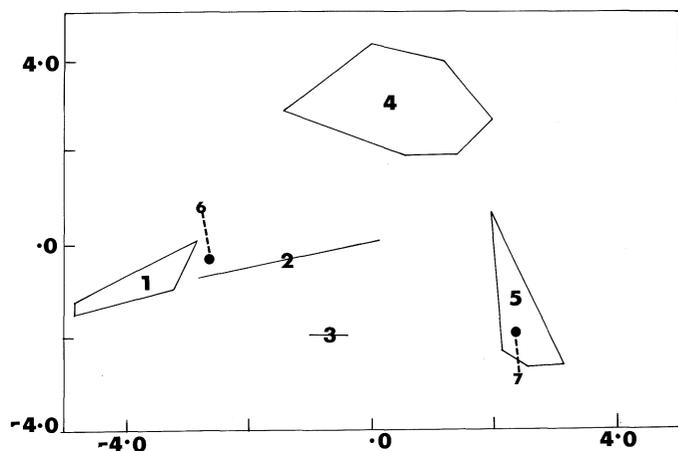
**Fig. 3.** Discriminant analysis of *Uromys*. Function 1 (abscissa) accounts for 42.5% of the total variance, and is most highly correlated with greatest skull length and snout length; Function 2 (accounting for 35.9% of total variance) is positively correlated with all variables except braincase width. 1 = *U. rex*, 2 = *U. imperator*, 3 = *U. hadrourus*, 4 = *U. anak*, 5 = *U. caudimaculatus*, 6 = *U. porculus*, 7 = *U. neobritannicus*.

*U. hadrourus* and *U. anak* are arrayed around one end of a linear clinal spread from *U. rex* via *U. porculus* to *U. imperator*. The result is difficult to interpret, but is consistent with our conclusions (below) that *U. rex* is the most autapomorphic species in *U.* (*Cyromys*) and that *U. anak* is less like other species of *U.* (*Uromys*) than is *U. neobritannicus*.

### *Uromys* (*Cyromys*) Thomas, 1910

**Type species.** *Mus imperator* Thomas, 1888.

**Revised diagnosis.** The species of *Uromys* (*Cyromys*) can be distinguished from species of *U.* (*Uromys*) by possessing the following features: i) molar rows relatively short, molars relatively broad; ii) M3 larger relative to other teeth; iii) anterior lophid of $M_1$ distinct even in worn molars; iv) molars more complex, individual cusps more distinctly defined, with $M^1$ retaining a well-developed fossa lingual to posterior cingulum; v) anterior and ventral orbital walls slope away from centre of orbitotemporal fossa, so that walls can be seen in dorsal view; vi) frontotemporal sutures markedly ridge-like; vii) coronal suture strongly convex or biconvex backwards; viii) preorbital foramen slopes backwards, so that inferior margin readily visible in dorsal view; ix) ascending ramus flares laterally; x) tail scales consist of small central prominence surrounded by large fleshy area. All of the dental features listed here are probably plesiomorphic for the species of *Uromys* and closely related genera (see discussion). However, the tail morphology is unique among near relatives and is presumably synapomorphic for the subgenus.

Additional useful diagnostic features for the

subgenus are as follows. The rostrum is broad, and the incisive foramina are strongly bowed outward; although the temporal sutures are markedly ridge-like, there are no post-sutural processes. The nasals are posteriorly broadened, and the posterior part of the lateral walls of the rostrum are steep, nearly vertical and partially concealing the lachrymal in dorsal view. The zygomatic arches do not swing down to the level of the molar alveoli. The nasal tips are abbreviated and slightly downturned. The incisors are opisthodont. The paroccipital processes are long, their tips level with the inferior margins of the occipital condyles and the auditory bulla. The insertion scar of the *M. temporalis* on the mandible is marked by a strong anterior ridge.

Although *U.* (*Cyromys*) differs strongly from *U.* (*Uromys*), and a good case could be made for separating them generically, we prefer at least for the present to retain them in one genus in order to emphasise their sister-group status with respect to their closest relatives (*Melomys*, *Solomys*).

### *Uromys* (*Cyromys*) *imperator* (Thomas, 1888)

**Type material.** HOLOTYPE, BM 88.1.5.33, adult female skin and skull collected at Aola, northern Guadalcanal, Solomon Islands, by C.M. Woodford.

**Revised diagnosis.** *Uromys* (*Cyromys*) *imperator* is the largest of the species of *Cyromys*. The pads of the feet are reduced in size relative to other *Cyromys*, and the molars relatively much broader. It is similar externally to *U. rex*, with its dark grey, somewhat woolly fur (as aptly described by Thomas, 1888), grading to white below, and its very short ears. In comparison with *U. rex*, however, the head and body is longer, and the tail shorter with smaller scales (9-11 per cm versus 7-9 per cm). The skull is characterised by a median posterior palatal spine; very square posterior nasals which end comparatively far forward, anterior to a line connecting the posterior ends of the lachrymals; a relatively vertical ascending ramus with a low, rounded coronoid process; and a small dentary ridge and tubercle.

**Discussion.** *Uromys imperator* is still known with certainty only from the original three specimens collected by Charles Woodford at Aola on Guadalcanal in 1887. Woodford probably purchased the specimens from local hunters, and it is unlikely that they were collected far from the coast as Woodford (1890) mentions repeatedly the near impossibility of travelling far inland for fear of neighbouring tribes. A flat skin without a skull in the Australian Museum (AM M19739) may, however, also represent this species. Its tail scales are less rasp-like than the Museum's specimens of *U. rex*, and the size is considerably larger, although smaller than the previously known specimens of *U. imperator*. It was collected by a Captain G. Hart. Other specimens collected by Captain Hart in the Museum Collections are from Lavoro Plantation in far northern

Guadalcanal, and were collected in August 1933. On balance, we think this likely to be *U. rex* because of the larger foot pads, but the difficulty of identification reinforces our conclusion that the two species are extremely close.

Recently the remains of *U. imperator* have been found in archaeological deposits in northern Guadalcanal (Flannery & Roe, in preparation). Extensive questioning of the older people of Guadalcanal suggest that it may well be extinct, there having been few or no reliable sightings over the last 40 years, and also suggest that within living memory it was encountered only in montane mossy forest. This is surprising, considering that the archaeological deposits within which its remains have been found are now located in savannah areas near sea level, far distant from any mossy forest, and that Woodford's specimens probably came from near the coast.

Because of its short tail and reduced pads on the feet, Thomas (1888) considered this species to be terrestrial. This hypothesis is strengthened both by information related to one of us (TFF) by older men who had seen it in their youth, and from an examination of the adult male in the Natural History Museum specimen (BM 1888.1.5.32) which has considerable amounts of clay and earth adhering to the claws, forepaws and muzzle, suggesting that it was dug from a burrow.

### *Uromys* (*Cyromys*) *rex* (Thomas, 1888)

**Type material.** HOLOTYPE, BM 88.1.5.34, adult male skin and skull collected at Aola, Guadalcanal, Solomon Islands by C.M. Woodford.

**Revised diagnosis.** Larger than *U. porculus* but smaller than *U. imperator*. Differing further from *U. imperator* in its relatively narrower molar rows and shorter, broader skull with an especially broad, deep rostrum; its extreme development of the frontotemporal ridges; the more arched posterior nasal ends which are level with the posterior ends of the lachrymals; the absence of a post palatal spine; the very oblique ascending ramus with strongly-developed tubercle and ridges, and slender, pointed coronoid. Externally it differs in its longer tail, larger pads on the hindfeet, and larger, more rasp-like tail scales (7-9 per cm versus 9-11 per cm).

**Discussion.** *Uromys* (*Cyromys*) *rex* is the only species of *U.* (*Cyromys*) for which the soft palate is known (Fig. 2). AM M19740 is an aged individual which shows an intriguing soft palate configuration. There are seven interdental ridges, as opposed to the five that are seen in the species of *Melomys* and *Xenuromys*. The interdental ridges are, however, irregular and incomplete. The increased number of ridges is clearly apomorphic and reminiscent of the condition of *U.* (*Uromys*), where between 10 and 12 interdental ridges can be present. Their irregularity and incompleteness in the only specimen of *U.* (*Cyromys*) thus far known, however, does not resemble the condition in *U.* (*Uromys*). We are unsure of how to interpret this feature. It may be pathological (the animal is extremely aged), or it may be the normal condition, in which case it must be regarded as a synapomorphy for *U.* (*Cyromys*) or *U. rex*. Within *U.* (*Cyromys*), *U. rex* is the most derived of the three species in many respects, despite its superficial resemblance to *U. imperator*.

The original series of seven specimens were collected at Aola by Woodford in 1887. The greater numbers of this species relative to the other two species of *Uromys* found on Guadalcanal by Woodford may suggest that even at this time it was the commonest taxon. It is the only one of the species of *Uromys* (*Cyromys*) to have been collected since Woodford's work. The Australian Museum holds a specimen in alcohol with the skull extracted (AM M13594) which was collected on Guadalcanal. Unfortunately, it lacks other data. A flat skin (AM M19739) belonging either to this species or *U. imperator* (see above, under *U. imperator*) is also held in the Australian Museum. There are two specimens (skins with skulls) in the Bernice P. Bishop Museum, Honolulu, Hawaii, USA (BBM 23988 and 24101), collected at Tabila, Guadalcanal, in June, 1964, by Peter Shanahan.

*Uromys rex* is still to be found on Guadalcanal, the most recent known specimen (AM M19746) being collected by one of us (TFF) in a relict outlier of tall rainforest in the Poha Valley north of Honiara in 1987. It was climbing a liane high in the canopy when sighted. In its size, external morphology and habits it is convergent upon *Solomys sapientis* and *S. salebrosus*. It seems plausible that this species has been able to survive because of its arboreal habits while the terrestrial *U.* (*C.*) *imperator* has evidently become extinct.

### *Uromys* (*Cyromys*) *porculus* (Thomas, 1904)

**Type material.** HOLOTYPE, adult male BM 89.4.3.8, collected at Aola, Guadalcanal, by C.M. Woodford.

**Revised diagnosis.** Smaller than any other species of *Uromys* (*Cyromys*), and brown rather than grey above with fur not woolly in texture; also unique by virtue of its possession of grey based belly fur and in having a more finely scaled tail (13-14 scales per cm). The skull is longer and narrower than in *U. rex*, and the molars relatively narrower than in *U. imperator*. It differs additionally from *U. rex*, and resembles *U. imperator*, in its less prominent frontotemporal ridges and its subvertical ascending ramus, and from both *U. rex* and *U. imperator* in its more nearly parallel zygomatic arches and broad-arched nasofrontal suture.

**Discussion.** Although the only known specimen was described in 1904, the date of registration (1889), and the fact that it was collected by Woodford at Aola, suggest that this specimen was probably collected at the same time as the original *U. rex* and *U. imperator* material or shortly thereafter. The very short tail of this species suggests that it may have been terrestrial. Questioning local people by one of us (TFF) reveals that today there is no clear local knowledge of this species, and it is probably extinct. If this is so, then evidently both terrestrial species of Guadalcanal *Uromys* are probably now extinct, while the only arboreal species survives.

The only known skull of *U. porculus* has the molars so worn that few details of the crown remain. The soft palate is unknown. We assign it to *Uromys (Cyromys)*, rather than to *Solomys*, for the following reasons. The anterolateral spur of the bulla is very large, as is typical of the species of *Uromys*, but not *Solomys* or *Melomys*. This enlargement of the anterolateral spur of the bulla appears to be synapomorphic of *Uromys* if any other of the Melanesian mosaic-tailed murid genera (*Melomys*, *Solomys*, *Pogonomelomys*) is taken as an outgroup. A second feature typical of the species of *Uromys* is that the bony palate extends to a level near the posterior end of M³. This is also a derived condition for *Uromys*, being unknown in other mosaic-tailed rats. Furthermore, the palate shows no sign of thickening or the development of a large post palatal spine as is seen in the species of *Solomys*. The skull is elongate and narrow (a common feature in *Uromys*). As *U. porculus* shows no derived features typical of other Melanesian murid genera, we are confident that we are correct in placing it within *Uromys*. The placement within *Uromys (Cyromys)* is somewhat more problematic; but it lacks all of the derived features for *U. (Uromys)*, and possesses the apparently derived states of the orbitotemporal fossa, frontotemporal and coronal sutures, preorbital foramen and ascending ramus orientation which characterise *U. (Cyromys)*. Also, the tail scales are widely spaced, mainly flat but slightly raised distally, rounded or bluntly pointed, and some have one to three longitudinal ridges. Within the subgenus it clearly retains primitive features in its external morphology and the morphology of the zygomatic arches and posterior nasals. Cladistically, it is the sister taxon to *U. rex* and *U. imperator*.

### *Uromys (Uromys)* Peters, 1867

**Type species.** *Mus macropus* Gray, 1866 (= *Hapalotis caudimaculatus* Krefft, 1867).

**Revised diagnosis.** The species of *Uromys (Uromys)* can be distinguished from the species of *Uromys (Cyromys)* by possessing the following features: i) incisive foramina very shortened, narrow, slit-like; ii) molars simple and elongated, M3 greatly reduced in size; iii) bony palate greatly lengthened posteriorly; v) interdental ridges multiplied, with more than seven, and as many as 12 present; vi) anterior cingulum of $M_1$ greatly reduced, obliterated on only moderately worn teeth; vii) cranial characters listed under *U. (Cyromys)* primitive in their states in *U. (Uromys)*.

The following additional features are also useful in identifying species of the subgenus *U. (Uromys)*. The lingual marginal ridges of the molar alveoli are enlarged. There are no frontotemporal ridges, but laterally directed processes of varying size are present behind the sutures. The medial and anterior walls of the orbitotemporal fossa are vertical, as is the preorbital foramen. The posterior ends of the nasals are not broadened, the zygomatic arches swing down to the level of the molar alveoli, the nasals slightly protrude anterior of the premaxillae, the incisors are orthodont, the paroccipital processes are short (not descending lower than the inferior margin of the external auditory meatus), the ascending rami of the dentary do not flare laterally, the toothrows are comparatively well spaced.

### *Uromys caudimaculatus* (Krefft, 1867)

**Type material.** SYNTYPE, AM S1848, skull only (the body apparently being lost). Cape York.

**Revised diagnosis.** *Uromys caudimaculatus* differs from *U. anak* and *U. neobritannicus* in possessing a posterior palatal spine, an only rudimentary postorbital process; narrow, tapering posterior nasals which terminate anterior to the posterior ends of the lachrymals; in having the hindfoot not usually longer than 22% of the head-body length and ear length more than 43% of condylobasal length; the incisive foramina are more than 20% of the palatal length, while the toothrow is less than 20% of condylobasal length. The colour is a medium brown-grey, the feet are white, the tail scales arranged in clear rings and longer than broad, with a white tail tip. It differs from *U. hadrourus* in its larger size, less inflated braincase, and larger postorbital process and anterolateral bullar spurs, shorter ears and longer white tail tip, greater frontal convexity, narrower feet and less posteriorly extensive nasals. It differs from *U. emmae* n.sp. in its more elongate rostrum, narrower and longer hindfoot, relatively smaller teeth, longer ears, more inflated frontals, and in having the distalmost portion of the tail white.

**Notes.** We have considered whether there might not be two or even three distinct species among what was hitherto called *U. caudimaculatus*. As far as the mainland (Australian and New Guinean) forms are concerned, this might be possible. The work of Donnellan (1989), based upon chromosomes, suggests that these populations may represent distinct species, since a possible rearrangement (tandem fusions) in the Australian population should provide barriers to gene

flow. C-banding in the New Guinean population, however, is necessary before tandem fusion can be identified with certainty. A morphological study also shows that a distinct form inhabits Australia and southern New Guinea as far east as Kaimare in the Gulf of Papua, a second homogeneous taxon is found throughout the rest of the eastern half of New Guinea, and a third form is found in the western part of the island. Unfortunately, the characters that support this division are not entirely consistent, and when the insular populations are taken into consideration they form such a complex mosaic pattern that it is impossible to allocate the insular forms satisfactorily to one or other of the mainland species. Thus, while recognising the striking differences between the three mainland forms, and the lack of intermediates in some regions on the mainland, we have declined to recognise them as full species, but instead regard them as subspecies. Study of further material will be necessary to confirm or refute this hypothesis.

The Discriminant Function analysis (Fig. 4) tends to separate the three major mainland groups, but not cleanly. Clustering with the Australian/south New Guinea sample are specimens from Yapsiei and Yapen Island, and an Aru Islands specimen is in the slight overlap zone between the Australian/south New Guinean and the main Papua New Guinean samples. The Irian Jayan samples are close to one another, but a specimen from Kaimare (which in most respects apart from its metrical characters resembles the Australian form) falls within the Irian Jayan cluster. The only taxon recognised here as a full species that does fall cleanly outside any major cluster is the holotype of *U. emmae* n.sp.

Within Papua New Guinea there is a series of overlapping clusters: Mount Hagen area/south-east Papua/Mount Sisa/Dobodura. Specimens from Telefomin and Mount Karimui fall on the edge of the Mount Hagen cluster; one from the Torricelli Mountains falls, curiously, with the Mount Sisa specimens. One Mount Elimbari specimen falls outside any of these. Within Irian Jaya there is again a gradient: Alkmaar district/ Setakwa/Mimika River/Utakwa, with a specimen from the Weyland Range falling, oddly, in the Papua New Guinea cluster.

## *Uromys caudimaculatus caudimaculatus*
(Krefft, 1867)

**Synonyms.** *Mus macropus* (Gray, 1866) (not of Waterhouse); *Uromys aruensis* Gray, 1873; *Uromys validus* Peters & Doria, 1881; *Uromys exilis* Troughton & Le Soeuf, 1929; *Uromys sherrini* Thomas, 1923.

**Revised diagnosis.** Distinguished from other subspecies as follows: i) hindfoot short, 18-22% of head and body length; ii) size large (condylobasal length of adults 63-72 mm); iii) fur colour "rabbity" grey brown or tawny, with underparts yellow or white; iv) feet white with a distinct brown line or block above; v) tail long, with only slight mottling in transition zone; vi) scales arranged in clear rings; frontal region of skull convex; vii) bullae somewhat flattened.

**Discussion.** There is more regional variation within *U. c. caudimaculatus* than in any other subspecies.
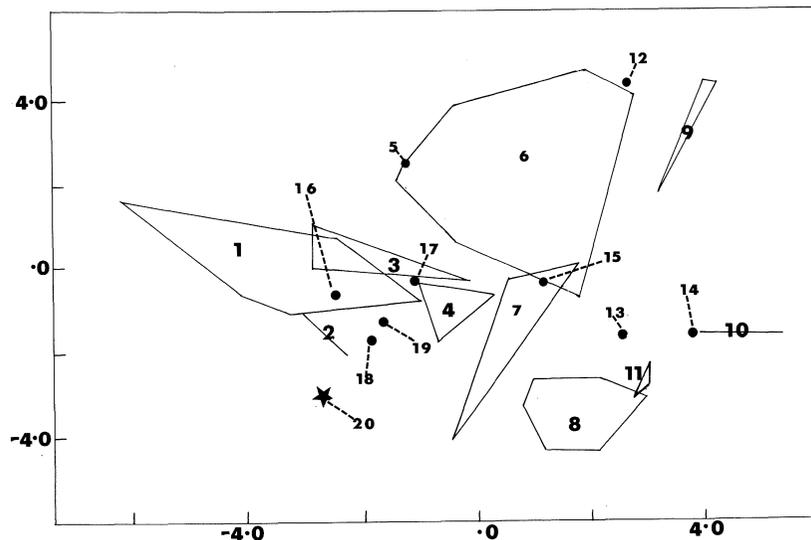


**Fig. 4.** Discriminant analysis of *U. caudimaculatus* and *U. emmae*. The numbers refer to groupings as follows: 1 = Hagen region, 2 = Mount Karimui, 3 = south-east Papua, 4 = Mount Sisa, 6 = Australian mainland, 7 = Dobodura, 8 = Alkmaar region, 9 = Hinchinbrook Island, 10 = Utakwa River, 11 = Setakwa River. Individual specimens from Yapen (5), Yapsiei (12), Mimika (13), Kaimari (14), Aru Island (15), Telefomin (16), Torricellis (17), Mount Erimbari (18) and Weyland Range (19), fitted in after the calculation of the Functions, are plotted separately, as is the type of *U. emmae* (20). That *U. emmae*, despite being fitted into a pre-calculated analysis, fell outside the dispersion of any *U. caudimaculatus* sample, is highly significant.

Indeed, some of the more distinct regional forms have previously been recognised as subspecies. Individuals from the Aru Islands are smaller than those from elsewhere, and differ morphologically in possessing a distinct dorsal stripe. Those from the trans-Fly plains are again a little smaller than individuals from Australia, possess an indistinct dorsal stripe, have slightly less of the tail white, and have less warm tones in the fur. The Australian sample is, in contrast, remarkably morphologically homogeneous throughout its range. Baverstock *et al.* (1982), however, recognised two chromosome races within it: the southern race is characterised by the possession of two to 12 B chromosomes while the northern race lacks B chromosomes but possesses large blocks of distal C-positive heterochromatin on between 18 and 28 of the 46 chromosomes. Although these two chromosome races seem to be isolated from one another, and no chromosome intermediates are known, we could detect no differences based upon morphology or morphometrics to support the division of the Australian sample into two taxa.

**Distribution.** This subspecies is distributed from north-east Queensland throughout the trans-Fly plains to the Gulf of Papua and the Aru Islands.

### *Uromys caudimaculatus papuanus* (Ramsay, 1883)

(not preoccupied by *papuanus* von Meyer, 1876, a nomen nudum)

**Synonyms.** *Uromys prolixus* Thomas, 1913; *U. ductor* Thomas, 1913; *U. lamington* Troughton, 1937.

**Type material.** HOLOTYPE. A search of the collections of the Australian and Macleay Museums, Sydney has failed to reveal the existence of this specimen, and we suspect that it has been lost. The type locality is given as Port Moresby or the lower slopes of the Astrolabe Range.

**Revised diagnosis.** Distinguished from other subspecies as follows; i) hindfoot long (21-24% of head and body length); ii) tail averaging longer (110-135% of head and body length); iii) size small (condylobasal length 56-64 mm; head and body length 250-288 mm, see Table 1); iv) feet buffy or brown; v) tail (which is partly white for over half of its length) strongly mottled with brown coalescing spots on its terminal portion, and scales not arranged in such clear rings; vi) underside creamy, smudged in grey; vii) frontals flat; viii) bulla more rounded.

**Discussion.** The Discriminant Analysis (Fig. 4) reveals considerable diversity within this subspecies, but it is difficult to see how it could be split up with two exceptions: i) Yapsiei (two specimens): in the Discriminant Analysis, these specimens resemble

nominotypical *U. c. caudimaculatus*. Univariate analysis reveals that the hindfoot is relatively long (24-25% of head and body length) and the ear markedly so in one of the specimens (44 and 58% of condylobasal length in the two specimens); ii) Mount Karimui (two specimens): these are distinguished from all other samples in the Discriminant Analysis. Univariate analysis reveals a small body size (mean condylobasal length 54.6 mm, head and body 232.5 mm).

We feel that either of these populations may eventually be shown to be distinct, but given the small sample size it would be rash to recognise them as such at present.

**Distribution.** This subspecies is distributed throughout the mainland of Papua New Guinea, except for the trans-Fly plains and the Gulf of Papua, where it is replaced by the nominate race.

### *Uromys caudimaculatus multiplicatus* (Jentink, 1907)

**Synonyms.** *Uromys nero* Thomas, 1913; *U. scaphax* Thomas, 1913; *?U. waigeoensis* Frechkop, 1932.

**Type material.** HOLOTYPE, Leiden Museum (no number), collected at Sentani Lake (2°37'S 141°30'E), Irian Jaya, by the Humboldt Bay Expedition on April 18, 1903.

**Revised diagnosis.** Can be distinguished from other subspecies as follows: i) tail much shorter than head and body; ii) hindfoot short (18-22% of head and body); iii) size small as in *U. c. papuanus* (condylobasal length 57-64 mm; iv) head and body 273-310 mm, see Table 2); v) feet diffusely white above; vi) tail yellow under base with very little (maximum one third) of its length white above, very little or no mottling, tail scales in clear rings; vii) fur tends to be soft, thick, with grizzling due to yellow or red brown tips to hairs; viii) frontals flat; ix) bullae rounded.

**Discussion.** There are differences between the type series of *U. nero* and the juvenile holotype of *U. multiplicatus* and others of this subspecies (those from the Setakwa and Mimika Rivers, Alkmaar and Bivak Island), the former being darker and of larger size. This may represent simple clinal changes with increasing altitude. The holotype of *U. waigeoensis* is described as being very large (head and body length 370 mm), but no other differences from the present subspecies seem apparent.

**Distribution.** This subspecies is distributed throughout mainland Irian Jaya, possibly including Waigeo Island.

**Related taxa of uncertain status.** *Uromys siebersi* Thomas, 1923, is from the Kei Islands. This poorly

known taxon (known from two skins and a single skull) exhibits a mosaic of features that make it difficult to determine whether it should be placed with *U. c. caudimaculatus* or *U. c. papuanus*, or recognised as a distinct subspecies. On the basis of metrical characters it falls near the south-west New Guinean samples. On the basis of its pelage colouration, tail and skull morphology, however, it is very close to Aru Islands *U. c. caudimaculatus*, differing in that it is slightly smaller, the tail is slightly more mottled at the transition, and the frontals are less convex. In these features it resembles *U. c. papuanus*. Thus it is intermediate between these two subspecies.

The single specimen known from Yapen Island (to the north of New Guinea) also somewhat resembles *U. c. caudimaculatus* from the Aru Islands on morphology, and falls within that subspecies on the basis of metrical characters. Because it is represented by only a single specimen, the allocation of the Yapen form must remain uncertain at present.

### *Uromys hadrourus* (Winter, 1984)

**Synonyms.** *Melomys hadrourus* Winter, 1984.

**Type material.** HOLOTYPE, QM J504, adult female, skin and torso in spirit, skull extracted, collected near the summit of Thornton Peak (1,220 m, 16°09'30"S 145°21'45"E) on 16 Nov. 1973 by J. Winter.

**Revised diagnosis.** *Uromys hadrourus* differs from other species of *Uromys* as follows: i) smallest member of the genus; ii) white tail tip that lacks mottled interdigitation with dark proximal area of tail is unique; iii) the postorbital processes reduced; iv) braincase more inflated; v) anterolateral bullar spurs proportionally smaller.

It resembles *U. caudimaculatus* in its palate spine, palate form, rounded braincase, suppressed dentary tubercle, long incisive foramina (25% of palate length), small teeth, tail scales arranged in rings and longer than broad, and its general fawn colour and white feet with a marked brown dorsal line. It differs in its thinner preorbital bar, anteriorly angled lambdoidal suture, flattened interorbital region, less downwardly bowed zygomatic arches, reduced coronoid processes, lesser extent of white on the tail, broad feet, and restriction of white ventrally to the throat and chest.

**Discussion.** *Uromys hadrourus* is thus far known from only five museum specimens, all collected at above 300 m on the Thornton Peak massif, north-eastern Queensland. This massif is isolated from other areas of upland rainforest by the Daintree and Bloomfield Rivers and sclerophyll forest.

Winter (1984) described *U. hadrourus* as a large species of *Melomys*. Although he discussed the possibility that it may represent a small species of *Uromys*, he discounted this on the basis of its small size, noting nonetheless that the well-developed tail and thickened upper incisors of *U. hadrourus* were striking similarities shared with the species of *Uromys*. Our cladistic analysis shows that *U. hadrourus* shares many derived features with the species of *Uromys*, but none with other mosaic-tailed rats. Such features include the posterior lengthening of the bony palate and the large anterolateral spur of the bulla which are synapomorphic for this genus. Phenetically, *U. hadrourus* is very close to other species of *U. (Uromys)* in skull shape, details of dental morphology and the thickness of the tail.

*Uromys hadrourus* is clearly a member of the *U. caudimaculatus* group of the subgenus *Uromys*, and even shares a few possibly derived features with *U. c. caudimaculatus* which are not seen in *U. c. papuanus* and *U. c. multiplicatus*: notably the white feet with a vaguely expressed brown longitudinal line on the upper surface. Other similarities are, however, plesiomorphic, and on balance it seems likely that it is the sister species to the entire species *U. caudimaculatus*.

### *Uromys anak* Thomas, 1907

**Type material.** HOLOTYPE, BM 7.5.22.2, adult male skin and skull, from Efogi (9°00'S 147°45'E), Owen Stanley Range at not less than 4,000 ft (1200 m). Collected 2 Oct. 1906 by C.A.W. Monckton.

**Revised diagnosis.** *Uromys anak* differs from all species of *U. (Uromys)* except *U. neobritannicus* and *U. boeadii* n.sp. in lacking a white tail tip. It differs from *U. neobritannicus* in its less well-developed postorbital processes, and in having the interorbital region more concave, and in its brown and white mixed underparts. It differs from members of the *U. caudimaculatus* group in that its tail scales are broader than long, its palatal foramina are short (only 14-19% of palate length), the molars are large (more than 20.5% of condylobasal length); in its less bowed zygomatic arches, larger postorbital processes continued downward as swollen ridges, posteriorly extended nasals, flatter braincase, more flattened auditory bullae, less anteriorly protruding nasals and deeper rostrum.

**Notes.** The Discriminant Analysis (Fig. 5) shows an almost clean division between samples from Mount Simpson and the Mount Hagen region, and these are here recognised as distinct subspecies. Two specimens from Telefomin and one from Mount Elimbari also stand well apart from the rest. Unfortunately no specimen from the Huon Peninsula is complete enough to enter into the analysis. As a high-altitude species, it is possible that a number of distinctive and semi-isolated subspecies will eventually be discernible.

*Uromys anak anak* Thomas, 1907

**Revised diagnosis.** Distinguished from other subspecies as follows: i) colour less dark than *U. a. rothschildi*; ii) body smaller; iii) tail longer; iv) hindfoot shorter.

**Notes.** The nominotypical subspecies is widely distributed along the New Guinean Central Cordillera above about 1000 m, from Mount Dayman in the Owen Stanleys in the east to the upper Bubu River region in the west.

*Uromys anak albiventer* **n.subsp.**

Figs 6,7, Table 1

**Type material.** HOLOTYPE, CSIRO Division of Wildlife and Ecology, Canberra no. CM.8532, adult male, skin and skull, from Uinba, Kubor Range, Papua New Guinea. Collected on 22 June 1963.

**Diagnosis.** Distinguished from other subspecies as follows: i) coat more brown-toned; ii) venter much more broadly white, from throat to groin; iii) teeth smaller.

**Discussion.** From Upper Bubu River region, as far west apparently as the Weyland Range. Of two specimens from Saiko, Bubu River, in the BM, one is
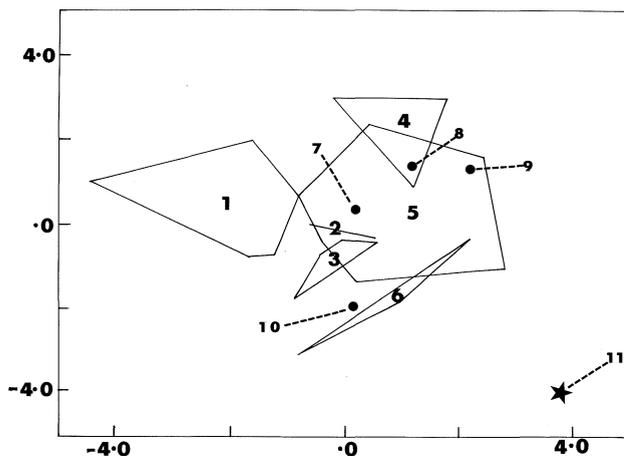


**Fig. 5.** Discriminant analysis of *Uromys anak* and *U. boeadii*. The numbers refer to groupings as follows: 1 = south-eastern peninsula, mainland Papua New Guinea (*U. a. anak*), 2 = Mount Erimbari, 3 = Habbema region, 4 = Bubu River (intermediate sample), 5 = Hagen region (*U. a. albiventer*), 6 = Telefomin. Individual specimens from Teri, Rawlinson Range (*U. a rothschildi*), Okapa (7), Rawlinson Range (8), Tari (9) and Weyland Range (10) are plotted separately, as is the type of *U. boeadii* (11, which, until this analysis, we had considered a probable subspecies of *U. anak*). Note that *U. boeadii*, despite being fitted into a pre-calculated analysis, falls even farther beyond the dispersion of *U. anak* than does the type of *U. emmae* from *U. caudimaculatus*.

entirely typical of this subspecies, while the other has the ventral white restricted as in nominotypical *anak*. In the Discriminant Analysis, both specimens fall with the present subspecies.

To this subspecies belong a series of seven specimens (6 skins with skulls, 1 skull only) in the British Museum (Natural History), from the Kratke Mountains (Buntibasa, Kuraka, Apimuri) and east of the Hagen Range (Degabaga, Menebe). Certain other specimens may yet turn out to represent distinctive subspecies. These are from Lamende Range, near Mount Giluwe, and from Telefomin and Mount Elimbari. The Mount Giluwe specimen (BM 53.370) has the largest skull seen by us; the molars are however very small (molar row length 12.2 mm), and the tail is short (106% of head and body). The dorsal colouration is dark, and the venter has no white, being all grey; in these features it resembles *U. a. rothschildi*. The two Telefomin specimens are very small in size, but have large teeth. Five specimens from Mount Elimbari are also rather small in size, but have small teeth, and relatively long tails and ears. Only further material will allow us confidently to determine the nature of these variant populations.

*Uromys anak rothschildi* Thomas, 1912

**Type material.** HOLOTYPE, BM 12.1.31.2, adult female skin and skull, collected by C. Keyser in the Rawlinson Mountains (6°43'S 147°06'E), Huon Peninsula, Papua New Guinea.

**Revised diagnosis.** Differs from other subspecies in the following combination of features: i) very dark, brown-black dorsum, with a paler (but not white) venter; ii) very large size with large teeth; iii) relatively short tail (100-113% of head and body length); iv) short hindfoot (19-21% of head and body length).

**Discussion.** This poorly known subspecies inhabits the isolated Huon Peninsula of northern New Guinea.

*Uromys neobritannicus* Tate & Archbold, 1935

**Type material.** HOLOTYPE, AMNH 99881, skull only of an adult male collected on New Britain, Bismarck Archipelago by J.W. Eyerdam.

**Revised diagnosis.** *Uromys* (*U.*) *neobritannicus* differs from all other species of *Uromys* as follows: i) hypertrophy of the postorbital processes; ii) uniformly black tail (otherwise in subgenus only in *U. anak* and *U. boeadii* n.sp., from which it also differs by much larger postorbital processes, square posterior ends of nasals which do not extend as far posteriorly, reddish body colour with deep yellow venter, and more numerous tail scales [16 per cm]); iii) unlike *U. anak*, but like

*U. boeadii* n.sp., there are no swollen vertical ridges below postorbital processes, despite the large size of the processes; iv) one of the largest species, equal in size to *U. anak*.

**Discussion.** *Uromys neobritannicus* is thus far known only from six individuals, all collected on New Britain. The holotype is a skull only, localised only as far as New Britain. The second specimen (AMNH 119467) is a male skin and skull that was collected at Talasea (on the Mundo Willaumez Peninsula) by Fr Schumm (Tate, 1951). The third known specimen is held in the Museum of Victoria. It is a subadult female (no. 6890) collected on the Mundo Willaumez Peninsula on the north coast of New Britain by Clive Champion. Three additional specimens (one in spirits (AM M20690), two skins and skulls (AM M20689, AM M21118)), from the Fulleborn area East New Britain, are in the Australian Museum.

Recent work on New Ireland by one of us (TFF) failed
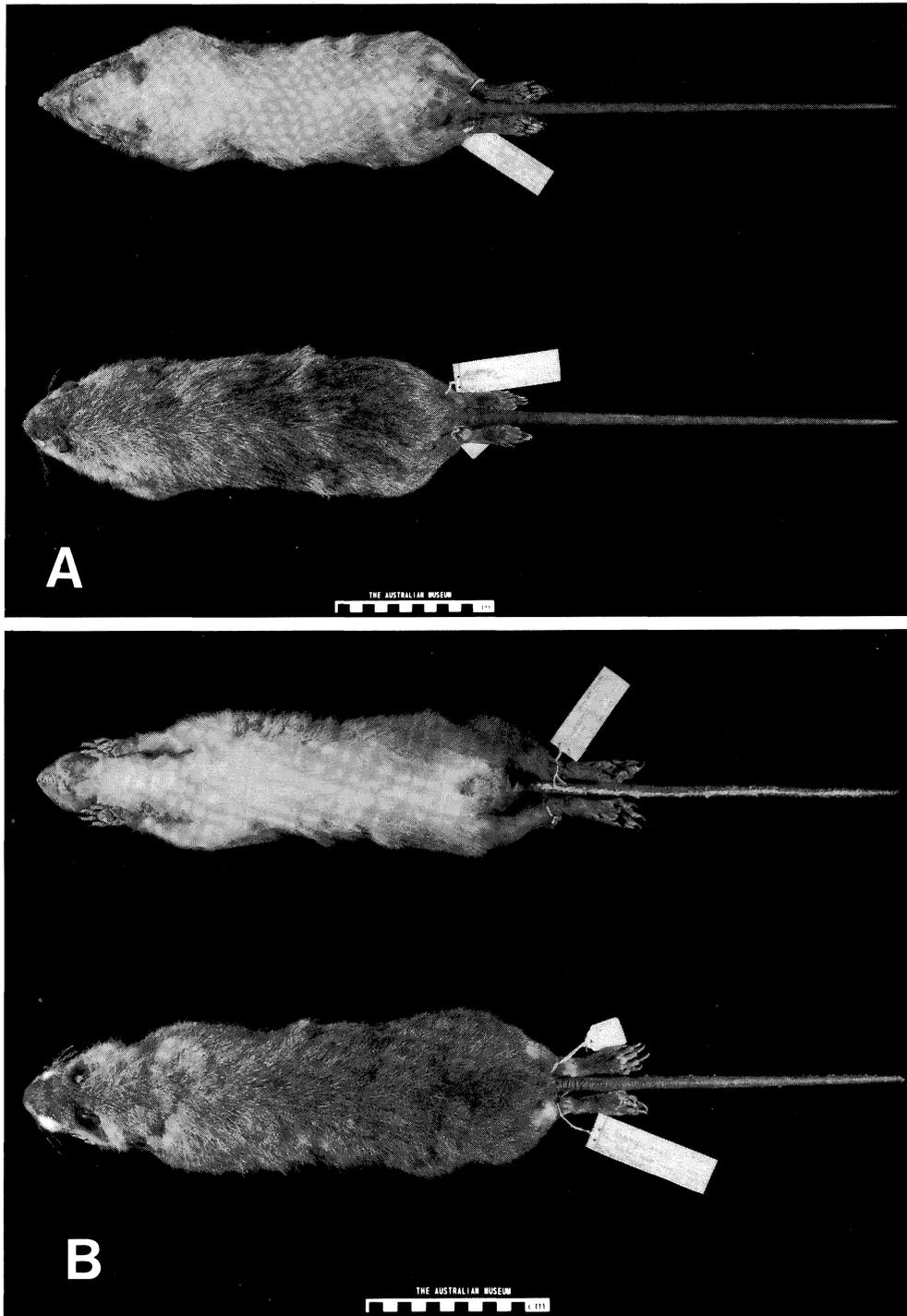


**Fig. 6.** Comparison of skins of A, *Uromys anak anak* (CSIRO 12337) and B, *U. a. albiventer* (CSIRO 8532).

to find it there despite extensive fieldwork and analysis of extensive archaeological material (Flannery & White, 1991), and it seems unlikely that the species inhabits any of the smaller islands off New Britain.

**Relationships.** *Uromys neobrittanicus* is clearly the sister species to *U. anak*, from which it differs in a few skull characters and in colour; of these it is likely that the condition seen in the present species is the plesiomorphic one, with the exception of the striking postorbital processes (a gross enlargement of the small tubercles of *U. anak*), and the more numerous tail scales.

## *Uromys boeadii* n.sp.

### Figs 8, 9, Table 2

**Type material.** HOLOTYPE, AMNH 222242, young adult male skin and skull, collected by Philip Temple on 22 March 1963, 25 km north-east of Biak, Pulau Biak, Geelvinck Bay, Irian Jaya, Indonesia.

**Etymology.** For Bp. Boeadi, Indonesia's most eminent mammalian taxonomist, and one of that country's leading biologists.

**Diagnosis.** This new species is phenetically closest to the *U. anak*/*U. neobrittanicus* group, agreeing with the members of this group in its uniformly black tail, the deep rostrum, the tendency towards development of distinct postorbital processes, and the posteriorly extended nasal bones. It differs from them in the following ways: i) size much smaller; ii) postorbital processes poorly developed; iii) posterior ends of nasal bones only just reaching level of anterior orbital margins; iv) tail scales longer than broad, and arranged in clear rings. It differs additionally from *U. anak* as follows: i) lack of prominent inflation of frontotemporal sutures; ii) flat interorbital area. It differs from *U. neobrittanicus* as follows: i) less tail scales (7-9 per cm of length); ii) deep black-brown colour with sharply marked median pectoral streak.

**Description.** The holotype (and only known) skin and skull are in good condition. The overall colour is deep blackish brown, tending to be darker on the foreparts and with a lighter sheen on the hindparts. The pelage consists largely of long, dark guard hairs, somewhat paler towards the base, with a few light-coloured guard hairs and crimped grey-white underhairs mixed in. The venter is sparsely furred, with the lighter skin tone showing through; the ventral hairs are mostly brown, but there is a sharply marked creamy-white streak, 92 mm long, in the midline of the chest, along the approximate extent of the sternum, beginning as a thin streak at about the level of the axillae, broadening suddenly 22 mm further back, and narrowing gradually behind (Fig. 8). Hands and feet are lighter brown owing to the sparseness
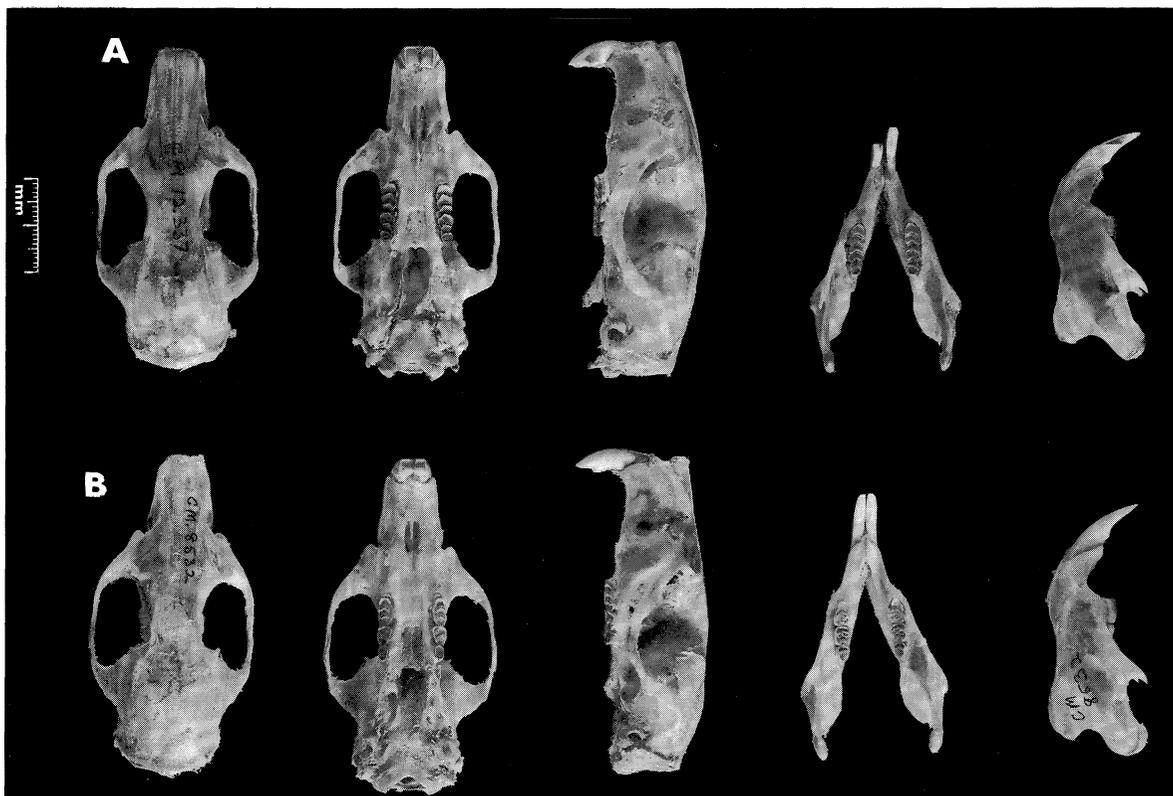


**Fig. 7.** Comparison of skulls of A, *U. a. anak* (CSIRO 12337) and B, *U. a. albiventer* (CSIRO 8532).
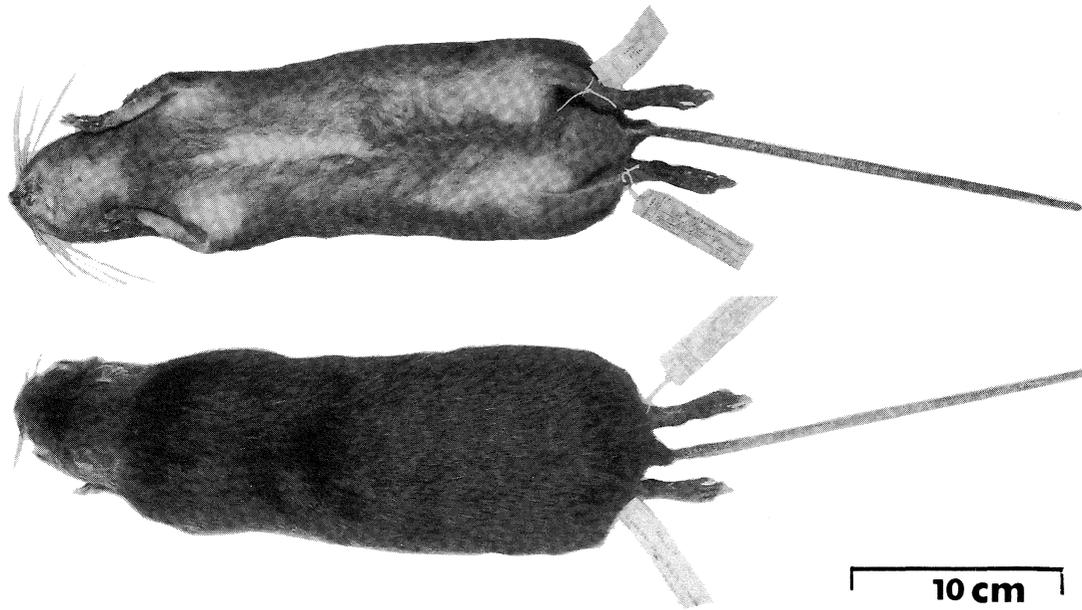
**Fig. 8.** Study skin of holotype of *U. boeadii* (AMNH 222242).
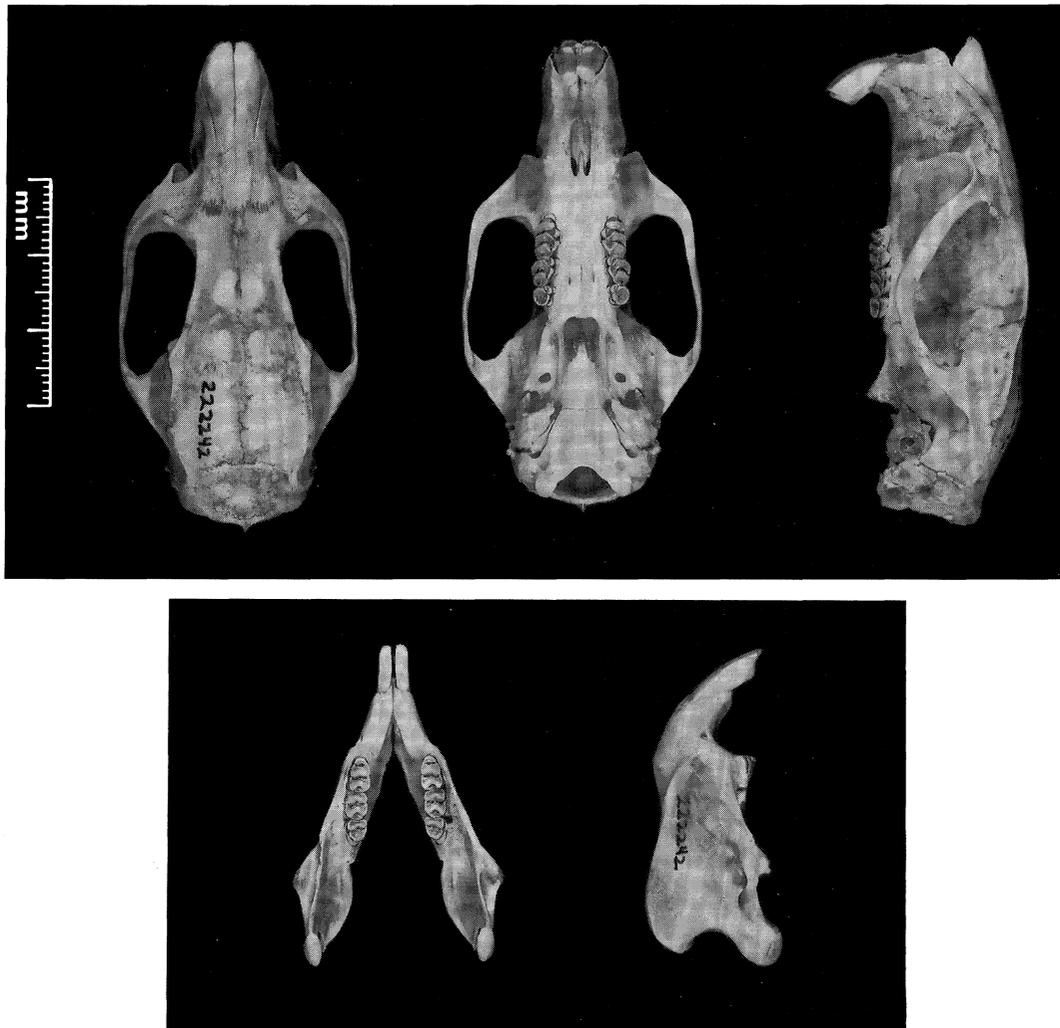


**Fig. 9.** Skull and dentary of holotype of *Uromys boeadii* (AMNH 222242).

of the hair covering; vibrissae are long and black. The tail scales are somewhat longer than broad, flattened, and arranged in rings.

The skull is deep, especially the rostrum, as in *U. anak* and *U. neobrittanicus*, but unlike these the nasals are relatively short, and the postorbital processes are only slightly developed. The parietal crests are well developed, extending forward to form clear supraorbital ridges. The premaxilla extends back on either side nearly to the zygomatic plate. The zygomatic arches sweep downward to just above the level of the posterior molar alveoli, then curve up again to their posterior roots above the external auditory meati. The incisive foramina are slit-like. The palate ends squarely somewhat posterior to the third molars; the mesopterygoid fossa is broad, parallel-sided. The bullae are small (Fig. 9).

**Discussion.** Consideration must always be given to the problem of what level of taxonomic recognition should be awarded to entirely allopatric taxa. In the present case, the evidence is overwhelming that, cladistically, *U. boeadii* is the plesiomorphic sister-taxon to the *U. anak/neobrittanicus* clade, or to all *Uromys* (*Uromys*); consequently, if these are to be maintained as separate species, *U. boeadii* must be given species rank as well.

While most of its features are evidently plesiomorphic, the restriction of the white zone to a pectoral streak and the complete absence of any white in the inguinal region would appear to be autapomorphic states of this new species, perhaps its only ones.

## *Uromys emmae* n.sp.

Figs 10-12, Table 2

**Type material.** HOLOTYPE, AM M7200, adult female skin and skull. Collected by Col. C.B. Phillips of the USA Typhus Commission on Owi Island (1°16'E 136°13'S), Schouten Group, Geelvinck Bay, Irian Jaya, Indonesia. The specimen was registered on 1 July 1946, and was probably collected during 1944-1945.

**Etymology.** For the junior author's daughter, Emma.

**Diagnosis.** *Uromys emmae* can be distinguished from all other species of *Uromys* except *U. caudimaculatus* in having a mottled section of the tail, where the light tip contacts the darker proximal part. It differs from *U. caudimaculatus* in the following ways: i) hindfoot shorter, broader; ii) body fur shorter, coarser; iii) white mottling on tail restricted to distal third, where it is limited in extent, and terminal 1 cm brown (in other species white tail section much more extensive); iv) rostrum relatively and absolutely shorter; v) preorbital foramen hidden behind zygomatic plates (most of it visible in other species); vi) frontals not inflated, supraorbital ridging better developed, incisive foramina shorter (only 18.4% of palate length); vii) molars relatively larger (21% of condylobasal length); viii) posterior ends of nasals extend further posteriorly; preorbital bar thinner; ix) zygomatic arches less swung downwards.

**Description.** The holotype skin is in good condition



**Fig. 10.** Study skins in dorsal view of A, holotype of *U. emmae* and B, *U. caudimaculatus papuanus* Mount Karimui area, AM M13812.

except that the right pinna is missing, the interorbital region has been damaged by a rat trap, and part of the venter is soiled (Figs 10, 11). The guard hairs of the dorsum are tipped with Clove Brown, while the fur is tipped with Straw. The bases of all of the dorsal fur is Dull Grey. The overall effect of the dorsal colouration is somewhat less rufescent than most *U. caudimaculatus*. A ring of slightly darker hairs surrounds the eyes. The hindquarters are Prout's Brown, with the tipping of the hairs being less conspicuous than anteriorly, and the guard hairs reduced in number. The venter is sparsely furred, the hairs being dirty white from the anus to the chin. The vibrissae are black. The dorsal surface of the feet are clothed in fine, pure white hairs except on the metatarsum proximal to digits 2-3, where some light brown hairs are present. The feet are unusually broad and short with smooth plantar pads (Fig. 13). They are only 50.5 mm long (su) but 13.5 mm wide at the base of the fifth metatarsal. Tate (1951) gives measurements of the hindfoot for the holotypes of *U. nero*, *U. aruensis*, *U. scaphax*, *U. prolixus*, *U. ductor*, *U. seibersi* and *U. sherrini*. The length-width ratio for this sample is as follows: X = 0.18, range = 0.15-0.19, s.d. = 0.014 (n=8). Measurements of *U. caudimaculatus* held in the Australian Museum conform closely to Tate's sample. This compares with a ratio of 0.27 for *U. emmae*. It is highly unlikely that preparation method could have affected these measurements, both because the measurements of *U. emmae* taken in the field and from the study skins are similar, and because the proportions of the foot are altered little by preparation relative to other body parts. The mammary formula is 0 + 2 = 4 and, to judge from the size of the nipples, the animal

was lactating when caught. Over the proximal 120 mm of the tail the tail scales are raised to a conical point, the tail resembling a file. The scales become progressively more flattened distally, forming irregular tesserae near the tip. Limited white mottling is present over the distal one third of the tail, but white encircles the tail only in two narrow places. The terminal 1 cm is dark. There is a single hair per tail scale, visible only under magnification, which is one half to one third of a scale in length.

The skull is cracked through just anterior to the parietal-frontal suture; damage typically inflicted by the bar of a rat trap. The teeth are moderately worn and several have been glued into their sockets. The rostrum is short and narrow relative to that of other species of *Uromys*. The premaxillary/maxillary suture is positioned just anterior to the zygomatic plate, the entire masseteric foramen being hidden behind the zygomatic plate when the skull is viewed from the side (Fig. 12). The incisive foramina are remarkably short, narrow and parallel sided. The frontals in the interorbital region are slightly dished, and weak supraorbital ridging developed. The parietal crests are weakly developed and are subparallel. The palate and upper molars are essentially similar in morphology to those of *Uromys caudimaculatus*. The mesopterygoid fossa is narrow relative to *U. caudimaculatus*. The pterygoids are damaged. The bullae are small and resemble those of *U. caudimaculatus*. Except in their smaller size, the dentary and lower dentition do not differ from those of *U. caudimaculatus*.

**Discussion.** As in the case of *U. boeadii*, careful consideration has been given as to whether the taxon
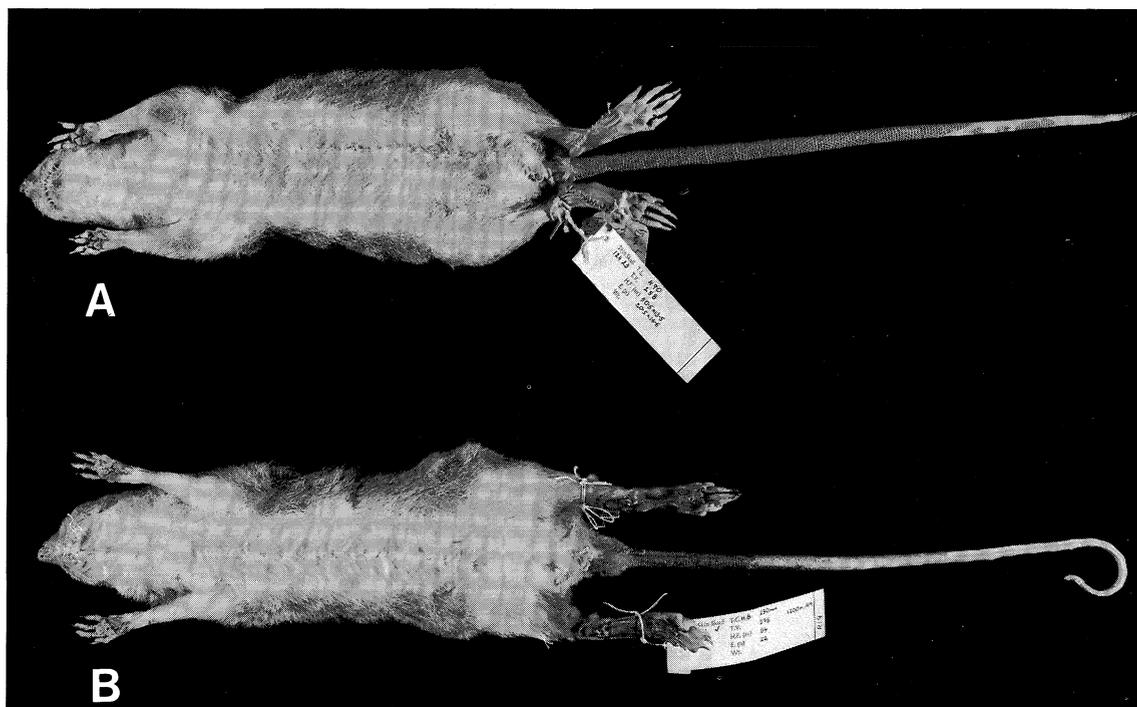


**Fig. 11.** Study skins in ventral views of A, holotype of *U. emmae* and B, *U. caudimaculatus papuanus* Mount Karimui area, AM M13812.

*U. emmae* should be recognised as a new species, or as a subspecies of *U. caudimaculatus*, always a difficult question to resolve when dealing with insular taxa for which the criterion of reproductive isolation is immaterial and sample size is small. We decided that *U. emmae* should be described as a full species for the following reasons. 1) It differs from *Uromys caudimaculatus* in a number of features that are not observed to vary among the previously recognised subspecies of the latter taxa. These features include the short, very broad hindfoot; short rostrum; recession of the masseteric foramen behind the zygomatic plate, and short, sparse coat. 2) Some of the distinguishing features of *U. emmae* argue for a quite different ecological niche from that of *U. caudimaculatus*; in particular the short, broad hindfoot and the shortened rostrum denote considerable specialisation. Short, broad feet and a foreshortened snout are commonly seen in Melanesian murid taxa that are highly arboreal (eg, the species of *Pogonomys*, *Chiruromys* and *Melomys rufescens*), while

elongated hindfeet and a long skull are typical of terrestrial taxa (eg, *Xenuromys barbatus*, *Melomys lorentzi*). The combination of a short, broad hindfoot and short snout may well indicate that *U. emmae* is more arboreal than *U. caudimaculatus*. (3) It shares plesiomorphic features with *U. hadrourus*: nasofrontal suture well posterior to the level of the preorbital foramen; thin preorbital bar; uninflated interorbital profile; weaker zygomatic arches; and broader feet, recalling *U. (Cyromys)*. It retains other apparently plesiomorphic states not seen in either *U. hadrourus* or *U. caudimaculatus*, including relatively small ears (39% of condylobasal length), short incisive foramina, and relatively large teeth. In all of these features it resembles *U. anak* and *U. neobrittanicus*.

In addition to *U. boeadii* and *U. emmae*, the terrestrial mammalian fauna of the Geelvinck Bay islands, including Owi Island (Palau Awai) and Biak Island (P. Biak) includes a number of endemic taxa. A highly distinctive and diminutive race of spiny bandicoot (*Echymipera kalubu philipi*) has previously
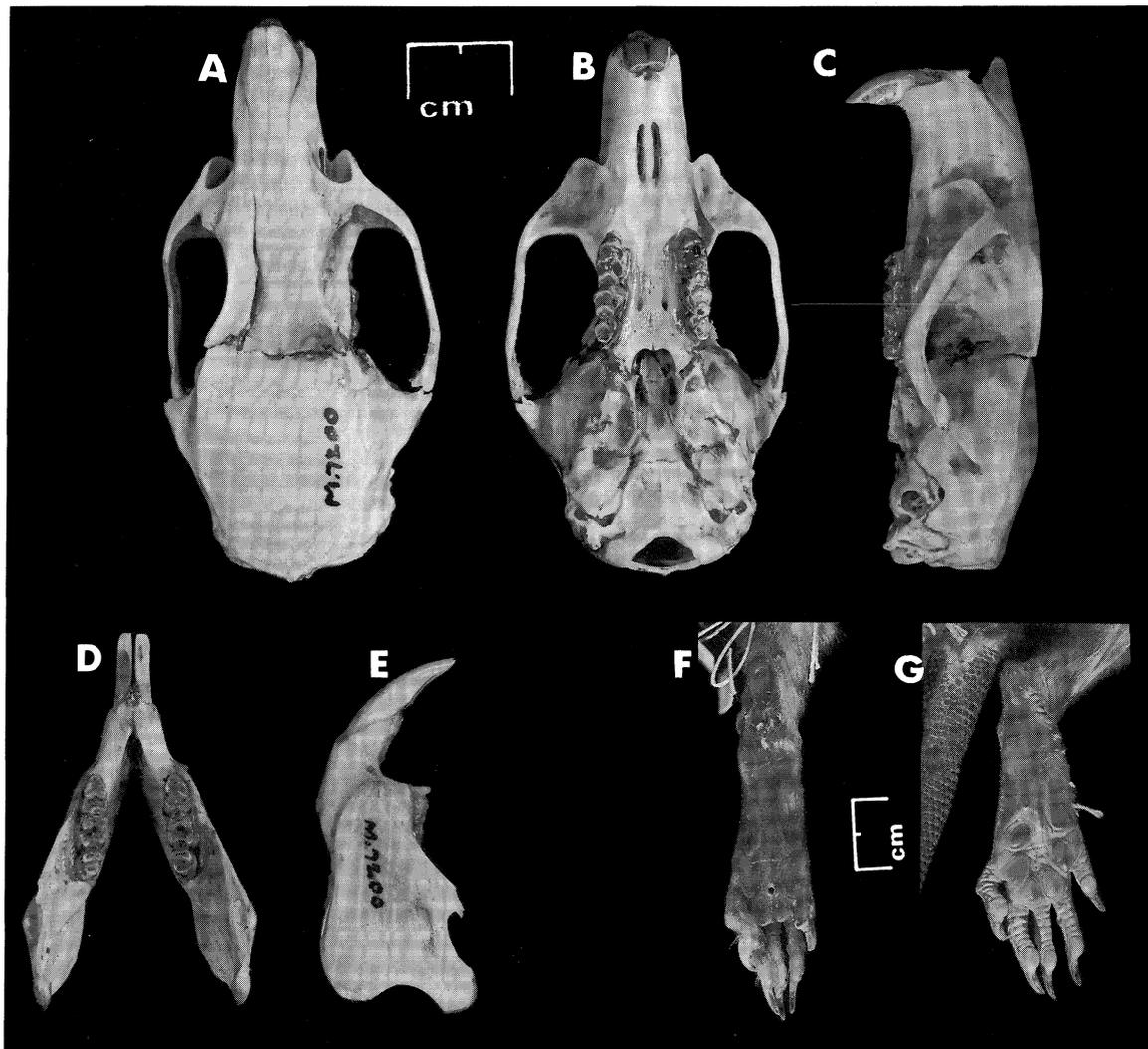


**Fig. 12.** Holotype cranium of *U. emmae* in: A – occlusal, B – dorsal and C – lateral views, and dentary in D – occlusal, and E – lateral views. F – pes of *U. caudimaculatus* AM M13812, Mount Karimui, and G – holotype of *U. emmae*.

been named (Troughton, 1945). Troughton (1945) also described *Petaurus kohlsi* from Owi, but this is a junior synonym of *Petaurus breviceps biacensis* Ulmer, 1940, a taxon so distinctive that it may represent a distinct species unique to Owi and Biak Islands. Two *Rattus* species, *R. jobiensis* and *R. exulans*, are also found on Owi. The former is known only from Owi, Biak and nearby Japen Islands, while the latter species is a widespread Human commensal. Thus the degree of endemism among the mammals of the Owi-Biak Island group (which were connected during the late Pleistocene), is very high. The occurrence of *R. jobiensis* on Yapen as well as Owi-Biak is intriguing, especially as it is *Uromys caudimaculatus* (as documented by BM 46.642, which is a large individual of cbl = 63.0, bzw = 32) is present on Japan, the two endemic Geelvinck *Uromys* species not being known from there. It is possible that the occurrence of *R. jobiensis* on Yapen could be due to accidental human transportation, as it is the only mammal taxon with such a distribution, and other species of *Rattus* have been widely distributed by this means in other parts of the Pacific.

## Discussion

**Interrelationships.** Table 3 lists the characters used by us in constructing a cladogram for *Uromys*, and Table 4 is a list of the character states for each species. Figure 13 shows the one cladogram produced by Hennig86 using the coding given in Table 4, except that characters 12, 15, 24, 25, 35, 43, 44 and 48 are dropped as only one taxon in each case shows the derived condition. There is a basic split between the two subgenera. Within *U.* (*Cyromys*), *U. porculus* is the sister species to *U. rex* and *imperator*. Within *U.* (*Uromys*), *U. boeadii* is sister to all other species; next there is a split between *U. anak* and *neobrittanicus* on the one hand, and the *caudimaculatus* group on the other; within the latter, *U. caudimaculatus* and *hadrourus* are closer than either is to *U. emmae*.

Node 15, defining subgenus *Cyromys*, is defined by the derived states of characters 5, 7, 11, 13, 20, 22, 23, 26, 27, 32 and 38. The condition of character 42 is equivocal. At node 13, the characters showing derived states in common between *U. rex* and *imperator* are numbers 2 and 9.

Node 16, defining subgenus *Uromys*, is defined by the derived states of characters 1, 3, 18, 38, 40, 41 and 45; the condition of characters 11, 21 and 29 is equivocal. At node 14, all of *U.* (*Uromys*) except *U. boeadii* have the derived states for characters 4, 6, 8 and 19; characters 21 and 29 are equivocal, and character 11 shows a possible reversal. At node 11, *U. anak* and *U. neobrittanicus* share the derived states of characters 10, 21, 32 and 33, and characters 21 and 29 have possible reversals.

At Node 12, *U. emmae*, *U. caudimaculatus* and *U. hadrourus* share derived states for characters 1, 3, 10, 16, 29, 31, 32, 37 and 47. Finally at node 10 *U. caudimaculatus* and *U. hadrourus* share derived conditions for states 18, 36 and 39.



**Fig. 13.** Most parsimonious cladogram for the genus *Uromys* produced by Hennig86.

The sole Hennig86 cladogram has a tree length of 56 and a consistency index of 73, which is high for a tree based on nine terminal taxa (plus *Melomys* as outgroup).

We entered the taxa into MacClade and tested the cladogram by branch-swapping. Figure 14 depicts the four shortest cladograms calculated by the MacClade program. Three have a length of 74, with a consistency index of 84, but one other option (*U. porculus* as a sister species to all instead of just *U. rex* and *U. imperator*) has a length of 75, for a consistency index of 83.

Laying aside *U. boeadii* for the moment, the species of *Uromys* (*Cyromys*) in all trees clearly form the sister group to *Uromys* (*Uromys*). Many features seen in *U.* (*Cyromys*) are less complete expressions of the condition seen in the species of *U.* (*Uromys*); others are the plesiomorphic condition. Characters which show primitive states compared to *U.* (*Uromys*), again excluding *U. boeadii*, are characters 2, 9, 19, 20, 40, 41, 42 and 46.

The species of *Uromys* (*Cyromys*) however do possess some synapomorphies that unite them as a group; characters 8, 14, 21, 23, 26, 27 and 28. In addition, the morphology of the tail is highly distinctive, although in the binary coding used here it appears similar to that of the *U. anak/neobrittanicus* group. The tail scales are soft, and have a small hard prominence in the centre of each scale region. All other species of *Uromys* have flat, hard scales arranged in a

mosaic pattern, and lack the soft skin between the widely separated hard tubercles.

The fourth possible cladogram, however, would put *U. porculus* as the sister species to all the rest (Fig. 13d). In such a case *U. boeadii* is constructed to be the sister group to all *U.* (*Uromys*), the other positions having longer tree lengths and lower consistency indices. Despite this finding of equal parsimony for this option, the remaining branches share no unequivocal derived states; we therefore note this option as unlikely and will concentrate on cladograms a to c.

Within *Uromys* (*Uromys*), interrelationships are a little clearer (*U. boeadii* again excepted for the moment). We recognise two distinct groups. The first group represented in our cladogram is the clade containing *U. anak* and *U. neobritannicus*. Despite the considerable phenetic similarities between these taxa, very few possible synapomorphies could be found that may link them. The most obvious is the hypertrophy of the postorbital processes; in both species they are larger than in any other *Uromys* (although because they are not wholly absent in *U. caudimaculatus* and *U. emmae* the binary coding does not show this fully), but in *U. neobritannicus* they are greatly developed. The form of the tail scales is unique. Rostral deepening, and the posterior position of the posterior nasal ends, are certainly further synapomorphies, though both are convergent on *U. rex*.



Fig. 14. Four equally parsimonious cladograms of genus *Uromys*: (a) *U. boeadii* is sister species to other members of *U.* (*Uromys*).

The second group contains *U. hadrourus, U. caudimaculatus* and *U. emmae*. These species share a number of synapomorphies within *Uromys*: characters 1 (convergent on *U. imperator*), 10 (convergent on *U. rex* and *U. imperator*), 16, 29, possibly 30, 31, 32, 37 and 47. *Uromys hadrourus* is the most distinctive member of the group because of its small size, inflated braincase, reduced postorbital processes and slightly smaller anterolateral bullar spurs; some of these features may be correlated with its small size, and all appear to be unique within *Uromys*. On the other hand, it shares a few synapomorphies with *U. caudimaculatus* which are absent in *U. emmae*: characters 18, 36 and 39 (convergent on *U. (Cyromys)*. With *U. caudimaculatus* it shares only character 7; with *U. emmae*, no synapomorphies. The balance of evidence therefore supports the hypothesis that *U. hadrourus* is a highly autapomorphic sister species of *U. caudimaculatus*, with *U. emmae* a sister group to them both.

The phyletic position of *U. boeadii* remains to be considered. Our Hennig86 analysis placed it definitively as the sister species to the rest of *U. (Uromys)*; whereas the MacClade branch-swapping revealed three equally parsimonious options: it could be the sister-group to the species of *U. (Uromys)* (Fig. 14a), to the species of *U. (Cyromys)* (Fig. 14b), or to all the other species of the genus *Uromys* (Fig. 14c). Inspection of the actual character state distributions, however, puts a different complexion on the matter: the first model is supported by characters 2, 4, 19, 40, 41, 42 and 46; the second and third (and the slightly less parsimonious interpretations that it is the sister-group to the *U. anak/ neobrittanicus* or *U. caudimaculatus/hadrourus/emmae* groups) are supported by several characters but only at the cost of several convergences: thus, it shares the derived condition of character 22 with the *anak/ neobrittanicus* group, but this is convergent with *U. rex*. Our favoured hypothesis, therefore, is that the new species *Uromys boeadii*, superficially so similar to *U. anak*, is actually the plesiomorphic sister-group to all other species of subgenus *Uromys*.

Our hypothesis of the monophyly of *Uromys* necessitates some convergence within the mosaic tailed rats. Species of *Uromys (Uromys)* are very similar in their simplified dentitions to some *Melomys* species (eg, *M. rufescens, M. rubex*). During our initial inquiries into *Uromys*, we considered the possibility that this simplified dentition might be indicative of monophyly in this group; but the subsequent detection of the suite of convincing synapomorphies in the palate and bulla linking *U. (Uromys)* and *U. (Cyromys)* species convinces us that the simplified dentition in the species of *Uromys* and *Melomys* must be due to convergence. This is because the species of *U. (Cyromys)* possess plesiomorphically relatively complex molars.

We have deliberately deferred discussion of the question of the relationships of *Uromys* to its closest relatives, *Melomys* and *Solomys*. We are confident of the



**Fig. 14** (cont'd). Four equally parsimonious cladograms of genus *Uromys*: (b) *U. boeadii* is sister species to *U. (Cyromys)*.

monophyly of *Uromys* relative to these taxa, but the complexity of the (surely paraphyletic) *Melomys* group places this task well beyond the scope of the present study.

**Zoogeography.** The species of *Uromys* are dispersed over a wider area than almost any other genus of Melanesian murid. Two species are found in north-eastern Queensland, two on the island of New Guinea, one each on P. Owi, P. Biak and New Britain, and three on Guadalcanal in the Solomon Islands (Fig. 1). The three species restricted to Guadalcanal are in many respects the most plesiomorphic, and present the most enigmatic zoogeographic problem. Guadalcanal is close to the middle of the Solomon Islands chain. During times of lowered sea level as little as 1 km of open water separated it from the southern tip of Greater Bukida, a landmass that incorporated all the eastern islands of the Solomons from Buka to Nggela (Diamond, 1974). All of the Greater Bukidan fragments, as well as Ugi Island to the south of Guadalcanal, lack species of *Uromys* but are inhabited by various species of the endemic Solomon Islands murid genus *Solomys*, which differ so widely from the species of *Uromys* that they are probably only distantly related to them. The presence of three species of *Uromys* on an island in the middle of an island chain otherwise inhabited by the species of *Solomys* is intriguing. It may be that fortuitous rafting of an ancestral *U.* (*Cyromys*), perhaps

from the islands of eastern New Guinea onto Guadalcanal, permitted the establishment of the genus there; certainly Guadalcanal has a different geologic history from Greater Bukida (Ravenne *et al.*, 1982). Whatever the origins of the species of *U.* (*Cyromys*), it is remarkable that they should be restricted to Guadalcanal, given its geographic location and distance from any possible source. The implications for speciation processes, in the apparent absence of notable geographic barriers, on the single island inhabited by three closely related species, are also noteworthy.

Further difficulties in interpreting zoogeography present themselves when one considers the species of *Uromys* that inhabits the Bismarck Archipelago. A single species, *U. neobritannicus*, is present on New Britain – a close relative of the mainland New Guinean *U. anak*. Analysis of a large amount of archaeological material, and a detailed mammal survey (Flannery & White, 1991) make it clear that *Uromys* is totally absent from New Ireland, and has not been present there over the last 30,000 years. It therefore seems highly unlikely that New Ireland acted as a stepping stone for the species of *Uromys* between New Guinea and the Solomons. Indeed, that *U. neobritannicus* has failed to cross the narrow (30 km at present) strait into New Ireland, where there are no similar-sized murids, but abundant apparently suitable habitat, is eloquent of the difficulties the species of *Uromys* face in dispersing over water barriers.

*Uromys neobritannicus* presents other problems for



**Fig. 14** (cont'd). Four equally parsimonious cladograms of genus *Uromys*: (c) *U. boeadii* is sister species to all other species of the genus.

the zoogeographer, for its nearest relative (*U. anak*) is a montane species rarely if ever encountered below about 1,000 m along the Central Cordillera. *Uromys caudimaculatus* replaces it at lower altitudes in northern New Guinea (Stein, 1933). Intuitively one would expect that a relative of the lowland *U. caudimaculatus* would inhabit New Britain rather than the montane *U. anak*. One possibility may be that before the evolution of *U. caudimaculatus* (or the extension of the *caudimaculatus* group into New Guinea) the eastern New Guinean lowlands were inhabited by a *U. anak*-like species that dispersed to New Britain. Subsequently, the presence of *U. caudimaculatus* or an ancestral taxon caused the restriction of the *U. anak* group to higher altitudes on New Guinea. A similar explanation might account for the survival of the relatively plesiomorphic *U. boeadii* on Biak in the absence of *U. caudimaculatus*.

Speciation within the *caudimaculatus* group and *U. hadrourus* is complex. *Uromys hadrourus* must have become isolated on the Thornton Peak Massif at an early period within the speciation of the group. It is presently sympatric with *U. caudimaculatus*, which may be a more recent invader from New Guinea. But why should *U. hadrourus* be restricted to the Thornton Peak Massif? It clearly cannot live in lowland rainforest, so this may account for its absence from much of Cape York. It cannot ever have reached as far south as the Bellenden Ker area, otherwise one would expect it to inhabit the

upland rainforests of the Atherton Tablelands. A further possibility is that it may be a highly differentiated localised derivative of *U. caudimaculatus*.

*Uromys caudimaculatus* may have diversified during the Pleistocene, when increased aridity would have separated an ancestral taxon into three parts in the closed forests of (broadly speaking) northern Australia, Papua New Guinea and Irian Jaya respectively. These taxa have come into close proximity if not parapatry as the closed forests expanded during interglacial periods; while it is not known whether or not they intergrade, our reasons for adopting a conservative course, and retaining them all in a single species, are given under that heading.

## Summary

The genus *Uromys* is monophyletic, and includes nine species in two subgenera. Three species belonging to subgenus *Cyromys* are confined to Guadalcanal, Solomon Islands; six species in the nominotypical subgenus are spread through New Guinea (including its offshore islands), New Britain and north-eastern Australia. We recognise two new species: *U. emmae*, related to *U. caudimaculatus* and *U. hadrourus*, and the relatively plesiomorphic *U. boeadii*; both these two species live on islands in Geelvinck Bay, Irian Jaya. The



**Fig. 14** (cont'd). Four equally parsimonious cladograms of genus *Uromys*: (d) *U. porculus* is sister species to all other species in the genus, and *U. boeadii* is part of the *U.* (*Uromys*) clade.

Thornton Peak rat, described as *Melomys hadrourus*, is transferred to *Uromys*; it is the sister species of *U. caudimaculatus*. Three subspecies are recognised within each of the two widespread species, *U. caudimaculatus* and *U. anak*.

# References

Diamond, J., 1984. Biogeographic mosaics in the Pacific. Pp. 1–4. **In** F.J. Radovsky, P.H. Raven & S.H. Sohmer (eds). Biogeography of the Tropical Pacific. Lawrence, Kansas.

Flannery, T.F. & J.P. White, 1991. Animal translocations. National Geographic Research and Exploration 7: 96–113.

Laurie, E.M.O. & J.E. Hill, 1954. List of Land Mammals of New Guinea and Celebes. British Museum (Natural History) Trustees, London, 175 pp.

McAllan, I.A.W. & M.D. Bruce, 1989. Some problems in vertebrate nomenclature 1. Mammals. Bolletino del Museo Regionale di Scienze Naturali di Torino 7: 443–460.

Musser, G., 1981. The giant rat of Flores and its relatives east of Borneo and Bali. Bulletin of the American Museum of Natural History 169: 69–175.

Ravenne, C., C.E. de Broin & F. Aubertin, 1982. Structure et histoire de la région Salomon-Nouvelle-Irlande. Pp. 327–341. **In** Contribution a l'etude géodynamique du Sud-ouest Pacifique. ORSTOM, Paris.

Ridgway, R., 1886. Color standards and color nomenclature. Washington, DC (privately printed).

Rümmler, H., 1938. Die Systematik und Verbreitung der Muriden Neuguineas. Mitteilungen aus dem Zoologischen Museum in Berlin 23: 2–297.

Tate, G.H.H., 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia and New Guinea. Bulletin of the American Museum of Natural History 97: 187–430.

Winter, J.W., 1983. Thornton Peak Melomys. P. 379. **In** R. Strahan (ed.). The Complete Book of Australian Mammals. Angus & Robertson, Sydney.

Woodford, C.M., 1890. A Naturalist among the Head-hunters, being an Account of 3 Visits to the Solomon Islands in the Years 1886, 1887 and 1888. George Philip & Son, London.

APPENDIX

Table 1. Localities and selected measurements for *Uromys anak* and *U. caudimaculatus* examined during our study.

| | Condylobasal | | | Molar Row | | | Head + Body Length | | | Tail:H+B |
|---|---|---|---|---|---|---|---|---|---|---|
| | Mean | s.d. | n | Mean | s.d. | n | Mean | s.d. | n | Range |
| *U. caudimaculatus* | | | | | | | | | | |
| *U.c. caudimaculatus*: | | | | | | | | | | |
| Cape York Peninsula | 68.3 | 2.36 | 5 | 12.5 | 0.38 | 11 | 334 | 25.9 | 4 | 99-123 |
| Cooktown/Townsville | 69.9 | 1.40 | 6 | 11.5 | 0.65 | 15 | 282 | 19.7 | 7 | 101-128 |
| Atherton Tablelands | 67.4 | 2.23 | 4 | 12.0 | 0.58 | 17 | 296 | 20.0 | 4 | 106-130 |
| Hinchinbrook Island | 67.2 | 2.23 | 4 | 12.0 | 0.41 | 4 | 281 | 13.3 | 5 | 110-124 |
| Kaimare (young adult) | 63.4 | - | 1 | 12.4 | - | 1 | 268 | - | 1 | 93 |
| Katau (type) | - | - | - | 11.0 | - | 1 | - | - | - | 100 |
| Western Division | 62.4 | 2.19 | 6 | 11.3 | 0.74 | 6 | 278 | 7.5 | 6 | 95-111 |
| *U.c. papuanus* and cf. *papuanus*: | | | | | | | | | | |
| Smallest size (Mount Hagen) | 59.6 | 1.74 | 11 | 11.2 | 0.27 | 17 | 264 | 10.4 | 11 | 105-132 |
| Largest size (Telefomin) | 60.2 | 1.88 | 5 | 11.6 | 0.30 | 6 | 269 | 12.7 | 6 | 105-132 |
| Mount Karimui | 54.6 | - | 2 | 11.4 | - | 2 | 232.5 | - | 2 | 120-125 |
| Yapsiei | 60.1 | - | 1 | 11.6 | - | 1 | 230 | - | 1 | 112-135 |
| Torricelli Mountains | 64.5 | - | 1 | 11.6 | - | 1 | 272 | - | 1 | 122 |
| Dobodura/Mount Lamington | 59.9 | 2.13 | 5 | 11.8 | 0.40 | 5 | 258 | 9.6 | 5 | 100-112 |
| *U.c. multiplicatus* and cf. *multiplicatus*: | | | | | | | | | | |
| Alkmaar/Mimika/Setakwa | 59.6 | 1.78 | 8 | 11.1 | 0.37 | 13 | 295 | 15.9 | 8 | 79-88 |
| Utakwa | 64.1 | - | 2 | 11.9 | 0.36 | 3 | 283 | - | 2 | 83-84 |
| Weyland Range | 63.7 | - | 1 | 12.3 | - | 2 | 273 | - | 2 | 105-114 |
| Waigeu (Frechkop) | - | - | - | 14(?!) | | 1 | 370 | - | 1 | 88 |
| *U.c.* subsp. | | | | | | | | | | |
| Yapen | 63.0 | - | 1 | 12.0 | - | 1 | 294 | - | 1 | 109 |
| *U.c.* subspp. (described as *siebersi* and *aruensis*): | | | | | | | | | | |
| Great Kai Island | 59.5 | - | 1 | 13.3 | - | 1 | 280 | - | 1 | 84 |
| Aru Island | 63.2 | - | 1 | 11.7 | 0.52 | 3 | 275 | - | 2 | 104 |
| *U. anak* | | | | | | | | | | |
| *U.a. anak* | 69.1 | 0.96 | 6 | 13.5 | 0.24 | 7 | 319 | 8.4 | 6 | 119-130 |
| *U.a. albiventer*: | | | | | | | | | | |
| Kubor Range | 70.6 | 1.94 | 5 | 12.5 | 0.40 | 8 | 329 | 7.2 | 5 | 106-129 |
| Erimbari | 67.5 | 2.39 | 4 | 12.8 | 0.51 | 5 | 313.5 | - | 2 | 116-123 |
| Telefomin | 67.0 | - | 2 | 13.3 | - | 2 | 309 | - | 2 | 100-113 |
| Mount Giluwe | 73.3 | - | 1 | 12.2 | - | 1 | 340 | - | 1 | 106 |
| *U.a. rothschildi* | 70.8 | - | 1 | 13.0 | 0.44 | 3 | 355 | - | 1 | 100 |

Table 2. Measurements of type specimens of *Uromys emmae* and *U. boeadii*.

|  | U. boeadii | U. emmae |
|---|---|---|
| head body length | 255 | 232 |
| tail length | 235 | 258 |
| hindfoot (su) length | 62.0 | 50.5 |
| ear (notch) length | 25.0 | 20.5 |
| ear width | – | 16.5 |
| condylobasal length | 61.3 | 53.0 |
| bizygomatic breadth | 32.2 | 28.0 |
| incisive foramen length | 7.8 | 5.7 |
| interorbital breadth | 10.9 | 9.2 |
| upper molar row length | 11.5 | 11.1 |
| $M^1$ breadth | 3.3 | 3.1 |
| palate width (external) at $M^1$ | 11.8 | 11.1 |
| palate width (external at $M^3$ | 12.5 | 11.5 |
| nasal length | 25.1 | 19.3 |
| nasal breadth (anterior) | 7.9 | 6.1 |
| nasal breadth (posterior) | 4.0 | 3.5 |

Table 3. Derived characters used in cladistic analysis. Each character was binary coded only – 0 = absent, 1 = present.

1. Strong spine at back of palate
2. Incisive foramina slit-like
3. Zygomatic arches posteriorly flared
4. Posterior walls of rostrum inflated, sloping-sided
5. Lingual margins of molar alveoli thickened, ridge-like
6. Prominently swollen frontotemporal sutures
7. Postorbital processes (behind frontotemporal sutures)
8. Medial walls of orbitotemporal fossa sloping, not vertical
9. Anterior wall of orbit subvertical
10. Posterior nasal ends tapered, narrow-arched
11. Posterior nasal ends extend behind anterior orbital margins
12. Lacrimal extends at least as far back as nasals
13. Coronal suture straight or only slightly bowed backward
14. Preorbital foramen not vertical
15. Lambdoid suture anteriorly angulated
16. Braincase rounded
17. Interorbital region inflated
18. Zygomatic arches swing down towards molar alveoli
19. Nasals protrude in front of snout
20. Nasal ends slightly upturned
21. Incisors opisthodont (not orthodont)
22. Skull, especially rostrum, deepened
23. Long paroccipital processes
24. Ascending ramus vertical, not backsloping
25. Coronoid process low, rounded
26. Dentary tubercle and ridge strongly developed
27. Ascending rami flare outward
28. Tail shorter than head + body
29. Ear length greater than 40% of condylobasal length
30. Hindfoot length usually less than 20% of head + body
31. Feet light coloured (white or light brown)
32. White on terminal part of tail
33. Tail scales large, ridged, in rings
34. Tail scales broader than long
35. Underside with restriction of white zone
36. Incisive foramina long, greater than 20% of palate length
37. Bullae inflated
38. Feet narrow, their breadth less than 20% of their length
39. Toothrow short, less than 20% of condylobasal length
40. $M^3$ reduced
41. Anterior lophid of mandibular M1 reduced
42. Molars simplified
43. Pads of feet reduced in size
44. Molars broadened
45. Tail scales 9 or less per cm
46. Palate greatly lengthened posteriorly
47. Interparietal bone elongated
48. Anterolateral bullar spurs reduced
49. Preorbital foramen hidden behind zygomatic plates

Table 4. Distribution of character states among species of *Uromys*. 0 = plesiomorphic, 1 = apomorphic. The columns are ordered sequentially as in Table 3.

| | |
|---|---|
| *rex* | 0010010101111100000011111111100001000001000000000 |
| *imperator* | 1010010101001100000010100111000010000010001110000 |
| *porculus* | 0000010100001100000010100111000010000010000010000 |
| *anak* | 0101111010101000101101000000000011000001110001000 |
| *neobrittanicus* | 0101101010101000001101000000000011000001110011000 |
| *boeadii* | 0101000000000000001001000000010000000001110001000 |
| *emmae* | 1111101011001001001100000000111100001001110001101 |
| *caudimaculatus* | 1111101011001001111100000000111100011111110001100 |
| *hadrourus* | 1111100011001011011100000000111100111011110001110 |