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NOTE

MORPHOLOGY-BASED REVISION OF *MUREXIA* AND *ANTECHINUS* (MARSUPIALIA: DASYURIDAE)

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The unremarkable, rat-like appearance of 16 named forms of small Irian Jayan and Papua New Guinean dasyurids previously assigned to *Antechinus* Waterhouse, 1837, and *Murexia* Tate & Archbold, 1937, has resulted in persistent taxonomic confusion. In this paper the two genera are systematically revised and a hypothesis of phylogenetic relationships proposed. I conclude that the New Guinea taxa assigned to *Antechinus* (pre-1984) represent three related but morphologically primitive taxa that lack clear signs of relationship to each other. They are referred to monotypic *Micromurexia* (for *M. habbema*), *Phascomurexia* (for *P. naso*), and *Murexechinus* (for *M. melanurus*) all but distantly related to Australian antechinuses. New Guinea *Murexia* is monotypic (*M. longicaudata*) and highly plesiomorphic. It has no especially close relationship with the more derived *rothschildi* which has traditionally been assigned to *Murexia* but is assigned here to *Paramurexia* gen. nov.; the Murexinae is not supported, and the Australian *Antechinus* forms a monophyletic group with *Phascogale*. ☐ *Murexia, Antechinus, Marsupialia, New Guinea, taxonomy*.

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Two laconic remarks made by Schlegel (1866) in the original description of *Phascogale longicaudata*, had significance well beyond their immediate 19th century context ... 'Cette espèce rappelle, par sa taille, le jeune du rat ordinaire' [*This species calls to mind, by its build, the young of the common rat* ...], '... et offrant en général absolument les mêmes caractères que les Antechinus de l'Australie ...' [... *and offering in general absolutely the same characteristics as the Antechinus of Australia* ...].

Ever since Schlegel's time, the unremarkable, rat-like appearance of his *P. longicaudata* has consistently confounded its affinities with the suite of other equally unremarkable, rat-like dasyurids from New Guinea.

Schlegel's other observation that *P. longicaudata* shared attributes with the Australian *Antechinus* was later echoed by Thomas (1899) in his description of the Papua New Guinean species *Phascogale melanura*, '*P. melanurus clearly belongs to the group comprising the small < Antechini > of Australia, Ph. minima, flavipes* etc., and of which *Ph. longicaudata* is the largest member ...'.

Tate & Archbold (1941) assigned 3 New Guinean dasyurids *Phascogale tafa, P. melanurus* and a new species, *habbema* to the Australian *Antechinus* on the basis of their 'generalised forms'. In so doing Tate & Archbold

finally formalised the close link suggested by Schlegel & Thomas between the small dasyurids of Australia and those of Irian Jaya/Papua New Guinea.

Acceptance of the trans-Torresian distribution of *Antechinus* prevailed until 1984, when Woolley presented results of studies of phallic morphology in New Guinea dasyurids, indicating a very dubious relationship between Australian and New Guinean members of *Antechinus*, and thus challenging the integrity of the Phascogalinae (sensu Archer, 1982a) not long after consensus from a diversity of opinion indicated that *Antechinus* in Australia was not monophyletic (but included what we now regard as *Dasykaluta rosamondae, Pseudantechinus macdonnellensis, P. ningbing, Parantechinus apicalis* and *Pa. bilarni*). This was followed (Van Dyck, 1988) by a clarification of specific epithets applicable to '*Antechinus*' of New Guinea (*melanurus, habbema* and *naso*) but more importantly providing morphological confirmation that these species (and *Murexia*) deserved generic reclassification, that their inclusion in *Antechinus* was, as Woolley had suggested, inappropriate.

Kirsch et al. (1990), using DNA hybridisation, and Baverstock et al. (1990), using albumin immunology, confirmed the closer relationship between New Guinea 'antechinuses' and New

Guinea *Murexia* than with Australian *Antechinus*. Krajewski et al. (1993) concluded that New Guinea *Antechinus* and *Murexia* formed a clade that was the sister-group of Australian antechinuses. Krajewski et al. (1994) called for the abolition of the Murexinae and Phascolosoricinae, in favour of the Phascogalinae and the Dasyurinae (respectively). Krajewski et al. (1996), on the basis of analysis of cytochrome b sequencing, concluded that the Phascogalinae (sensu Archer, 1982a) actually consisted of 3 clades corresponding to *Phascogale*, Australian *Antechinus*, and New Guinean 'antechinuses' and *Murexia*. They also proposed monophyly of *Murexia* and all *Antechinus* apart from *Phascogale*, and recommended assignment of the New Guinea antechinuses *A. habbema*, *A. melanurus*, *A. naso* and *A. wilhelmina* (provisionally) to *Murexia*.

Since Schlegel's description of *P. longicaudata*, 15 species or subspecies of *Murexia* and *Antechinus* have been described from New Guinea. The primary objective of this study is to clarify the generic relationships of the New Guinea species previously assigned to *Antechinus*. At a specific level, there has been, since then, reasonable concurrence with other authors (Woolley, 1989; Krajewski et al., 1996), however, at the generic and subspecific levels there are major discrepancies between conclusions from morphological and molecular analyses.

Species assigned to *Antechinus* herein are: *A. stuartii* Macleay, 1841, *A. leo* Van Dyck, 1980, *A. subtropicus* Van Dyck & Crowther, 2000, *A. agilis* Dickman, Crowther & King, 1998, *Phascogale godmani* Thomas 1923, *Phascogale swainsonii* Waterhouse 1840, *Phascogale bella* Thomas 1904, *Phascogale flavipes* Waterhouse 1837, *Phascogale flavipes adusta* Thomas 1923, and *Dasyurus minimus* Geoffroy [Saint-Hilaire] 1803. *Antechinus habbema* Tate & Archbold, 1941 is assigned to *Micromurexia* gen. nov., *Phascogale naso* Jentink, 1911 is assigned to *Phascomurexia* gen. nov., *Phascogale melanura* Thomas, 1899 is assigned to *Murexechinus* gen. nov. and *Phascogale rothschildi* Tate, 1938 is assigned to *Paramurexia* gen. nov. *Murexia* now contains only *Phascogale longicaudata* Schlegel, 1866.

METHODS

Terminology of cranial morphology follows Archer (1976a), dental and external morphology follows Archer (1976b, 1981), and tooth number

follows Luckett (1993). Cranial and dental measurements were made with NSK electronic digital calipers (to 0.01mm). All specimens compared in diagnoses were adults with fully erupted $P^{3/3}$.

Specimens were examined from the Australian Museum, Sydney (AM M); Australian National Wildlife Collection, Division of Wildlife Research, Canberra (CM); Bernice Bishop Museum, Honolulu (BBM); Natural History Museum, London (BMNH); Rijksmuseum van Natuurlijke Histoire, Leiden (RMNH); American Museum of Natural History, New York (AMNH); Museum National D'Histoire Naturelle, Paris (MNHN); Museo Civico Del Storia Naturale, Genova (MCSN); Museum of Comparative Zoology, Harvard College, Cambridge (MCZ); Zoologisches Museum der Humboldt-Universität zu Berlin (ZM); Queensland Museum, Brisbane (QMJ or JM).

I have examined type material of the species recognized herein (listed above) and species here placed in synonymy with them. Types of other *Antechinus* species not dealt with in the taxonomic section are: *Phascogale godmani* Thomas, 1923 (BMNH 1922.12.18.46), *Phascogale swainsonii* Waterhouse, 1840 (BMNH 60.1.5.18), *Phascogale swainsonii mimetes* Thomas, 1924 (BMNH 24.10.1.1), *Dasyurus minimus* Geoffroy, [Saint-Hilaire] 1803 (MNHM 1987-223), *Phascogale affinis* Gray, 1841 (BMNH 41.1241), *Phascogale (Antechinus) minimus maritima* Finlayson, 1958 (SAM M4985), *Phascogale bella* Thomas, 1904 (BMNH 4.1.3.102), *Phascogale flavipes* Waterhouse, 1837 (BMNH 1855.12.24.75), *Phascogale flavipes rufogaster* Gray, 1841 (BMNH 1841.1251), *Antechinus flavipes rubeculus* Van Dyck, 1982 (QM JM2676), *Phascogale leucogaster* Gray, 1841 (BMNH 1841.1244), *Phascogale flavipes adusta* Thomas, 1923 (BMNH 1922.12.18.54), *Antechinus stuartii* Macleay, 1841 (neotype AM M5294), *Antechinus subtropicus* Van Dyck & Crowther, 2000 (QMJ17407), *Antechinus leo* Van Dyck, 1980 (QMJM2372).

I present only the most economical primary synonymy. Species diagnoses attempt to describe absolute diagnostic features, while more relative diagnostic characters, appear in Remarks. In most instances subjective synonyms are dealt with in detail to provide reasonable justification for taxonomic decisions made here, and to remove subjectivity.

Pelage colours were compared with Ridgway (1912) and statistical significance between means was established through Students T-tests.

PHYLOGENETIC ANALYSIS

Binary coding of character states was rarely possible, and most characters were scored multistate. Both the branch and bound algorithm of Hennig '86 V1.5 (Farris, 1988) and PAUP version 4.0b2 (Swofford 1998) were used to analyse the data matrix in Table 8. A heuristic search of the data was completed using step-wise addition sequences, tree-bisection-reconnection (TBR) branch swapping, MULPARS, and zero branches collapsed to yield polytomies. The strict consensus (Bremer, 1990) of the most parsimonious trees was computed using PAUP and Hennig '86. Successive approximations character weighting (successive weighting) was implemented using PAUP with a base weight of 1000. Clados Version 1.2 (Nixon, 1992) was used to study character evolution. In the character matrix, *A. stuartii*, *A. agilis* and *A. subtropicus* are merged into the single taxon *Antechinus stuartii* for the analysis. In addition, a heuristic search of the data was invoked using 500 bootstrap pseudoreplicates, Branch-swapping, Tree-bisection-reconnection, MuTrees and a Concensus Tree formulated using the 50% majority-rule criterion (not shown).

TAXONOMIC HISTORY OF THE PHASCOGALINAE

Suprageneric clasification within the Dasyuridae was reviewed and revised by Archer (1982a) and challenged by Westerman & Woolley (1993), and Krajewski et al.(1994, 1996). Goldfuss (1820) assigned Australian carnivorous marsupials to the tribe Dasyurini. From this tribe Waterhouse proposed the Dasyuridae and the Myrmecobiidae. Bonaparte (1838) removed *Thylacinus* from the Dasyuridae to the Thylacinidae, but proposed the Phascogalinae, within the Dasyuridae to, presumably, accomodate the smaller representatives. Gill (1872) erected a suborder, the Dasyuromorphia, to accomodate the Myrmecobiidae and the Dasyuridae (which contained subfamilies Sarcophilini, Dasyurinae and Phascogalinae). But Thomas (1888) did not adopt the Phascogalinae, and divided the Dasyuridae into the Myrmecobiinae and Dasyurinae. Iredale & Troughton (1934) (classifying only Australian mammals) recognised 3 subfamilies in the Dasyuridae:

Phascogalinae (*Antechinus, Planigale, Phascogale, Dasycercus, Dasyuroides, Sminthopsis* and *Antechinomys*), Dasyurinae and Thylacininae. Simpson (1945) assigned *Dasyurus, Dasyurops, Dasyurinus, Satanellus* and *Sarcophylus* to the Dasyurinae, which, along with the Phascogalinae, Myrmecobiinae and Thylacinidae accounted for the Polprotodontia. Tate (1947) instead, divided the Dasyuridae into the Dasyurinae (based on the reduction of P^3, and I^2 being smaller than I^4) and the Phascogalinae to which he assigned *Antechinus, Murexia, Thylacinus, Sminthopsis, Antechinomys, Planigale* and *Phascogale*. Similarly, Laurie & Hill (1954) accomodated New Guinean representatives of *Murexia, Sminthopsis, Planigale* and *Antechinus* in the Phascogalinae. Ride (1964) recognised four marsupial orders, one of which, the Marsupicarnivora contained the superfamily Dasyuroidea made up of the Thylacinidae and Dasyuridae. The Dasyuridae contained Myrmecobiinae and the Dasyurinae (containing all dasyurid genera other than *Myrmecobius*). Kirsch (1977) used Gill's (1872) Dasyuromorphia to accomodate the Dasyuroidea which contained the Myrmecobiidae and the Dasyuridae.

POLYPHYLY OF THE PHASCOGALINAE. Several studies that suggested *Antechinus* was not monophyletic were based on phallic morphology (Woolley, 1982), interpretation of enzyme data (Baverstock et al., 1982) and cranial and dental examinations (Archer, 1982a; Kirsch & Archer, 1982). They specifically impacted on what we now regard as *Dasykaluta rosamondae, Pseudantechinus macdonnellensis, P. ninbing, Parantechinus apicalis* and *Pa. bilarni*. The broad spectrum of species, historically representing the Phascogalinae, was reduced by Archer (1982a), with restriction of its constituents to *Phascogale* and *Antechinus* (the New Guinea 'antechinuses', and 7 thin-tailed Australian antechinuses) on the putative synapomorphies of enlargement of I^1, reduction in M^4 complexity, and slight reduction in posterior premolar size. At the same time Archer erected the Murexinae, for *Murexia longicaudata* and *M. rothschildi*, in recognition of the primitive nature of the dentition and basicranium.

Woolley's (1984) studies of phallic morphology in New Guinea dasyurids indicated a more than dubious relationship between Australian and New Guinean members of *Antechinus*, again challenging integrity of the Phascogalinae. This was followed (Van Dyck, 1988) by a clarification
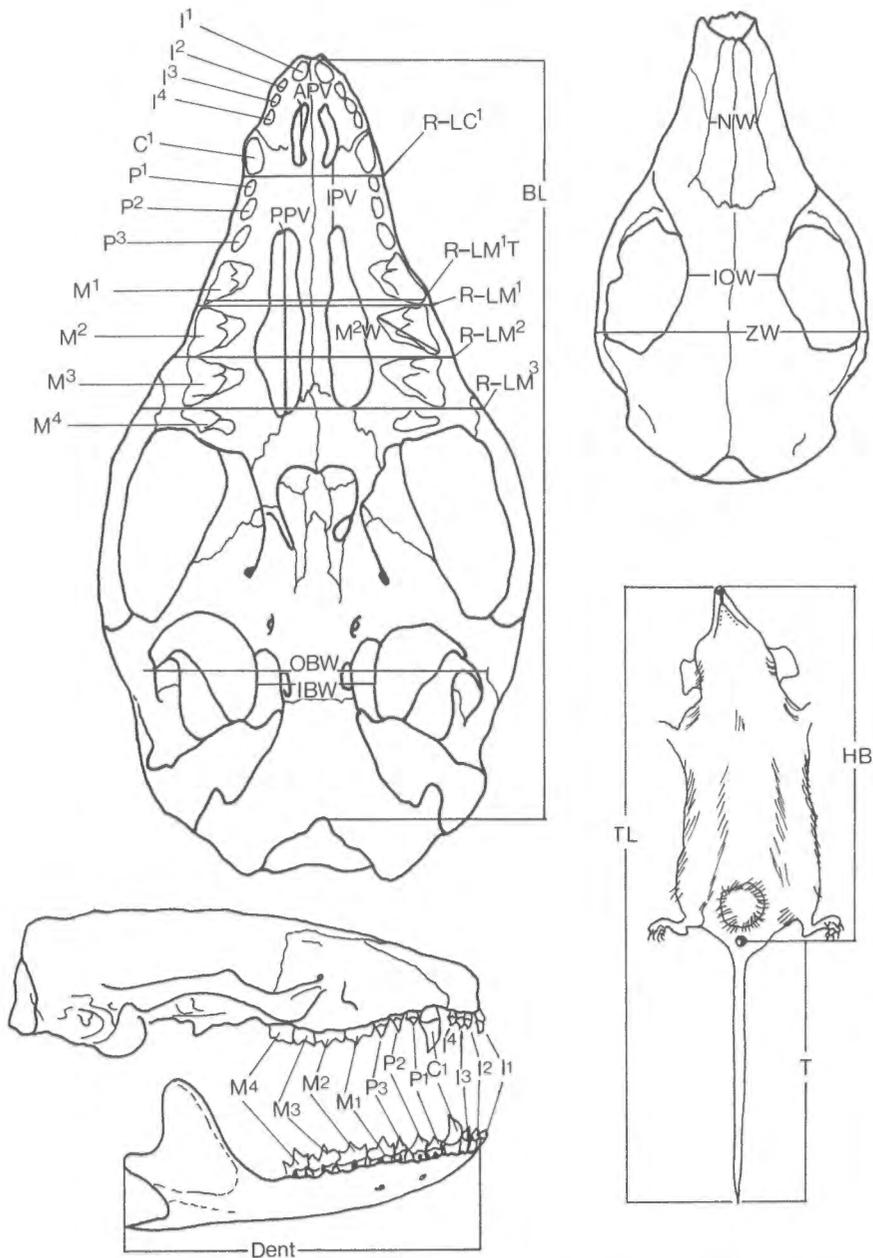
FIG. 1. Tooth numbering and limits of measured dimensions. Abbreviations are: APV = anterior palatal vacuity length; BL = basicranial length; Dent = dentary length; HB = head and body length; IBW = distance between right and left auditory bullae; IOW = interorbital width; IPV = inter-palatal vacuity length; M^2W = width of second upper molar; NW = nasal width the level of the premaxillary/nasal/maxillary junction; OBW = basicranial width from outside right and left auditory bullae; PPV = posterior palatal vacuity length; $R-LC^1$ = rostral width at the level of the upper canines; $R-LM^1$ = rostral width at the level of the first upper molars; $R-LM^1T$ = width between the ectolophs of right and left first upper molars; $R-LM^2$ = rostral width at the level of the second upper molars; $R-LM^3$ = rostral width at the level of the third upper molars; T = tail length; TL = total length, body and tail; ZW = zygomatic width.

of specific epithets applicable to the 'Antechinus' of New Guinea (*melanurus*, *habbema* and *naso*) but more importantly providing morphological confirmation that these species deserved generic reclassification, that their inclusion in *Antechinus* was inappropriate. The specific epithets were tentatively confirmed by Woolley (1989), who again drew attention to distinction between Australian and New Guinean 'ant- echinuses'. Kirsch et al. (1990), using DNA hybridisation, and Baverstock et al.(1990), using albumin immunology, confirmed the closer relationship between small New Guinean 'antechinuses' and New Guinean *Murexia* than with Australian *Antechinus*. While both studies concluded, however, that New Guinean 'antechinuses' were monophyletic with *Murexia*, Baverstock et al. (1990) concluded that Australian species of *Antechinus* and *Phascogale* formed a monophyletic group (also see Aplin et al., 1993), while Kirsch et al., (1990) found *Phascogale* to be part of a broader context i.e., the sister group of all Australian and New Guinean *Antechinus* and *Murexia*. Kirsch's results (with respect to *Phascogale*) were confirmed by Krajewski et al, (1993) who also concluded that New Guinea species of *Antechinus* and *Murexia* formed a clade that was the sister-group of Australian antechinuses. On the basis of cytochrome-*b* and MC'F data, however, Westerman & Woolley (1993) suggested *Murexia longicaudata* and *M. rothschildi* were allied to the Dasyurinae, not the Murexinae.

Krajewski et al, (1994) called for abolition of Muricinae (sic) and Phascolosoricinae, in favour of Phascogalinae and Dasyurinae respectively. Krajewski et al. (1996) presented the following results of phylogenetic analysis of cytochrome b sequences from 10 species of the Phascogalinae: the subfamily consisted of 3 clades corresponding to 1. *Phascogale* 2. Australian *Antechinus*, and New Guinean 'antechinuses' and 3. *Murexia*. There was monophyly of *Murexia* and all *Antechinus* apart from *Phascogale*; a sister-species relationships existed between *A. melanurus* and *A. naso*, and between *A. stuartii* and *A. swainsonii*. They also suggested early divergence of *A. habbema*. But finally, and most importantly, Krajewski et al. recommended assignment of the New Guinea antechinuses *A. habbema*, *A. melanurus*, *A. naso* and *A. wilhelmina* (provisionally) to *Murexia*. This was echoed by Armstrong et al. (1998).

Morphological comparisons presented here suggest that *M. habbema*, *M. longicaudata*, *P. naso*, *P. rothschildi* and *M. melanurus* represent a suite of related but morphologically primitive taxa that lack clear signs of close relationship but that have minor autapomorphies to distinguish them from one another. They are largely plesiomorphic in their teeth and skulls relative to Australian *Antechinus* and other dasyurid genera.

SYSTEMATICS

Family DASYURIDAE

Antechinus Macleay, 1841

Dasyurus (in part) Geoffroy [Saint-Hilaire] 1803.
Phascogale (in part) Temminck 1824.
Phascologale (in part) Thomas 1888.

TYPE SPECIES. *Antechinus stuartii* Macleay, 1841. Based on a drawing and written description by J. Stuart. Neotype AM M5294, adult ♂ in ethanol and skull from Waterfall [Royal] National Park, New South Wales.

SPECIES INCLUDED. *godmani* (Thomas, 1923); *swainsonii* (Waterhouse, 1840); *minimus* (Geoffroy [Saint-Hilaire], 1803); *bellus* (Thomas, 1904); *flavipes* (Waterhouse, 1837); *adustus* (Thomas, 1923); *subtropicus* Van Dyck & Crowther, 2000; *leo* Van Dyck, 1980, *agilis* Dickman et al., 1998.

GENERIC DIAGNOSIS. Penis with a bifid tip. Tail shorter than the head-body length (the tail does not possess a terminal brush or ventral crest as in *Phascogale*, *Dasyuroides*, *Dasycercus*, *Antechinomys*, *Sminthopsis longicaudata*). Pelage not including dorsal striping (as in *Paramurexia*, *Myoictis*, *Phascolosorex*, *Thylacinus*) or spots (as in *Dasyurus*). M^1 of reduced protocone breadth, with complete or incomplete anterior cingulum but with the anterior margin indented posteriorly, and never anteriorly convex (as in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus*, *Myoictis*). P^3 might be relatively reduced, never reduced to a spicule or lost from the premolar row (as in *Dasyurus*, *Sarcophilus*, *Dasykaluta*, *Parantechinus*, *Dasyuroides*, some *Planigale*). M$_1$ with reduced paraconid but never greatly reduced as in *Parantechinus*, *Pseudantechinus*, *Dasyurus*, *Sarcophilus*). Tail not incrassate (as in some *Sminthopsis*, *Pseudantechinus*, *Dasykaluta*, *Dasycercus*). Auditory bullae not enormously enlarged (as in *Ningaui*, *Dasykaluta*, *Pseudantechinus*, *Dasyuroides*, *Phascogale*, some *Sminthopsis*). Squamosal and frontal bones not in contact (as in *Sminthopsis*, *Thylacinus*, *Neophascogale*, *Phascolosorex*, *Planigale ingrami*, *Myoictis*, *Antechinomys*). Metacristids and hypocristids not transverse to the long axis of the skull (as in *Sminthopsis*, *Thylacinus*,

Ningaui). Skull non-dolichocephalic (unlike *Planigale*). Striated foot pads. Rudimentary pouch. Post-mating mortality of males.

DESCRIPTION. *Dentition*. Upper Incisors: I^1 is not needle-like, taller-crowned than other incisors and may be very procumbent in some species (*adustus*) or totally non-procumbent in others (*minimus*). Right and left I^1 may be separated by a small gap (*leo*) or may touch (most others), however in *swainsonii* and *minimus* R and LI^1 form a V-shaped cutting wedge. I^1 crown may be narrow, long, pointed and curved, the arc of this curve orienting along the incisor row (*godmani*) or almost lensate, triangular, uncurved and flaring (*swainsonii*, *minimus*), alternatively, it may be massive, strongly curved, and almost caniniform (*adustus*). In most species it is separated from I^2 by a distinct diastema (however, in *swainsonii* and *minimus* it is not). I^{2-4} may be relatively compressed laterally (lensate) with broad roots (*swainsonii*) or narrowly rooted with heavier, more massive crowns (*bellus*, *leo*). I^{2-4} are invariably cingulated, this may be relatively weakly defined leading to a lack of differentiation between wide roots and crowns (*godmani*, *minimus*, *swainsonii*) or heavy (*adustus*). Relative crown size in I^{2-4} varies from overall approximate equality (*swainsonii*, *minimus*, *godmani*) to a condition of decreasing size, $I^2>I^3>I^4$ (*leo*, *flavipes*, *adustus*, *stuartii*, *agilis*, *subtropicus*). I^4 lacks a secondary posterior cusp. It is also characterised by an increased crown height and a narrow root. In overall crown size $I^2>I^3>I^4$. Only in *adustus* is I^4 conspicuously enlarged but not to the extent seen in *P. calura* and *P. tapoatafa*.

Upper Canines: May be relatively long (not as long as in *Micromurexia*, *Murexia*, *Phascomurexia*), curved, needle-like and weakly cingulated (*godmani*, *swainsonii*, *minimus*) or more robust as in *leo*. There is no anterior cusp but a very small posterior cingular cusp is sometimes present (*leo*, *flavipes*, *adustus*, *stuartii*, *agilis*, *subtropicus*, *swainsonii*).

Upper Premolar: Rows may be long with the premolars widely spaced and exceptionally slender (*swainsonii*, *minimus*), or alternatively, the teeth may be crushed and bulbous (*leo*, *flavipes*, *adustus*). Posterior cusps on P^3 may be seen in *swainsonii*, *minimus* and *godmani*. In all species $P^3>P^2>P^1$ and in none is P^3 lost.

Upper Molars: The anterior cingulum on M^1 originates in a small but prominent stylar cusp A, and, in species where the cingulum is broad and complete, continues into the trigon basin (*adustus*, *stuartii*, *agilis*, *subtropicus*, *swainsonii*). In those species where the cingulum is narrow and almost incomplete, it becomes indistinct at the base of the paracone apex (*bellus*, *leo*, *flavipes*). The anterior margin of M^1 is indented posteriorly, and never anteriorly convex (as in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus*, *Myoictis*). M^2 is invariably longer than M^3 in which the ectoloph is indented to the greatest extent in *bellus*, *leo* and *flavipes*. Stylar cusp B lies at the termination of the anterobuccally oriented preparacrista. It is more reduced than in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus* and *Myoictis*, but it is never reduced to a minute spur or entirely lost. The paracone of M^1 is approximately half the height of the metacone, it is never fused with stylar cusp B. Stylar cusp D of M^1 and M^2 is usually taller and more prominently conical than in *Micromurexia*, *Murexia*, *Phascomurexia*, *Paramurexia*, *Murexechinus* and *Myoictis* and reaches its greatest development for the genus in *swainsonii*. The condition in *godmani* most closely approximates that reduced condition in New Guinea taxa mentioned above. Stylar cusps C and E are usually not prominent and a posterior cingulum is usually absent in *bellus*, *leo*, *minimus* and *godmani*. M^4 protocone is variably reduced but minute in *bellus* and *leo*, slightly larger in *adustus*, *minimus*, *stuartii*, *agilis*, *subtropicus* and *godmani*, and largest in *swainsonii*.

In M^2 and M^3, the broad anterior cingulum which contacts the metastylar corner of M^1 tapers very quickly as it progresses along the base of the paracrista and usually degenerates labially, well buccal to the base of the paracone apex (in *A. adustus* the anterior cingulum is usually just complete). No protoconule is visible. M^2 lacks stylar cusps A, C and E. Stylar cusp D is slightly reduced in M^2 to a very small, sharp peak.

In M^4 the broad anterior cingulum usually terminates quickly away from metastylar corner of M^3, however a continuous anterior cingulum is often present in *adustus*, *stuartii*, *agilis*, *subtropicus* and *flavipes*. A posterior cingulum is absent. M^4 shows some metacone development in *leo*, *swainsonii*, *minimus* and *godmani* but generally the metacone is greatly reduced.

Lower Incisors: I_1 crown is invariably larger than I_2 which is subequal to I_3 except in *swainsonii* in which $I_1>I_2>I_3$. Lower incisors are oval in anterolateral view and gouge-like in occlusal view. I_1 and I_2 are almost prostrate in *flavipes*,

slightly more erect in *bellus, leo, adustus, minimus* and *godmani*, and most erect in *adustus* and *swainsonii*. I_3 is usually incisiform except in *minimus* where it is premolariform in lateral view with a large posterior cusp. The lower canine rests against this cusp. In occlusal view a small notch separates the posterior cusp from a prominent posterolingual lobe which wraps posteriorly around the canine and the crown enamel of primary and posterior cusps folds noticeably so that the crest of the two cusps bisects the tooth longitudinally. In some species the heel is narrower on I_3 than I_1 (*bellus* in particular).

Lower Canines: C_1 may be caniniform and strongly sickle-shaped (*godmani, minimus*) or thicker and more erect (*leo, adustus, flavipes, stuartii, agilis, subtropicus*). In *swainsonii* however, C_1 is premolariform with minimal curvature from root to crown. The canine may be weakly cingulated buccally and lingually (*bellus, godmani, swainsonii, agilis, subtropicus, stuartii*). *A. leo* has weak buccal cingula but is strongly cingulated lingually, while strong buccal and lingual cingula are found in *minimus* and *adustus*.

Lower Premolar: Rows may be long, with the premolars widely spaced and exceptionally slender (*swainsonii*, slightly less so in *minimus* and *godmani*), or alternatively, the teeth may be more crushed and bulbous (*leo, bellus, flavipes, adustus*) and in these the P_3 is often oriented more transversely in the tooth row. Lower premolars are cingulated. Postero-lingual lobing occurs in *bellus, leo* and *flavipes*. P_3 is never absent. The bulk of each premolar mass is concentrated anteriorly to the line drawn transversely through the middle of the two premolar roots.

Lower Molars: M_1 talonid is wider than the trigonid and the anterior cingulum is present but usually poorly developed or absent (variably absent in *stuartii* and *swainsonii*). If the cingulum is present it terminates at the posterior base of the protoconid. There is a very weak buccal cingulum in most species but again, it is not always present in *stuartii* and *swainsonii*. It is confined between the bases of the protoconid and hypoconid as a thickened bulge of enamel. The paraconid which is more reduced than in *Micromurexia, Murexia* and *Phascomurexia* but similar to that seen in *Paramurexia* and *Murexechinus*, appears in occlusal view as a small steeply-sided or low spur, the lingual edge of which makes an appreciable swelling on the

endoloph of M_1 in *bellus, godmani, minimus* but little or no contribution in *leo, swainsonii, adustus, agilis, subtropicus, flavipes* or *stuartii*. The metacristids are roughly oblique to the long axis of the dentary. The cristid obliqua extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point directly below the tip of the protoconid in *bellus, leo, godmani*, but slightly lingual to that in the other species (*stuartii* sometimes slightly buccal). From the base of the metaconid posteriorly, the talonid endoloph may follow the line of the dentary past the base of the entoconid and along the dentary line to the hypoconulid as in *leo, swainsonii, minimus, adustus* or it may take a sharp lingual orientation until it meets the base of the entoconid where it then orients buccally to meet the hypoconulid (*bellus, godmani, stuartii*). In M_1 the entoconid is usually minute or low.

In M_2 the talonid is usually wider than that of the trigonid. The anterior cingulum is poorly developed in all species and terminates lingually to accommodate the hypoconulid notch and continues very weakly into the buccal cingulum which terminates slightly anterior to a vertical line drawn through the tip of the hypoconid. Buccal cingula are strongly present only in *A. leo*, and posterior cingula in *leo, bellus, swainsonii* and *adustus*. The paraconid is well-developed throughout but is the smallest trigonid cusp. It is slightly taller than the entoconid which is well developed in *godmani, swainsonii*, variably in *stuartii* and weakly developed in the rest. Its greatest reduction is seen in *bellus, leo* and *flavipes*. The hypoconid is shorter than the entoconid. The metacristid is more steeply inclined from the protoconid to the metacristid fissure than from the entoconid to the metacristid fissure. The cristid obliqua extends to the base of the protoconid, intersecting the trigonid at a point directly below the protoconid tip, but well buccal to the metacristid fissure. From the base of the entoconid posteriorly, the talonid endoloph follows the line of the dentary axis in *leo, godmani, swainsonii, minimus* and *adustus*, but takes a more lingual orientation in *bellus* and *stuartii*, and a more buccal orientation in *flavipes*.

In M_4 of most species the talonid is slightly wider than the trigonid. The anterior cingulum is poorly developed in all but *leo* and *adustus* and buccal and posterior cingula are weak in all but *leo* and *bellus*. The cristid obliqua intersects the trigonid at a point more buccal to the longitudinal vertical mid-line through the protoconid tip than

in M_2. This intersection does not, however, reach the point directly below the metacristid fissure. The endoloph of the talonid in M_3 orients directly along the line of the dentary in *bellus, godmani, adustus* but takes a more buccal orientation in *leo, swainsonii, minimus, flavipes* and variably in *stuartii*. The entoconid is relatively tall only in *minimus, godmani, adustus* and variably in *stuartii, agilis* and *subtropicus*.

The M_4 trigonid is wider than the talonid. The anterior buccal and posterior cingula are as in M_2 and M_3. The paraconid is shorter than the metaconid. Talonid cusps are reduced to 2 in *bellus, adustus, stuartii, agilis, subtropicus, swainsonii, minimus* and *godmani* and 1 in *leo* and *flavipes*. The hypoconid is reduced relative to M_3. The cristid obliqua is a high crest which intersects the trigonid directly below the metacristid fissure, this being markedly more lingual than intersections of the cristid obliqua for M_1-M_3.

Skull, Externals, etc. The skulls of *swainsonii, minimus* and *godmani* are the most elongate (skull width across lachrymals: length I^1 to lachrymal canal 76-84%), followed by *leo, flavipes, stuartii, agilis, subtropicus* (85-93%) and the broadest rostrum is found in *bellus* and *adustus* (94-102%). Nasal fluting is rarely found, but the condition is sometimes suggested in *leo*. The tympanic wing of the alisphenoid is generally poorly developed in all except *bellus* where there is moderately greater expansion. The pars mastoidea and adjacent squamosal are poorly expanded in all species and only in *bellus* is the skull 'Roman nosed'. It is slightly domed in *swainsonii* and *minimus*. Squamosal/frontal contact does not occur in any species, nor do palatine vacuities. Anterior palatal vacuities are very large in *swainsonii, minimus* and smallest in *bellus*. Posterior palatal vacuities are largest in *swainsonii* and *subtropicus*. Only in *bellus, leo* and *godmani* is the supratragus folded. The tail is shorter than the head-body length, but it is further reduced in *swainsonii* and *minimus*. All hind foot pads are striated and very long claws are found in *swainsonii* and *minimus*. All species lack body stripes and all females possess a rudimentary (ephemeral) pouch in which nipple number may vary from 6 (*godmani, adustus*) to 10 (*leo, bellus*) to variable (all others). All males die soon after mating.

REMARKS. The analysis that follows suggests that *Phascogale* is monophyletic with *Antechinus*, and represents antechinuses in their most derived state. This is supported by albumin immunology assessment (Baverstock et al., 1990; Aplin et al., 1993) but not through cytochrome b sequence analysis (Krajewski et al., 1993, 1996). Until some consensus is reached between the biochemical and morphological schools on this and broader New Guinea issues discussed later, I am reluctant to propose that *Phascogale* should accomodate all Phascogalines (sensu Archer, 1982a) or that *Antechinus*, revert to subgeneric status to accomodate all antechinuses.

Micromurexia gen. nov.

Antechinus (in part) Macleay, 1841.

TYPE AND ONLY SPECIES. *Antechinus habbema* Tate & Archbold, 1941: 8), based on AMNH 109812, adult ♂ puppet skin with skull extracted, from 9km NE of Lake Habbema, N slope of Mt Wilhelmina, Irian Jaya, 4°05'S, 138°50'E, at 2,800m.

GENERIC DIAGNOSIS. M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. Talonid on M_4 relatively unreduced, retaining an entoconid, hypoconid and hypoconulid. Tail longer than the head-body length.

It is distinguished from *Phascolosorex* and *Myoictis* by its lack of dorsal body stripes, and from *Neophascogale* by lacking a white tail-tip.

Micromurexia is separable from *Phascomurexia* by the absolutely shorter length of its upper and lower molar rows.

Micromurexia differs from *Murexechinus* by: ears lack post-auricular patches and pelage more uniform shade throughout rather than rufous post-auricular patches and definite warming of tones toward rump; claws slightly curved and slender rather than strongly curved and thick; tail dorso-ventrally bicoloured rather than uniform black (sometimes uniform dark brown); I^1 narrow, needle-like and minutely crowned rather than broad, claw-like and heavily crowned; I^{2-4} uncingulated, narrow and with minimal curvature of the crown rather than strongly cingulated buccally and lingually, blade-like and robust; C^1 extremely long and slender rather than short and thick; premolars uncrowded and narrow with P^1 separate from P^2 rather than premolars crowded, wide and robust; lower molars with greatly developed entoconids (e.g., M_3 entoconid taller than paraconid in *Mi. habbema*) rather than lack of development in *Mu.*

melanurus (where in M3 entoconid is shorter than paraconid); nasals raised and fluted.

Miicromurexia is separable from *Murexia* by its smaller values for the following measurements (the ranges (R) associated with each measurement do not overlap (Tables 1, 4)); BL, ZW, OBW, IBW, R-LC^1, R-LM^1, R-LM^2, R-LM^3, R-LM^{1}T, I^1-M^4, P$^{1-3}$, M$^{1-4}$, M^{2}W, I$_1$-M$_4$, P$_{1-3}$, M$_{1-4}$, M$_2$W, TL and HF.

Micromurexia is separable from *Paramurexia* by its smaller values for the following measurements (ranges (R) associated with each measurement do not overlap (Tables 1, 5)); BL, ZW, OBW, IBW, R-LC^1, R-LM^1, R-LM^2, R-LM^3, R-LM^{1}T, I^1-M^4, M$^{1-4}$, M^{2}W, I$_1$-M$_4$, P$_{1-3}$, M$_{1-4}$, M$_2$W. It lacks a black, dorsal body stripe.

Micromurexia habbema
(Tate & Archbold, 1941)
(Figs 2, 3, 6, 7)

Antechinus habbema Tate & Archbold, 1941: 3.
Antechinus hageni Laurie, 1952: 296.

HOLOTYPE. American Museum of Natural History, AMNH 109812. Adult male puppet skin with skull extracted (both skin and skull in excellent condition, but teeth badly worn).

TYPE LOCALITY. 9km NE of Lake Habbema, north slope of Mt Wilhelmina, Irian Jaya, 4°05'S, 138°50'E at 2,800m

COLLECTOR. W.B. Richardson, 21 October 1938.

DIAGNOSIS. As for genus.

DESCRIPTION. Holotype AMNH 109812. *Pelage* (Fig. 2). Fur of the mid-back (7.7mm long) with the basal 6.4mm Slate Color, median 1mm Clay Color and apical 0.3mm black (Fuscous). The back appears overall to be Sepia. Medially thickened Fuscous spines (guard hairs) are interspersed through the fur and are up to 12mm long on the rump (basal 7.5mm Slate, median 2.5 Fuscous, apical 2mm colourless) and reduce to 2mm where they terminate between the eyes on the crown of the head. Fur on and below the shoulders, thighs flanks and chin lacks black (Fuscous) tips on guard hairs and these areas and belly appear Cream Buff to Chamois. The harshness of the guard hairs is reduced from rump to crown by the apical 2mm being colourless — this giving a warmer tone to the fur colour compared to specimens from Mt Wilhelm. At the anterior corner of each eye a small patch of dark hairs sweeps to midway along the top and bottom eyelid thereby creating a half eye-ring. The remainder of fur around the eye is an orange-brown (Sepia). A warm patch of Clay Color hairs is found anterior to each pinna. The soft ventral fur (8mm long on the belly) is Dark Neutral Gray on the basal 6mm and Pale Cinnamon-Pink on the apical 2mm and is interspersed with Cream-Buff medially thickened guard hairs 10mm long. The belly is thus an overall patchy Greyish Olive. Forefeet are very thinly covered with Hair Brown (greyish-brown) hairs. Hindfeet are more thickly covered with a mixture of white and Hair Brown hairs, giving the feet a peppered appearance. The tail (Figs 6, 7) is weakly bicoloured with short dorsal hairs averaging 2mm along its length and increasing to 4mm at its tip. These dorsal hairs are a uniform Saccardo's Umber. Hairs on the ventral surface are longer, averaging 5mm along its length increasing to 7mm at the tip. (This ventral 'crest' has been screwed around to the right hand side during preparation of the puppet skin). These ventral hairs are also uniform Saccardo's Umber.

Vibrissae. Approximately 17 mystacial vibrissae occur on each side and are up to 18mm long. The more dorsal mystacial vibrissae are coloured Fuscous Black while those lower are colourless; supra-orbital vibrissae (Fuscous Black becoming clear) number 1 left and 2 right; genals (Fuscous Black and colourless) number 8 left and 7 right; ulna-carpals (colourless) number 4 right and 5 left; submentals (colourless) number 4.

Tail (Figs 6, 7). The tail is much longer than the head and body length but in the holotype the tip of the tail has been broken off. It is thin and tapers toward the tip.

Hindfoot. Long hallucal and post-hallucal pads are narrow and fused. Apical granules are fleshy, enlarged, elongate and striate. There is an auxiliary apical granule outside and adjacent to the first interdigital pad. No other auxiliary granules are visible.

Ears. Pinnae large, with complex supratragus, posterior margin thickened, distal end reflected ventrally, reflected tip slightly concave.

Dentition (Fig. 3). Upper Incisors: I^1 is narrow and needle-like, slightly procumbent and heavily worn on the crowns, taller crowned than all upper incisors and separated by a small diastema from I^2. Left and right I^1 are widely separated and the crowns appear to be directed away from each other. Crown height for I$^{2-4}$ is difficult to judge as all are badly and irregularly worn. I^4 appears to be greater in crown height than I^3 which appears to be greater than I^2. All upper incisors are badly worn but appear to lack buccal and lingual
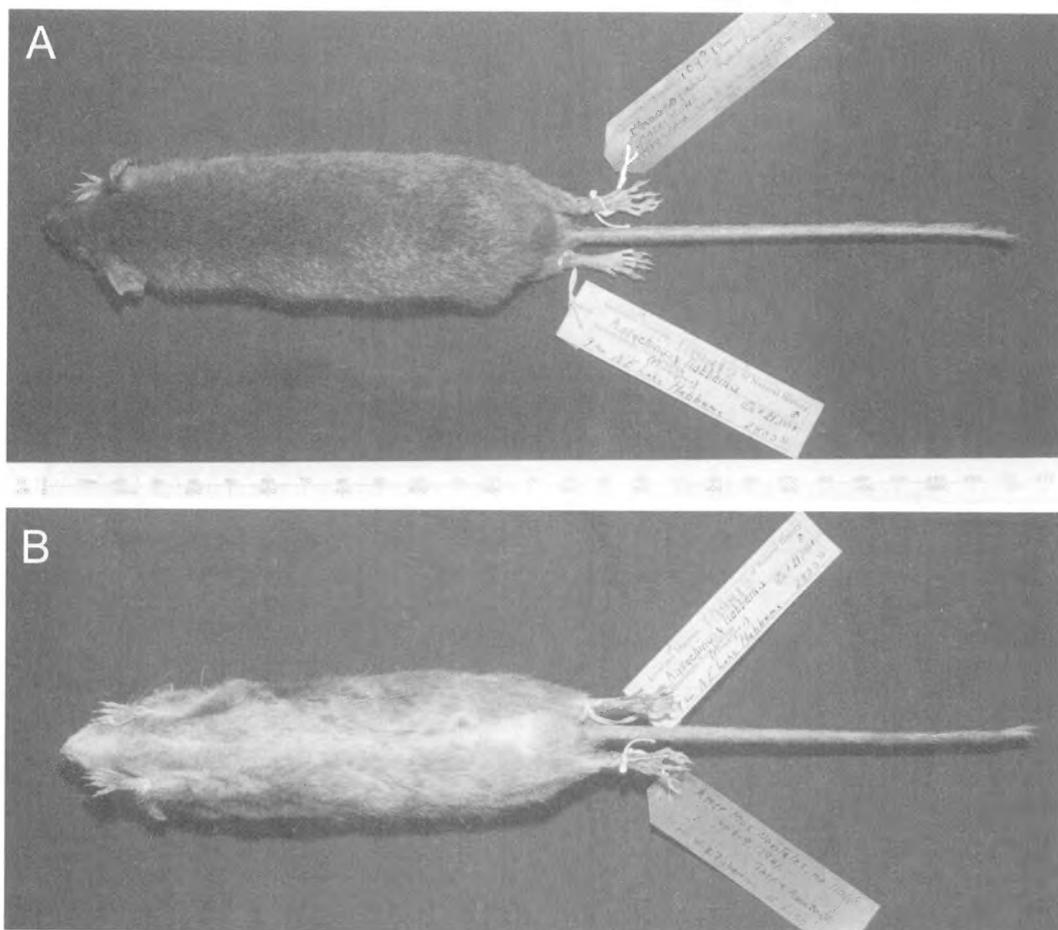
FIG. 2. Holotype of *Antechinus habbema* Tate & Archbold, 1941 (now *Micromurexia habbema*). AMNH 109812, study skin; A, dorsal view; B, ventral view. TL = 252mm; HB = 112mm; TV = 140mm; HF = 21mm; E = 13mm.

cingula. I^4 carries no anterior or posterior cusp, although excessive wear may have eliminated these. Roots of I^4 are wide.

Upper Canines: C^1 is slender and caniniform with no appreciable boundary between root and crown. There are no buccal or lingual cingula. R and L C^1 are abnormally worn with thegotic wear anteriorly and posteriorly over the tip. Posterior notching occurs at the root level. The thegotic wear appears to have been caused by poorly occluding R and L C_1.

Upper Premolars: The premolar row is long, narrow and characterized by the separation of P^1 from P^2 and P^3. There is a diastema between C^1 and P^1, but LP^2 touches LP^3; RP^2 is separated from RP^3. P^1 and P^2 carry strong buccal and weak lingual cingula but P^3 lacks a lingual cingulum

and its buccal cingulum is weak. P^1 crown is shorter than P^2 crown which is shorter than P^3. P^3 has a massive posterior root. There are small but clearly definable anterior cingular cusps on P^1 and P^2. No posterior cusps are visible although the poorly occluding lower jaw has caused excessive, abnormal wear to P^1 resulting in its posterior half having been worn away.

Upper Molars: All upper molars are excessively worn. The posterior tip of P^3 lies in the parastylar corner of M^1. In M^1 stylar cusp A is worn away. The anterior cingulum below stylar cusp B is so badly worn that it is impossible to tell if it is complete. Stylar cusp B and the M^1 paracone are worn off and there is no protoconule present. Stylar cusp C is not visible on either L or RM^1 and stylar cusp E is not visible. M^1 has a weak

posterior cingulum. The RM^1 metacone is worn off to be coplanar with the trigon basin. Stylar cusp D is worn away.

In M^2 the paracone is worn almost away and the anterior cingulum is difficult to detect, however it seems narrow, contacting the metastylar corner of M^1 and tapering quickly down to the base of the protocone apex. There is no visible protoconule. M^2 lacks stylar cusps A, C and E. Stylar cusp D is very high but this is probably an artefact of the metacone's wearing away. There is a weak posterior cingulum on LM^2. RM^2 is worn down to the level of the posterior cingulum.

In M^3 the anterior cingulum is worn but is probably narrowly present. There is slight evidence of an anterior cingulum at the base of the paracone. Stylar cusp D is reduced to a very small blunt peak. Stylar cusps C and E are absent.

In M^4 the anterior cingulum appears complete. The paracone is greatly worn and a posterior cingulum is absent. The protocone is reduced and narrow. A small crest analogous to the metacone is present. In occlusal view the angle between postprotocrista and premetacrista is close to $80°$.

Lower Incisors: I_1 is taller in crown height than I_2. I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is slightly taller in crown height than I_3. I_3 is small, premolariform in lateral view with an inconspicuous posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent posterolingual lobe, and crown enamel of the primary and posterior cusp folds slightly lingually such that the longitudinal crest of the 2 cusps bisects the tooth, with 1/3 of enamel buccal to the crest and 2/3 lingual.

Lower Canines: C_1 is slender and caniniform, with erect projection and slight curvature from root to crown tip. It has weak buccal and lingual cingulation and no posterior cusp. Both R and L C_1 sustain appalling, abnormal thegotic wear in the form of deep posterior cuts where the ill-occluding C^1 has stabbed into the posterior half of the lower canine.

Lower Premolars: P_{1-3} are unevenly spaced with RP_1 almost touching RP_2 which almost touches RP_3. LP_1 is widely separated from LP_2 which nearly touches LP_3. They are weakly cingulated buccally and lingually. In crown height P_2 is taller than P_3 which is taller than P_1. All premolars are narrow. All possess posterior cusps. P_1 possesses a minute anterior cusp. The bulk of each premolar

mass is concentrated posteriorly to a line drawn transversely through the middle of the two premolar roots. Postero-lingual lobes are not a feature of the slender lower premolars.

Lower Molars: All lower molars are worn, they are narrow and lie in a relatively short premolar row. The M_1 talonid is much wider than the trigonid and the anterior cingulum is poorly developed. It originates at the anterior base of the paraconid and terminates at the anterior base of the protoconid. There is a very weak buccal cingulum. The well-developed paraconid appears in occlusal view as a small oblique spur, the lingual edge of which makes no appreciable swelling on the endoloph of M_1. In lateral view the paracristid is almost $45°$ to the horizontal from the paraconid to the paracristid fissure, and $25°$ from the paracristid fissure to the protoconid (measured from the vertical, posteriorly). The metacristid is slightly oblique to the long axis of the dentary while the hypocristid is transverse. The protoconid and paraconid are worn, and the talonid basin eroded so badly that the cristid obliqua is short and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid slightly lingual to that point probably directly below the worn-off tip of the protoconid.

The hypocristid terminates midway between the hypoconulid without veering toward the very tall, broad entoconid. From the base of the metaconid posteriorly, the talonid endoloph takes a very sharp lingual orientation then swings back buccally, posterior to the entoconid, until the base of the hypoconulid.

In M_2 the talonid is wider than the trigonid. The anterior cingulum is poorly developed originating lingually at a very weak and worn parastylid notch against which the M_1 hypoconulid is abutted. There is no buccal cingulum. A narrow, weak posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is badly worn and is the smallest trigonid cusp (even the entoconid is taller). The entoconid is tall and there is no metastylid present. The cristid obliqua extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point which cannot be assessed from the badly worn protoconid and metaconid. The hypocristid extends from slightly anterior and buccal to the hypoconulid to the tip of the hypoconid. From the base of the metaconid posteriorly, the endoloph bulges out lingually around the entoconid swelling, and buccally to the hypoconulid tip.

In M_3 the trigonid is narrower than the talonid. A small parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3. The posterior cingulum is as in M_2. The cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid, and directly below the metacristid fissure. The entoconid is very tall. The endoloph takes a more buccal orientation than that seen in M_2 so that only a swelling of entoconid is seen in occlusal view. The rest of M_3 morphology is as in M_2.

In M_4 the trigonid is wider than the talonid. The anterior cingulum is as in M_2 but more poorly developed and a posterior cingulum is absent. Of the 3 main trigonid cusps the metaconid is slightly taller than the paraconid, but both are dwarfed by the protoconid. The hypoconid of M_4 is small in comparison to that on M_3. Between the hypoconid and the base of the metacristid the cristid obliqua forms a low, worn crest which contacts the trigonid wall below the metacristid fissure. There is no reduction of talonid crown enamel below the cristid obliqua so the talonid appears (in occlusal view) as a wide shelf extending from the trigonid wall. The entoconid is prominent as are the hypoconulid and hypoconid.

Skull (Fig. 3). The skull of *habbema* has a high, domed braincase, depressed and concaved frontals, raised and fluted nasals and a squarish, 'dog-faced' rostrum. The left and right alisphenoid tympanic bullae are widely separated and very weakly enlarged. The foramina pseudovale are very large and are not bisected by a bridge of the alisphenoid. The eustachian canal opening is large and the entocarotid foramina are just anterior to the foramen pseudovale. The internal jugular canal foramina are small, the canals are low and obscure. The posterior lacerate foramina are large and exposed but the entocarotid foramina are small and hidden. The premaxillary vacuities extend from the level of the I^2 root back to the level of the posterior edge of the C^1 root. The large maxillary vacuities extend from the level of the metacone root of M^1 and back to the level of the protocone root of M^4. Single large palatine vacuities (left and right) occur posterior to the maxillary vacuities.

SYNONYM

Antechinus hageni Laurie, 1952 (Figs 4, 5)

HOLOTYPE. BMNH 50.1829, adult ♂ puppet skin and skull (both in excellent condition).

TYPE LOCALITY. Mt Tomba, SW slopes of Hagen Range, Central Highlands, PNG, 05°50'S, 144°02'E. altitude 2,501m. Coll. F. Shaw Mayer, 30 June 1947.

The holotype differs from the holotype of *habbema* in the following respects.

Pelage (Fig. 4). It has a more luxurious fur covering than *A. habbema*. The fur of the mid-back is 12mm long with the basal 9.75mm Slate Color, median 1.25 Clay Color and the apical 1mm black. Medially-thickened Fuscous Black guard hairs are up to 15.5mm long on the rump and reduce to 5.7mm where they terminate at the crown of the head posterior to the rhinarium. The tail is bicoloured with mid-dorsal hairs averaging 2.8mm (Clove Brown) and mid-ventral hairs averaging 5.8mm (Olive Buff). At the tail tip, dorsal hairs are as long as 5.3mm (Clove Brown) while the ventral crest hairs are up to 13.5mm (Olive Buff).

Hindfoot. The left hind foot hallucal and post-hallucal pads are fused, while in the right foot they are separate. Auxillary apical granules occur outside first and third interdigital pads on left and right hind feet. A post, third-interdigital granule occurs on left and right hind feet.

Dentition (Fig. 5). Teeth are unworn and allow description of features lost in the *habbema* type.

Upper Incisors: I^1 is narrow, needle-like, slightly procumbent with an extremely high crown. Left and right I^1 are widely separate and the tops of the crowns are directed away from each other in the direction of the dentary line. It is difficult to detect a gradation of crown size in the upper incisors, but it appears as if I^4 crown is larger than I^3 which is larger than I^2. All are weakly cingulated buccally. I^4 has no anterior or posterior cusp.

Upper Canines: C^1 is very long and slender with an extremely weak buccal cingulum indicating the very high crown, at least mid-way up the exposed tooth.

Upper Premolars: $P^3 > P^2 > P^1$. All carry strong buccal cingula but no lingual cingula. All are spaced, with contact occurring only between M^1 and P^3. There is no posterior cusp on P^3.

Upper Molars: The posterior tip of P^3 is in the parstylar corner of M^1 but lingual to, and just below stylar cusp A in the left dentary, and level with stylar cusp A in the right dentary. Stylar cusp A is prominent. The anterior cingulum of M^1 is very broad and complete, and stylar cusp B is much greater in mass than the paracone. There is a small protoconule present as well as a small bulge of enamel directly below it on the face of
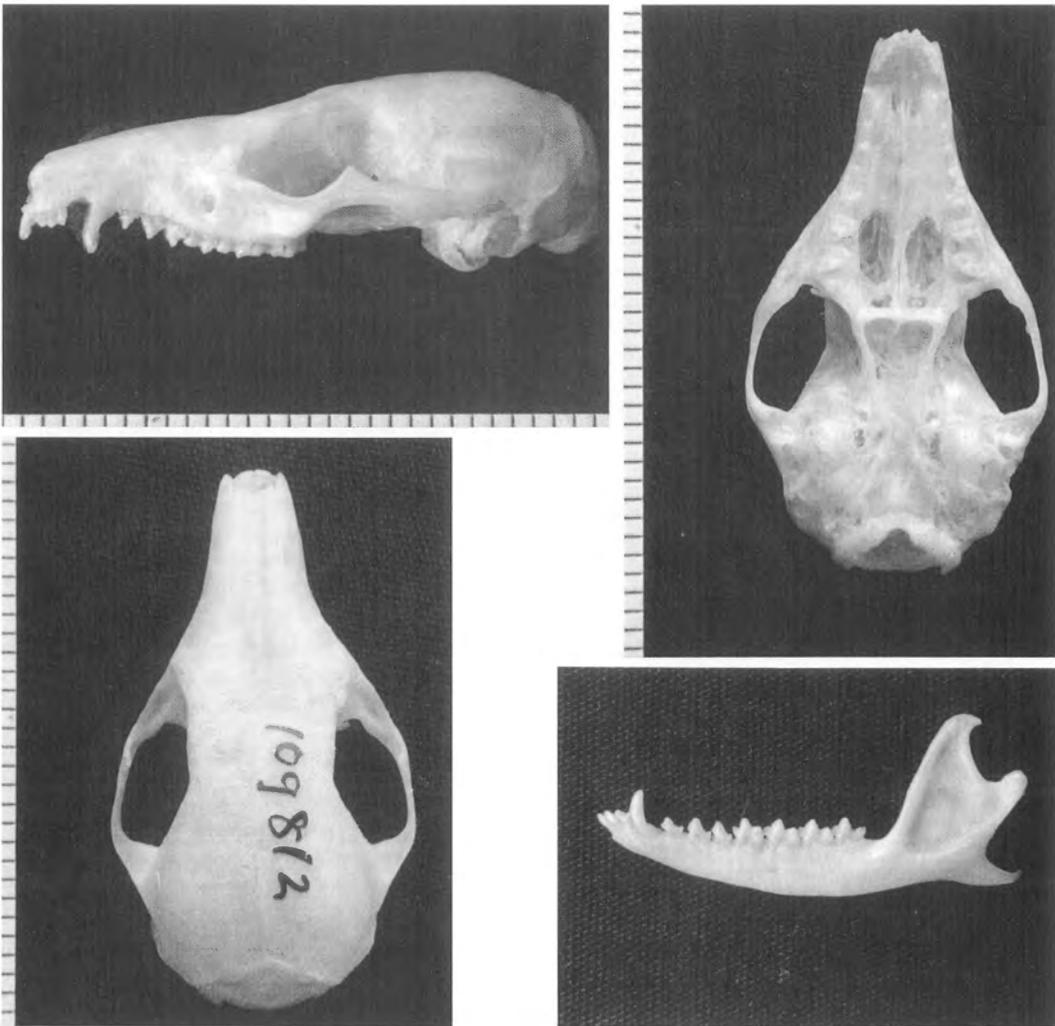
FIG. 3. Holotype of *Antechinus habbema* Tate & Archbold, 1941 (now *Micromurexia habbema*). AMNH 109812, cranium and dentary. Sex = m; BL = 26.75; ZW = 16.51; IO = 7.73; OBW = 10.71; IBW = 4.46; R-LC^1 = 5.14; R-LM^1 = 9.30; R-LM^2 = 11.10; R-LM^3 = 13.08; R-LM^{1}T = 7.35; M^{2}W = 1.71; I^1-M^4 = 14.70; P$^{1-3}$ = 3.35; M$^{1-4}$ = 6.24; Dent = 21.38; I$_1$-M4 = 12.87; P$_{1-3}$ = 3.57; M$_{1-4}$ = 6.81; M$_2$W = 1.06.

the anterior protocrista. Stylar cusps C and E are absent. There is no posterior cingulum.

In M^2 the anterior cingulum is very broad and complete as far as the small protoconule. Stylar cusps A, C and E are absent. Stylar cusp D is tall in M^2, and is considerably taller than in M^1. There is no posterior cingulum present.

In M^3 the anterior cingulum is broad and complete but narrow at the base of the paracone. Stylar cusps A, C and E are absent and D is reduced to a low cutting crest.

In M^4 the protocone is reduced but still relatively broad. There is some metacone development although this is minimal and does not constitute a true metacone. It is such that in occlusal view the angle made between the post-protocrista and the premetacrista is close to 80°.

Lower Incisors: In crown height I$_1$ is greater than I$_2$ which is greater than I$_3$. I$_3$ is premolariform in lateral view with a very low open notch formed by primary and secondary cusps.

Lower Canines: C_1 slender, tall, erect, with very slight curvature from root to crown, with very weak buccal and lingual cingulation. Diastema between C_1 and P_1 is equal to that between P_1 and P_2 which is greater than the diastema between P_2 and P_3. P_3 touches M_1. In overall size P_2 is larger than P_3 which is larger than P_1.

Lower Molars: The anterior cingulum on M_1 is very poorly developed and the paracristid (in lateral view) is vertical from the paracristid fissure to the protoconid. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the protoconid tip. Hypocristid is complete from hypoconulid to hypoconid. The entoconid is very large.

In M_2 the talonid is equal in width to the trigonid. There is a slight buccal cingulum. The very tall entoconid is of equal height to the paraconid. The cristid obliqua extends from the hypoconid to the posterior trigonid wall intersecting the trigonid at a point lingual to that point directly below the protoconid tip but buccal to that point directly below the metacristid fissure.

In M_3 the trigonid is wider than the talonid. The cristid obliqua intersects the trigonid at a point well lingual to that point directly below the tip of the protoconid but buccal to the point directly below the tip of the metacristid fissure.

In M_4, although there is greater reduction in the 'buccal cingulum' than in the holotype of *habbema*, the 3 cusps of the talonid — the entoconid, hypoconulid and hypoconid are very well developed and prominent.

Skull (Fig. 5). As for the holotype of *habbema* but in *hageni* the premaxillary vacuities extend from the I^2 root back to the level of the middle of the C^1 root. The large maxillary vacuities extend from the level of the protocone root of M^1 and extend back to the level of the metacone root of M^3. There are no palatine vacuities.

ADDITIONAL DIAGNOSTIC FEATURES

Micromurexia habbema differs from all other dasyurids in the combination of: 1, extremely thin, spur-like crown in I^1 which is needle-like and only slightly procumbent; 2, a slightly cingulated upper incisor row where $I^2<I^3<I^4$; 3, extremely long, thin, needle-like upper canines in which the root and crown are undifferentiated, and in which there is no posterior cusp; 4, an upper premolar row in which the cingulated teeth are uncrowded yet in which P^1 and P^2 are slightly rounded with accompanying postero-lingual lobing; 5, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave; 6, M^1 stylar cusp B large and only slightly smaller than stylar cusp D; 7, M^4 protocone broad and anterior cingulum complete; 8, M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone; 9, M^4 metacone relatively large; 10, a poorly cingulated lower premolar row in which the narrow teeth are widely spaced and where P_3 is slightly smaller than P_2; 11, uncingulated P_3; 12, well-developed paraconid on M_1; 13, 3 well-developed cusps on M_4 talonid; 14, tall entoconid on M_2; 15, metacristids and hypocristids not transverse to the long axis of the dentary; 16, fluted nasals; 17, poorly developed tympanic wing of the alisphoid which is contrasted by an expanded pars mastoidea and adjacent squamosal; 18, skull markedly domed posterior of the frontals; 19, tail with small ventral crest along entire length, the tail being longer than the head-body length; 20, polyoestrous, and only 4 nipples.

In addition to the diagnosis, *habbema* differs significantly (P<0.001) from *P. naso* as follows (measurements are means, mm): shorter total length TL (246:275); shorter tail T (135:149); shorter ear length E (16.95:18.40); shorter basicranial BL (26.70:30.13); narrower zygomatic ZW (15.56:17.45); narrower outside bullae OBW (10.43: 11.57); narrower inside bullae IBW (4.72: 5.81); narrower rostral widths L-RC^1 (5.00:5.91), L-RM^1 (8.87:10.57), L-RM^2 (10.49:12.97), L-RM^3 (12.76:15.48); shorter upper tooth row I^1-M^4 (15.02:17.32); shorter upper premolar row P^{1-3} (3.85:4.63); narrower upper second molar M^2W (1.73:2.02); shorter dentary Dent (21.46: 24.23); shorter lower tooth row I_1-M_4 (13.12: 15.18); shorter lower premolar row P_{1-3} (4.08:4.73); narrower lower second molar M_2W (1.11:1.31); semi-straight, slender claws rather than strongly curved and thick; tail well-haired dorsally and ventral crest hairs long throughout rather than tail almost naked dorsally with weaker ventral crest developing at the tip. The likely presence of auxiliary apical granules outside the interdigital pads of the hind feet and non-fused hallucal/post-hallucal pads, rather than no auxiliary granules and always fusion between hallucal and post-hallucal pads; the tip of the tail skin never white, often white in *P. naso* (49%).

M. habbema differs significantly (P<0.001) from *Mu. melanurus* by ear length E (16.95: 15.83); narrower zygomatic width ZW
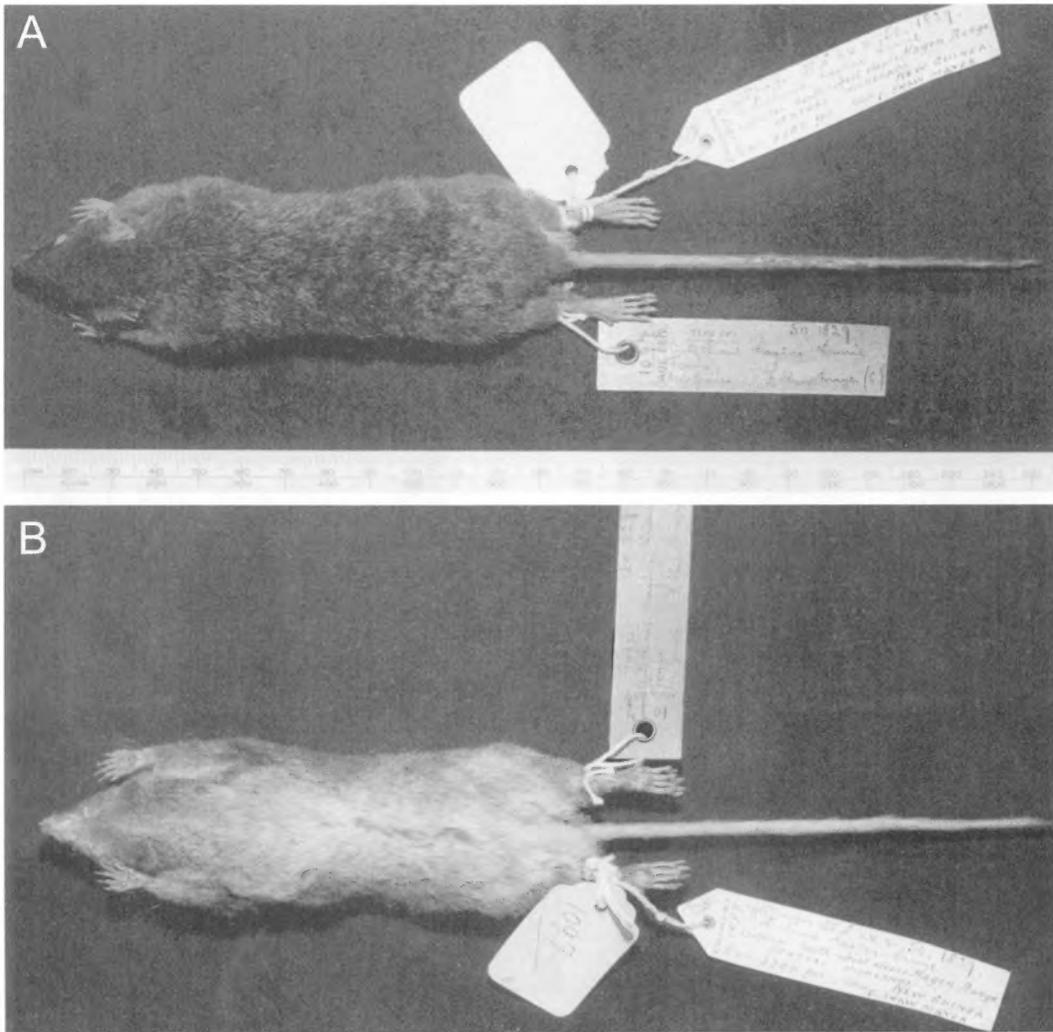
FIG. 4. Holotype of *Antechinus hageni* Laurie, 1952 (now *Micromurexia habbema*). BMNH 50.1829, study skin; A, dorsal view; B, ventral view. TL=234mm; HB=109mm; TV=125mm; HF=21mm; E=17.5mm.

(15.56:16.89); broader interorbital width IO (7.62:7.09); narrower postcranial width measured outside bullae OBW (4.72:5.12); narrower width inside bullae IBW (4.72:5.12); narrower rostral widths L-RC^1 (5.00:5.43), L-RM^1 (8.87:9.71), L-RM^2 (10.49:11.91), L-RM^3 (12.76:14.12); longer upper premolar row P$^{1-3}$ (3.85:3.37); shorter upper molar row M$^{1-4}$ (6.38:6.78); narrower upper second molar M^{2}W (1.73:1.89); longer lower premolar row P$_{1-3}$ (4.08:3.45); shorter lower molar row M$_{1-4}$ (6.86:7.37); narrower lower second molar M$_2$W (1.11:1.22); the likely presence on the hind foot of auxiliary apical granules and unfused hallucal/post-hallucal pads rather than no auxiliary apical granules and always fused hallucal/post-hallucal pads.

M. habbema differs significantly (P<0.001) from *Murexia longicaudata* by: shorter dentary DL (21.46:36.17); shorter tail T (135:197); shorter ear E (16.95: 20.50); semi-straight slender claws rather than strong, thick, curved claws; tail well-haired dorsally with long ventral crest throughout rather than semi-naked tail with very weak ventral crest; silky fur rather than short spinous fur; hindfoot without the post metatarsal
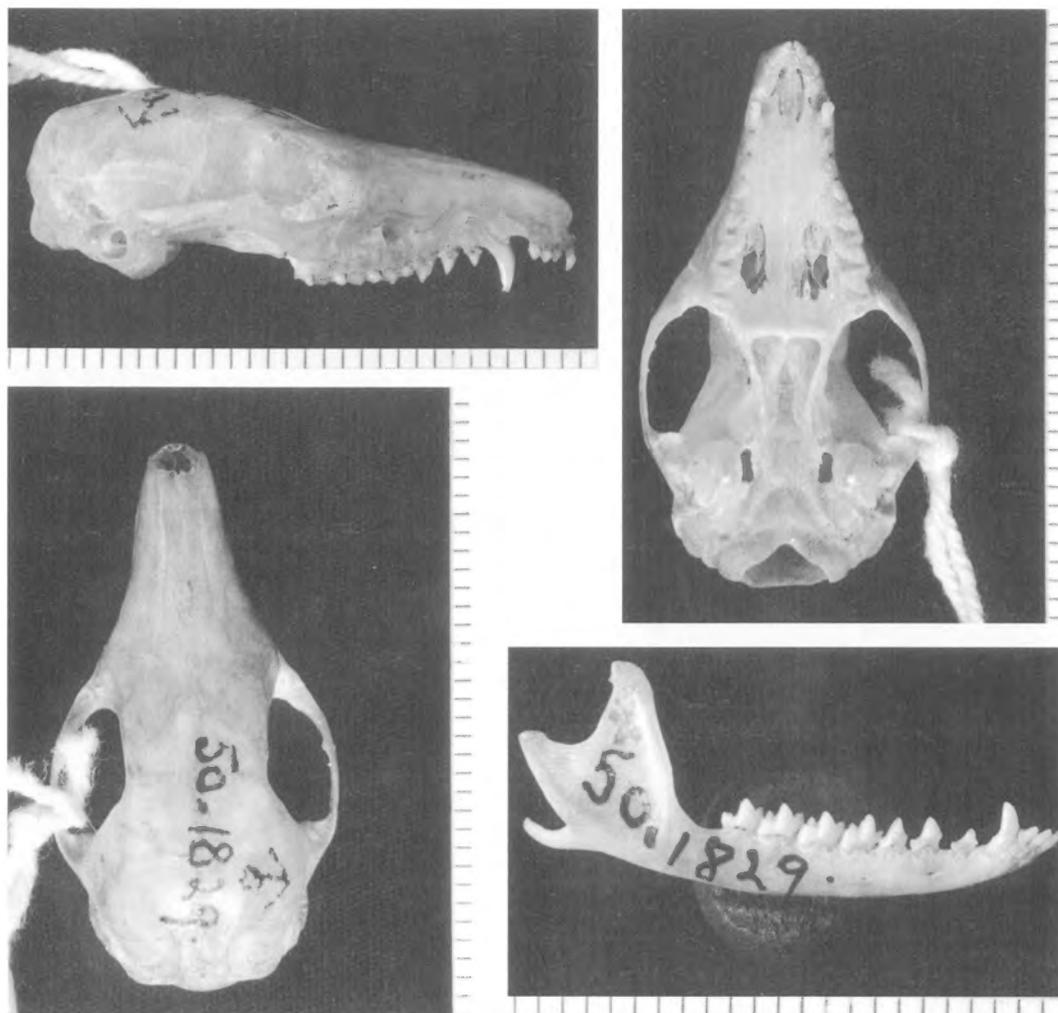
FIG. 5. Holotype of *Antechinus hageni* Laurie, 1952. BMNH 50.1829, cranium and dentary. Sex = m; BL = 27.71; ZW = 16.00; IO = 7.78; OBW = 10.86; IBW = 4.90; R-LC^1 = 5.24; R-LM^1 = 9.57; R-LM^2 = 11.18; R-LM^3 = 13.27; R-LM^{1}T = 7.50; M^{2}W = 1.69; I^1-M^4 = 15.58; P$^{1-3}$ = 4.18; M$^{1-4}$ = 6.24; Dent = 22.26; I$_1$-M$_4$ = 13.58; P$_{1-3}$ = 4.43; M$_{1-4}$ = 6.75; M$_2$W = 1.11.

pads often present in *longicaudata*; the likely presence of auxiliary apical granules on the hind foot, rather than no auxiliary apical granules.

M. habbema differs significantly (P<0.001) from *P. rothschildi* as follows: shorter upper premolar row P$^{1-3}$ (3.85: 4.77); shorter dentary Dent (21.46: 28.33); shorter tail T (135: 168); shorter hind foot HF (22: 27); shorter ear E (16.95: 19.92); semi-straight, slender claws rather than strongly curved claws; hindfeet lack post-metatarsal pads.

REMARKS. *Taxonomic History*. Six years after *Antechinus habbema* was described, Tate (1947) announced that he and Archbold had inadvertently described the species from a mismatched skin and skull. To remedy the situation Tate (1947) proposed to restrict use of *habbema* to the skin of the holotype which he, in turn, made a junior synonym of the species *mayeri* (originally described as *tafa centralis*, here regarded as *Phascomurexia naso*). The skull he assigned to a new species, *A. wilhelmina* (here regarded as

Murexechinus melanurus) which he described in the same paper.

The description of *hageni* Laurie, 1952, from Mt Tomba (Hagen Range), 550km E of the type locality of Tate & Archbold's *habbema* (Lake Habbema, Irian Jaya), was quickly followed by Laurie & Hill's (1954) submersion of *hageni* into Tate's *wilhelmina*. Laurie's synonymy was followed thereafter, and subsequent references to the third New Guinea 'antechinus' species (the others being *naso* and *melanurus*) have been made under *wilhelmina* e.g., Honacki et al. (1982), Corbet & Hill (1980), Kirsch & Calaby (1977), Ziegler (1977), Baverstock et al. (1990). Other authors (Westerman & Woolley, 1993; Woolley, 1994; Krajewski et al., 1996, Armstrong et al., 1998) regard *wilhelmina* as a fourth New Guinea species of 'antechinus' (with *habbema*, *naso* and *melanurus*). I have examined the holotype of *habbema*, *hageni*, *tafa centralis* and *wilhelmina* and I have no doubts that, despite the similarities in skins of the 2 former and skulls in the 2 latter species, Tate was mistaken in his assumption that a mismatch had occurred. Justification for the retention of *habbema* as the senior synonym, and the rejection of Tate's assumption is as follows.

The skin. External body dimensions (e.g. HB, TV, E, HF) for the skin of the *habbema* holotype are at odds with those of the *tafa centralis* holotype and the series. The *habbema* holotype is an old adult ♂ in which the combined head, body and tail length is 252mm. While this is average for the series of adult *habbema* males (N=26), only two adult males from the entire *naso* series (i.e., *naso*, *tafa*, *tafa centralis*, *mayeri misim*, *Murexia longicaudata parva* types and series, N=26) were recorded with such a low corresponding value. Even few adult females of *M. naso* (2 of 22) had corresponding values as low. The hind foot measurement of the *habbema* holotype is given as 21mm. No male examined in the entire *naso* series (N=25) had a hind foot as small as the *habbema* holotype. Ear (crown) measurements for the *habbema* holotype is given as 13mm. No specimen of *naso* for which crown-ear measurements were provided (N=12) had an ear as small as 13mm.

The tail of the *habbema* holotype is well-haired with relatively long hairs dorsally (2mm increasing to 4mm near the tip) and a long ventral 'crest' (hairs 5mm increasing to 7mm near its tip [tip broken], 13mm in the *hageni* holotype). This compares badly with the typically semi-naked tail of the *tafa centralis* holotype where dorsal hairs are very short (uniformly 1mm) as are hairs on the ventral crest (3mm) but increasing to 14mm at the ventral tip (see Figs 6, 7).

The hind feet of *habbema* are narrow in comparison to feet of *tafa centralis*. The original description of the *habbema* holotype emphasised this quality, 'Differing by the much smaller, more delicate feet and hands ... the width of foot across base of 5th metatarsal, 3.7, in *A. t. centralis*, 5.1, and in the type of *A. t. tafa* (f), 4.3.' (Tate & Archbold, 1941: 9). Claws of the pes of *habbema* are semi-straight, thin and short in comparison to the stronger, thicker and more noticeably curved claws (which results in them looking shorter from above) of *tafa centralis* (see Fig. 7).

The skull. In the holotype of *wilhelmina* (and for *melanurus* as a whole) I^1 is broad, slightly procumbent, claw-like and curved posteriorly. In the holotype of *A. habbema* (and for the species) I^1 is narrow and needle-like with a minute crown (can be better seen in the *hageni* holotype which is relatively unworn). I^{2-4} in the *wilhelmina* holotype are blade-like and robust with buccal and lingual cingula. In the *habbema* holotype I^{2-4} are poorly cingulated, narrow and with minimal lingual curving of the crown.

C^1 in the *wilhelmina* holotype is heavy and short but caniniform. In the *habbema* holotype the canine is extremely long and slender with a very short crown.

The upper premolar row (in particular P^{1-2}) in the *wilhelmina* holotype is characterised by wide, robust premolars crowded into a relatively short row. In the *habbema* holotype the premolars are long, uncrowded and narrow, with P^1 separated from P^2 by a small diastema.

Lower molars (M_2, M_3, M_4) in the *wilhelmina* holotype lack entoconids. These however are well developed in the holotype of *habbema*. The *wilhelmina* holotype also lacks the complex M_4 talonid of the *habbema* holotype with its 3, well-developed cusps.

Flagging confidence in Tate's decision to synonymise the skull of *habbema* with *wilhelmina* is further aggravated by his comment (Tate, 1947:131) that 'Furthermore the skull which was associated with the type skin of *A. habbema* exactly matches the skulls of *A. wilhelmina*'. He also failed to rationalise the other 4 specimens which, with AMNH 109812, comprised the type series, and he made no comment regarding the corresponding mismatched *tafa centralis* skull and *wilhelmina* skin which must have generated from the initial 'mismatch'. Even

if Tate had actually mismatched the *habbema* skin and skull and there was still doubt about the distinction of the *habbema* skin, the skull alone exhibits all the features characteristic of a species which mark it as neither *naso* nor *melanurus* (including *wilhelmina*).

DISTRIBUTION. *M. habbema* is known from mid to upper-montane areas of the central cordillera (4°05'-8°03'S and 138°50'- 146° 53'E), central Irian Jaya to central Morobe Province, PNG (Fig. 8). It occurs at altitudes of 1600-3660m and has been collected in rainforest, mid-mountain forest, beech forest, mossy forest and subalpine grassland. Full floristic details of collection localities appear in Archbold et al. (1942: 263-266) and Brass (1964: 189-216).

FIG. 6. Tail morphology of holotypes of: *Antechinus habbema*, AMNH 109812 (below) and *Antechinus tafa centralis*, AMNH 109823 (above).

REPRODUCTION. All pouches examined contained 4 teats. Lactating ♀♀ had been collected in (date included in parenthesis) June (25), July (1, 3, 19, 24, 25, 27), August (no dates), October (31), November (7). No specimens (♂ or ♀) were examined which had been collected in December, January, February, March, April or May. Woolley (1994) recorded 2 lactating ♀♀ in December.

DESCRIPTION. *Mean Measurements* (mm). External: total length (head, body, tail) (♂) 251 (♀) 240; tail (to cloaca) (♂) 135 (♀) 133; hindfoot (su) (♂) 22.22 (♀) 22.15; ear (notch) (♂) 17.26 (♀) 16.54. Skull: basicranial length (♂) 27.31 (♀) 25.97; M^{1-4} length (♂) 6.43 (♀) 6.30; M^2 width (♂) 1.75 (♀) 1.70 (Table 1).

P4. In *habbema* P^4 is 3-rooted (AMNH 190885, 190887, 190894, 190904, 190908). In AMNH 190885 RP^4 shows a poorly developed protocone while the paracone and metacone merge, LP^4 shows a well-developed protocone and paracone and metacone. Stylar cusps are poorly developed. A similar pattern of development is seen in AMNH 1090887 but here stylar cusp B and the metastylid are developed. P_4 may be double or single-rooted. Of 4 specimens examined for P_4, 2 had single-rooted R and LP_4 and 2 had double-rooted R and LP_4. All lowers were premolari-form, however those of AMNH 190885 showed signs of 3 small and triangularly arranged cusps.

Pelage. There is considerable variation in the pelage colour of study skins, however some of this may be due to bleaching induced by a period of storage in ethanol prior to skinning. In such specimens from the eastern extremity of the range (Mt Tomba AM M9562, 9566) skins are very light and appear almost golden brown with the black patch absent from the anterior corner of each eye and the tail colour much diluted.

Tail. The tail is well-haired, but not densely so. A ventral crest is present, and the colour of the tail varies from light (in the east) to black (in the west). In three specimens from Mt Wilhelm, AMNH 109808, 109810, 109813 the tail is more lightly coloured dorsally and the caudal brush is a darker Sepia. These specimens are also characterised by a more crowded, shorter, upper premolar row (contact between P^1-P^2, P^2-P^3, P^3-M^1, in 109813; P^2-P^3, P^3-M^1 contact in 109810, 109808) and palatine vacuities.

Hind Foot. Variable. hallucal and post-hallucal pads may be completely fused, or completely unfused, or any intermediate stage of fusion. Left and right hind feet may differ in the one individual. There may be a large auxiliary granule outside the first and/or third interdigital pads. An auxiliary hallucal (or 'post-first-interdigital') pad is also variable (Fig. 9; Table 2).

SPECIMENS EXAMINED. Bulldog Road, 2400m, 07°31'S 146°40'E (BMNH 96748); Collins Sawmill, 2300m, 05°59'S 145°25'E (AMNH 190919); Giluwe Mt., 2684 m, 06°03'S 144°53'S (CM 29, CM 37); Giluwe Mt., 2700-2750m,
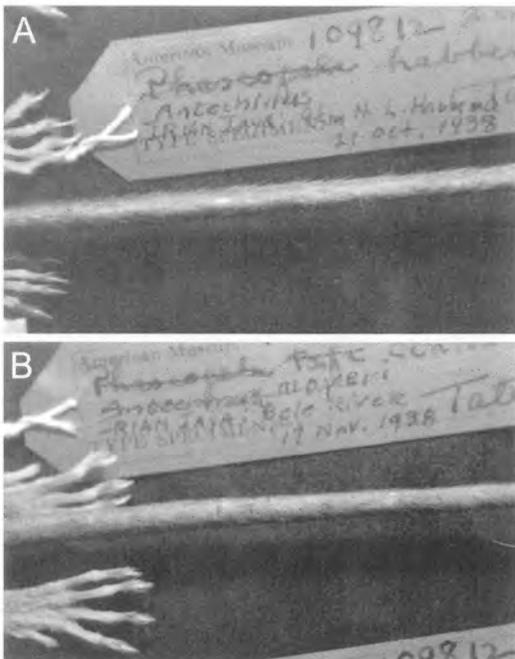
FIG. 7. Hind feet, tail and claws in the holotypes of: A, *Antechinus habbema*, AMNH 109812; and B, *Antechinus tafa centralis*, AMNH 109823.

06°03'S 144°53'E (BMNH53.204); Giluwe Mt., 2735m, 06°03'S 144°53'E (CM 12); Habbema Lake, 9km NE, 2706-2800m, 04°05'S 138°50'E (AMNH 152739); Habbema Lake, 9km NE, 2800m, 04°05'S 138°50'E (AMNH 109808, AMNH 109810, AMNH 109812, AMNH 109813); Hagen Mt., 2135-2400m, 05°54'S 144°09'E (AMNH 156370, AMNH 156372, AMNH 156373, AMNH 156389, AMNH 156391, AMNH 156393); Hagen Mt., 2592m, 05°54'S 144°09'E (AMNH 156367, AMNH 156376, AMNH 156395-156398); Hagen Mt., 3355-3660m, 05°54'S 144°09'E (AMNH 156378); Kaindi Mt., 2250-2350m, 07°21'S 146°43'E (BBM 29156, BBM 29183, BBM 29193, BBM 51049, BBM 51055, BBM 51073, BBM 51079, BBM 53411); Keglsugl, 2300m 05°50'S 145°06'E (AMNH 190880, BBM 100822); Marafunga, 2500-2350m, 05°58'S 145°08'E (BBM 55576); Marafunga, 2500m, 05°58'S 145°08'S (BBM 55562); Nondugl, 1600-1800m, 05°52'S 144°45'E (AMNH 183455, AMNH 222617); Nondugl, 1600-1800m, 05°52'S 144°45'E, (BMNH 56.7); Nondugl, 2135-2400m, 05°52'S 144°45'E, (AMNH 156364, AMNH 159392, AMNH 156394, AMNH 183594-183596); Nondugl, 2745-3660m, 05°52'S 144°45'E (AMNH 156361); Pengagl Creek, 2800m, 05°40'S 145°05'E (AMNH 190891, AMNH 190894, AMNH 190900, AMNH 190901, AMNH 190912); Smiths Gap, 2500m, 08°03'S 146°53'E (BBM 97023, BBM 97036); Tomba Mt., 2500m, 05°50'S 144°02'E (BMNH 50.1831, BMNH 50.1832, AM M9562, AM M9564, AM M9566); Tomba Mt., 2501m, 05°50'S 144°02'E (BMNH 50.1829); Wilhelm Mt., 2500-3570m, 05°46'S 144°59'E

(AMNH190881-190890, AMNH190892, AMNH 190896-190899, AMNH190902-190911, AMNH 190913-190918, AMNH100712); Wilhelm Mt., 2800m, 04°05'S 138°50'E (AMNH192270-76); Yanka, 1981m, 05°45'S 144°07'S (BMNH 50.1833).

Phascomurexia gen. nov.

Phascogale (in part) Temminck 1824.
Antechinus (in part) Macleay 1841.
Murexia (in part) Laurie 1952.

TYPE AND ONLY SPECIES. *Phascogale naso* Jentink, 1911: 236, based on RMNH 35134, adult ♂ puppet skin with skull, from Hellwig Mountains, Irian Jaya, 4°32'S 138°41'E at ~2,000m.

GENERIC DIAGNOSIS. M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. Talonid on M_4 relatively unreduced. Tail longer than the head-body length.

It is distinguished from *Phascolosorex* and *Myoictis* by its lack of dorsal body stripes, and from *Neophascogale* by its lack of reduced premolars and the lack of a thickly-haired tail.

Phascomurexia is separable from *Micromurexia* by the absolutely longer lengths of its upper and lower molar rows, M1-4.

Phascomurexia differs from *Murexechinus* by ears always lacking post-auricular patches rather than ears possessing rufous post-auricular patches; pelage uniform brown throughout rather than agouti with definite warming of tones toward rufous rump; tail semi-naked dorsally with weak ventral crest developing toward tip rather than tail well-haired dorsally with ventral crest hairs long throughout; I^1 narrow and needle-like rather than broad and claw-like; I^{2-4} uncingulated rather than cingulated; I^1 long and slender rather than short and squat; premolar row long with un-crowded, narrow premolars rather than premolar row short with broad crowded premolars.

Phascomurexia is separable from *Murexia* by the shorter lower tooth row I_1-M_4.

Phascomurexia naso is separable from *Paramurexia* by the narrower second upper and lower molars M2. *M. naso* also lacks a black dorsal body stripe.

Phascomurexia naso (Jentink, 1911)
(Figs 10, 11)

Phascogale naso Jentink, 1911: 236.
Phascogale tafa Tate & Archbold, 1936: 3.
Antechinus tafa centralis Tate & Archbold, 1941: 8.
Antechinus mayeri misim Tate, 1947: 130.
Murexia longicaudata parva Laurie, 1952: 294.

| Measurement		N	mean±r	OR	SD	V	CV
BL	Male	37	27.31±0.15	24.30-28.89	0.91	0.83	3.33
	Female	30	25.97±0.15	24.35-27.85	0.83	0.69	3.20
	Total	70	26.70±0.13	24.30-28.89	1.09	1.19	4.08
ZW	M	37	16.07±0.12	14.30-17.55	0.76	0.58	4.73
	F	27	14.92±0.10	13.77-15.92	0.53	0.28	3.55
	T	67	15.56±0.11	13.77-17.55	0.87	0.76	5.59
IOW	M	39	7.66±0.04	7.12-8.10	0.24	0.06	3.13
	F	30	7.55±0.04	6.99-7.90	0.20	0.04	2.65
	T	72	7.62±0.03	6.99-8.10	0.23	0.05	3.02
OBW	M	32	10.54±0.06	9.89-11.25	0.33	0.11	3.13
	F	27	10.28±0.07	9.59-10.88	0.38	0.15	3.70
	T	62	10.43±0.05	9.59-11.25	0.38	0.14	3.64
IBW	M	32	4.77±0.04	4.28-5.28	0.24	0.11	5.03
	F	27	4.67±0.05	4.32-5.30	0.24	0.06	5.14
	T	62	4.72±0.03	4.28-5.30	0.24	0.06	5.08
R-LC^1	M	39	5.17±0.04	4.60-5.73	0.28	0.08	5.42
	F	30	4.81±0.03	4.53-5.33	0.17	0.03	3.53
	T	72	5.00±0.04	4.49-5.73	0.30	0.09	6.00
R-LM^1	M	39	9.09±0.08	8.03-10.04	0.50	0.25	5.50
	F	30	8.58±0.06	8.20-9.57	0.31	0.09	3.61
	T	72	8.87±0.06	8.03-10.04	0.49	0.24	5.52
R-LM^2	M	28	10.68±0.10	9.79-11.92	0.54	0.29	5.06
	F	22	10.23±0.07	9.63-11.22	0.33	0.11	3.23
	T	53	10.49±0.07	9.63-11.92	0.51	0.26	4.86
R-LM^3	M	30	13.14±0.12	12.02-14.69	0.66	0.43	5.02
	F	23	12.24±0.08	11.66-13.09	0.38	0.15	3.10
	T	56	12.76±0.10	11.66-14.69	0.72	0.52	5.64
R-LM^{1}T	M	33	7.63±0.04	7.17-8.30	0.24	0.06	3.15
	F	26	7.37±0.04	7.04-7.89	0.18	0.03	2.44
	T	62	7.52±0.03	7.04-8.30	0.25	0.06	3.32
I^1-M^4	M	39	15.29±0.05	14.46-15.94	0.33	0.11	2.16
	F	30	14.66±0.07	13.70-15.85	0.41	0.17	2.80
	T	72	15.02±0.06	13.70-15.94	0.48	0.23	3.20
P$^{1-3}$	M	40	3.94±0.05	3.35-4.72	0.30	0.09	7.61
	F	30	3.72±0.04	3.30-4.17	0.24	0.06	6.45
	T	73	3.85±0.03	3.30-4.72	0.29	0.09	7.53
M$^{1-4}$	M	40	6.43±0.03	6.10-6.74	0.17	0.03	2.64
	F	30	6.30±0.03	6.00-6.63	0.16	0.03	2.54
	T	73	6.38±0.02	6.00-6.74	0.18	0.03	2.82
M^{2}W	M	40	1.75±0.01	1.45-1.89	0.08	0.01	4.57
	F	30	1.70±0.01	1.57-1.85	0.07	0.00	4.12
	T	73	1.73±0.01	1.45-1.89	0.08	0.01	4.62
Dent	M	39	22.08±0.19	19.20-27.71	1.20	1.45	5.43
	F	30	20.72±0.13	19.04-22.86	0.73	0.53	3.52
	T	72	21.46±0.14	19.04-27.71	1.22	1.48	5.68
I$_1$-M$_4$	M	39	13.36±0.06	12.59-14.18	0.36	0.13	2.69
	F	30	12.83±0.09	12.20-14.68	0.47	0.22	3.66
	T	72	13.12±0.06	12.20-14.68	0.48	0.23	3.66
P$_{1-3}$	M	40	4.23±0.05	3.57-4.94	0.29	0.09	6.86
	F	30	3.88±0.05	3.35-4.43	0.28	0.08	7.22
	T	73	4.08±0.04	3.35-4.94	0.33	0.11	8.09
M$_{1-4}$	M	40	6.92±0.03	6.51-7.41	0.19	0.04	2.75
	F	30	6.78±0.03	6.57-7.11	0.15	0.02	2.21
	T	73	6.86±0.02	6.51-7.41	0.19	0.04	2.77
M$_2$W	M	40	1.12±0.01	1.05-1.25	0.04	0.00	3.57
	F	30	1.09±0.01	1.03-1.20	0.04	0.00	3.67
	T	73	1.11±0.00	1.03-1.25	0.04	0.00	3.60
TL	M	26	251±2.16	224-279	11.00	140.00	4.38
	F	19	240±1.38	229-260	6.00	43.00	2.50
	T	45	246±1.64	224-279	11.00	125.00	4.47
T	M	35	135±1.69	109-157	10.00	111.00	7.41
	F	22	133±1.28	119-143	6.00	47.00	4.51
	T	57	135±1.19	109-157	9.00	88.00	6.67
HF	M	34	22.22±0.28	19-25	1.61	2.58	7.25
	F	24	22.15±0.26	19.5-24	1.29	1.66	5.82
	T	58	22.19±0.19	19-25	1.48	2.20	6.67
E	M	31	17.26±0.17	15-19	0.97	0.93	5.62
	F	23	16.54±0.17	15-18	0.83	0.69	5.02
	T	54	16.95±0.13	15-19	0.98	0.96	5.78
W	M	15	34.59±1.07	28.35-45.36	4.14	17.10	11.97
	F	14	25.92±0.69	22.68-31.18	2.59	6.72	9.99
	T	29	30.40±1.03	22.68-45.36	5.55	30.85	18.26
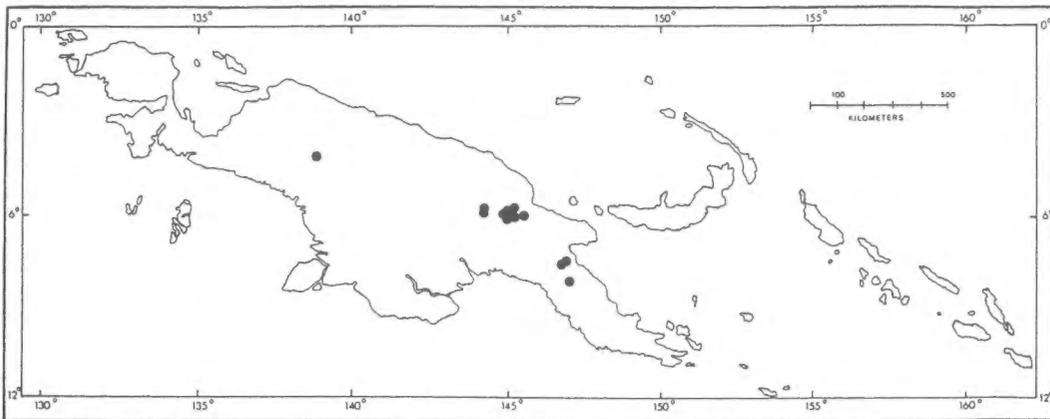
FIG. 8. Distribution of *Micromurexia habbema*.

HOLOTYPE. Rijksmuseum van Natuurlijke Histoire, Leiden, RMNH 35134. Adult ♂ puppet skin and skull extracted (both in excellent condition).

TYPE LOCALITY. Hellwig Mountains, Irian Jaya, 4°32'S 138°41'E, ~2,000m. Coll. H.A. Lorentz, 16 October 1909.

DIAGNOSIS. As for genus.

DESCRIPTION. HOLOTYPE. *Pelage* (Fig. 10). Fur of the mid-back (8mm long) has basal 3mm Neutral Gray becoming Fuscous at 4.5mm, median 1mm Buffy Brown and apical 1.5mm Fuscous. The back appears to be a Greyish Sepia. Medially thickened guard hairs are interspersed through the fur and are 7mm long on the rump and reduce to 2.5mm at the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks both black tips and the median Buffy Brown band and these areas appear Mouse Gray. The belly is Pale Olive-Buff and the fur is luxuriously soft, a pale grey becoming silvery-white (not cream) along the belly mid-line. The fur is 7.5mm long on the belly and 6mm long on the interramal region with the basal 2/3 Light Neutral Gray and the apical 1/3 Pale Olive-Buff. It is interspersed with similarly coloured, medially thickened spines 7.5mm long. The forefeet are thinly covered with Hair Brown hair.

Hindfeet are more thickly covered with the same coloured hairs. The tail is weakly dorso-ventrally bicoloured with a very sparse covering of short hairs averaging 1.2mm (dorsally) along its length. These dorsal hairs are uniformly Sepia-coloured. Ventrally the hairs (3mm long near the base, increasing to form a ventral crest of hairs 6.5mm long) are coloured Ochraceous-Tawny.

Vibrissae. Approximately 20 mystaceal vibrissae occur on each side, up to 30mm long. The more dorsal mystaceal vibrissae are coloured Fuscous while those lower are colourless; supra-orbital vibrissae (Fuscous) number 0 left and 2 right;

TABLE 1. Absolute measurements for *Micromurexia habbema*. See 'Methods' for limits of measured dimensions. Abbreviations (as for Tables 3-6) are as follows: N = number of specimens in the sample; mean ± r = sample mean ± one standard error; OR = observed range; SD = standard deviation; V = variance; CV = coefficient of variation; M = male; F = female; BL = basicranial length; ZW = zygomatic width; IOW = interorbital width; OBW = basicranial width from outside right and left auditory bullae; IBW = distance between right and left auditory bullae; R-LC^1 = rostral width at the level of the upper canines; R-LM^1 = rostral width at the level of the first upper molars; R-LM^2 = rostral width at the level of the second upper molars; R-LM^3 = rostral width at the level of the third upper molars; R-LM^{1}T = width between the ectolophs of right and left first upper molars; I^1-M^4 = length of upper tooth row (alveolar); P$^{1-3}$ = length of upper premolar row (alveolar); M$^{1-4}$ = length of upper molar row; M^{2}W = width of upper second molar; Dent = dentary length, I$_1$-M$_4$ = length of lower tooth row (alveolar); P$_{1-3}$ = length of lower premolar row (alveolar); M$_{1-4}$ = length of lower molar row (alveolar); M$_2$W = width of second lower molar; APV (not taken for all species) = anterior palatal vacuity length; PPV (not taken for all species) = posterior palatal vacuity length; IPV (not taken for all species) = inter-palatal vacuity length; NW (not taken for all species) = nasal width at the level of the premaxillary/nasal/maxillary junction; TL = total length, body and tail; T = tail length; HF = length of hind foot (su); E = length of ear (from notch); W = weight in grams.
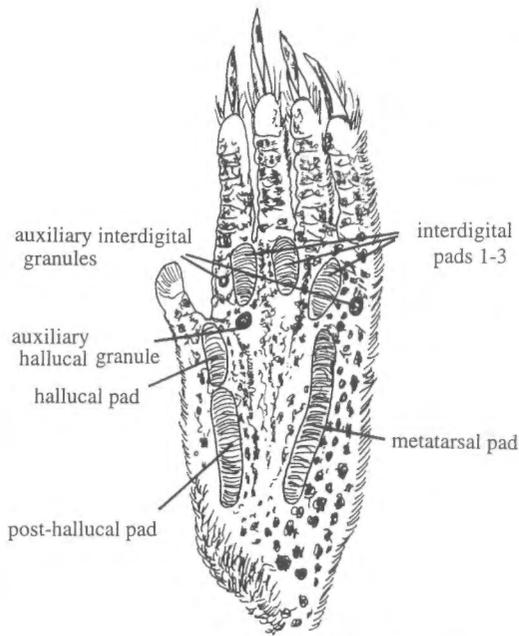
FIG. 9. Hindfoot padding in *Micromurexia habbema*.

genals (Fuscous and colourless) number 9 left and right; ulna-carpals number 5 left and right and submentals (colourless) number 4.

Tail. ~1.25 longer than the nose-vent length. It is thin and tapers toward the tip.

Hindfoot. The long hallucal and post-hallucal pads are narrow and fused. Interdigital pads are separate and the enlarged apical pad is elongate and striate. The metatarsal pad is very long and striate. The terminal pads of the digits are also striate.

Ears. The pinnae are large with a complex supratragus which has a pronounced, thickened posterior margin and the distal end is reflected ventrally. The reflected tip is slightly concave.

Dentition (Fig. 11). Upper Incisors: I^1 is narrow, peg-like, slightly procumbent and relatively uncurved. R and LI^1 have crowns worn posteriorly so that the height of I^1 is equal to that of other upper incisors. I^1 is separated by a diastema from I^2. R and LI^1 are obliquely inclined toward one another but contact does not occur. All upper incisors lack buccal and lingual cingula yet there is no lack of differentiation in root and crown. I^4 carries no anterior or posterior cusp. The roots of I^4 are narrow. In crown size I^4 is greater than I^3 which is greater than I^2.

TABLE 2. Hindfoot morphology in *Micromurexia habbema*.

Hindfoot Condition		x/N	%
Right hallucal/post-hallucal pads	Unfused	69/89	77
	Fused	20/89	22
Left hallucal/post-hallucal pads	Unfused	71/90	79
	Fused	19/90	21
Right and left hallucal/post-hallucal pads	Unfused	66/90	73
	Fused	16/90	18
Right hallucal/post-hallucal fused, left Unfused		5/90	6
Left hallucal/post-hallucal fused, right Unfused		3/90	3
Auxiliary granules on both feet		51/69	74
No auxiliary granules on feet		9/69	13
Auxiliary granules on left foot only		6/69	8
Auxiliary granules on right foot only		3/69	4
Auxiliary granules on both feet		51/69	74
Right: # with granules at 1		5	10
# with granules at 3		9	18
# with granules at 1 and 3		37	72
Left: # with granules at 1		7	14
# with granules at 3		8	16
# with granules at 1 and 2		36	71
Aux. granules on left foot only		6/69	9
# with granules at 1		1	17
# with granules at 3		4	67
# with granules at 1 and 3		1	17
Aux. granules on right foot only		3/69	4
# with granules at 1		1	33
# with granules at 3		-	
# with granules at 1 and 3		2	67
Right feet, hallucal/post-hallucal pads:			
Fused, pads with aux. hallucal granule		1/7	14
Fused, pads without aux. granule		6/7	86
Unfused, pads with aux. granule		21/34	62
Unfused, pads without aux. granule		13/34	39
Left feet, hallucal/post-hallucal pads:			
Fused, pads with aux. granule		4/7	57
Fused, pads without aux. granule		3/7	43
Unfused, pads with aux. granule		25/33	76
Unfused, pads without aux. granule		8/33	24

Upper Canines: C^1 slender, erect, caniniform, with forward projection and an indistinct boundary between the root and crown. There is no buccal or lingual cingulum, and no anterior or posterior cusp. R and LC^1 have crowns broken off and abnormal thegotic wear is evident on the anterior surface of both canines.

Upper Premolars: The premolar row is long and diastemata separate all premolars. C^1 and P^1 are, however, very closely approximated, P^3 contacts M^1 and the diastema separating P^1 and P^2 is largest. All premolars carry strong buccal cingula. Weak lingual cingula are found on P^1 and P^2, but P^3 lacks a lingual cingulum. P^1 crown is shorter than P^2 which is shorter than P^3. Small anterior cusps occur on P^1 and P^2 with a less discernible anterior cusp on P^3. There are very small posterior cingular cusps on P^2 and P^3. No upper premolars possess postero-lingual lobes.

Upper Molars: The posterior tip of P^2 rests in the parastylar corner of M^1 but lingual to and just below a weak stylar cusp A. The anterior cingulum below stylar cusp B is short, broad and complete. Stylar cusp B and the paracone are relatively unworn and a large protoconule is present at the base of the paracone apex. The protoconule is accompanied by a large bulge of enamel directly below it on the face of the anterior protocrista. The paracone is well developed and approximately half the height of the metacone. Stylar cusps C and E are not visible on either R or LM^1. M^1 has an indistinct posterior cingulum. Stylar cusp D is large but erect and narrow, not contributing greatly to the bulk of endoloph enamel.

In M^2 a narrow, almost incomplete anterior cingulum contacts the metastylar corner of M^1 and tapers quickly as it progresses down and along the base of the paracrista and finally degenerates labially to the base of the paracone apex. A protoconule is present with an associated anterior protocrista bulge as in M^1. M^2 lacks stylar cusps A, C and E. There is a very indistinct posterior cingulum and stylar cusp D is reduced and erect.

In M^3 the anterior cingulum is incomplete and narrower than that in M^2. It becomes indistinct after covering 1/2 the distance between stylar cusp B and the base of the paracone. There is a small protoconule but no associated enamel bulge. Stylar cusp D is greatly reduced to a minute conical peak. Stylar cusp E is weakly present but C is absent.

In M^4 the parastylar corner is grossly developed. The broad anterior cingulum is complete but a posterior cingulum is absent. The protocone is very broad. In occlusal view the angle made between the post-protocrista and post paracrista is close to $135°$ indicating little metacone development.

Lower Incisors: L and RI_1 both show abnormal thegotic wear caused from ill-occluding L and RI^2. I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. In crown size I_1 is greater than I_2 which is greater than I_3. I_3 has a posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent posterolingual lobe, and the crown enamel of the primary and posterior cusps folds noticeably so that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform and characterised by slight curvature and erect projection. It has weak buccal, and slightly stronger lingual cingulation and no posterior cusp. The posterior surface of LC_1 shows abnormal thegotic wear caused by the broken LC^1.

Lower Premolars: P_{1-3} are unevenly spaced, a slight diastema separates C_1 and P_1, a wider diastema occurs between P_1 and P_2, but P_2 and P_3 almost contact. All premolars are weakly cingulated buccally and lingually. In crown size P_2 is greater than P_3 which is greater than P_1. All premolars are relatively broad and elongate. All possess posterior cusps, none possess anterior cusps. The bulk of each premolar mass is concentrated posteriorly to the line drawn transversely through the middle of the two premolar roots.

Lower Molars: All lower molars are relatively broad. The M_1 talonid is wider than the trigonid and the anterior cingulum is poorly developed. It continues around the posterior base of the protoconid into a weak buccal cingulum. The narrow paraconid appears in occlusal view as a small, steeply-sided spur, the lingual edge of which makes no appreciable swelling on the endoloph. The paracristid is almost $45°$ to the horizontal from the paraconid to the paracristid fissure and vertical from fissure to protoconid. The metacristid is roughly oblique to the long axis of the dentary while the hypocristid is perpendicular. The cristid obliqua is very short and extends from the hypoconid to the posterior wall of the trigonid, intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoncoid. The entoconid is well developed as is a high entocristid slung between entoconid and metaconid. From the base of the metaconid posteriorly, the talonid endoloph shows an appreciable lingual incursion of enamel from the line of the endoloph. The weak buccal
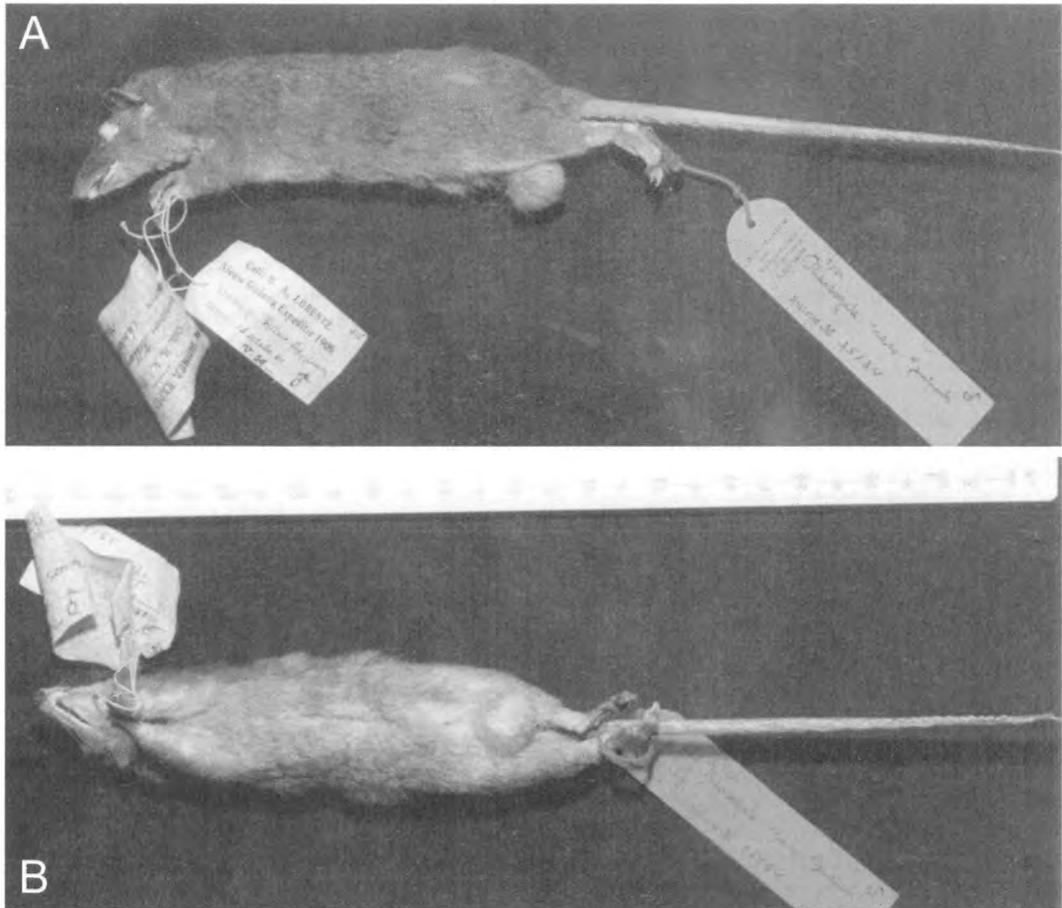
FIG. 10. Holotype of *Phascogale naso* Jentink, 1911 (now *Phascomurexia naso*). RMNH 35134, study skin; A, lateral view; B, ventral view. TL = 290mm; HB = 145mm; TV = 145mm; HF = 27mm; E = 16mm.

cingulum continues into a heavy posterior cingulum.

In M_2 the talonid is slightly narrower than the trigonid. The anterior cingulum is poorly developed but almost complete, breaking down just below the hypoconid. A narrow posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is well developed and is the smallest trigonid cusp. A large, broad entoconid is twice the height of the metastylid. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point well lingual to that point directly below the protoconid tip but well buccal to the metacristid fissure. From the base of the metaconid posteriorly, the endoloph is characterised by a significant lingual swelling of the entoconid foundation.

In M_3 the trigonid is wider than the talonid. A prominent parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3. Buccal and lingual cingula are continuous as in M_2 but weakly developed. The reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn throughout the tip of the protoconid, but slightly buccal to the metacristid fissure. A large but worn entoconid is found on M_3. The endoloph on the talonid of M_3 takes a more buccal orientation, under the reduced influence of a smaller entoconid, than that seen in M_2. The rest of the morphology is as in M_2.

In M_4 the trigonid is wider than the talonid. The anterior cingulum is as in M_2. The posterior cingulum is absent. Of the three main trigonid
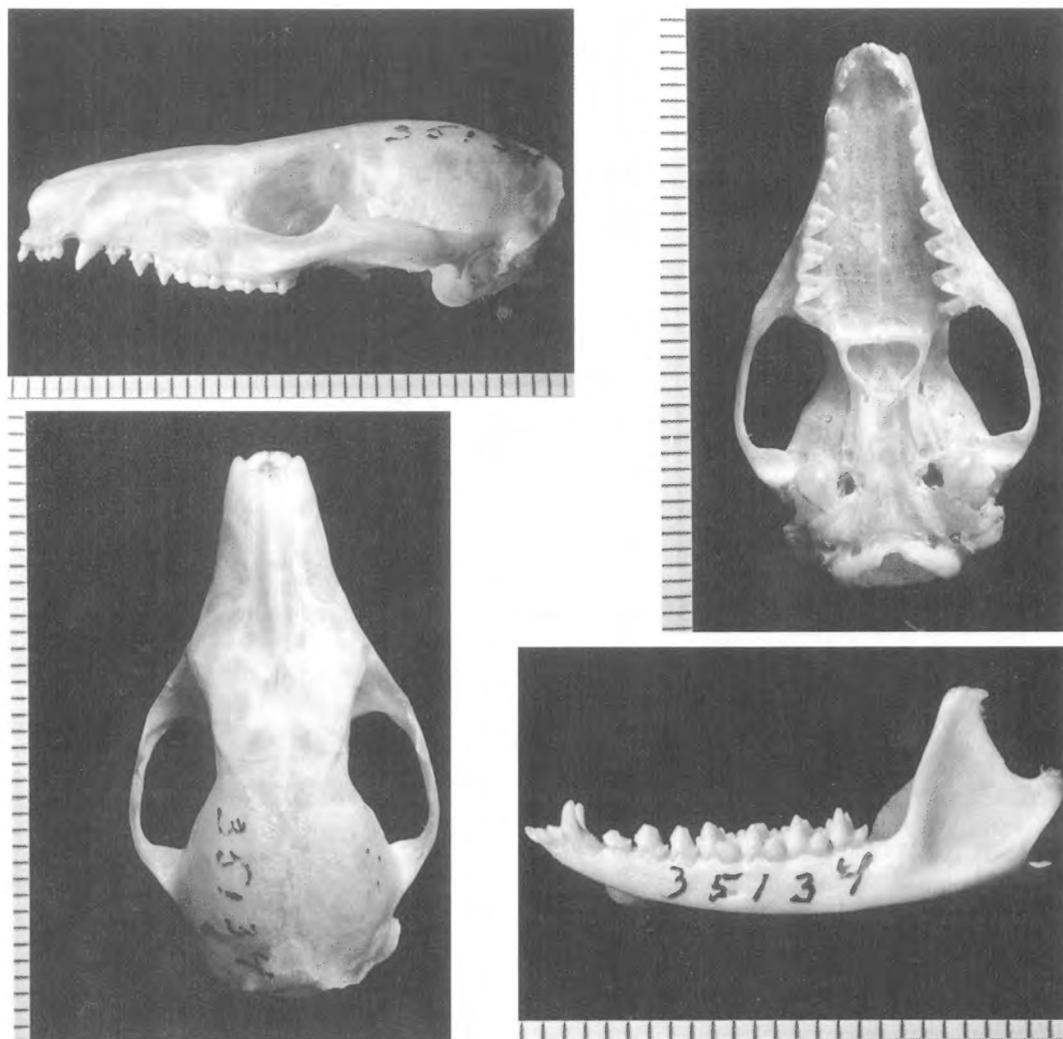
FIG. 11. Holotype of *Phascogale naso* Jentink, 1911 (now *Phascomurexia naso*). RMNH 35134, cranium and dentary. Sex = m; BL = 31.87; ZW = 19.44; IO = 8.22; OBW = 12.51; IBW = 6.60; $R-LC^1$ = 6.57; $R-LM^1$ = 11.29; $R-LM^2$ = 13.63; $R-LM^3$ = 16.59; M^2W = 2.00; I^1-M^4 = 17.65; P^{1-3} = 4.99; M^{1-4} = 7.72; Dent = 26.16; I_1-M_4 = 15.72; P_{1-3} = 4.66; M_{1-4} = 8.28; M_2W = 1.36.

cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of M_4 is much more reduced than in M_3. Between the hypoconid and the base of the metacristid, the cristid obliqua forms a low, weak crest which contacts the trigonid wall directly below the metacristid fissure. A broad distinct M_4 buccal cingulum anchors the talonid to the trigonid. There is no entoconid, the hypoconulid is taller than the hypoconid and both are clearly distinct.

Skull (Fig. 11). The skull of the *naso* holotype has a high, domed brincase, depressed and concave frontals, greatly raised and fluted nasals and a squarish 'dog-faced' rostrum. The right and left alsphenoid tympanic bullae are widely separated and very weakly enlarged. The foramen pseudovale therefore appears very large and is not bisected by the inner wing of the entocarotid canal. The transverse canals are widely separated and just anterior to the foramen pseudovale. The eustachian canal foramina are large. The internal

jugular canal foramina are small, the canals low and obscure. The posterior lacerate foramina are large and exposed and the entocarotid foramina are large and exposed. The premaxillary vacuities extend from the level of the I^2 root back to 1/3 the distance along the C^1 root. In the holotype, dry skin still covers the maxillary vacuities but they appear to be large, extending from the posterior root of P^3 to the protocone root of M^3. It is impossible to detect palatine vacuities.

SYNONYMS

Phascogale tafa Tate & Archbold, 1936
(Figs 12, 13)

HOLOTYPE. AMNH 104050, adult ♀ (skin and skull in excellent condition).

TYPE LOCALITY. Eastern slopes of Mt Tafa, Central Division, PNG, 8°22'S 147°23'E, at 2,130m. Coll. by R. Archbold & A.L. Rand, 25 May 1933.

The type of *tafa* differs from the *naso* holotype in the following respects.

Pelage (Fig. 12). The pouch area is stained rusty red and 4 elongated nipples are visible. The tail is more evenly haired than the *naso* type (which is sparsely haired almost to the point of patchy balding) and the last dozen hairs in *tafa* are white; there is, however, no white skin at the tip of the tail. Belly hair is slightly more silver and greater in extent than the more narrow band in the *naso* type.

Hindfoot. There are no significant differences in hindfoot morphology.

Dentition (Fig. 13). There are few significant differences in tooth morphology. R and L I^1 are unworn in *tafa* and in crown height I^1 is greater than all other incisors. I^4 is greater than I^3 which is greater than or equal to the height of I^2. There is no abnormal wear on the upper canines, but their small size and straight carriage demonstrates the sexually dimorphic nature of canine size and shape in the species. The posterior cingula of M^{2-4} are more strongly developed, and stylar cusps in M^3 are almost undetectable.

In the lower incisors RI_1 is missing, there is a slight, even gap between LP_1, LP_2 and LP_3, but RP_2 and RP_3 touch, thereby causing the diastema between P_1 and P_2 to be large. The rest of the molar morpohology is as in the *naso* type.

Skull (Fig. 13). In AMNH 104050 the nasals are not raised as highly, or fluted to the same extent as in the *naso* holotype, the maxillary vacuities extend from the level of the posterior edge of the M^1 protocone root back to the level of the M^3 protocone root. There are no palatine vacuities.

Antechinus tafa centralis Tate & Archbold, 1941
(Figs 14, 15)

HOLOTYPE. AMNH 109823, large adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. Bele River, 18km N of Lake Habbema, Irian Jaya, 4°05'S 138°42'E.At 2,200m.Coll. W.B. Richardson, 17 November 1938.

The type of *tafa centralis* differs from *naso* in the following respects.

Pelage (Fig. 14). There are no significant pelage differences between the *tafa* and *tafa centralis* types. There are no white hairs in the tail crest.

Dentition (Fig. 15). There are few dental features in *tafa centralis* that differ significantly from *naso*. RI^1 is missing as is LP_1. The only significant diastema in the upper premolar row occurs between P^1 and P^2. In the lower right premolar row there is even spacing between all premolars and LP_3 is not in contact with LM_1, however, in the lower left premolar row LP_3 contacts LM_1.

Skull (Fig. 15). The nasals are lower and less fluted than in *naso*, and are more poorly developed than in *tafa*. Although the rostrum is typically high, the poor development of the nasals gives the top of the snout a flat appearance. Maxillary vacuities are large and wide, extending from the protocone root of M^1 back as far as the metacone root of M^3.

Antechinus mayeri misim Tate, 1947
(Figs 16, 17)

HOLOTYPE. MCZ 29924, adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. Mount Misim, PNG, 7°13'S 146°50'E. Altitude 1,784m. Coll. H. Stevens, 24 April 1933.

The type of *mayeri misim* differs from the type of *naso* in the following respects.

Pelage (Fig. 16). The fur is thin and silky, having the appearance of sparse pelage often seen in young dasyurids raised and weaned in captivity on an impoverished diet. The more typical luxurious fur in a female (MCZ 29923), collected in the same area two days after the *m. misim* type was collected, suggests that the sparse condition of the type may be abnormal. The tail is typically bare dorsally, but has been 'corkscrewed' around the wire used in the preparation of the study skin.
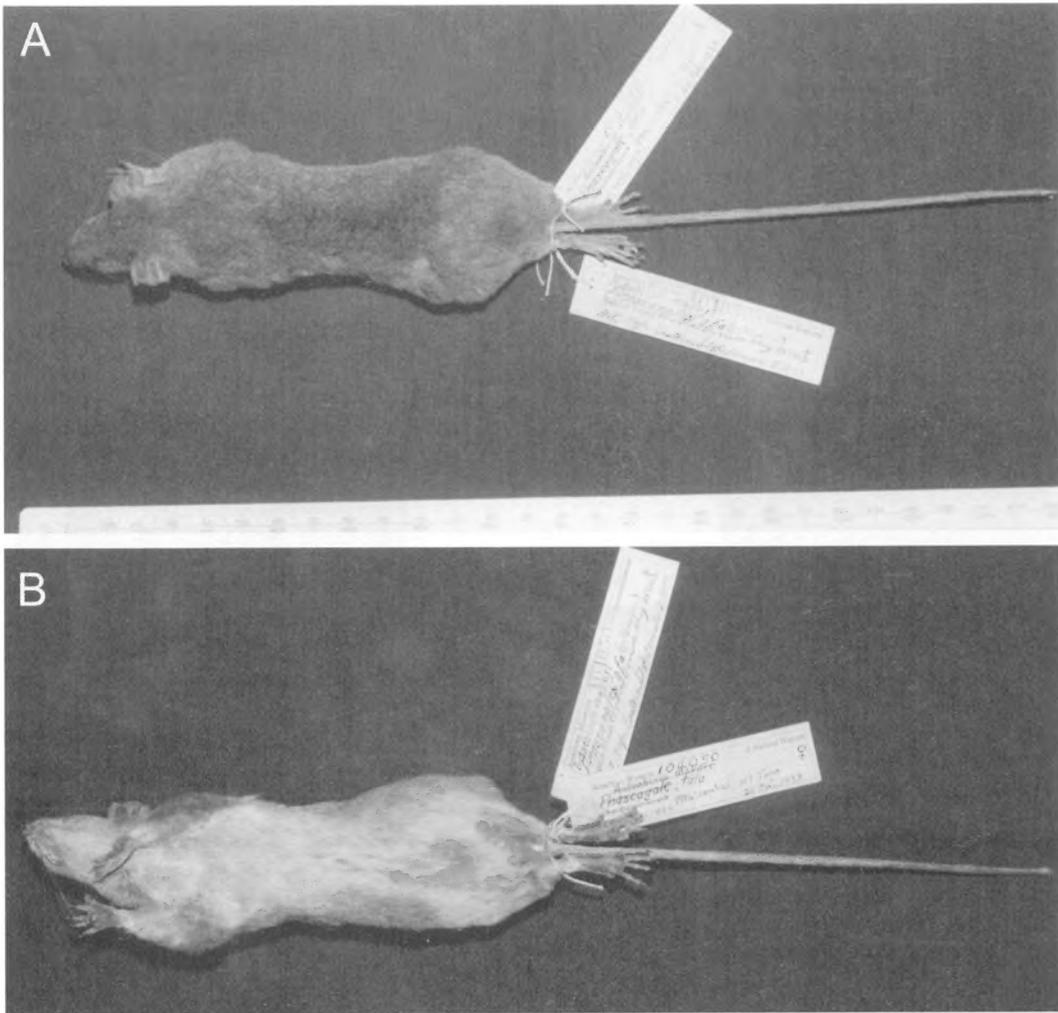
FIG. 12. Holotype of *Phascogale tafa* Tate & Archbold, 1936 (now *Phascomurexia naso*). AMNH104050, study skin; A, dorsal view; B, ventral view. TL = 279mm; HB = 134mm; TV = 145mm; HF = 25.

Dentition (Fig. 17). The *A. m. misim* type is a subadult male with emerging $P^3/_3$ and unworn dentition. L and RI^1 are widely separate and parallel. Unworn incisors show clearly I^2 crown lower than I^3 which is lower than I^4, with no cusps. Paracone and stylar cusp B appear closely approximated in M^{1-3} but this may be a function of youth and the lack of tooth wear. Upper and lower cingula are particularly weak throughout. There is no metacone development on M^4. Entoconids are strongly developed on M_{2-4} and contribute greatly to the lingual bulging of the talonid endolophs. The subadult dentition suggests a very large animal when adult.

Skull (Fig. 17). Nasal fluting is minimal and both pre- and maxillary vacuities are long and broad. A small palatine vacuity occurs behind each maxillary vacuity.

Murexia longicaudata parva Laurie, 1952
(Figs 18, 19)

HOLOTYPE. BMNH 50.1114, adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. Baiyanka, Ramu River Divide, SE Bismarck Range, 5°35'S 144°51'E. At 2,287m. Coll. F. Shaw Mayer, 6 June 1940.
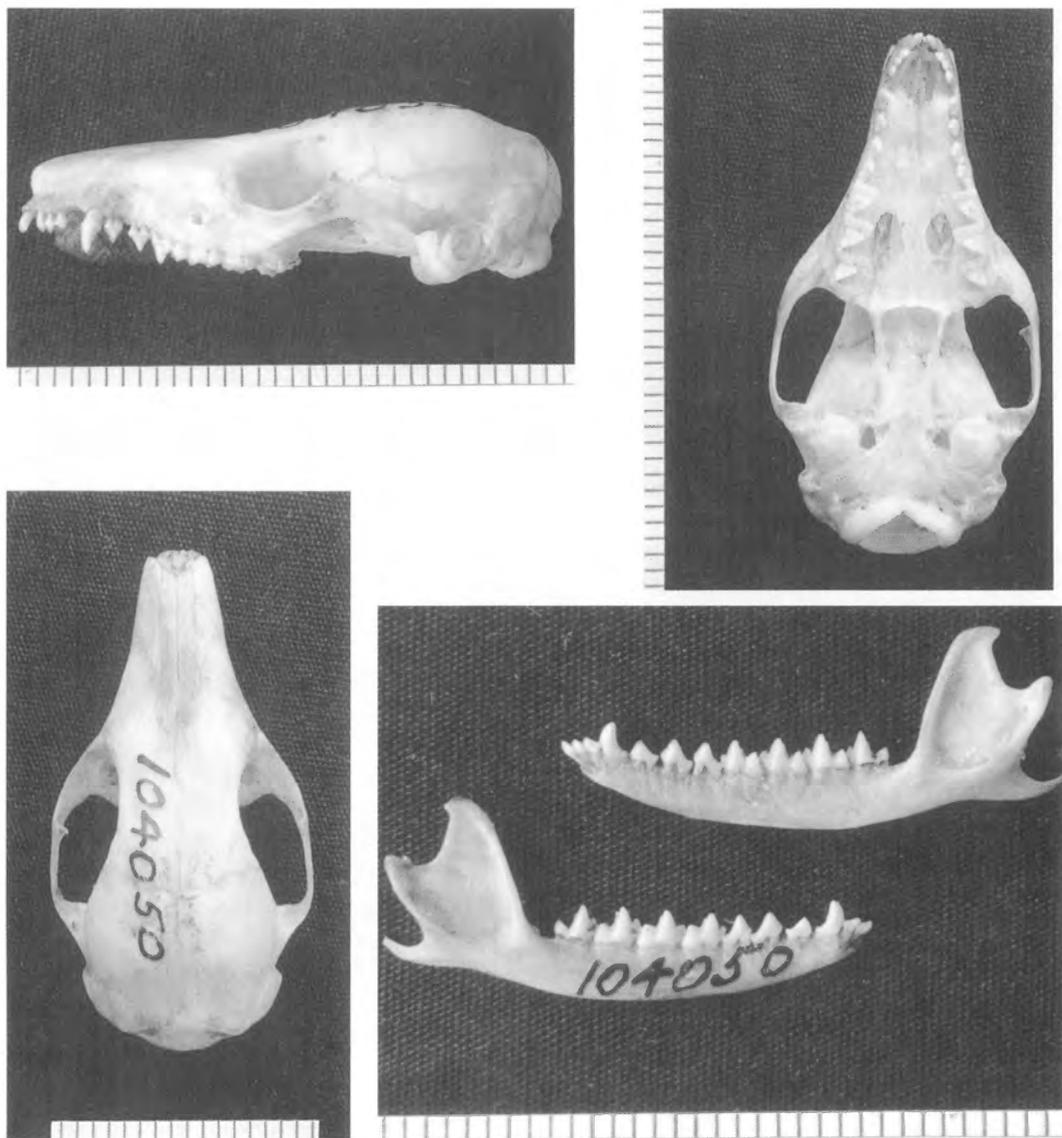
FIG. 13. Holotype of *Phascogale tafa* Tate & Archbold, 1936. AMNH 104050, cranium and dentary. Sex =f; BL = 29.71; ZW = 17.06; IO = 7.67; OBW = 11.66; IBW = 5.64; R-LC^1 = 5.88; R-LM^1 = 10.35; R-LM^2 = 13.19; R-LM^3 = 15.45; R-LM^{1}T = 8.27; M^{2}W = 2.08; I^1-M^4 = 17.20; P$^{1-3}$ = 4.46; M$^{1-4}$ = 7.51; Dent = 23.54; I$_1$-M$_4$ = 15.40; P$_{1-3}$ = 4.58; M$_{1-4}$ = 8.12; M$_2$W = 1.27.

The type of *longicaudata parva* differs from the holotype of *naso* in the following respects.

Pelage (Fig. 18). The fur is longer and more silky than the *P. naso* type. Guard hairs interspersed thinly through the fur are up to 10mm long on the rump and reduce to 5.6mm where they terminate at the crown of the head between the eyes. The silver belly fur is much more extensive than that of the *P. naso* type. Hairs on the tail are long, averaging 1.2mm dorsally and 5mm long ventrally (mid-). At the ventral tip these hairs increase to 14mm long. The tail and hairs are white for the distal 23mm. Mystaceal vibrissae number approximately 21 each side and are up to

33mm long. Supra-orbital vibrissae number 2 left and 2 right, genals number 8 left and 8 right; ulna-carpals number 3 right and 4 left and submetals number 6.

Dentition (Fig. 19). BMNH 50.1114 is a young specimen with only slightly worn dentition. R and LI^1 are slightly procumbent and while they are oriented toward one another they do not touch. I^2, I^3 and I^4 are subequal in crown height and length. C^1 is almost straight with no buccal or lingual cingulum. P^3 is larger than P^2 which is larger than P^1. There is no anterior cusp on P^3. M^1 has a strong posterior cingulum. In M^2 the anterior cingulum is narrow but complete. A protoconule is present on the trigon basin and a small bulge of enamel on the face of the anterior protocrista accompanies it. Stylar cusp D is just posterior to the metacone and a distinct posterior cingulum is present. In M^3 the anterior cingulum is complete and broader than that of M^2. There is a prominent anterior cingulum at the base of the paracone and a small protoconule.

Stylar cusp D is almost undetectable. Neither stylar cusps C or E are present. In M^4 the metastylar corner is well developed. The protocone is very broad and there is some prominent metacone development, making an angle of 90° between the posterior paracrista and the posterior protocrista. In the lower incisors, I$_1$ is much larger than I$_3$ which is equal to or slightly larger than I$_2$. There is an inconspicuous posterior cusp on I$_3$. The C$_1$ is only slightly curved and in the premolar row L and RP$_2$ are greater than P$_3$ which are greater in size than P$_2$. Small diastemata appear between LP$_2$ and LP$_3$, LP$_3$ and LM$_1$, LP$_1$ and LP$_2$, RP$_2$ and RP$_3$ and RP$_1$ and RP$_2$ (each side given in descending order of diastema magnitude).

In M$_1$ the cristid obliqua extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly buccal to that point directly below the tip of the protoconid. M$_1$ also shows a very well-developed entocristid. In M$_3$ the entoconid takes a great reduction in size and is absent in M$_4$.

Skull (Fig. 19). Nasal fluting and rostrum height are accentuated in the *M. l. parva* types. The large maxillary vacuities extend from the level of the protocone root of M^1 back to the metacone root of M^3. A small palatine vacuity occurs posterior to each maxillary vacuity.

ADDITIONAL DIAGNOSTIC FEATURES

Phascomurexia naso differs from all other dasyurids in the combination of the following features: 1, thin, spur-like crown in I^1 which is needle-like and almost procumbent; 2, uncingulated upper incisor row where I^2<I^3<I^4; 3, long, thin (but bulkier and shorter than in *Micromurexia*) upper canines in which the root and crown are more differentiated than in *Micromurexia*, and in which there is no posterior cusp; 4, an upper premolar row in which the narrow, slightly cingulated teeth are uncrowded, and in which P^1 and P^2 are not rounded or postero-lingually lobed, nor does the P^3 show a posterior cusp; 5, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave; 6, M^1 stylar cusp B very large and in M^2 only slightly smaller than stylar cusp D, in some specimens stylar cusp C is visible; 7, M^4 protocone slighty more reduced than in *Micromurexia* and anterior cingulum complete; 8, M^1 and M^2 stylar cusp D slightly heavier than in *Micromurexia*; 9, M^4 metacone relatively large; 10, heel of I$_3$ wider than that of I$_1$; 11, a lightly cingulated lower premolar row in which the narrow teeth are widely spaced and where P$_3$ is only slightly smaller than P$_2$; 12, cingulated P$_3$; 13, well-developed paraconid on M$_1$; 14, three poorly-developed cusps on the M$_4$ talonid; 15, tall entoconid on M$_2$ but very small or absent on M$_4$; 16, metacristids and hypocristids are not transverse to the long axis of the dentary; 17, very fluted nasals which, in lateral view, might be convex at the junction of the premaxillaries; 18, poorly developed tympanic wing of the alisphoid which is contrasted by a greatly expanded pars mastoidea and adjacent squamosal; 19, skull domed posterior of the frontals; 20, tail almost naked dorsally with weak ventral crest developing toward the tip (48% tails white-tipped); 21, polyoestrous and nipple number low (4).

In addition to those features noted in the diagnosis *naso* also differs significantly (P<0.001) from *M. habbema* as follows (measurements are means, mm); longer total length TL (275:246); longer tail T (149: 135); longer ears E (18.40: 16.95); longer basicranial length BL (30.13: 26.70); greater zygomatic width ZW (17.45: 15.56); wider outside bullae OBW (11.57:10.43); wider inside bullae IBW (5.81:4.72); wider rostral widths L-RC^1 (5.91:5.00), L-RM^1 (10.57: 8.87), L-RM^2 (12.97:10.49), L-RM^3 (15.48: 12.76); longer upper tooth row I^1-M^4 (17.32: 15.02); longer upper premolar row P$^{1-3}$ (4.63:
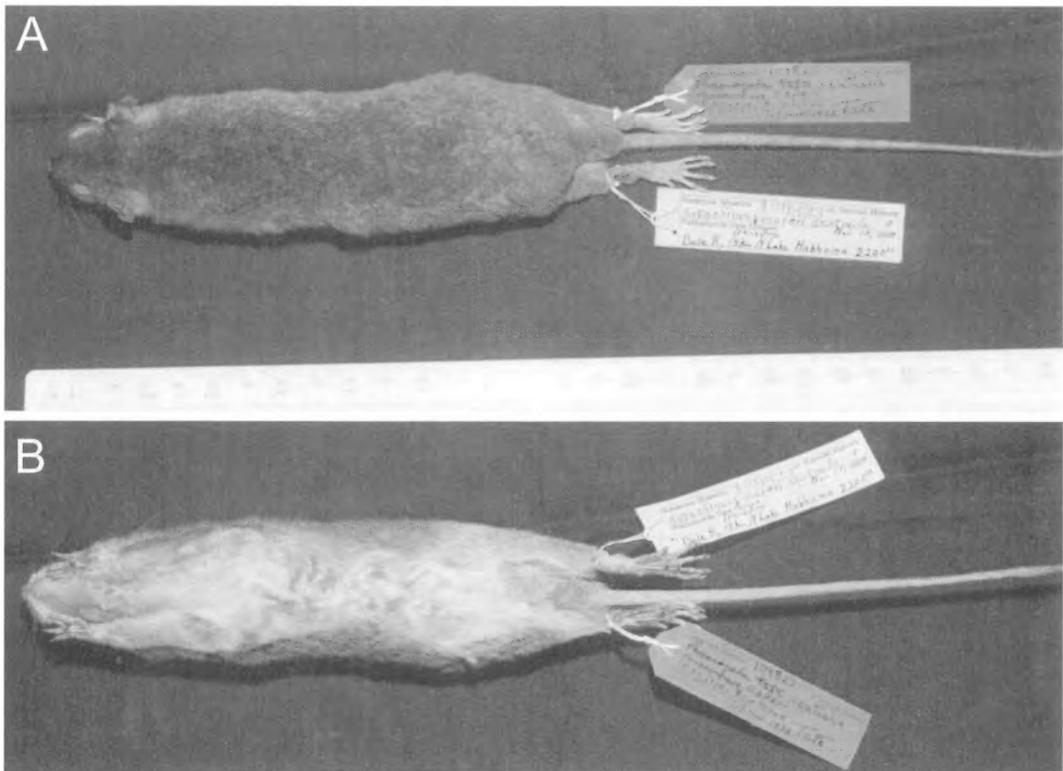
FIG. 14. Holotype of *Antechinus tafa centralis* Tate & Archbold, 1941 (now *Phascomurexia naso*). AMNH 109823, study skin; A, dorsal view; B, ventral view. TL = 281mm; HB = 135mm; TV = 146mm; HF = 26mm.

3.85); wider upper second molar M^2W (2.02:1.73); longer dentary Dent (24.23:21.46); longer lower tooth row I_1-M_4 (15.18:13.12); longer lower premolar row P_{1-3} (4.73:4.08); wider lower second molar M_2 W (1.31:1.11); strongly curved, thick claws rather than claws semi-straight and slender; tail almost naked dorsally with weak ventral crest developing toward the tip rather than tail well-haired dorsally and ventral crest hairs long throughout; the absence of auxiliary apical granules on the interdigital pads of the hind feet and hallucal/post-hallucal pads always fused rather than the likely presence of auxiliary apical granules and non-fused hallucal/post-hallucal pads; the tip of the tail skin often white (48%) rather than never white (in *Micro. habbema*).

P. naso differs significantly (P<0.001) from *M. melanurus* as follows (measurements are means, mm): longer basicranial length BL (30.13: 26.83); wider interorbital width IOW (7.56: 7.09); wider inside bullae IBW (5.70: 5.12);

wider rostral widths R-LM^1 (10.57: 9.71), R-LM^2 (12.97:1.91), R-LM^3 (15.48:14.12); wider maxillary R-LM^1T (8.50:7.69); longer upper tooth row I^1-M^4 (17.32:14.88); longer upper premolar row P^{1-3} (4.63:3.37); longer upper molar row M^{1-4} (7.61: 6.78); wider second upper molar M^2 W (2.02:1.89); longer dentary Dent (24.23:21.31); longer lower tooth row I_1-M_4 (15.18:12.96); longer lower premolar row P_{1-3} (4.73:3.45); longer lower molar row M_{1-4} (8.32:7.37); wider second lower molar M_2 W (1.31:1.22); longer TL (275: 247); longer tail T (149: 133); longer hind foot HF (25.35:22.27); longer ear E (18.40: 15.83); the tip of the tail often white (48% of individuals examined) and usually lightly coloured throughout rather than tail always dark (dark brown to black) and never with white tip.

P. naso differs significantly (P<0.001) from *Murexia. longicaudata* as follows: shorter basicranium BL (30.13: 43.64); narrower zygomatic width ZW (17.45: 25.33); narrower
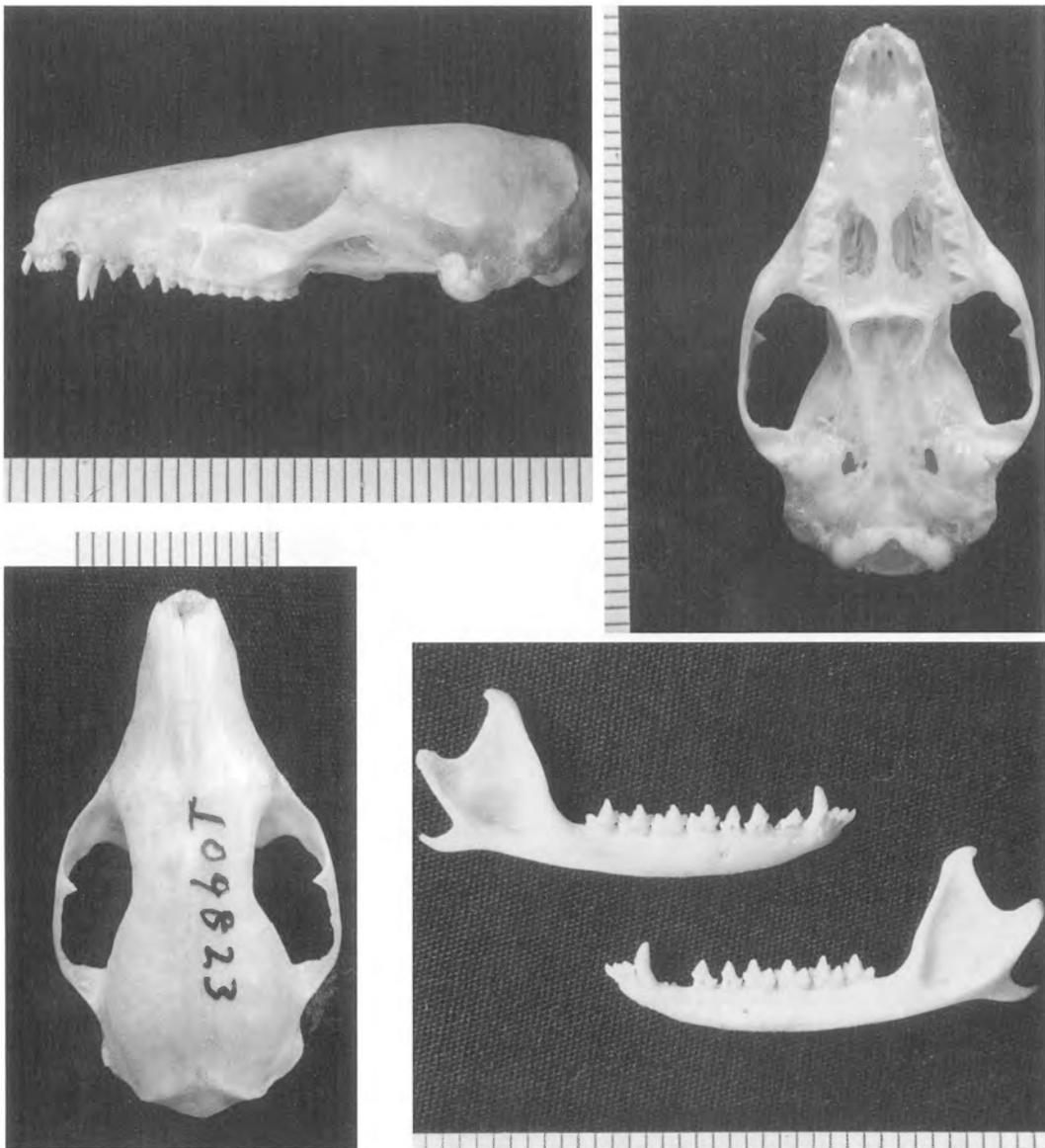
FIG. 15. Holotype of *Antechinus tafa centralis* Tate & Archbold, 1941. AMNH 109823, cranium and dentary. Sex = m; BL = 31.92; ZW = 19.14; IO = 7.86; OBW = 12.12; IBW = 5.85; R-LC^1 = 6.75; R-LM^1 = 10.92; R-LM^2 = 13.49; R-LM^3 = 16.63; R-LM^{1}T = 9.12; M^{2}W = 2.03; I^1-M^4 = 17.61; P$^{1-3}$ = 4.77; M$^{1-4}$ = 7.57; Dent = 26.16; I$_1$_M$_4$ = 15.59; P$_{1-3}$ = 5.50 M$_{1-4}$ = 8.08; M$_2$W = 1.33.

outside bullae OBW (11.57: 14.59); narrower inside bullae IBW (5.81: 8.44); narrower rostrum R-LC^1 (5.91-8.40), R-LM^1 (10.57: 14.71), R-LM^2 (12.97: 17.80), R-LM^3 (15.48: 21.24); narrower maxillae R-LM^{1}T (8.50: 11.95); shorter upper tooth row I^1-M^4 (17.32: 25.01); shorter upper premolar row P$^{1-3}$ (4.63: 7.49); shorter upper molar row M$^{1-4}$ (7.61: 10.10); narrower second upper molar M^2 W (2.02: 2.75); shorter dentary Dent (24.23: 36.17); shorter lower premolar row P$_{1-3}$ (4.73: 7.92); shorter lower molar row M$_{1-4}$ (8.32: 10.90); narrower second lower molar M$_2$W (1.31: 1.71); shorter total length TL (275: 398); shorter tail T (149: 197);
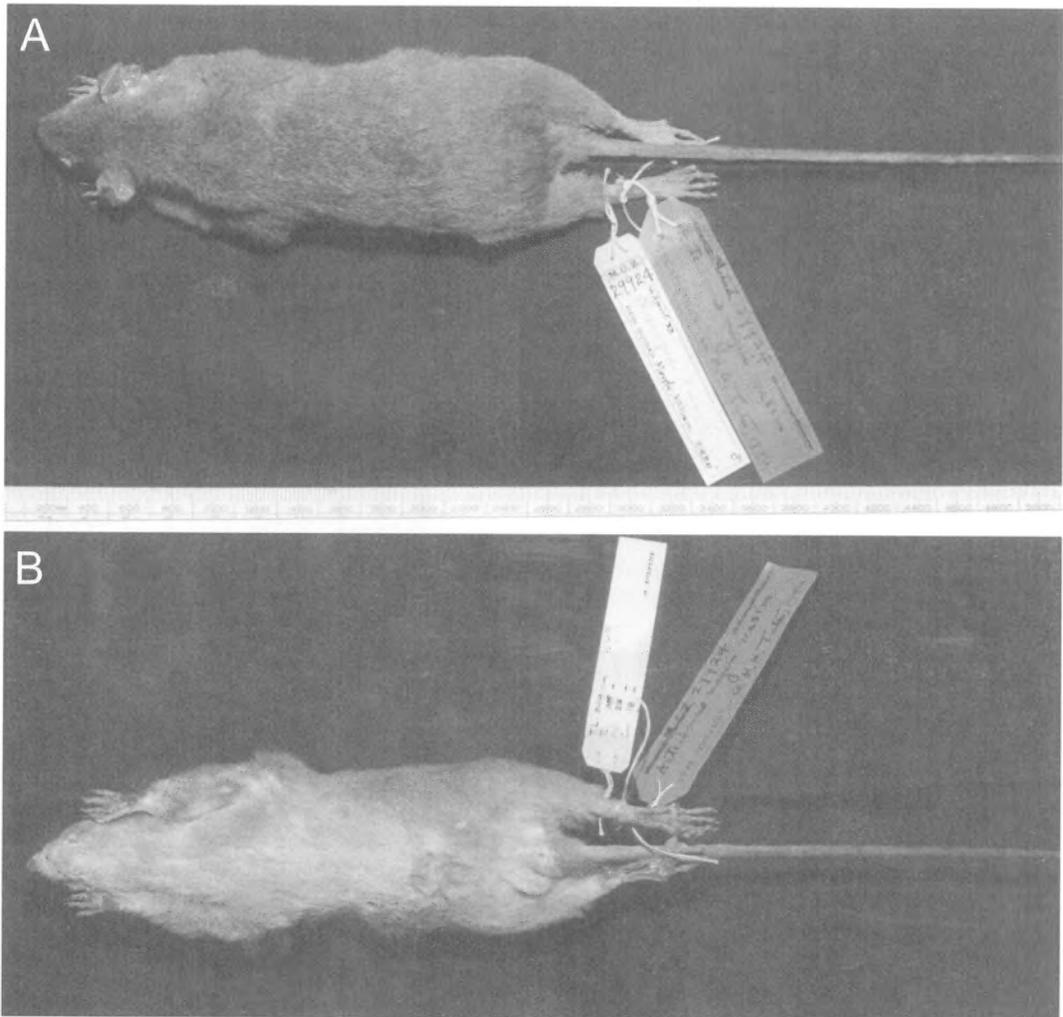
FIG. 16. Holotype of *Antechinus mayeri misim* Tate, 1947 (now *Phascomurexia naso*). MCZ 29924, study skin; A, dorsal view; B, ventral view. TL = 249mm; HB = 112mm; TV = 137mm; HF = 25mm.

shorter hind foot HF (25.35: 35.22); shorter ear E (18.40: 20.50); fur long and luxurious rather than short and harsh; ventral tail crest well developed rather than very poorly developed; no post-metatarsal granule on hind foot rather than well developed post-metatarsal granule often present.

Phascomurexia naso differs significantly (P<0.001) from *Pa. rothschildi* as follows: shorter basicranial length BL (30.13: 35.41); narrower zygomatic width ZW (17.45: 21.29); narrower outside bullae OBW (11.57: 13.21); narrower inside bullae IBW (5.81: 7.27); narrower rostrum R-LC^1 (5.91: 7.72), R-LM^1 (10.57: 12.20), R-LM^2 (12.97: 14.79), R-LM^3 (15.48: 17.65); narrower maxillae R-LM^{1}T (8.50: 10.08); shorter upper tooth row I^{1}M^5 (17.32: 19.68); shorter upper molar row M$^{1-4}$ (7.61: 8.71); shorter dentary Dent (24.23: 28.33); shorter lower tooth row I$_1$-M$_4$ (15.18: 17.39); shorter lower molar row M$_{1-4}$ (8.32: 9.48); no post-metatarsal heel pads on hind foot rather than heel pads well developed.

REMARKS. *Taxonomic History*. It is strange that the disorder associated with the history of this species could have persisted as long as it did.
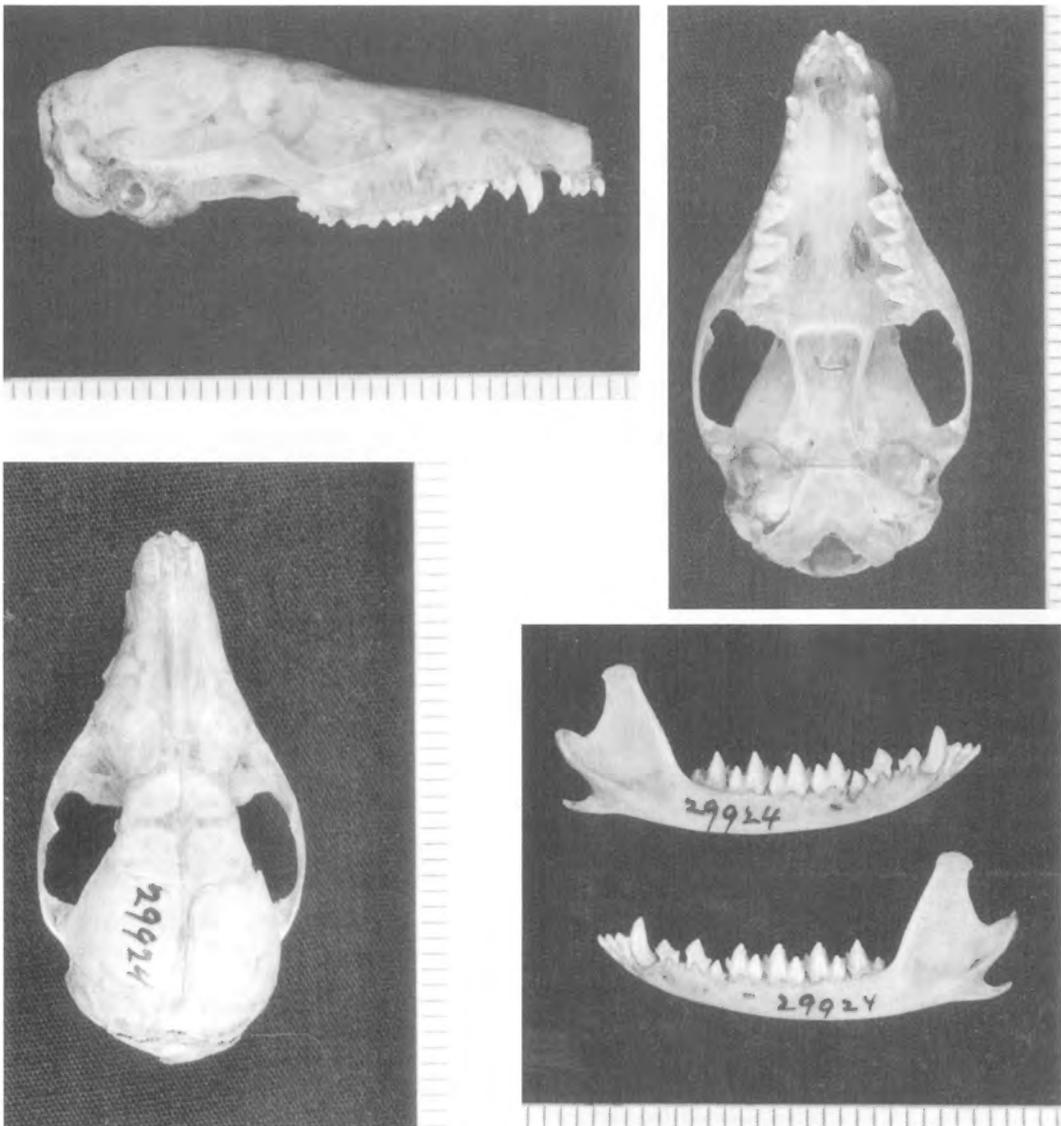
FIG. 17. Holotype of *Antechinus mayeri misim* Tate, 1947. MCZ 29924, cranium and dentary. Sex = m; BL = 30.81; ZW = 17.42; IO = 6.86; OBW = 11.94; IBW = 6.08; R-LC^1 = 5.93; R-LM^1 = 10.80; R-LM^2 = 13.33; R-LM^3 = 15.48; R-LM^{1}T = 8.98; M^{2}W = 2.29; I^1-M^4 = 18.37; P$^{1-3}$ = 4.94; M$^{1-4}$ = 18.45; Dent = 24.99; I$_1$-M$_4$ = 17.10; P$_{1-3}$ = 4.76; M$_{1-4}$ = 9.74; M$_2$W = 1.43.

Jentink's original description of *naso* (1911) was more than adequate for its day considering the brevity of some type descriptions and obscurity of some journals (and newspapers) where many descriptions appeared. In addition, Jentink's specimen was (and still is) in extremely good condition. It is therefore remarkable that *naso* should have been virtually lost from the literature

for 43 years from the day of its description until its resurfacing in Laurie & Hill (1954).

Tate was aware of *P. naso* when he and Archbold described *P. tafa* (1936) — the two species were listed together by Tate as 'unplaced' forms ('... in the subgeneric sense ...' [Tate & Archbold, 1937: 339]). Tate's awareness of *naso* at this time was limited to Jentink's written
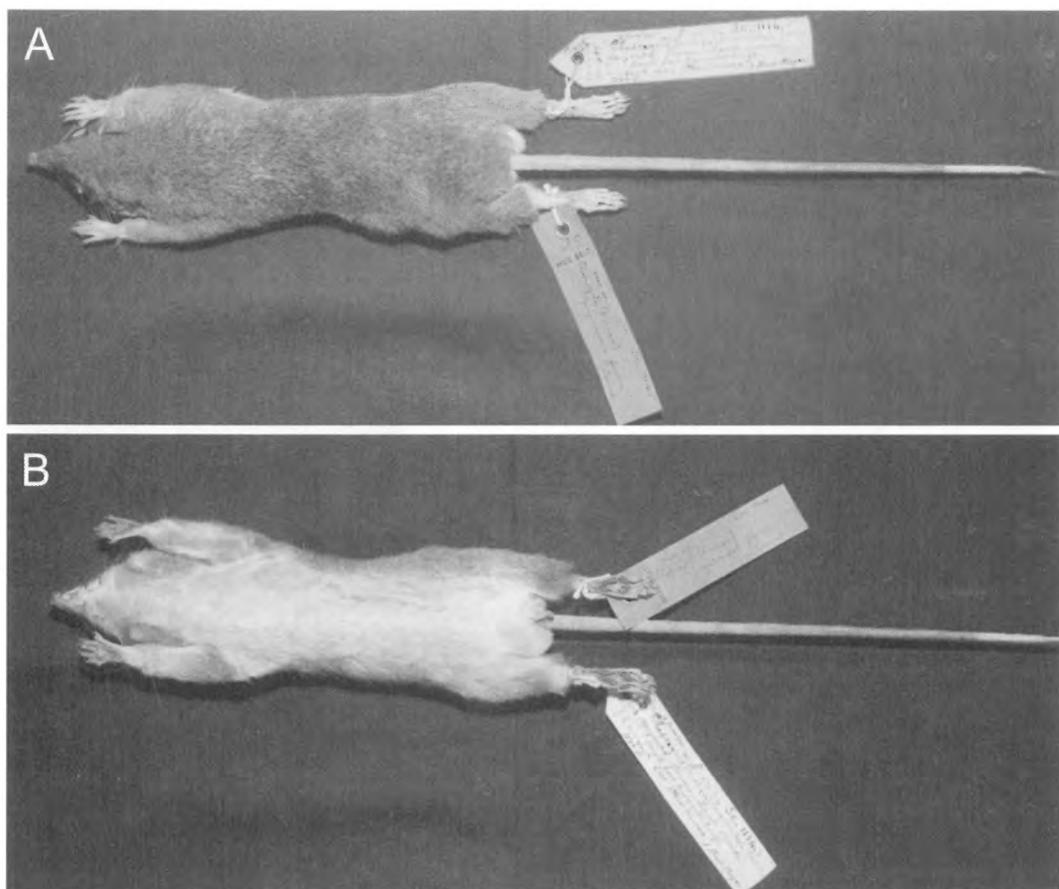
FIG. 18. Holotype of *Murexia longicaudata parva* Laurie, 1952 (now *Phascomurexia naso*). BMNH 50.1114, study skin; A, dorsal view; B, ventral view. TL = 307mm; HB = 132mm; TV = 175mm; HF = 26mm.

description as he had not, prior to 1937, examined type material in overseas institutions, and, as far as I am aware, the only other existing specimens (apart from the types of *tafa* and *naso*) were, presumably, 2 specimens collected by Stein in the Weyland Range, 1931 and held in East Berlin.

The specific title chosen by Jentink 1911, *naso*, drew attention to the fluted, raised condition of the nasals — '... so that a kind of small ram's nose is imitated, giving the head of the animal a peculiar aspect, quite different from that of the other *Phascogale* - species' (p. 236). Tate must have been strongly influenced by this part of the description and concluded that 'The only species from New Guinea to which *rona* [*Sminthopsis virginiae*] might conceivably be allied is *naso* Jentink' (Tate & Archbold, 1937:345; Tate & Archbold, 1936:2). Tate must have been unaware

of the variable nasal fluting in *naso* and, as AMNH 104050 exhibited reduced fluting, he evidently assumed it to be undescribed and published it as *tafa*. Hereafter (1937), *naso* was not referred to again by Tate.

It seems inconceivable that Tate could have missed the holotype of *naso* during his examination of types (*longicaudata*, *lorentzi*, *nouhuysii*, *melas*, *thorbeckiana*) in the Rijksmuseum van Natuurlijke Histoire, Leiden ('... I give some detailed measurements of the specimen [*Phascogale longicaudata*], made by me in Leiden ...' Tate 1947: 117).

It is possible that Tate accidentally overlooked Jentink's *naso* in the Leiden Museum, but it would be unkind to suggest a vague possibility that the potentially humiliating experience of discovering the real identity of *P. naso* in Leiden
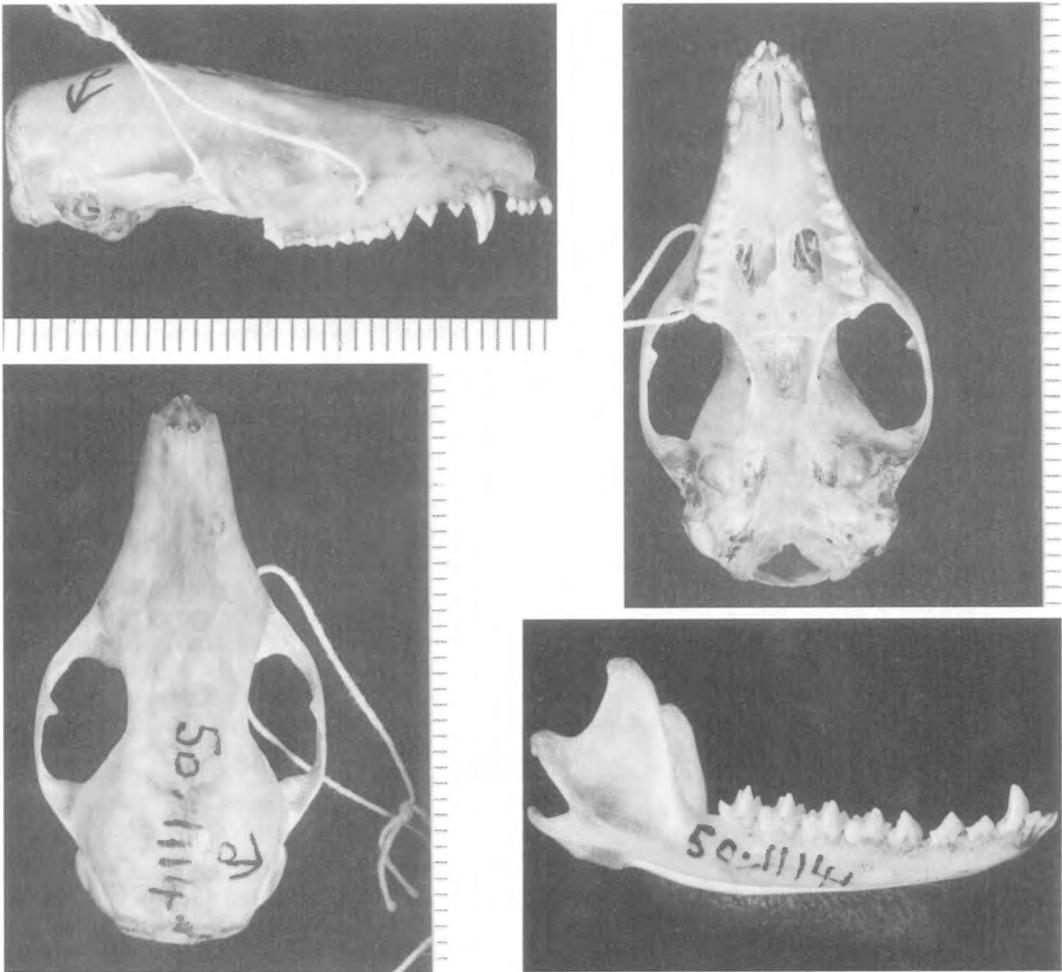
FIG. 19. Holotype of *Murexia longicaudata parva* Laurie, 1952. BMNH 50.1114, cranium and dentary. Sex = m; BL = 31.95; ZW = 19.06; IO = 7.63; OBW = 11.67; IBW = 6.25; R-LC^1 = 5.35; R-LM^1 = 11.16; R-LM^2 = 13.71; R-LM^3 = 16.80; R-LM^{1}T = 8.97; M^{2}W = 2.03; I^1-M^4 = 18.27; P$^{1-3}$ = 5.20; M$^{1-4}$ = 7.89; Dent = 26.17; I$_1$-M$_4$ = 15.92; P$_{1-3}$ = 5.65; M$_{1-4}$ = 8.49; M$_2$W = 1.29.

just one year after describing *P. tafa* (Tate & Archbold, 1936) was too much for Tate's pride, and the specimen was academically overlooked from then on. Whatever the reason, it is most unlikely that Tate, after having examined the specimen, chose to ignore it because he could not come to grips with its identity and affinities.

In 1941, satisfied that *P. tafa* was eligible for subgeneric status of *Antechinus*, Tate & Archbold described *centralis*, a new subspecies of *tafa*. The specimen was a large ♂, considerably bigger than the ♀ *tafa* holotype. The subspecies was erected solely for 2 cranial features: increased size of the maxillary vacuities and an increase in the internal width of the mesopterygoid fossa behind the palate (2 demonstrably variable characters in similarly sized animals). They admitted that the other size differences were due to sexual dimorphism within the species and that the new subspecies was '... separable from true *tafa* only by cranial characters ...' (Tate & Archbold, 1941: 8). The degree of nasal inflation and fluting in *centralis* was even more reduced than that of the *tafa* type, so it is not surprising that the name of *naso* again did not appear in association with this new form.

Six years later (in 1947) Tate submerged his and Archbold's species *tafa* (and *tafa centralis*) into Dollman's (1930) *mayeri* . This was done in spite of the following background to the decision:

1) that Dollman had indicated in his original description that *mayeri* was most closely allied to *melanurus*.

2) that Tate's examination of AMNH 101978 (typical *melanurus* features and which had been identified personally by Dollman as *mayeri*) convinced him and Archbold to (justifiably) relegate *mayeri* to subspecific status as *Phascogale (Antechinus) melanura mayeri* (Tate & Archbold, 1937).

3) that Tate had examined the holotype of *mayeri* — a specimen exhibiting all the dental and cranial features nominated by Tate (1947) to characterise specimens of *A. melanurus*. (The skin of *A. mayeri*, while lighter than typical *melanurus* displays rufous post-auricular patches and a long-haired, black tail, features which never appeared in any of Tate & Archbold's *tafa* types or in any of the AMNH series associated with them (see descriptions of *A. mayeri* (= *Murexechinus melanurus*) and *A. melanurus* (= *Murexechinus melanurus*) later for detailed cranial, dental and pelage data).

4) that Tate himself noted (1947: 128) the unusually low altitude from which the type of *mayeri* had come '... *mayeri* from only 3500 feet' (which is outside the range of *M. naso* but well within those limits ascribed by Tate to *M. melanurus*).

Then in the face of the very dubious separate identities of *A. mayeri centralis* and *A. mayeri tafa*, Tate added another subspecies, *misim* to the *mayeri* list. Once again here, another form was described which was externally '... indistinguishable from the races *centralis* and *tafa*' (Tate 1947: 130). The grounds for its subspecific status lay in its large teeth, and there can be no denying that up until the time of its description no other larger specimen appeared to exist. Tate made no mention, however, that this specimen was a subadult male with only newly emerging $P^3/_3$, and although it was physically smaller than many other specimens which Tate had access to in his own collection, the large value of the dental measurements in the type description make it appear as if the specimen was of a unique form rather than of a young specimen whose large dental proportions would eventually match correspondingly large physical measurements at adulthood.

Tate's dilemma with his *mayeri* group of New Guinea dasyurids is best expressed in his own words, 'All four of these races stand so close to one another that later reviewers may decide that they should be merged together' (Tate, 1947: 129).

The encompassing confusion associated with Tate's dasyurid taxonomy is no more apparent than in his introduction to 'The Members of the *Antechinus flavipes* Group in New Guinea' (Tate 1947: 128). Here he summarised the characteristics of his three proposed groups of *Antechinus* in New Guinea: 1) *melanurus*; 2) *modestus*, *tafa*, *centralis*, *mayeri*; 3) *wilhelmina* (allusion to the name supplied later).

For inexplicable reasons, on the following page, Tate synonymised *modestus* (Thomas) with *melanurus* (Thomas) thereby lifting *modestus* from group 2 and adding it to group 1, and then introduced a further unmentioned '*misim*' to group 2 on page 130. A typographical error could explain the swapping of the names *modestus* for *misim* in the list of p. 128 but can not explain why *modestus* was omitted from group 1 with *melanurus*. If a typographical error had occurred it could be expected that the altitude data provided for *modestus* on p. 128 would simply correlate with that of the *misim* description on p. 130. These values are, however, different (5,000 and 5,850 feet respectively).

In 1952 Laurie described *Murexia longicaudata parva*, a large male of almost identical size to the type of *A. naso* (Jentink, 1911). It can only be assumed that Laurie's comparative assessment of the species was an 'in-house' process as no specimens other than her type and 5 paratypes existed in British Museum collections at the time of the description (or since). Unfortunately, at that time, many similar and some almost identical specimens were to be found in the collections of such natural history museums as the Rijksmuseum in Leiden, the Humboldt-Universitat in East Berlin and the American Museum (Natural History) in New York. Tate had never mentioned in his description of *A. tafa* that the last dozen hairs that comprised the tip of the long ventral crest were coloured white. Perhaps Laurie's attention would have been steered toward *P. naso* if this were the case. But despite this, in 1954 when Laurie and Hill's research revealed the valid identity of *A. naso* for *tafa*, *tafa centralis* and *mayeri misim* they not only failed to associate Laurie's *Murexia longicaudata parva* with Jentink's *naso* but they
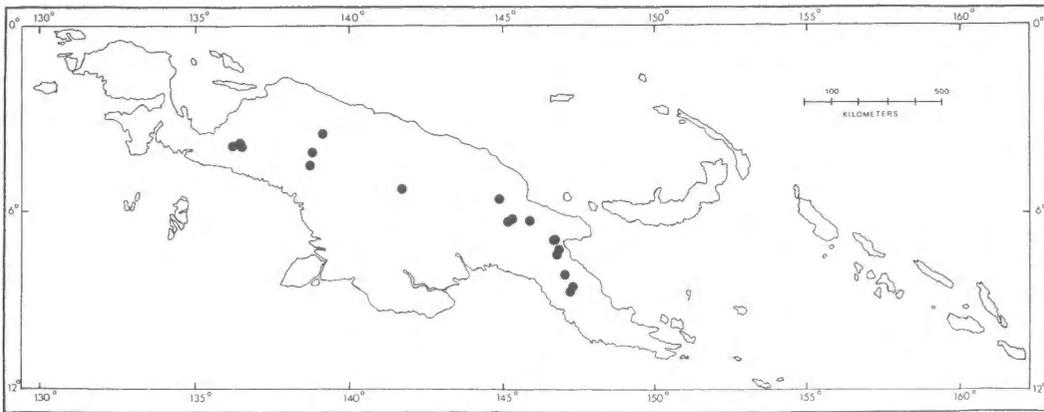
FIG. 20. Distribution of *Phascomurexia naso*.

also failed to recognise that the *A. mayeri* type (held in their own collection) was synonymous with *P. melanurus* and not with *naso*. Ziegler (1977) also referred to *naso* as including *mayeri*, but made a confusing reference (p. 125) to *mayeri* appearing in the '... list of Kirsch and Calaby' (1977) which actually contained the three New Guinea species *naso*, *wilhelmina* and *melanurus* without making a reference to *mayeri*. Honacki et al. (1982) note, however, that Ziegler recognised that *naso* '... probably includes *Murexia longicaudata parva*' (p. 28). And Archer (1982a), erecting the subfamily Murexinae, aired reservations about *M. l. parva* thus, '*Murexia longicaudata parva* is so similar in dental and cranial morphology to plesiomorphic species of *Antechinus* [New Guinea species] that the generic boundary can only be maintained by resorting to external morphology' (p. 428). Archer, in fact, was comparing not an example of *Murexia* with N.G. antechinuses, but another 'antechinus' — *A. naso*. Jenkins & Knutson (1983) assigned the holotype of *M. l. parva* in their care to *Murexia longicaudata*. Van Dyck (1982a) discussed the status and affinities of *A. godmani* and suggested a close phenetic relationship between *A. godmani* and *A. mayeri*. The use of the name *mayeri* by Van Dyck was ill-advised, coming from label names accompanying the specimens used in the comparison. The name *naso* should be substituted in all cases for *mayeri* in this work.

DISTRIBUTION. *Phascomurexia naso* is known from mid to lower montane areas of the central cordillera between 3°32'S 139°10'E Irian Jaya, and 8°35'S 147°09'E Central Morobe Province, Papua New Guinea (Fig. 20). It occurs in a narrow altitudinal range from 1400-2800m and has been collected in rainforest, mid-montane forest, beech forest, pandanus forest and mossy forest. Full floristic details of collection localities appear in Archbold et al., (1942:246) and Brass (1964: 182).

REPRODUCTION. All pouches examined contained 4 teats. Lactating females had been collected in (dates including in parentheses), January (19), February (9), April (16, 29), May (19, 20), August (26), September (27). Dwyer (1977) noted the capture of lactating females in June (20) and December (13). Among other months mentioned already, Woolley (1994) noted lactating females from November.

DESCRIPTION. *Mean Measurements* (mm). External: total length (head, body, tail) ($\male$) 281, ($\female$) 268; tail (to cloaca) ($\male$) 152, ($\female$) 146; hind foot (su) ($\male$) 25.87, ($\female$) 24.83; ear (notch) ($\male$) 19.21, ($\female$) 17.65. Skull: basicranial length ($\male$) 30.79, ($\female$) 29.22; M^{1-4} length ($\male$) 7.64, ($\female$) 7.57; M^2 width ($\male$) 2.04, ($\female$) 2.01. (Table 3).

P4 Morphology. 3 juveniles, AMNH 190872, 190873 and 152028. In two specimens P^4 was single-rooted and premolariform with a single cusp. In AMNH 152028 P^4 was double-rooted but again premolariform. P_4 was a single-rooted, formless spur.

Pelage and Tail. There is no reasonable justification for retaining subspecific groups within *P. naso*. There are however some variable features which deserve recognition. Tail colour varies not only with longitude but also greatly within specimens from eastern localities. Of 52

TABLE 3. Absolute measurements for *Phascomurexia naso*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	Male	22	30.79 ± 0.43	27.17 - 33.74	2.02	4.08	6.56
	Female	16	29.22 ± 0.16	28.07 - 30.42	0.63	0.39	2.16
	Total	38	30.13 ± 0.29	27.17 - 33.74	1.77	3.13	5.87
ZW	M	21	17.99 ± 0.29	15.51 - 20.28	1.35	1.83	7.50
	F	16	16.75 ± 0.11	15.94 - 17.67	0.42	0.18	2.51
	T	37	17.45 ± 0.20	15.51 - 20.28	1.22	1.50	6.99
IOW	M	22	7.75 ± 0.07	6.92 - 8.26	0.31	0.10	4.00
	F	19	7.56 ± 0.05	7.17 - 7.95	0.23	0.05	2.97
	T	41	7.66 ± 0.05	6.92 - 8.26	0.29	0.09	3.79
OBW	M	22	11.76 ± 0.11	11.05 - 12.74	0.50	0.25	4.25
	F	16	11.30 ± 0.08	10.72 - 11.69	0.30	0.09	2.65
	T	38	11.57 ± 0.08	10.72 - 12.74	0.48	0.23	4.15
IBW	M	22	5.89 ± 0.09	4.98 - 6.60	0.41	0.17	6.96
	F	16	5.70 ± 0.08	4.96 - 6.35	0.32	0.11	5.61
	T	38	5.81 ± 0.13	4.96 - 6.60	0.39	0.15	6.71
R-LC^1	M	22	6.10 ± 0.10	5.26 - 7.01	0.48	0.23	7.87
	F	19	5.69 ± 0.06	5.16 - 6.24	0.27	0.07	4.75
	T	41	5.91 ± 0.07	5.16 - 7.01	0.45	0.20	7.61
R-LM^2	M	22	10.73 ± 0.13	9.81 - 12.11	0.60	0.36	5.59
	F	19	10.39 ± 0.14	9.60 - 12.24	0.62	0.39	5.97
	T	41	10.57 ± 0.10	9.60 - 12.24	0.64	0.40	6.05
R-LM^3	M	19	13.17 ± 0.19	11.76 - 14.62	0.82	0.68	6.25
	F	16	12.73 ± 0.16	11.64 - 14.52	0.63	0.40	4.95
	T	35	12.97 ± 0.13	11.64 - 14.62	0.77	0.60	5.94
R-LM^4	M	20	15.84 ± 0.20	14.01 - 17.21	0.90	0.82	5.68
	F	16	15.03 ± 0.16	13.92 - 16.85	0.63	0.40	4.19
	T	36	15.48 ± 0.15	13.92 - 17.21	0.89	0.79	5.75
R-LM^{2}T	M	21	8.64 ± 0.10	7.81 - 9.56	0.44	0.19	5.09
	F	19	8.34 ± 0.08	7.87 - 9.11	0.36	0.13	4.32
	T	40	8.50 ± 0.07	7.81 - 9.56	0.43	0.19	5.06
I^1-M^4	M	22	17.70 ± 0.17	15.92 - 19.23	0.82	0.68	4.63
	F	19	16.89 ± 0.14	15.85 - 18.85	0.59	0.35	3.49
	T	41	17.32 ± 0.13	15.85 - 19.23	0.83	0.69	4.79
P$^{1-3}$	M	22	4.83 ± 0.11	3.80 - 5.90	0.50	0.25	10.35
	F	19	4.40 ± 0.06	4.02 - 4.89	0.24	0.06	5.45
	T	41	4.63 ± 0.07	3.80 - 5.90	0.45	0.20	9.72
M$^{1-4}$	M	23	7.64 ± 0.06	7.09 - 8.21	0.27	0.07	3.53
	F	19	7.57 ± 0.08	7.15 - 8.69	0.34	0.11	4.49
	T	42	7.61 ± 0.05	7.09 - 8.69	0.31	0.09	4.07
M^{2}W	M	23	2.04 ± 0.01	1.90 - 2.22	0.07	0.01	3.43
	F	19	2.01 ± 0.02	1.89 - 2.16	0.08	0.01	3.98
	T	42	2.02 ± 0.01	1.89 - 2.22	0.08	0.01	3.96
Dent	M	22	25.03 ± 0.29	21.73 - 26.93	1.36	1.85	5.43
	F	19	23.31 ± 0.22	21.49 - 25.87	0.98	0.96	4.20
	T	41	24.23 ± 0.23	21.49 - 26.93	1.47	2.17	6.07
I$_1$-M$_4$	M	23	15.55 ± 0.13	14.21 - 16.60	0.60	0.37	3.86
	F	18	14.70 ± 0.08	14.01 - 15.40	0.32	0.10	2.18
	T	41	15.18 ± 0.10	14.01 - 16.60	0.65	0.43	4.28
P$_{1-3}$	M	22	4.96 ± 0.10	3.91 - 5.72	0.48	0.23	9.68
	F	19	4.47 ± 0.04	4.28 - 4.90	0.17	0.03	3.80
	T	41	4.73 ± 0.07	3.91 - 5.72	0.44	0.20	9.30
M$_{1-4}$	M	23	8.40 ± 0.10	7.42 - 10.01	0.46	0.21	5.48
	F	19	8.22 ± 0.08	7.60 - 9.24	0.34	0.12	4.14
	T	42	8.32 ± 0.06	7.42 - 10.01	0.42	0.18	5.05
M$_2$W	M	23	1.32 ± 0.01	1.24 - 1.43	0.04	0.00	3.03
	F	19	1.31 ± 0.01	1.23 - 1.38	0.04	0.00	3.03
	T	42	1.31 ± 0.01	1.23 - 1.43	0.04	0.00	3.05
TL	M	20	281 ± 4.47	231 - 307	20	432	7.12
	F	18	268 ± 2.36	247 - 285	10	101	3.73
	T	38	275 ± 2.76	231 - 307	17	14	6.18
T	M	20	152 ± 3.13	109 - 175	14	219	9.21
	F	19	146 ± 2.29	126 - 164	10	111	6.85
	T	39	149 ± 2.08	109 - 175	13	173	8.72
HF	M	19	25.87 ± 0.33	23 - 29	1.45	2.10	5.60
	F	19	24.83 ± 0.45	20 - 28	1.96	3.83	7.89
	T	38	25.35 ± 0.29	20 - 29	1.80	3.24	7.10
E	M	12	19.21 ± 0.44	17 - 23	1.52	2.31	7.91
	F	13	17.65 ± 0.46	14 - 21	1.67	2.78	9.46
	T	25	18.40 ± 0.36	14 - 23	1.78	3.16	10.08
W	M	2	49 ± 3.54	44 - 54	5	25	10.20
	F	-	-	-	-	-	-
	T	2	49 ± 3.54	44 - 54	5	25	10.20

specimens examined for tail colour, 25 had white tail tips (ranging from the most distal tail hairs being white, up to 62mm along the tail from the tip) and 27 had uniformly dark tails. White colouring is evident in both tail hair and skin pigment. No specimens west of Telefomin (141°38'E) had white-tipped tails (N=19) while specimens from the east (e.g., Central Morobe Province) showed 24 with white tips and 5 without. One specimen (QM JM6169) from Ofektamin near Telefomin (centre of the *P. naso* range) shows pelage and tail colouration unlike any other specimen. This large adult male has its tail uniformly coloured a dark slate grey with a slightly browner, weak ventral crest. There is no white tip. The mid-back is typically *P. naso* coloured (a dull sepia) but rump and neck are a rich golden brown. It also shows a black stripe passing from the mystaceal vibrissae to the anterior corner of the eye. In cranial and dental features it is indistinguishable from other large *P. naso* specimens.

Size. Largest specimens appear to occur at the east-west extremities of the overall range, with AMNH 1919 from Araboe-bivak (136°26'E) Irian Jaya, measuring BL = 33.72mm and AMNH 221473 from Mt Albert Edward (147°18'E) Papua New Guinea, measuring BL = 33.03mm.

SPECIMENS EXAMINED. Albert Edward Mt., 2257m, 08°22'S 147°18'E (AMNH 221473); Araboe-bivak, 1750m, 03°51'S 136°26'E (RMNH 1919, RMNH 3725); Baiyanka, 2287m, 05°35'S 144°51'E (BMNH 50.1114-50.1116); Bernhard Camp 15km SW, 1500m, 03°32'S 139°10'E (AMNH 152031); Bernhard Camp 15km SW, 1800m, 03°32'S 139°10'E (AMNH 152026-152030); Enarotali, 1765 m, 03°56'S 136°13'E (RMNH 520, RMNH 755-756); Enarotali, 1800m, 03°56'S 136°13'E (AMNH 221629, AMNH 222049); Erimbari Mt., 2850m, 06°12'S 145°10'E (QM JM 1095-1096); Gono, 1900m, 06°20'S 145°12'E (AMNH 190875); Habbema Lake 18km N, 2200m, 04°05'S 138°42'E (AMNH 109823, AMNH 151069); Habbema Lake 18km SW, 2150m, 03°33'S 139°09'E (AMNH 152037); Habbema Lake 9km NE, 2800m, 04°05'S 138°50'E (AMNH 109809, AMNH 109814, AMNH 109816-109818); Hellwig Mts, 2000m, 04°32'S 138°41'E (ZM 35134); Kaindi Mt., 1900m, 07°21'S 146°43'E (BBM 54653); Kaindi Mt., 2100m, 07°21'S 146°43'E, (AMNH 190872-190874, BBM 101625, BBM 101640); Kaindi Mt., 2200m, 07°21'S 146°43'E (BBM 105356, BBM 105363, BBM 105369, BBM 105379); Kaindi Mt., 2300m, 07°21'S 146°43'E (BBM 29184, BBM 51029, BBM 53436); Kaindi Mt., 2350m, 07°21'S 146°43'E (BBM 53380); Kamila (Okapa area), 1900m, 06°37'S 145°35'E (AMNH 190877-190879); Kunupi, 1400-1800m, 03°50'S 135°30'E (ZM 91679-91680); Misim Mt., 1900m, 07°13'S 146°50'E (BBM 29088); Misim Mt., 1769m, 07°13'S 146°50'E (MCZ 29923); Misim Mt., 1784m, 07°13'S 146°50'E (MCZ

29924); Moimo, 1830m, 07°59'S 147°01'E (BBM 98044, BBM 98115); Ofektamin, 1500m, 05°12'S 141°38'E (QM JM6169); Paniai, 1750m, 03°55'S 136°23'E (RMNH 518); Shungul Mt., 200m, 06°51'S 146°44'E (BBM 60300); Shungul Mt., 2300m, 06°51'S 146°44'E (BBM 98293); Sonofi (Kainantu area), 1891m, 06°20'S 145°43'E (AMNH 190876); Tafa Mt., 2130m, 08°35'S 147°09'E (AMNH 104040); Tapu, 2287m, 06°14'S 145°50'E (BMNH 50.117-50.1119).

Murexia Tate & Archbold, 1937

Phascogale (in part), Temminck 1824.
Phascologale (in part) Thomas 1888.

TYPE AND ONLY SPECIES. *Phascogale murex* Thomas, 1913 = *longicaudata.* Based on BMNH 12.2.4.1, adult ♂, puppet skin and skull, from Sattelburg, Houn Peninsula, NE PNG, 06°30'S 147°43'E.

GENERIC DIAGNOSIS. M^2 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. A relatively unreduced talonid on M_4 with 3 cusps. Tail longer than the head-body length.

It is distinguished from *Phascolosorex* and *Myoictis* by its lack of dorsal body stripes, and from *Neophascogale* by its lack of reduced premolars and lack of a thickly-haired white-tipped tail.

Murexia is immediately separable from *Micromurexia* by its larger valves for the following measurements (ranges (R) associated with each measurement do not overlap, Table 4); basicranial length BL, zygomatic width ZW, outside bullae width OBW, inside bullae width IBW, rostral widths $R-LC^1$, $R-LM^1$, $R-LM^2$, $R-LM^3$, maxilla width $R-LM^1T$, upper tooth row I^1-M^4, upper premolar row P^{1-3}, upper molar row M^{1-4}, upper second molar width M^2W, lower tooth row I_1-M_4, lower premolar row P_{1-3}, lower molar row M_{1-4}, lower second molar width M_2W, total length TL and hind foot HF.

Murexia is separable from *Phascomurexia* by the longer lower tooth row I_1-M_4.

Murexia is separable from *Murexechinus* by the longer upper and lower premolar rows P1-3.

Murexia is separable from *Paramurexia* by its lack of a black, longitudinal head-body stripe and accompanying black facial mask.

Murexia longicaudata (Schlegel, 1866)
(Figs 21, 22)

Phascogale longicaudata Schlegel, 1866: 356.
Phascogale murex Thomas, 1913: 80.
Phascogale murex aspera Thomas, 1913: 211.
Phascogale maxima Stein, 1932: 254.

HOLOTYPE. RMNH 35135, subadult ♂, very old, faded mount and skull extracted (skin faded, skull deformed with basioccipital region missing).

TYPE LOCALITY. Wonoembai, Aru Islands, Irian Jaya 6°00'S 134°30'E. <100m. Coll. M. von Rosenberg, 1865.

DIAGNOSIS. As for genus.

DESCRIPTION. HOLOTYPE. *Pelage* (Fig. 21) faded; head shows insect damage, and patches of fur are missing from the body. The head appears as a Tawny Olive, mid-back and shoulders appear as Sepia and rump in a warm Sepia.

Fur of the mid-back (4.3mm long) has basal 3.3mm Slate colour, median 0.6mm Cinnamon Buff and apical 0.4mm Fuscous Black. Sepia guard hairs are thickly interspersed through the fur and are 3.6mm on the head, 7.5mm on the mid-back and 9.0mm on the rump. Fur of the head is 2.17mm long with similarly pigmented basal, median and apical bands which are 2.11 mm, 0.3mm and 0.3mm respectively. Fur of the rump is 7.03mm long with similarly pig- mented basal, median and apical bands 4.7mm, 1.62mm and 0.71mm respectively, however the median band is coloured Mikado Brown.

The head lacks a stripe and there is no head patch or eye-ring. The ventral fur (5mm long on the belly and interramal region) is Deep Olive Buff (a 'dirty' off-gray) on the basal half and Warm Buff on the apical half and is interspersed with Cream-Buff guard hairs 6.4mm long. The belly is thus an overall Warm Buff. Forefeet are thinly covered with Sepia coloured hairs and hindfeet are similarly coloured. The tail is weakly bicoloured with dorsal hairs averaging 1.3mm and ventral hairs averaging 1.8mm along its length until the tip where hair length increases to 3.3mm dorsally and 4.7mm ventrally. Dorsal hairs appear a dark Clove Brown — this results from a combination of black guard hairs and Mikado Brown guard hairs. Ventrally the hairs are all the same colour, Burnt Umber.

Vibrissae. Approximately 9 mystaceal vibrissae occur on the left side and 14 occur on the right. The more dorsal of these are coloured a faded Sepia with those more ventral are colourless; supra-orbital vibrissae (Sepia) number 2 (left) and 2 (right); genals (Sepia and colourless) number 0 (left) and 9 (right), ulna-carpals (colourless) number 4 (right) and 0 (left); submentals (colourless) number 4.

Tail. Tail very long (much longer than the head and body), thin, tapering toward the tip.

Hindfoot. Interdigital pads separate. The apical granule is enlarged, elongate and striate. Hallucal and post-hallucal pads are long and fused. Metatarsal pads are long, narrow and striate.

Ears. Pinnae are large with a complex supratragus which has a pronounced thickened posterior margin and the distal end is reflected ventrally. The reflected tip is (presumably in the mount) concave.

Dentition (Fig. 22). Upper Incisors: I^1 is narrow, procumbent and slightly curved, taller crowned than all the other incisors and separated by a diastema from I^2. Left and right I^1 are just separate. In crown heights $I^4>I^3>I^2$. All upper incisors lack buccal cingula yet there is no lack of differentiation between root and crown. I^1 carries no anterior or posterior cusps. The roots of I^4 are narrow. The premaxillae of the holotype are grossly deformed having folded lingually and being also reflected posteriorly so that all right incisor crowns orient toward all left incisor crowns, and all crowns orient posteriorly.

Upper Canines: C^1 is slender, very long and caniniform with an indistinct boundary between root and crown. There are no buccal or lingual cingula, and no anterior or posterior cusps. Both R and LC^1 appear not to have erupted fully and are both abnormally deflected lingually. Long, deep grooves occur obliquely between I^4 and the lingual edge of C^1 where C_1 has occluded.

Upper Premolars: Premolars are abnormally square and crushed. In crown height $P^3>P^2>P^1$. All upper premolars carry strong buccal and weak lingual cingula. Small anterior and posterior cusps occur on all premolars. P^1 and P^2 possess postero-buccal lobes and P^3 does not contact M^1.

Upper Molars: The posterior tip of P^3 is not in the parastylar corner of M^1 but lingual to and well below stylar cusp A. The anterior cingulum below stylar cusp B is short, broad and complete. Stylar cusp B and the paracone are relatively unworn and no protoconule is present at the base of the paracone apex. The paracone on M^1 is approximately half the height of the metacone. Stylar cusp C is very well developed on LM^1 and RM^1, and stylar cusp E is visible. M^1 possesses a posterior cingulum.

In M^2 the broad, complete anterior cingulum which contacts the metastylar corner of M^1, tapers quickly as it progresses down and along the base of the paracrista and finally unites with the trigon basin of the paracone apex. No protoconule is visible. M^2 has a prominent stylar

cusp A, a small C and a just visible stylar cusp E. Stylar cusp D is robust and broad and there is a posterior cingulum.

In M^3 the anterior cingulum is as broad and long as in M^2. It is complete. Stylar cusp D is reduced to a very small, dense peak. Stylar cusp E is present, but stylar cusp C is not. A posterior cingulum is present.

In M^4 the metastylar corner is well developed. The anterior cingulum is complete and a posterior cingulum is also present. The protocone is reduced but broad. In occlusal view the angle made between the post-paracrista and the post-protocrista is close to 120°. There is slight development of the metacone.

Lower Incisors: The lower incisor row is abnormally crowded and the incisors crushed. LI_1 folds over, and anterior to RI_1. A supernumary incisor with degenerate I_1 morphology is fully erupted posterior to LI_1. The first lower incisor is slightly larger in crown height than I_2. I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is sub-equal in crown height to I_3. I_3 is slightly premolariform in lateral view with a conspicuous posterior cusp at the base of a crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the prominent posterolingual lobe, and the crown enamel of the primary and posterior cusps folds noticeably lingually such that the crest of the two cusps bisects the tooth longitudinally.

Lower Canines: C_1 is caniniform, with forward and erect projection and maximal curvature from root to crown tip. It has weak buccal and lingual cingulation and no posterior cusp. The dentary is abnormally widened below the premolars and canines.

Lower Premolars: P_{1-2} are abnormally crushed into each other and on to C_1. All are weakly cingulated buccally and lingually. In crown height $P_2>P_3>P_1$. P_1 and P_2 are abnormally broad and massive and P_3 is oblique to the dentary thereby avoiding contact with P_2. All possess weak cingular cusps and none possess anterior cusps. The bulk of each premolar mass is concentrated posterior to the line drawn transversely through the middle of the two premolar roots. Postero-lingual and postero-buccal lobes are featured in P_1 and P_2.

Lower Molars: All molars are narrow. The M_1 talonid is wider than the trigonid and the anterior cingulum is present but poorly developed. It

continues into a weak buccal cingulum. The paraconid is greatly reduced and appears in occlusal view as a small steeply-sided spur, the lingual edge of which makes a slight swelling on the endoloph of M_1. The paracristid is scarcely detectable from paraconid to paracristid fissure and is approximately 45° from the paracristid fissure to the protoconid. The metacristid is roughly oblique to the long axis of the dentary and the hypocristid is also oblique. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly lingual to that point directly below the tip of protoconid. The hypocristid extends from the tip of the hypoconid to the metastylid. The entoconid is low. From the base of the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid. In M_2 the trigonid is slightly narrower than the talonid. The anterior cingulum is very well developed and continues into a weak buccal cingulum which is slightly broken at the base of the protoconid. A strong posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid and anteriorly to the weak buccal cingulum. The paraconid is well developed and is the smallest trigonid cusp. The metastylid and minute entoconid are subequal in height but are both very poorly developed. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid, intersecting the trigonid at a point directly below the tip of protoconid but well buccal to the metacristid fissure. The hypocristid extends from the hypoconulid tip to the tip of hypoconid. From the base of the metaconid posteriorly, the endoloph follows a line buccal to that of a dentary axis.

In M_3 the trigonid is wider than the talonid. An indistinct parastylid wraps around the hypoconulid of M_2 and there is a weak anterior cingulum on M_3. Buccal and posterior cingula are as in M_2 but more poorly developed. The cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid, but slightly buccal to the metacristid fissure. There is a poorly developed entoconid on M_3. The endoloph on the talonid of M_3 takes a more buccal orientation than that seen in M_2. The rest of M_3 morphology is as in M_2 except that a small crest runs down from the hypoconulid to the origin of the hypocristid.

In M_4 the trigonid is wider than the talonid. The anterior cingulum is stronger than in M_2. Posterior and buccal cingula are weak. Of the
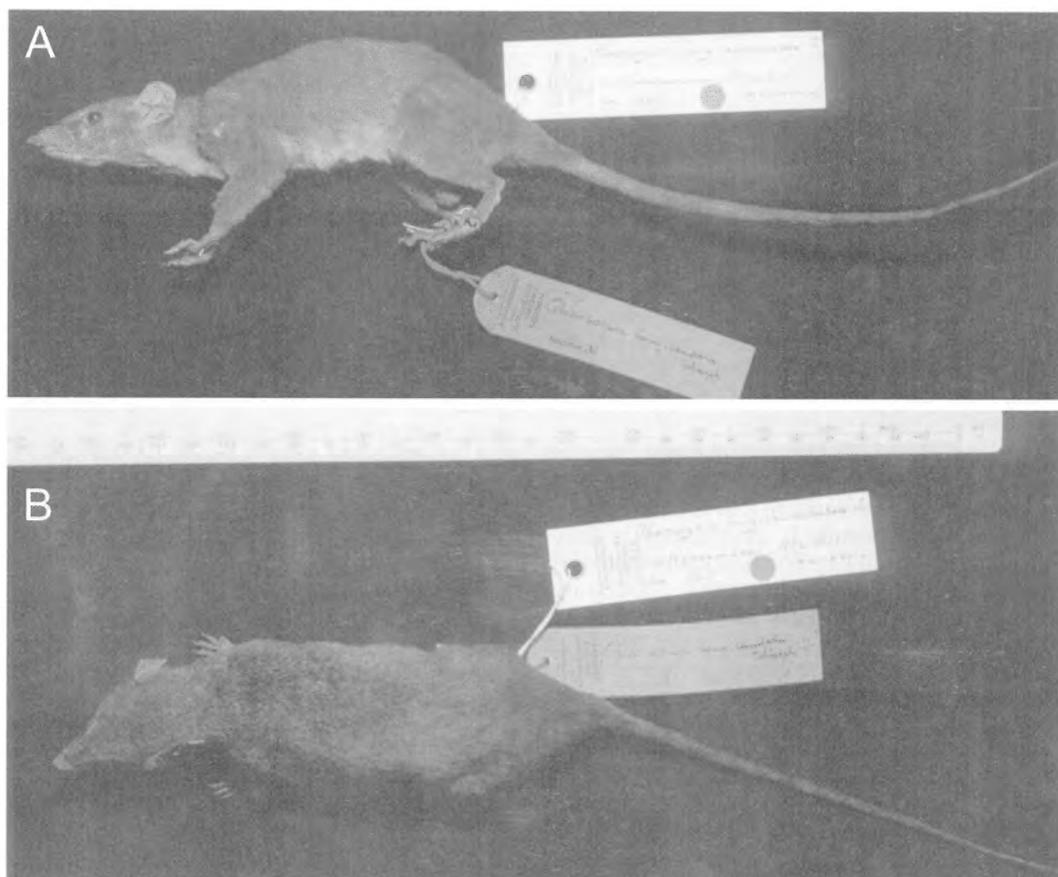
FIG. 21. Holotype of *Phascogale longicaudata* Schlegel, 1866 (= *Murexia longicaudata*). RMNH 35135, study skin; A, lateral view; B, dorsal view. Only external measurement available TL = 324mm; T = 175mm.

three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. The hypoconid of the M_4 talonid is much more reduced than in M_3. Between the hypoconid and the base of the metacristid, the cristid obliqua forms a low, weak crest which meets the trigonid lingual to the metacristid fissure. A significant feature of M_4 morphology is the retention of a broad buccal cingulum. The hypoconid is well formed as is the hypoconulid. The entoconid is represented by a barely discernible bump of enamel.

Skull (Fig. 22). The basicranium is missing from the holotype from the level of the entocarotid foramina posteriorly. The nasals are minimally inflated, creating a slight depression at the nasal-frontal suture in the interorbital region. The premaxillary vacuities extend from the level of the I^2 root back to midway along the C^1 root. The

very small maxillary vacuities extend from the level of the metacone root of M^1 and extend back to the level of the protocone root of M^3. Palatine vacuities are absent.

SYNONYMS

Phascogale murex Thomas, 1913
(Figs 23, 24)

HOLOTYPE. BMNH 12.2.4.1, adult ♂ puppet skin with skull extracted (skin in good condition, basicranium posterior to alisphenoid bullae, missing).

TYPE LOCALITY. Sattelburg, Huon Peninsula, NE PNG, 06°30'S 147°43'E. At 290m. Coll. O. Fritsche.

P. murex differs from the *longicaudata* holotype in the following respects.

Pelage (Fig. 23). The skin appears as a uniform Sepia. It has a well-developed, ventral tail crest.
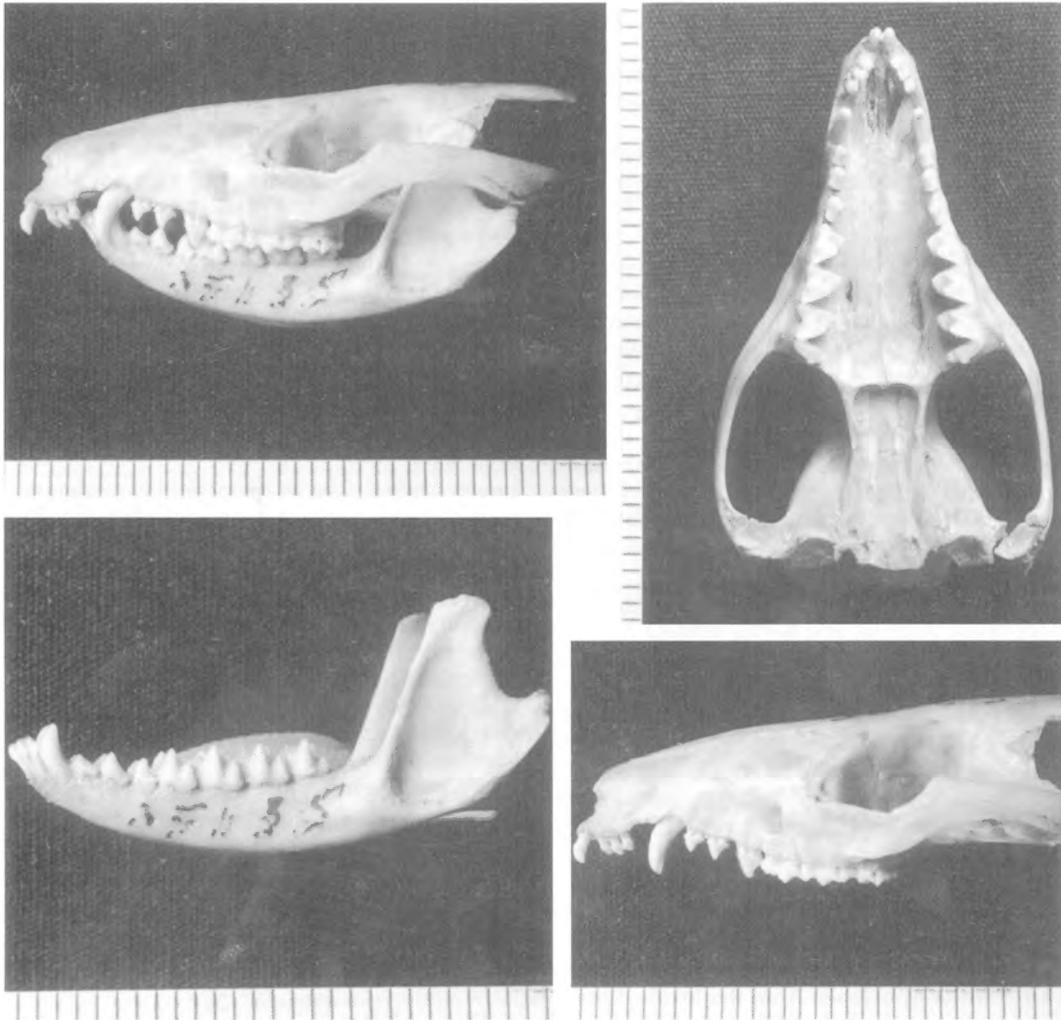
FIG. 22. Holotype of *Phascogale longicaudata* Schlegel, 1866, RMNH 35135, cranium and dentary. Sex = m; BL = -; ZW = 20.97; IO = 7.30; OBW = 12.69; IBW = 5.66; R-LC^1 = 6.88; R-LM^1 = 12.22; R-LM^2 = 14.88; R-LM^3 = 17.44; R-LM^{1}T = -; M^{2}W = 2.37; I^1-M^4 = 20.46; P$^{1-3}$ = 4.29; M$^{1-4}$ = 9.40; Dent = 27.39; I$_1$-M$_4$ = 15.87; P$_{1-3}$ = 4.29; M$_{1-4}$ = 9.40; M$_2$W = 1.56.

Dentition (Fig. 24). RP^3, RM^1, RM^3 and RI^1 are missing; . Despite the deformity of the holotype of *longicaudata*, *murex* exhibits a similar incisor gradient with I^1 procumbent and I^4>I^3>I^2. I^1 is very narrow and slightly built.

Upper Canines: C^1 is long, slender, fully erupted and displays no abnormal, oblique, lingual deflection as noted in the *longicaudata* holotype.

Upper Premolars: The premolars are narrow, elongate, and widely spaced. C^1 and P^1, and P^3 and M^1 are in close juxtaposition. A diastema

occurs between P^2 and P^3, but this is smaller than the large diastema which separates P^2 and P^3. Postero-lingual lobing is not featured in any of the upper premolars. In crown height P^3 is much greater than P^2 which is greater than P^1.

P^1 and P^2 are minute premolars, and P^3 is characterised by a long exposed anterior root. All premolars possess strong buccal cingula. P^1 and P^2 have both anterior and posterior cingular cusps. P^3 lacks an anterior cusp but possesses a small posterior cusp.

Upper Molars: The posterior tip of P^3 lies in the parastylar corner of M^1 and is lingual to and just below stylar cusp A. Stylar cusp B is very large but C is absent. In M^2 stylar cusps C and E are absent.

In M^3 stylar cusps C and E are just visible. In M^4 there is a great reduction in the length of the paracone which is broad, but very short. There is no development of the metacone.

Lower Incisors: There is no crushing among the lower incisors as in the *longicaudata* holotype. I_1 is much larger than I_2 or I_3. Only 3 right and 3 left incisors are present (i.e., the normal condition).

Lower Canines: C_1 is bulky and strongly curved.

Lower Premolars: The lower premolar row is uncrowded although C_1 and P_1 are closely juxtaposed. A large diastema occurs between P_2 and P_3. All premolars are narrow and elongate with no evidence of posterolingual lobing. In crown height $P_3>P_2>P_1$ and all possess buccal and lingual cingula.

Lower Molars: In M_1 the paraconid is very well developed. Anterior and buccal cingula are very strongly developed as is the entoconid.

M_2 has a well developed paraconid, strong buccal and anterior cingulation and a large entoconid. The trigonid is narrower than the talonid.

In M_3 the trigonid is wider than the talonid. The anterior, buccal and posterior cingula are complete, and the entoconid is large.

In M_4 all 3 talonid cusps are well developed. The hypoconid is larger than the entoconid which is larger than the hypoconulid.

Skull (Fig. 24). The premaxillary vacuity (4.32mm long) extends from the level of the I^2 root back to the level of middle of the C^1 root. The maxillary vacuities (3.31mm long) extend from the level of the M^1 protocone root back to the level of the M^2 metacone root.

Phascogale murex aspera Thomas, 1913
(Figs 25, 26)

HOLOTYPE. BMNH 13.6.18.90. Adult ♀ puppet skin with skull extracted (skin and skull in good condition).

TYPE LOCALITY. Utakwa River, Camp No. 3, Irian Jaya, 04°24'S 137°12'E. At 762m. Coll. C.B. Kloss, 1 December 1912.

P. murex aspera differs from the *longicaudata* holotype in the following respects (apart from the abnormalities).

Dentition (Fig. 26). As for *P. longicaudata* except C^1 is relatively small (always relatively smaller in ♀♀). The only diastema in the upper premolar row occurs between P^1 and P^2. Buccal cingula occur only on P^2 and P^3, weak lingual cingula occur on P^2 and P^3. On M^1 and M^2 stylar cusp C is large and stylar cusp E is very large. The anterior and posterior cingula are broad and complete. In M^3 anterior and posterior cingula are well developed, stylar cusps C and E are present and D is greatly reduced.

Lower Premolars: Premolars are tightly arranged though there is no crowding of the premolar row. In the left dentary the diastema separating P_1 and P_2 is greater than that which separates C_1 and P_1. In the right dentary these diastemata are equal. In crown size P_2 is slightly longer than P_1, but in crown height P_3 is taller than the other 2 premolars.

Lower Molars: The M_1 paraconid is moderately well developed and the entoconid is large. The M_3 trigonid is smaller than the talonid, the entoconid is large but it does not contribute to the bulk of the endoloph between metaconid and hypoconulid. In M_4 the cingulation is reduced (compared to that of M_3). The talonid shows moderate development of the three talonid cusps, with the hypoconid larger than the well developed hypoconulid which is larger than the small entoconid.

Skull (Fig. 26). The premaxillary vacuity (4.14mm long) extends from the level of the M^1 root to the posterior end of the C^1 root. The maxillary vacuities (3.01mm long) extend from the level of the M^2 protocone root back to the protocone root of M^3.

Phascogale maxima Stein, 1932
(Figs 27, 28)

HOLOTYPE. ZM 44228. Very large adult ♂ puppet skin with skull extracted (skin and skull in excellent condition).

TYPE LOCALITY. Yapen Island, Geelvink Bay, W Irian Jaya, 01°45'S 136°10'E. At 50m. Coll. G. Stein, 18 March 1931.

P. maxima differs from the *longicaudata* holotype in the following respects.

Pelage (Fig. 27). Head, back rump and the dorsal surface of the tail are coloured Saccardo's Umber. Sides of the body are Clay coloured and the belly is an Olive Buff. The tail is practically naked. There are approximately 20 left and 15 right mystacial vibrissae of which the longest are 30mm. The more dorsal are coloured Fuscous Black while those lower are colourless; supra-orbital vibrissae (Fuscous Black) number 1 (left)

and 0 (right); genals (Fuscous Black and colourless) number 8 (left) and 12 (right); ulna-carpals (colourless) number 2 each side; submentals (colourless) number 4. The fur has a very spinous texture and is difficult to rub against (from rump to head).

Dentition (Fig. 28). Upper Incisors: I^1 is narrow with the tips curved posteriorly. Left and right I^1 are just separate.

Upper Canines: C^1 is moderately broad but exceptionally long.

Upper Premolars: All premolars are narrow, elongate and widely spaced. The diastema separating P^2 and P^3 is greater than that separating P^1 and P^2 which is greater than that between the canine and P^1. In crown height $P^3 > P^2 > P^1$. Small anterior and posterior cingular cusps on P^1 and P^2, but not P^3.

Upper Molars: The posterior tip of P^3 is just buccal to the parastylar corner of M^1. The anterior cingulum below stylar cusp B is short, broad and incomplete. In M^2 the broad anterior cingulum tapers quickly as it progresses down and along the base of the paracrista and finally degenerates mid-way along the paracrista. LM^2 shows stylar cusps A and C while RM^2 shows A and E. In M^3 the anterior cingulum is as in M^2 but degenerates soon after it leaves the parastylar corner. Stylar cusp C is not present in M^3. In M^4 the metastylar corner is well developed (but much more indistinct than that seen in *Phascolosorex*). A posterior cingulum is absent.

Lower Incisors: LI_{1-3} missing; RI_1 is deformed.

Lower Premolars: The lower premolar row is very long and uncrowded. Diastemata (arranged in decreasing length) occur between P_2 and P_3, P_3 and M_1, P_1 and P_2, C_1 and P_1. In crown height $P_3 > P_2 > P_1$. All premolars are narrow and elliptical in occlusal view. All possess weak posterior cusps. There is no posterolingual lobing.

Lower Molars: In M_1 the paraconid is greatly reduced. In M_2 the anterior cingulum is very poorly developed. In M_3 the entoconid is well developed but does not contribute bulk to the endoloph between the metacone and the hypoconulid. In M_4 the anterior cingulum is stronger than that seen in M_2. A posterior cingulum is absent. The hypoconulid is the strongest M_4 cusp, while the hypoconulid and entoconid are small.

Skull (Fig. 28). The nasals are raised, slightly fluted and form a smooth semi-circular rostrum with a conspicuous concavity at the junction of the nasal and frontal bones just anterior to the anterolateral region. The interorbital width is very narrow. The right and left alsphenoid tympanic bullae are minute and widely separated. The foramina pseudovale are very large and open, the eustachian canal opening large and the posterior lacerate foramina are very small. The premaxillary vacuities extend from the level of the I^2 root back to the anterior of the C^1 root. The maxillary vacuities extend from the level of the protocone root of M^1 back to the level of the M^3 protocone root. Palatine vacuities are absent.

ADDITIONAL DIAGNOSTIC FEATURES

Murexia longicaudata differs from all other dasyurids in the combination of the following features: 1, widely spaced R and LI^1 that are needle-like and only slightly procumbent, extremely thin, and with a spur-like crown; 2, an uncingulated upper incisor row where $I^2 < I^3 < I^4$; 3, extremely long, relatively thin, needle-like upper canines in which the root and crown are undifferentiated, and in which there is no posterior cusp; 4, an upper premolar row in which the lightly cingulated teeth are uncrowded, narrow and without postero-lingual lobing; 5, a P^3, the anterior root of which, in larger individuals, elongates to the extent that P^3 is lowered into the upper molar plane where it acts as an increment to the molar row. Here the P^3 crown and much of the anterior root act as a sheering crest against the greatly enlarged primary cusp of the P_3; 6, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave; 7, M^1 and M^2 stylar cusp B large (slightly smaller than stylar cusp D in M^1, subequal in M^2); 8, M^4 protocone more narrow than in *Micromurexia* and *Phascomurexia* but anterior cingulum complete; 9, M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone; 10, M^4 metacone relatively large; 11, a poorly cingulated lower premolar row in which the narrow teeth are very widely spaced and where P_3 is larger than P_2; 12, cingulated P_3; 13, M_3 talonid narrower than trigonid; 14, well-developed paraconid on M_1; 15, three poorly developed cusps on the M_4 talonid; 16, tall entoconid on M_2; 17, metacristids and hypocristids are not transverse to the long axis of the dentary; 18, skull elongate, domed in smaller individuals but flat in the very large; 19, fluted nasals; 20, poorly developed tympanic wing of the alisphenoid with no contrasting expansion of the pars mastoidea and adjacent squamosal; 21, variable presence of a single post-metatarsal pad and calcaneal pad on hind

FIG. 23. Holotype of *Phascogale murex* Thomas, 1913 (= *Murexia longicaudata*). BMNH 12.2.4.1, study skin; A, dorsal view; ventral view. TL = 457mm; HB = 222mm; TV = 235mm; HF = 41mm.

foot; 22, tail almost naked brown with very weak ventral crest developing toward distal tip, the tail being generally longer than the head-body length; 23, polyoestrous and nipple number low (4); 24, penile morphology is simple; 25, body size can be large.

In addition to the features noted in the generic diagnosis *M. longicaudata* differs significantly ($P<0.001$) from *Mi. habbema* as follows (measurements are means, mm): longer dentary Dent (36.17:21.46); longer tail T (197:135); longer ear E (20.50: 16.95); strong thick claws rather than semi-straight slender claws; tail almost naked dorsally rather than well-haired; short, harsh fur rather than long silky fur.

M. longicaudata also differs significantly ($P<0.001$) from *P. naso* as follows: longer basicranial BL (43.64: 30.13); broader zygomatic width ZW (25.33: 17.45); broader basicranium measured outside bullae OBW (14.59: 11.57); broader inside bullae IBW (8.44: 5.81); wider rostrum at R-LC^1 (8.40: 5.91); R-LM^1 (14.71: 10.57), R-LM^2 (17.80: 12.97), R-LM^3 (21.24: 15.48); broader maxilla R-LM^{1}T (11.95: 8.50); longer upper tooth row I^1-M^4 (25.01: 17.32), longer upper premolar row P$^{1-3}$ (7.49: 4.63); longer upper molar row M$^{1-4}$ (10.10: 7.61); wider upper second molar M^{2}W (2.75: 2.02); longer dentary Dent (36.17: 24.23); longer lower molar row M$_{1-4}$ (10.90: 8.32); longer lower tooth row I$_1$-M$_4$ (22.73: 15.18); longer lower premolar row P$_{1-3}$ (7.92: 4.73); wider lower second molar M$_2$W (1.71: 1.31); longer total length TL (398: 275); longer tail T (197: 149); longer hind foot HF (35.22: 25.35); longer ear E (20.50: 18.40); fur short and harsh rather than long and luxurious; ventral tail-tip with poorly developed crest rather
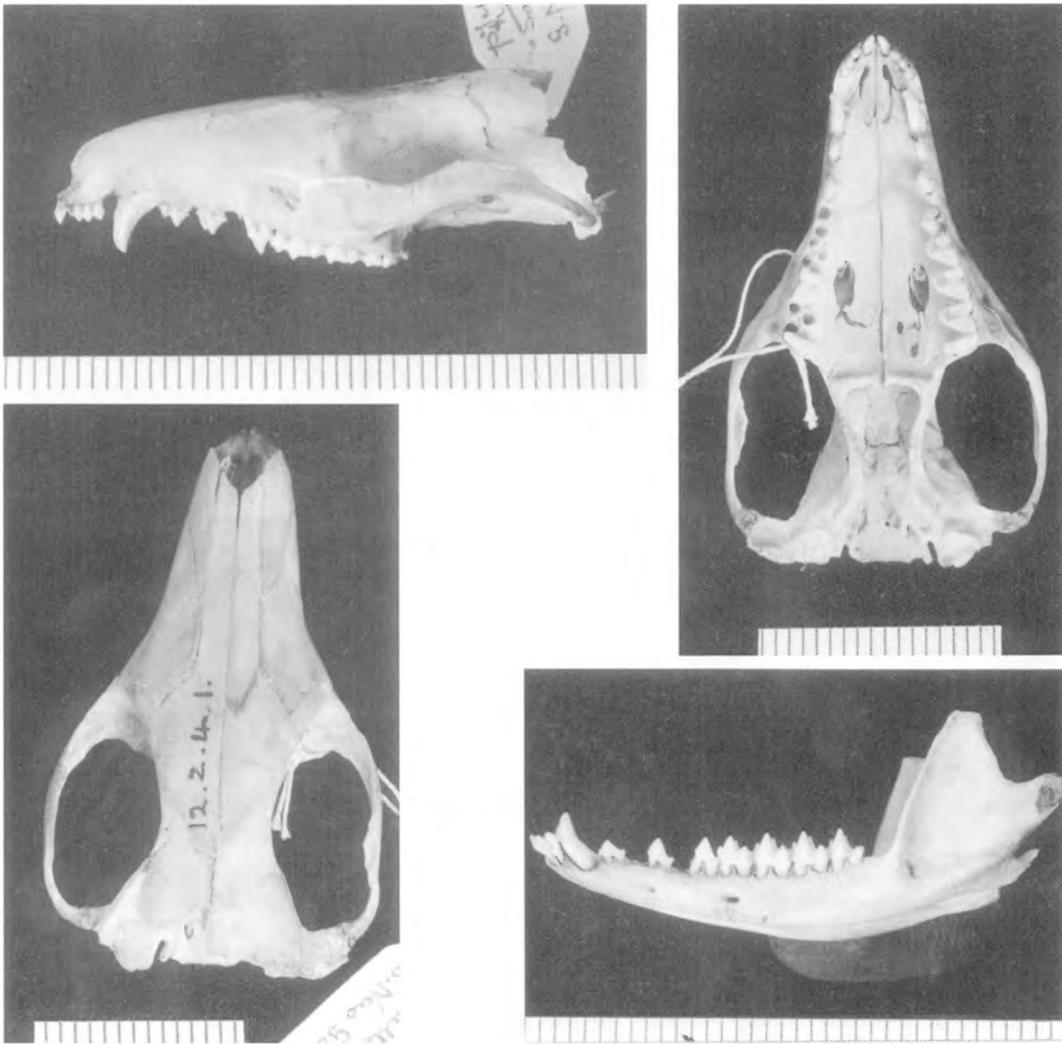
FIG. 24. Holotype of *Phascogale murex* Thomas, 1913. BMNH 12.2.4.1, cranium and dentary. Sex =m; BL = -; ZW = 23.84; IO = 7.71; OBW = -; IBW = 7.01; R-LC^1 = 8.12; R-LM^1 = 15.26; R-LM^2 = 17.94 R-LM^3 = 21.01; R-LM^{1}T = 11.45 M^{2}W = 2.58; I^1-M^4 = 24.12; P$^{1-3}$ = 7.85; M$^{1-4}$ = 9.08; Dent = 36.08; I$_1$-M$_4$ = 21.47; P$_{1-3}$ = 8.23; M$_{1-4}$ = 10.03; M$_2$W = 1.54.

than well developed crest; left and right upper first incisors separate rather than in contact.

M. longicaudata differs significantly (P<0.001) from *Murexechinus melanurus* as follows: longer basicranium BL (43.64: 26.83); broader zygomatic width ZW (25.33: 16.89); broader interorbital IOW (7.81: 7.09); broader outside bullae OBW (14.59: 10.99); broader inside bullae IBW (8.44: 5.12); wider rostrum at R-LC^1 (8.40: 5.43), R-LM^1 (14.71: 9.71), R-LM^2 (17.8: 11.91), R-LM^3 (21.24: 14.12); wider maxillae at R-LM^{1}T (11.95: 7.69); longer upper tooth row I^1-M^4 (25.01: 14.88); longer upper premolar row P$^{1-3}$ (7.49: 3.37); longer upper molar row M$^{1-4}$ (10.10: 6.78); wider upper second molar M^2 (2.75: 1.89); longer dentary DL (36.17: 21.31); longer lower tooth row I$_1$-M$_4$ (22.73: 12.96); longer lower premolar row P$_{1-3}$ (7.92: 3.45); longer lower molar row M$_{1-4}$ (10.90: 7.37); wider lower second molar M$_2$W (1.71: 1.22); longer total length TL (398: 247); longer tail T (197: 133); longer hind foot HF (35.22:22.27);
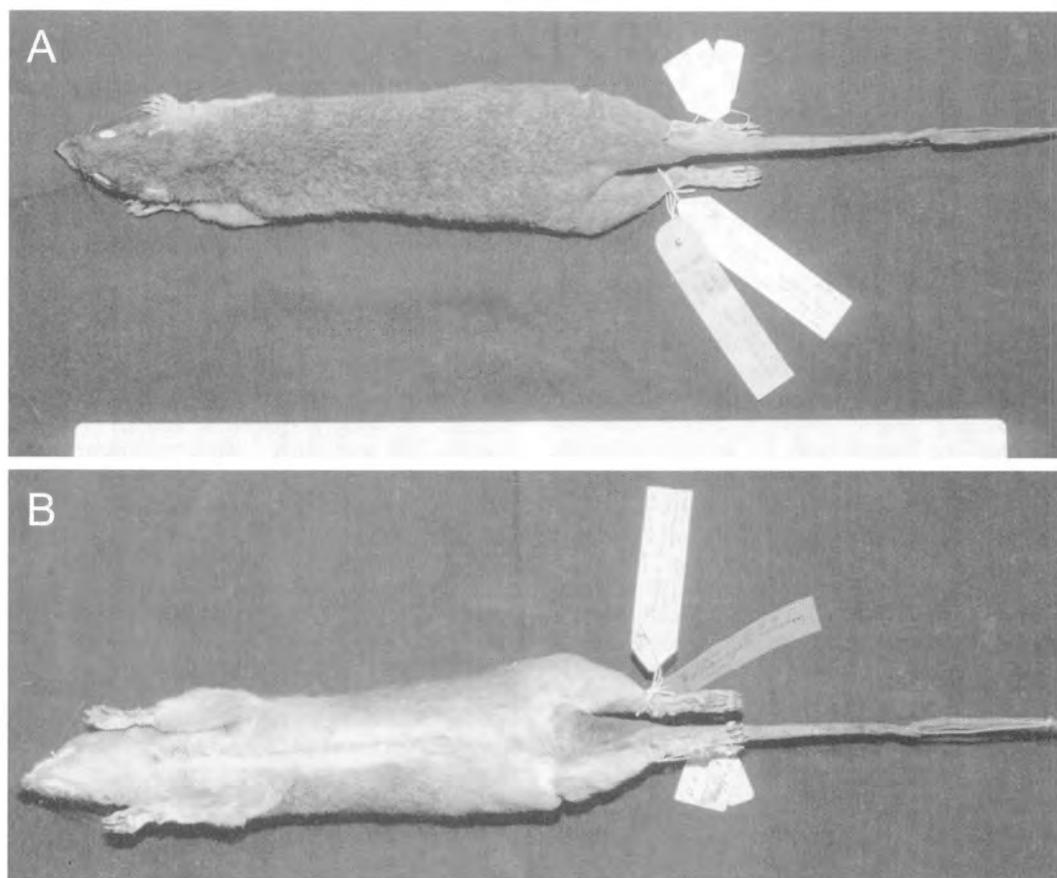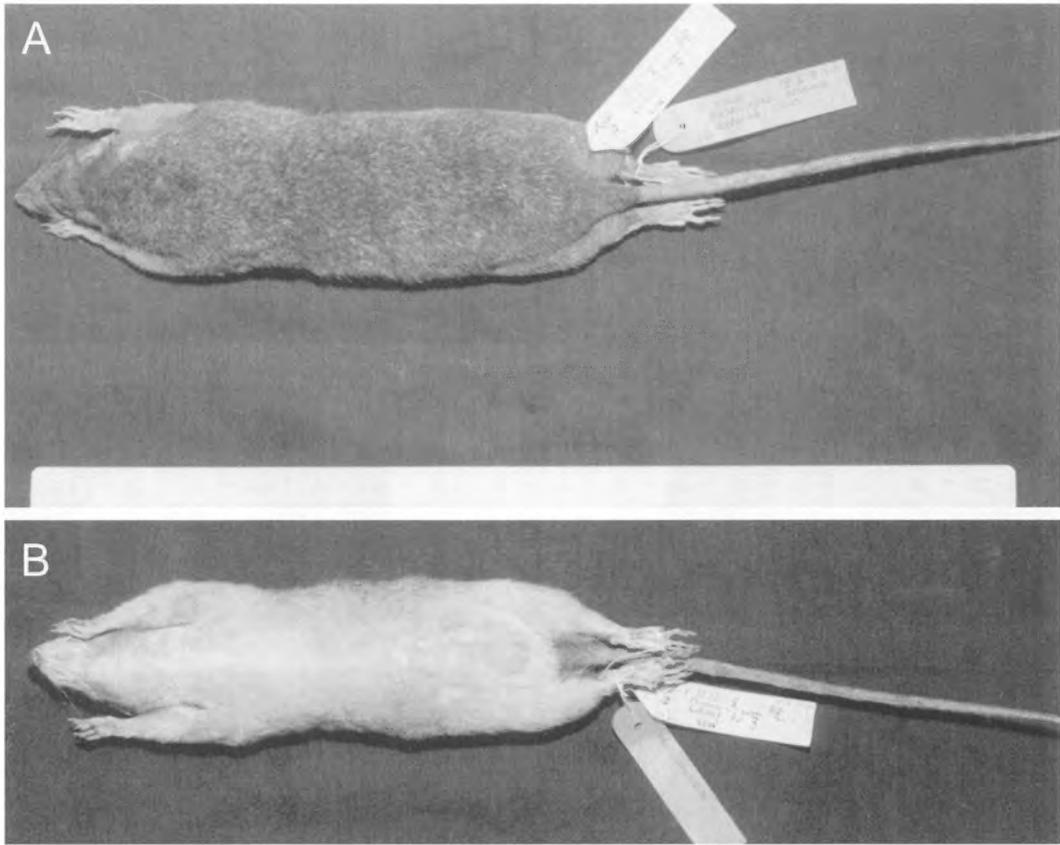
FIG. 25. Holotype of *Phascogale murex aspera* Thomas, 1913 (= *Murexia longicaudata*). BMNH 13.6.18.90, study skin; A, dorsal view; B, ventral view. TL = 349mm; HB = 169mm; TV = 180mm; HF = 33mm.

longer ear E (20.50: 15.83), ears always lack rufous post-auricular patches rather than ears always with patches; pelage uniform brown throughout rather than a definite colour change from agouti to warmer russet; pelage harsh, short and spinous throughout rather than fur long and soft; tail almost naked brown with very weak ventral crest developing toward distal tip rather than tail thickly-haired a uniform black (sometimes dark brown) with ventral crest hairs long throughout entire length; I^1 narrow and needle-like rather than broad and claw-like, $I^4 > I^3 > I^1$ rather than $I^2 \geq I^3 \geq I^4$; $C^1/_1$ very long and slender rather than short and thick; premolar row with uncrowded, narrow and widely spaced premolars rather than premolar row short with premolars crowded and broad; rostrum elongate rather than short and broad; nasals fluted rather the nasals flatter.

M. longicaudata differs significantly (P<0.001) from *Paramurexia rothschildi* as follows: broader skull at R-LM^2 (17.80: 14.79) and R-LM^3 (21.24: 17.65); longer upper tooth row I^1-M^4 (25.01: 19.68); longer upper premolar row P^{1-3} (7.49: 4.77); longer upper molar row M^{1-4} (10.10: 8.71); longer lower premolar row P_{1-3} (7.92: 4.07); I^1 long, narrow and needle-like rather than broad and claw-like; premolar row with uncrowded, narrow and widely spaced premolars rather than premolar row short with premolars crowded and broad; P^4 three-rooted rather than single-rooted; M^4 with metacone rather than without metacone; M_4 with entoconid rather than without; hind foot lacks specialisations such as large striate auxillary pad outside the third interdigital pad, greatly elongate metatarsal pad which almost contacts the third interdigital pad and highly developed, striate post-metatarsal and calcaneal pads.
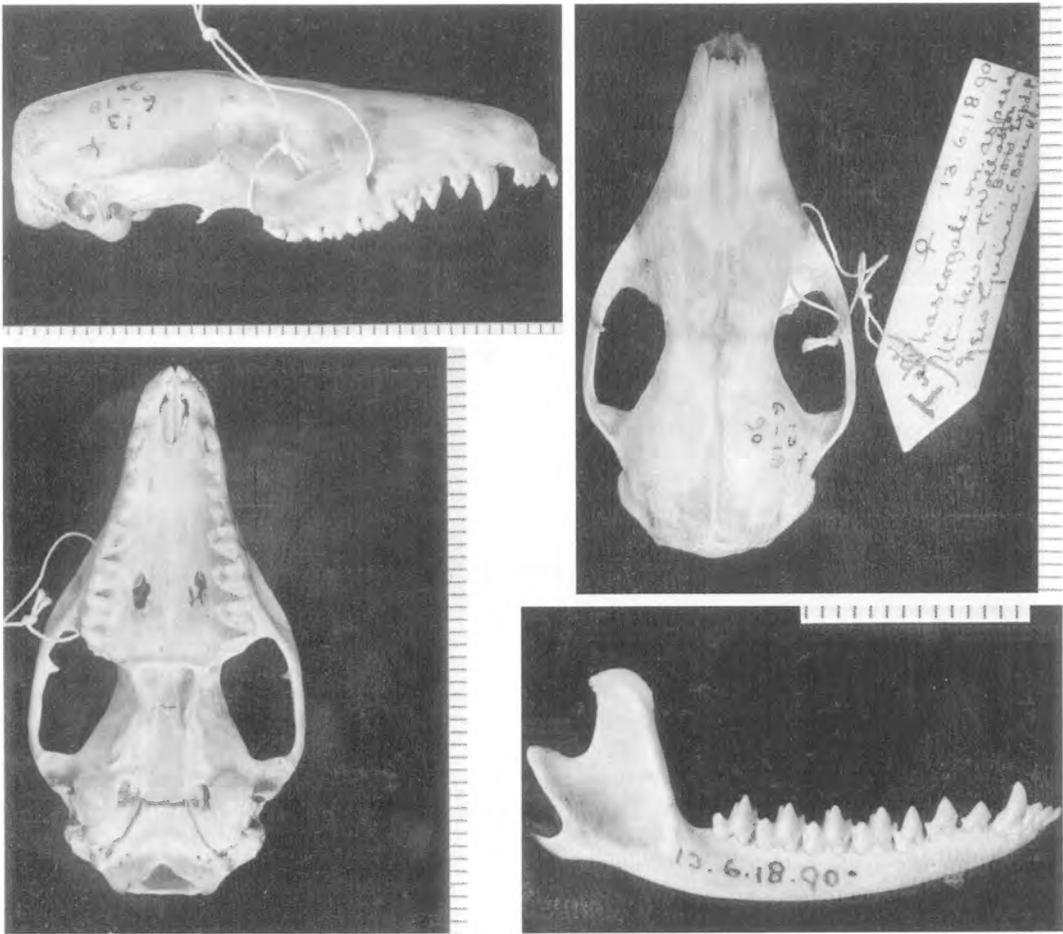
FIG. 26. Holotype of *Phascogale murex aspera* Thomas, 1913. BMNH 13.6.18.90, cranium and dentary. Sex = f; BL = 39.96; ZW = 23.01; IO = 8.69; OBW = 14.31; IBW = 7.37; R-LC^1 = 8.13; R-LM^1 = 14.19; R-LM^2 = 17.63; R-LM^3 = 20.34; R-LM^{1}T = 11.01 M^{2}W = 2.78; I^1-M^4 = 23.22; P$^{1-3}$ = 6.33; M$^{1-4}$ = 10.37; Dent = 32.39; I$_1$-M$_4$ = 20.84; P$_{1-3}$ = 6.24; M$_{1-4}$ = 11.27; M$_2$W = 1.90.

REMARKS. *Taxonomic History*. The distinctive appearance of *Murexia longicaudata* has assured it of a relatively stable taxonomic history at the generic level notwithstanding firstly, its unflattering introduction to Science, 'Cette espèce rapelle, par sa taille, le jeune du rat ordinaire' (Schlegel, 1866:356) and secondly, the mutliple deformities associated with the holotype skull (premaxillaries, upper and lower incisors, canines, premolars and the dentary). The species' extraordinary range in body size, however, has brought with it an array of described forms.

Although immature, the holotype is a very small male and would have matured to a small adult. This is reflected in the following measurements (in mm): M$^{1-4}$ =8.5, M$_{1-4}$ =9.4, M^2 width =2.37, M$_2$ width=1.56. The only specimens examined which approach this diminutive size are some very small individuals from the Kratke Mountains (at 8,000m) e.g., BMNH 50.1403, BMNH 50.1404, BMNH 50.1405. This locality occurs on virtually the same latitude (6°S) as Aru Islands but is situated approximately 1300 km to the east).

Thomas (1913) described *murex* on the basis of its large size, 'This fine Phascogale is readily distinguished by its greater size from its only near ally *Ph. longicaudata*, Schleg., a native of the Aru Islands' (p. 80). The external measurements accompanying Thomas' description appear to
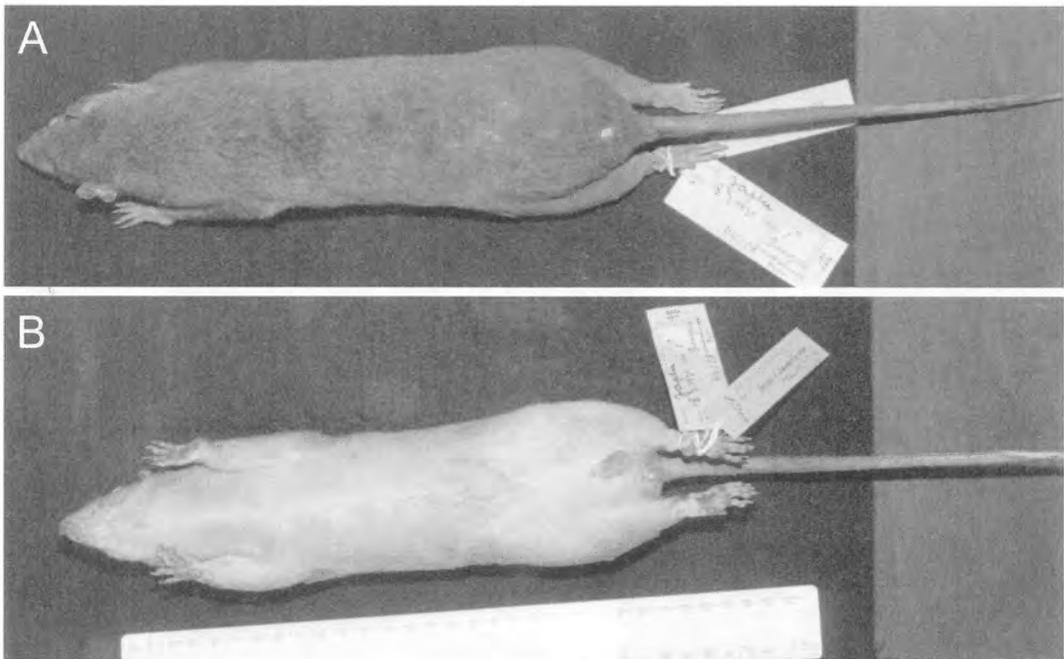
FIG. 27. Holotype of *Phascogale maxima* Stein, 1932 (= *Murexia longicaudata*). ZM 44228, study skin; A, dorsal view; B, ventral view. TL = 450mm; 'head-rump' = 235mm; 'tail' = 215mm; HF = 40mm.

support this claim, yet an examination of the type specimen reveals on obvious error with Thomas' measurements. He quotes 'Head and body 197mm; tail 167 ...' (p. 80) but these are not borne out in the skin which has a tail length much greater than its head and body length (in keeping with other intact *Murexia* examined). Thomas may have inadvertantly translocated the two measurements, but his *murex* male is, nevertheless, a small animal (M^{1-4} = 9.08, M_{1-4} = 10.03, M^2 width = 2.58, M_2 width = 1.54mm) not appreciably larger than the Leiden *P. longicaudata* holotype.

A few months later, it might have been with some misgivings that Thomas assessed the significance of a newly collected specimen presented to him by G.B. Kloss of the 1912 Wollaston Expedition to New Guinea. The animal which was collected from the Utakwa River, Irian Jaya was given to Thomas only weeks (or at the most months) after *P. murex* had appeared in print. This specimen was not only larger than the *P. murex* type but it represented (and still represents) one of the largest female *Murexia longicaudata* ever recorded. Thomas' description of *P. murex* was based on differences in size between it and the Leiden *P. longicaudata*

holotype. For four diagnostic measurements, the actual differences in size are of the following magnitude (in millimetres, see paragraphs 2 and 4 earlier) M^{1-4} = 0.58, M_{1-4} = 0.63, M^2 width = 0.21, M_2 width = 0.02. The difference between the new Utakwa River specimen and the Leiden holotype was of the following order: M^{1-4} = 1.87, M_{1-4} = 1.87, M^2 width = 0.41, M_2 width = 0.44; and between the Utakwa River specimen and *P. murex*: M^{1-4} = 1.29, M_{1-4} = 1.24, M^2 width = 0.20, M_2 width = 0.45. Using Thomas' criterion of size, if any specimen other than *longicaudata* rated full specific status then it was the Utakwa River specimen. Thomas, now in apparent anticipation of the enormous size variation within the species, chose to describe it as *aspera*, a subspecies of *P. murex*. (He was apparently unaware of 2 gigantic specimens of *Murexia* in Berlin (ZM13693, ZM60535) collected from the Urwald des Oertzengerbirges, Irian Jaya in 1908 and from Astrolabe Bay, PNG in 1888).

Although Thomas noted in the *P. murex aspera* (f) holotype the longer molar row, broader muzzle and shorter premolar row compared to the *P. murex* (m) holotype, his few specimens could not reveal to him that these features were
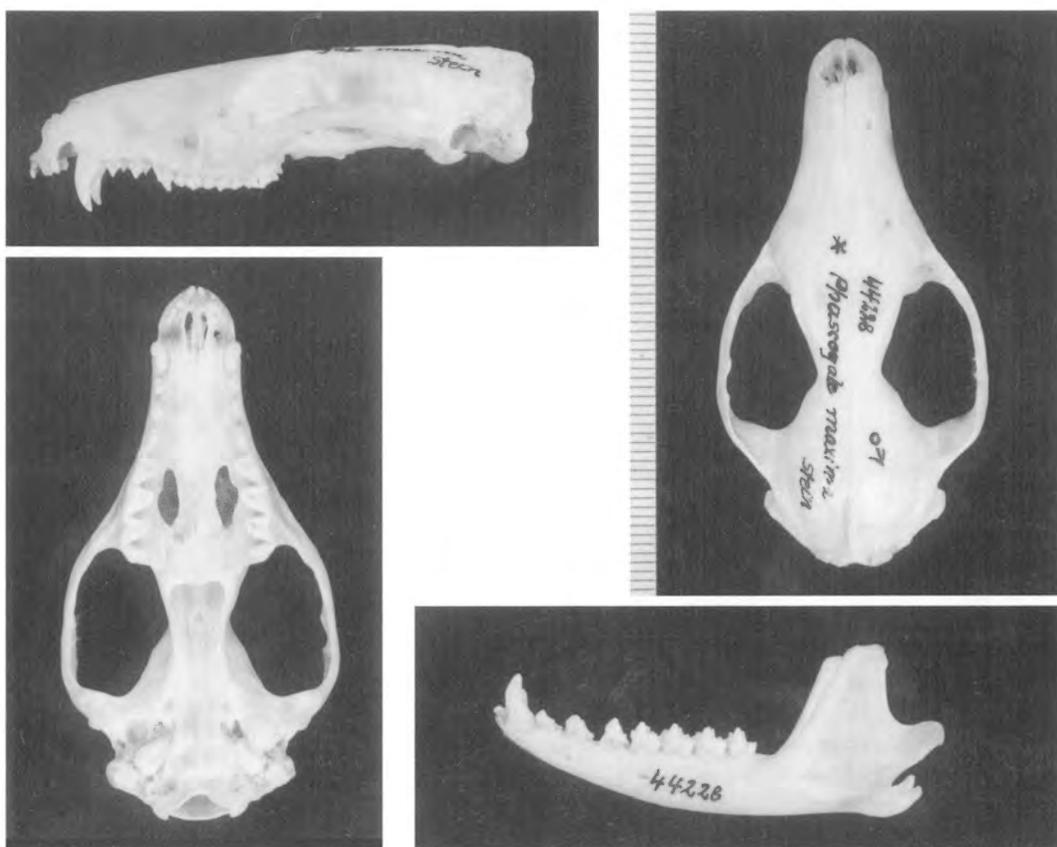
FIG. 28. Holotype of *Phascogale maxima* Stein, 1932. ZM 44228, cranium and dentary. Sex =m; BL = 53.69; ZW = 30.41; IO = 7.08; OBW = 17.24; IBW = 10.44; R-LC^1 = 9.58; R-LM^1 = 16.54; R-LM^2 = 19.99; R-LM^3 = 23.93; R-LM^{1}T = 13.80; M^{2}W = 3.21; I^1-M^4 = 29.41; P$^{1-3}$ = 8.67; M$^{1-4}$ = 11.54; Dent = 44.12; I$_1$-M$_4$ = 44.89; P$_{1-3}$ = 9.20; M$_{1-4}$ = 12.42; M$_2$W = 1.86.

normal examples of sexual dimorphism seen across the range of *Murexia*.

It is not clear if Stein (1932) was aware of *P. murex* and *P. murex aspera* when he described *P. maxima*, but no mention is made of them in his diagnosis. There is little doubt though, that even with this knowledge, Stein would have proceeded and named *maxima* on the basis of its enormous proportions. Specimens available to him at Berlin (probably) comprised ZM13693 and ZM60535, the two very large males mentioned earlier, (both larger than Stein's type) and one small specimen (ZM45801) which was of similar proportions to the Leiden *P. longicaudata*. (To my knowledge ZM13693 in East Berlin still represents the largest specimen ever recorded).

In his description Stein noted one very significant feature which up until then had gone unemphasised in *Murexia* — that of the upward gradient in lower premolar size from P$_1$ to P$_3$, a feature rarely encountered in the Dasyuridae, '... untere Pramolaren von einander und durch geringeren Zunschenraum auch von den Molaren getrennt, an Grosse zunehmend, so dab der letzte Pramolar die Hohe der Molaren hat'. (Stein 1932: 254-5).

Five years later in an extraordinary, uncharacteristically brief footnote, Tate & Archbold (1937) announced the new subgenus *Murexia* (for reasons which were diagnostically obscure and overlapping into other genera). The type they assigned to *Murexia* was *Phascogale murex* Thomas and to it they referred *P. m. aspera* Thomas and *P. maxima* Stein. At this stage Tate &
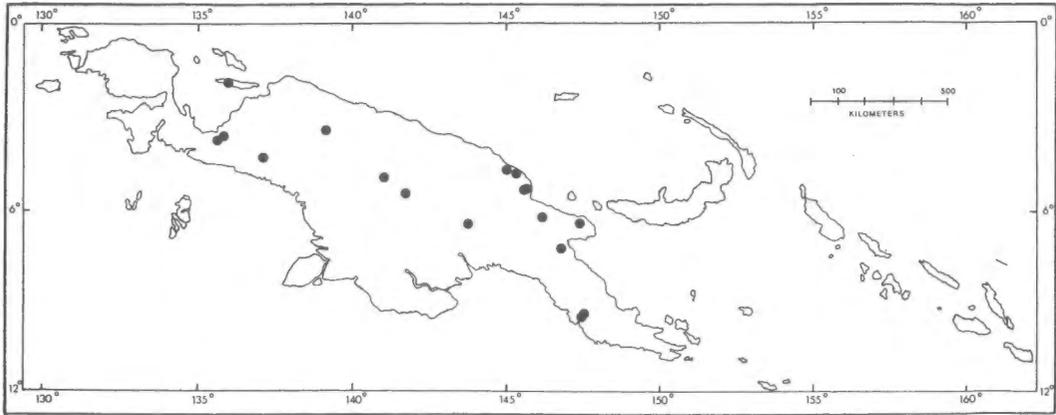
FIG. 29. Distribution of *Murexia longicaudata*.

Archbold could not assign *longicaudata* to a sub-generic position, but considered it most closely related to *Phascogale tafa* (= *Phascomurexia naso*). They also made no mention of Stein's observation of the lower premolar gradient until 10 years later when Tate (1947) noted this feature in *Murexia* and combined it with the characteristic incisor gradient and P4 morphology to suggest that *Murexia* was 'possibly the little-altered descendent of the early Tertiary marsupial that evolved into Thylacinus' (p. 117), a suggestion which has received considerable attention from Archer (1976b, 1982a, b). Tate (1947) acknowledged synonomy of *P. murex* Thomas and *P. longicaudata* Schlegel and recognised 3 subspecies; *longicaudata*, *murex* and *aspera* (wherein *maxima* was given junior synonymy), 'The only difference of importance between *longicaudata*, *murex*, *aspera* and *maxima*, after age and sex characters have been discounted is the one of size' (p.116).

Hereafter Tate's case for these 3 subspecies becomes very suspect. While *longicaudata* from Aru Islands was very small and the *maxima* race (within *longicaudata aspera*) was extremely large, the diagnosis of the intermediate subspecies *longicaudata murex* (Huon Peninsula) does not stand up to scrutiny. If, as Tate (1947:116, 118) suggested the race *aspera*, which was based on '... a young female ...' (in fact a lactating adult), was also represented by those specimens collected in the Gebroeders by F. Shaw Mayer ('... the morphological range of the smaller-sized group readily includes not only Thomas' type of *aspera* but also a series collected

by Shaw Mayer ...') then on the breadth of the range it is bold to suggest that there are significant grounds upon which to recognise *murex* as a valid (smaller) subspecies; e.g., measurements (in mm) for the *murex* type adult ♂ from Sattelburg, Irian Jaya vs a Gebroeder adult ♂ BMNH 33.6.1.84: ZW =23.84 vs 22.71, R-LC^1 =8.12 vs 7.64, R-LM^1 =15.26 vs 13.63, R-LM^2 =17.94 vs 17.03, R-LM^3 =21.01 vs 19.68, I^1-M^4 =24.12 vs 23.32, M$^{1-4}$ =9.08 vs 10.18, P$^{1-3}$ =7.85 vs 6.66, M^2 width =2.58 vs 2.74, Dent length=36.08 vs 33.27, I$_1$-M$_2$ =21.47 vs 20.86, M$_{1-4}$ =10.03 vs 10.66, P$_{1-3}$ =8.23 vs 7.04, M$_2$ width =1.54 vs 1.66.

While Tate (1947) asserted that the type of *murex* was '... still unique ...' and '... smaller than any other mainland race...' (p. 116) he ignored the rest of the Shaw Mayer collection made 2 years later (1932) in the Kratke Mts (at 1200m) and which consisted of adult males (e.g. BMNH 50.1400, 50.1401, 50.1404, 50.1406) all of which were much smaller than the *murex* type and scarcely larger than the *longicaudata* type.

Laurie & Hill (1954) however, did take note of the Mt Kratke specimens and refered to *murex* as a junior synonym of the small *longicaudata longicaudata*. The two other subspecies they recognised were *longicaudata aspera* (which includes *maxima*) and *longicaudata parva* (here regarded as *Phascomurexia naso*). *Murexia rothschildi* they regarded as the second *Murexia* species.

As far as I am aware there have been no subsequent references to subspecific forms of *Murexia* (apart from those refering to the dubious nature of *longicaudata parva*) since Laurie &

TABLE 4. Absolute measurements for *Murexia longicaudata*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	Male	28	46.45±1.51	33.26-59.03	8.00	64.06	17.22
	Female	12	37.55±1.10	31.28-44.47	3.81	14.48	10.15
	Total	41	43.64±1.26	31.28-59.03	8.06	65.02	18.47
ZW	M	28	26.86±0.75	19.55-34.45	3.98	15.86	14.82
	F	12	22.20±0.62	18.64-25.67	2.16	4.68	9.73
	T	42	25.33±0.63	18.64-34.45	4.08	16.68	16.11
IOW	M	29	7.69±0.09	7.01-8.69	0.46	0.22	5.98
	F	12	8.06±0.11	7.29-8.69	0.39	0.15	4.84
	T	43	7.81±0.07	7.01-8.69	0.47	0.22	6.02
OBW	M	28	15.06±0.33	11.80-17.95	1.72	2.95	11.42
	F	12	13.63±0.34	12.03-15.41	1.18	1.40	8.66
	T	42	14.59±0.26	11.80-17.95	1.69	2.84	11.58
IBW	M	29	8.85±0.29	6.33-11.78	1.59	2.54	17.97
	F	12	7.56±0.27	5.81-9.06	0.95	0.91	12.57
	T	43	8.44±0.23	5.81-11.78	1.53	2.34	18.13
R-LC[1]	M	28	8.89±0.27	6.50-11.31	1.44	2.07	16.20
	F	12	7.35±0.26	5.94-8.93	0.89	0.79	12.11
	T	42	8.40±0.22	5.94-11.31	1.45	2.11	17.26
R-LM[1]	M	28	15.31±0.36	11.96-18.40	1.92	3.67	12.54
	F	12	13.47±0.41	11.45-16.49	1.42	2.01	10.54
	T	42	14.71±0.30	11.45-18.40	1.94	3.77	13.19
R-LM[2]	M	27	18.55±0.41	14.63-21.77	2.14	4.58	11.54
	F	12	16.28±0.48	13.84-19.13	1.65	2.71	10.14
	T	41	17.80±0.35	13.84-21.77	2.22	4.92	12.47
R-LM[3]	M	28	22.16±0.50	17.54-26.18	2.66	7.06	12.00
	F	12	19.30±0.58	16.26-22.73	2.01	4.05	10.41
	T	42	21.24±0.43	16.26-26.18	2.76	7.64	12.99
R-LM[1]T	M	28	12.45±0.29	9.67-14.71	1.54	2.38	12.37
	F	12	10.95±0.33	9.23-12.75	1.14	1.30	10.41
	T	42	11.95±0.24	9.23-14.71	1.58	2.50	13.22
I[1]-M[4]	M	29	26.22±0.71	20.32-32.57	3.80	14.44	14.49
	F	11	22.14±0.60	18.48-25.99	1.99	3.97	7.59
	T	42	25.01±0.59	18.48-32.57	3.80	14.42	15.19
P[1-3]	M	19	8.11±0.30	5.28-10.91	1.63	2.66	20.10
	F	12	6.09±0.22	4.77-7.54	0.77	0.60	12.64
	T	43	7.49±0.25	4.77-10.91	1.67	2.78	22.30
M[1-4]	M	29	10.31±0.20	8.76-12.59	1.06	1.11	10.28
	F	12	9.59±0.21	8.69-10.77	0.72	0.51	7.51
	T	43	10.10±0.15	8.62-12.59	1.01	1.02	10.00
M[2]W	M	29	2.82±0.06	2.25-3.37	0.34	0.12	12.06
	F	12	2.61±0.07	2.29-3.01	0.23	0.05	8.81
	T	43	2.75±0.05	2.25-3.37	0.33	0.11	12.00
Dent	M	29	38.51±1.27	26.62-50.41	6.84	46.74	17.76
	F	12	30.99±0.88	25.92-36.95	3.06	9.33	9.87
	T	43	36.17±1.03	25.92-50.41	6.78	45.97	18.74
I_1-M_4	M	29	24.16±0.98	17.65-44.89	5.26	27.67	21.77
	F	12	19.61±0.49	17.12-22.72	1.69	2.87	8.62
	T	43	22.73±0.74	17.12-44.89	4.88	23.84	21.47
P_{1-3}	M	29	8.55±0.35	5.36-12.09	1.89	3.56	22.11
	F	12	6.58±0.34	5.12-9.57	1.17	1.36	17.78
	T	43	7.92±0.29	5.12-12.09	1.90	3.61	23.99
M_{1-4}	M	29	11.17±0.22	9.24-13.17	1.18	1.40	10.56
	F	12	10.30±0.24	8.62-11.55	0.84	0.71	8.16
	T	43	10.90±0.18	8.62-13.17	1.16	1.35	10.64
M_2W	M	29	1.74±0.04	1.40-2.21	0.22	0.05	12.64
	F	12	1.64±0.02	1.41-1.90	0.16	0.02	9.76
	T	43	1.71±0.03	1.40-2.21	0.21	0.04	12.28
TL	M	14	439±18.45	326-550	69	4881	15.72
	F	9	345±15.33	290-413	46	2191	13.33
	T	24	398±15.71	290-550	77	6042	19.35
T	M	23	207±7.29	155-283	35	1081	16.91
	F	11	177±5.72	150-215	19	392	10.73
	T	34	197±5.83	150-283	34	1178	17.26
HF	M	21	36.90±1.31	26.5-47	6.00	35.97	16.26
	F	11	32.00±0.88	27-37	2.92	8.55	9.13
	T	32	35.22±1.00	26.5-47	5.65	31.97	16.04
E	M	14	20.86±0.31	19-24	1.17	1.37	5.61
	F	5	20.00±0.49	18-21	1.10	1.20	5.50
	T	20	20.50±0.29	18-24	1.31	1.72	6.39

Hill, 1954). Woolley (1994) accorded full specific recognition, however, to *Murexia aspersa* (sic).

A most interesting feature in the history of *longicaudata* taxonomy is the absence of comment regarding the gross malformation in the holotype skull. The specimen was originally displayed as a mount (? hence the missing basicranium and lack of cranial and dental measurements accompanying the type description). But it must have been extracted prior to 1880 for Thomas lists its critical measurements in his Catalogue (1888: 299). Tate (1947) refered to the additional lower incisor as '... an anomalous (fourth) incisive tooth, possibly a milk tooth (?)' (p. 117), but the severely undershot dentary, crushed and broad premolars, incompletely erupted C^1, inwardly folded upper incisors and the abnormal height of the dentary below the premolars have always gone unstated.

DISTRIBUTION. *M. longicaudata* is widely distributed throughout Irian Jaya and PNG in lower to mid-montane forests below 1800m (Fig. 29). Floristic details of collection localities appear in Archbold et al., (1942: 231-243).

REPRODUCTION. All pouches examined contained 4 teats. Lactating females had been collected in (dates included in parentheses) February (13,17), March (22), April (2, 25), June (17, 27), August (10), December (1).

DESCRIPTION. *Mean Measurements* (mm). External: total length (head, body, tail) TL ($\male$) 439 ($\female$) 345; hind foot (su) HF ($\male$) 36.90 ($\female$) 32.00; ear (notch) E ($\male$) 20.86 ($\female$) 20.00. Skull: basicranial length BL ($\male$) 46.45 ($\female$) 37.55; M^{1-4} length ($\male$) 10.31 ($\female$) 9.59; M^2 width ($\male$) 2.82 ($\female$) 2.61. (Table 4).

Postmetatarsal and Calcaneal Pads. Of all males (adult, juvenile and subadult) examined for postmetatarsal and calcaneal pads (N = 18), 44% (N = 8) exhibited a single postmetarsal pad on both left and right hind foot. Three males (17%) exhibited a single postmetatarsal pad and a single calcaneal pad on both left and right hind foot.

Of all females examined for postmetatarsal and calcaneal pads (N = 4), 50% (N = 2) exhibited a single postmetatarsal pad on both left and right hind foot. No females exhibited calcaneal pads.

P4 Morphology. Only 3 juveniles were available for the study of deciduous premolars (AMNH 101970, AMNH 152035 and BMNH 33.6.1.71). In all cases L and RP^4 were 3-rooted with the paracone and metacone coalescing into one major cusp. The protocone was well developed, as was stylar cup B and the metastylid. In the lower molars L and RP_4 were single-rooted, formless spurs.

Body Size. Adult male *M. longicaudata* are significantly larger than adult females. (For basicranial length BL in males mean = 46.54mm, N = 28; for females mean = 37.55mm, N = 12, P<0.001). Females never attained the massive size seen in males, and the largest measure of BL recorded for an adult female (44.47mm) was less than the mean BL for males. Some of the largest specimens examined (ZM 60532, BL = 57.33 and ZM 13693, BL = 59.03) displayed dental abnormalities. In ZM 60532 an extra cusp is present on the posterior edge of the M^4 protocone. In ZM 13693 two small caniniform teeth incline against the posterobuccal surface of the LC^1.

The largest of adult male specimens examined (i.e., mean BL=50mm, N=9) were from localities north of 6°00'S (i.e., 01°45'S - 5°28'S). Within this latitudinal range, body size varied significantly and inversely with altitude (e.g., at altidues above 900m a.s.l. mean BL for adult males=45.97mm; at or below 900m mean BL= 54.24mm (P<0.01). South of 6°00'S a similar inverse relationship existed between body size and altitude (e.g., at altitudes above 900m a.s.l. mean BL for adult males = 34.43mm; at or below 900m mean BL=46.56mm (P<0.001).

The largest adult female specimens examined (i.e., mean BL=40mm, N=3) were also from northern localities (i.e., 3°30'S, at Bernhard Camp, 75m - 850m a.s.l.). North of 6°00'S body size varied significantly and inversely with altitude (e.g. at altitudes above 900m a.s.l. mean BL for adult females=37.73mm; at or below 900m mean BL=41.40mm (P<0.05). South of 6°00'S there was no significant relationship between body size and altitude in females.

The smallest adult males examined (i.e., mean BL=38mm, N=7) were from localities in 4°48'S 145°20'E - 6°32'S 147°17'E (i.e., Kratake Mts, Atitau, Gang Creek, at 1220m - 1311m a.s.l.).

The smallest adult females examined (i.e., mean BL=35mm, N=3) were from localities in 3°39'S 135°56'E - 6°32'S 147°17'E (i.e., The Gebroeders, Gang Ck, at 1375m-1525m a.s.l.).

Premolar Diastemata. In the upper premolar row of adult males, largest diastemata occurred most frequently between P^2-P^3 (41%, N=9) and P^3-M^1 (41%, N=9), while 18% (N=4) exhibited no diast- emata in the upper premolar row. No

specimen had the largest upper premolar diastema between P^1-P^2.

In the lower premolar row of adult males, largest diastemata occurred most frequently between P_3-M_1 (55%, N=12), less frequently between P_2-P_3 (36%, N=8), while 9% (N=2) exhibited no diastema in the lower premolar row. No specimen exhibited a condition where the largest lower premolar diastema occurred between P_1-P_2.

In the upper premolar row of adult females, largest diastemata occurred most frequently between P^2-P^3 (89%, N=8), while 11% (N=1) exhibited no diastema in the upper premolar row. No specimens exhibited a condition where the largest upper premolar diastema occurred either between P^1-P^2 or between P^3-M^1.

In the lower premolar row of adult females, largest diastemata occurred most frequently between P_2-P_3 (44%, N=4), less frequently between P_3-M_1 (11%, N=1), while 44% (N=1) exhibited no diastema in the lower premolar row. No specimen exhibited a condition where the largest lower premolar diastema occurred between P_1-P_2.

SPECIMENS EXAMINED. Astrolabe Ra., 450m, 9°30'S 147'20'E (AMNH 108558); Astrolabe Ra., 520m, 9°30'S 147°20'E (AMNH 108556-108557); Atitau, 1158m, 4°48'S 145°20'E (AMNH 198720); Bernhard Camp, 75m, 3°30'S 139°12'E (AMNH 152014-152018, AMNH152035); Bernhard Camp 4km SW, 850m, 3°30'S 139°12'E (AMNH 151997-2000); Derimapa Mt., 1220-1525m, 3°50'S 135°43'E (BMNH 1939.3235); Derimapa Mt., 1524m, 3°50'S 135°43'E (AMNH 101970-101971, BMNH 33.6.1.71-72, BMNH 336170); Derimapa Mt., 1830m, 3°50'S 135°43'S (BMNH 1939.3236); Derimapa Mt., 3°50'S 135°43'E (BMNH 33.6.1.84); Gang Creek, 1311m, 6°32'S 147°17'E (AMNH 194712); Gang Creek, 1372m, 3°62'S 147°17'E (AMNH 194710-11); Yapen I., 50m, 1°45'S 136°10'E (ZM 44228); Josephstaal, 4°44'S 145°00'E (AMNH 198721); Kratke Mts, 1200-1525m, 6°19'S 146°05'E (BMNH 50.1404-05); Kratke Mts, 1200m, 6°19'S 146°05'E (BMNH 50.1400, BMNH 50.1402); Kratke Mts, 1311m, 6°19'S 146°05'E (BMNH 50.1406); Kratke Mts, 6°19'S 146°05'E (BMNH 50.1401); Mabion Mt., 750m, 5°32'S 141°44'E (AMNH 105022); Namosado, 6°15'S 142°47'E (AMM14858, M15611); Oertzen Mts, 5m, 5°28'S 145°32'E (ZM 13693); Ogeramnangim Sarvwaged, 1785m, 3°39'S 135°56'E (ZM 45801); Sattelburg, 290m, 6°30'S 147°43'E (BMNH 12.2.4.1); Sibil Valley, 1250m, 5°00'S 141°00'E (RMNH 224, RMNH 16946); Sogeri, 450m, 9°25'S 147°26'E (AMNH 108554-5); Stephansort, 5m, 5°27'S 145°45'E (ZM 60532); The Gebroeders, 1525m, 3°39'S 135°56'E (AMNH 101972-3); Utakwa R., 762m, 4°24'S 137°12'E (BMNH 13.6.18.90); Wanuma, 671m, 4°51'S 145°19'E (AMNH 198719); Wau, 1159m, 7°20'S 146°43'E (AMNH 221630); Wonoembai Aru Is, 100m, 6°00'S 134°30'E (RMNH 35153, BMNH 50.1403).

Paramurexia gen. nov.

Phascogale (in part) Temminck, 1824.
Murexia (subgenus) (in part) Tate & Archbold, 1937.

TYPE AND ONLY SPECIES. *Phascogale (Murexia) rothschildi* Tate, 1938: 58.

GENERIC DIAGNOSIS. Broad, black, dorsal body stripe which commences at the nose and terminates at the base of the tail. M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but never indented or concave. Tail longer than head-body length.

It is distinguished from *Phascolosorex* by the narrow width of its body stripe and by its lack of reduced premolars, from *Myoictis* by its single dorsal body stripe and by its lack of reduced premolars, and from *Neophascogale* by its lack of reduced premolars and lack of a thickly-haired, white-tipped tail.

Paramurexia is separable from *Micromurexia*, *Paramurexia*, *Murexechinus* and *Murexia* by its single black, longitudinal head-body stripe and black facial mask.

Paramurexia rothschildi (Tate, 1938)
(Figs 30, 31)

Phascogale (Murexia) rothschildi Tate, 1938: 58.

HOLOTYPE. BMNH 1939.3233. Adult ♂ study skin and skull extracted (skin in good condition though slightly faded, skull in good condition).

TYPE LOCALITY. Head of the Aroa River, PNG, 8°50'S 147°06'E. Probably at 'about ± 4000 feet' (Tate, 1947). Coll. A.S. Meek, May 28, 1905.

DIAGNOSIS. As for genus.

DESCRIPTION. HOLOTYPE. *Pelage* (Fig. 30). Fur of mid-back dorsal stripe 6mm long with basal half Slate Gray and apical half Fuscous Black. Similarly pigmented guard hairs 7.4mm long are interspersed through the dorsal stripe. Fur of the mid-back immediately outside the 'black' dorsal stripe is 6mm long with basal 3.7mm Slate Colour, median 1.5mm Clay Colour and apical 0.8mm Fuscous Black. Fur beside the stripe thus appears overall to be a Saccardo's Umber. Guard hairs are interspersed through this fur and are 7.5mm long on the rump and reduce to 3mm on the crown of the head. Fur on and below the shoulders, thighs, flanks and chin lacks the black tips or coarse guard hairs and these areas and the belly appear as Cinnamon Buff.

The black dorsal stripe is 15mm at its widest. A distinct head-stripe runs from the tip of the nose expanding in width to the mid-back. Another less distinct stripe originates among the mystaceal vibrissae on each side. These Fuscous Black hairs progress posteriorly, passing over and under the eye and degenerate just to the anterior of the pinnae. A distinct eye-ring results from the combined effect of these dark hairs and the skin of the eyelids, which is darkly pigmented. A narrow band of short, black eyelash hairs completely encircles each eye. The remainder of the fur under each eye is a light fawn (Tawny Olive). The soft, ventral fur is 7mm long on the belly. The basal 4mm is Mouse Gray and the apical 3mm is Cinnamon Buff. The belly appears overall as Chamois coloured. Forefeet and hindfeet are thinly covered with Buffy Brown hairs. The tail is weakly bicoloured with mid-dorsal hairs 1.6mm long (Fuscous Black) and dorsal tip hairs 2mm long (Fuscous Black). Mid-ventral hairs are 4mm long and increase to 8mm at the tip. The full ventral crest begins as Fuscous-coloured but becomes silvery toward the tip.

Vibrissae. Approximately 26 mystacial vibrissae occur on each side and are up to 30mm long. The more dorsal vibrissae are Fuscous Black, while those lower are colourless; supra-orbital vibrissae (Fuscous Black) number 2 (left) and 2 (right); genals (Fuscous Black and colourless) number 10 (left) and 10 (right); ulna-carpals (colourless) number 6 each side; submentals (colourless) number 2.

Tail. The tail is longer than head and body. It is thin and tapers toward the tip.

Hindfoot (Fig. 33). The interdigital pads are separate. The apical granule is enlarged, elongate and striate. A greatly enlarged auxillary granule occurs outside the third interdigital pad. Hallucal and post-hallucal pads are fused and very elongate and broad. The metatarsal pad is greatly enlarged and elongate almost contacting the third interdigital pad. A very large, elongate calcaneal pad wraps around the heel. All pads are striate.

Ears. It was not possible to determine the state of the pinnae and supratragus from the type specimen. In other specimens, however, the supratragus is folded.

Dentition (Fig. 31). Upper Incisors: Left and (particularly) right I^1 are badly worn. They appear to have been narrow, peg-like and procumbent, taller crowned than all other incisors and separated from I^2 by a diastema. (In other specimens e.g., BMNH 50.1107, there is a small, auxillary posterior cusp on I^1 which gives I^1 the appearance of the tip of a crochet-hook). In crown size $I^4 > I^3 > I^2$. All upper incisors lack buccal cingula yet the crowns and roots are easily identified. I^4 carries no anterior or posterior cusps. The roots of I^4 are narrow.

Upper Canines: C^1 is thick, short and blunt with an indistinct boundary between root and crown. There is no buccal or lingual cingulum, and there is no anterior or posterior cusp.

Upper Premolars: The premolar row is short and the premolars broad with P^1 and P^2 bearing heavy posterolingual lobes. The premolars are, however, not crushed against one another. Slight diastemata occur between C^1 and P^1, P^1 and P^2 and P^2 and P^3. In crown height $P^3 > P^2 > P^1$. Small anterior and posterior cusps occur on P^1 and P^2. A small posterior cusp is present on P^3.

Upper Molars: Molars are heavily worn. The posterior tip of P^3 lies in the parastylar corner of M^1 but lingual to, and well below stylar cusp A. The anterior cingulum below stylar cusp B is short, broad and just complete. Stylar cusp B and the paracone are relatively worn and a minute protoconule is present at the base of the paracone apex. The minute protoconule is accompanied by a small bulge of enamel directly below it on the face of the anterior protocrista. The paracone on M^1 is very narrow and pinched. Stylar cusp C is not visible on either LM^1 or RM^1 and stylar cusp E is not visible. M^1 has a weak posterior cingulum.

In M^2 the broad anterior cingulum which contacts the metastylar corner of M^1 tapers quickly as it progresses down and along the base of the paracrista and finally degenerates labially to, and well before the trigon basin. No protoconule is visible. M^2 lacks stylar cusps A, C and E. Stylar cusp D is slightly reduced, narrow and there is a weak posterior cingulum.

In M^3 the anterior cingulum is as short as that of M^2, it becomes indistinct after covering 1/3 the distance between stylar cusp B and the base of the paracone. There is slight evidence of an anterior cingulum at the base of the paracone and there is no protoconule or protocone enamel bulge. Stylar cusp D is reduced to a very long, sharp crest. Stylar cusp E is absent, as is stylar cusp C.

In M^4 the metastylar corner is poorly developed. The broad anterior cingulum terminates quickly away from the metastylar corner of M^3 and a posterior cingulum is absent. The protocone is much reduced and narrow. In

occlusal view the angle made between the post-protocrista and the post-paracrista is close to 135°, reflecting little metacone development.

Lower Incisors: The small first lower incisor is larger in crown height than I_2. I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is larger in crown height than I_3. I_3 is incisiform in lateral view with a very weak posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view, a small notch separates the posterior cusp from the weak posterolingual lobe, and crown enamel of the primary and posterior cusps scarcely folds lingually such that the crest of the two cusps barely impacts on the tooth lingually.

Lower Canines: C_1 is caniniform, with forward, upward projection and strong curvature from root to crown tip. It has weak buccal and lingual cingulation and no posterior cusp. Some thegotic wear is present on the posterior surface of C_1.

Lower Premolars: Although the premolar row is short and the premolars broad, there are small diastemata between all premolars and between C_1 and P_1 and P_3 and M_1. All premolars are very strongly cingulated buccally and lingually. $P_2>=P_3>P_1$. P_1 is very broad and strongly built with heavy labial, lingual and posterior cingula as well as an anterior cusp. The bulk of each premolar is concentrated posteriorly to a line drawn transversely through the middle of the 2 premolar roots. P_1 (only) shows heavy posterolingual lobes.

Lower Molars: All molars are broad. The M_1 talonid is wider than the trigonid and the anterior cingulum is absent. The paraconid is greatly reduced to a minute bump of enamel.

The metacristid is roughly oblique to the long axis of the dentary while the hypocristid is very oblique. The cristid obliqua is very short and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The hypocristid terminates midway between the hypoconid and the metastylid. There is no entoconid. From the base of the metaconid posteriorly, the talonid endoloph follows the line of the dentary until the base of the hypoconulid. The metaconid is badly worn.

In M_2 the trigonid is slightly narrower than the talonid. The anterior cingulum is poorly developed, terminating lingually in a weak parastylid notch into which the hypoconulid of M_1 is tucked. The buccal cingulum is strong. A narrow, very weak, posterior cingulum extends from the hypoconulid to the posterior base of the hypoconid. The paraconid is worn and is the smallest trigonid cusp. There is no entoconid. The cristid obliqua extends from the hypoconulid to the posterior wall of the trigonid intersecting the trigonid at a point directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid extends from half way along the worn hypoconulid to the tip of hypoconid. From the base of the metaconid posteriorly, the endoloph follows the line of the dentary axis.

In M_3 the trigonid is slightly narrower than the talonid. A weak parastylid wraps around the hypoconulid of M_2 and there is a very weak anterior cingulum on M4. Buccal and posterior cingula are as in M_2 but more poorly developed. A reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid, but just buccal to the metacristid fissure. There is no entoconid on M_3. The endoloph on the talonid of M_4 takes a more buccal orientation than that seen in M_2. The rest of M_3 morphology is as in M_2 except that a small crest runs down from the hypoconulid to the beginning of the hypocristid.

In M_4 the trigonid is wider than the talonid. There is no anterior cingulum. A posterior cingulum is absent. Of the three main trigonid cusps the metaconid is equal in height to the paraconid but both are dwarfed by the protoconid. The hypoconid of the M_4 talonid is similar in size to M_3. Between the hypoconid and the base of the metacristid, the cristid obliqua forms low, weak crest which degenerates before contacting the trigonid wall. A significant feature of the M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua which results in the talonid appearing (in occlusal view) as a narrow oblique spur jutting off the trigonid wall. There is no entoconid and no cusps represent the hypoconulid or hypoconid. Small worn shelves, however, represent these cusps.

Skull (Fig. 31). The holotype exhibits minor fluting of the nasals. Alisphenoid tympanic bullae are widely separated and minutely inflated. The foramen pseudovale is large and not bisected by the bridge of the alisphenoid. The eustachean canal opening is large. The premaxillary vacuity (3.87mm long) extends from the level of the I^1 root back to the level of the posterior edge of the C^1 root. The very small

maxillary vacuity (6.62mm long) extends from the level of the posterior root of P^3 back to the level of the metacone root of M^3. There are no palatine vacuities present.

ADDITIONAL DIAGNOSTIC FEATURES

Paramurexia differs from all other dasyurids in the combination of the following features: 1, I^1 lightly built, curved (more claw-like) and slightly laterally compressed with heavier crown than *Micromurexia*, *Murexia* or *Phascomurexia*; 2, I^1 and I^2 widely separated; 3, a slightly cingulated upper incisor row where $I^2 < I^3 < I^4$; 4, I^4 without a posterior cusp; 5, upper canines long, thin (but bulkier and shorter than in *Micromurexia*, *Paramurexia*, and *Murexia*). The root and crown are more differentiated than in those genera and there is no posterior cusp; 6, an upper premolar row in which the moderately cingulated teeth are uncrowded from C^1 to P^2, but where P^3 usually touches P^2 and M^1; 7, P^1 are P^2 are rounded and show postero-lingual lobing; 8, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave; 9, M^1 and M^2 stylar cusp B large (slightly smaller than stylar cusp D in M^1, subequal in M^2); 10, M^4 protocone more narrow than in *Micromurexia* but anterior cingulum complete; 11, M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone; 12, M^4 metacone reduced more than in *Micromurexia*, *Paramurexia* and *Murexia*; 13, a lightly cingulated lower premolar row in which the more rounded teeth are slightly crushed, and where P_3 is smaller than P_2; 14, cingulated P_3; 15, M_3 talonid width subequal to the trigonid; 16, paraconid on M_1 more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; 17, three very poorly developed cusps on the M_4 talonid; 18, entoconid of M_2 is more reduced than in *Micromurexia*, *Paramurexia* and *Murexia* ; 19, metacristids and hypocristids are not transverse to the long axis of the dentary; 20, skull elongate and domed; 21, fluted nasals; 22, poorly developed tympanic wing of the alisphoid with contrasting expansion of the pars mastoidea and adjacent squamosal; 23, presence of a long postmetatarsal pad and calcaneal pad on hind foot; 24, tail thinly haired with short hairs and weak, light-coloured ventral crest developing at the distal end, the tail being longer than the head-body length; 25, polyoestrous and nipple number low (4); 26, penile morphology is simple.

In addition to those features noted in the generic diagnosis *P. rothschildi* is immediately separable from *Micromurexia. habbema* by its larger (the ranges (R) associated with each measurement do not overlap, Table 5); basicranial length BL, zygomatic width ZW, basicranial width measured outside bullae OBW, inside bullae width IBW, rostral widths R-LC¹, R-LM¹, R-LM², R-LM³, maxilla width R-LM¹T, upper tooth row I¹M⁴, lower tooth row I₁-M₄, lower molar row M₁₋₄, and lower second molar width M₂W. *P. rothschildi* also differs significantly (P<0.001) from *M. habbema* as follows: longer upper premolar row P¹⁻³ (4.77: 3.85); longer dentary Dent (28.33: 21.46); longer lower premolar row P₁₋₃ (5.03: 4.08); longer tail T (168: 135); longer ear E (19.92: 16.95); longer hind foot HF (27: 22); strongly curved claws rather than slender, semi-straight claws; hindfeet with post-metatarsal pads.

P. rothschildi is immediately separable from *Phascomurexia naso* by its wider second molars. (For M² in *P. rothschildi* mean=2.45, R= 2.32-2.69; in *P. naso* mean = 2.02, R=1.89-2.22. For M₂ in *P. rothschildi* mean=1.56, R= 1.46-1.72; in *P. naso* mean = 1.31, R=1.23-1.43). *P. rothschildi* also differs significantly (P<0.001) from *naso* as follows: longer basicranial BL (35.41: 30.13); greater zygomatic width ZW (21.29: 17.45); wider basicranium measured outside bullae OBW (13.21: 11.57); wider inside bullae IBW (7.27: 5.81); wider rostrum R-LC¹ (7.72: 5.91), R-LM¹ (12.20: 10.57), R-LM² (14.79: 12.97), R-LM³ (17.65: 15.48); wider maxillae R-LM¹T (10.08: 8.50); longer upper tooth row I¹-M⁴ (19.68: 17.32); longer upper molar row M¹⁻⁴ (8.71: 7.61); longer dentary Dent (28.33: 24.23); longer lower tooth row I₁-M₄ (17.39: 15.18); longer lower molar row M₁-M₄ (9.48: 8.32); post-metatarsal pads on hind feet.

P. rothschildi is immediately separable from *Murexechinus melanurus* by its larger ears. (For E in *rothschildi* mean=19.92, R=19-21.5; in *melanurus* mean= 15.83, R=14-18). *P. rothschildi* also differs significantly (P<0.001) from *melanurus* as follows: longer basicranium BL (35.41:26.83); greater zygomatic width ZW (21.29: 16.89); wider outside bullae OBW (13.21:10.99); wider inside bullae IBW (7.27: 5.12); wider rostrum R-LC¹ (7.72:5.43), R-LM¹ (12.20:9.71), R-LM² (14.79:11.91), R-LM³ (17.65:14.12); wider maxillae R-LM¹T (10.08:7.69); longer upper tooth row I¹-M⁴ (19.68: 14.88); longer upper premolar row P¹⁻³ (4.77: 3.37); longer upper molar row M¹⁻⁴ (8.71:
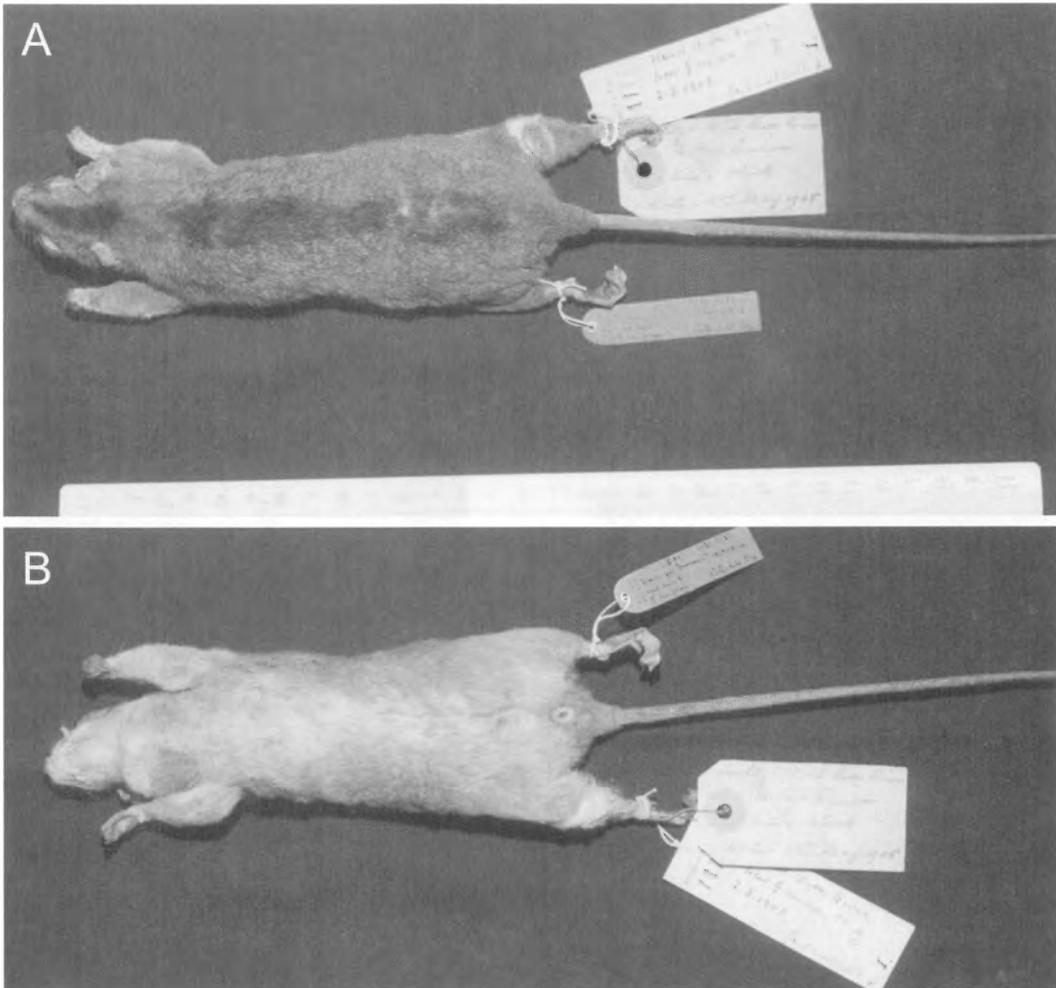
FIG. 30. Holotype of *Paramurexia rothschildi* Tate, 1938. BMNH 1939.3233, study skin; A, dorsal view; B, ventral view. TL = 350mm; HB = 170mm; TV = 180mm; HF = 13mm.

6.78); wider upper second molar M^2W (2.45: 1.89); longer dentary Dent (28.33: 21.31); longer lower tooth row I_1-M_4 (17.39:12.96); longer lower premolar row P_{1-3} (5.03:3.45); longer lower molar row M_{1-4} (9.48:7.37); wider lower second molar M_2W (1.56:1.22); face with black mask rather than rufous post-auricular patches; tail thinly haired with short hairs and weak, light-coloured ventral crest developing at the distal end rather than tail thickly haired a uniform black (sometimes dark brown) with ventral crest hairs long throughout.

P. rothschildi differs significantly (P<0.001) from *Murexia longicaudata* as follows: narrower skull at R-LM^2 (14.79: 17.80) and R-LM^3 (17.65: 21.24); shorter upper tooth row I^1-M^4 (19.68: 25.01); shorter upper premolar row P^{1-3} (4.77:7.49); shorter upper molar row M^{1-4} (8.71:10.10); shorter lower premolar row P_{1-3} (4.07:7.92); I^1 broad and claw-like rather than long, narrow and needle-like; premolar row short with premolars crowded and broad rather than premolar row uncrowded with premolars narrow and widely spaced; P^4 single-rooted rather than three-rooted; M^4 without a metacone rather than with a metacone; M_4 without an entoconid; hind foot with large auxiliary granule outside the third interdigital pad, elongate metatarsal pad which
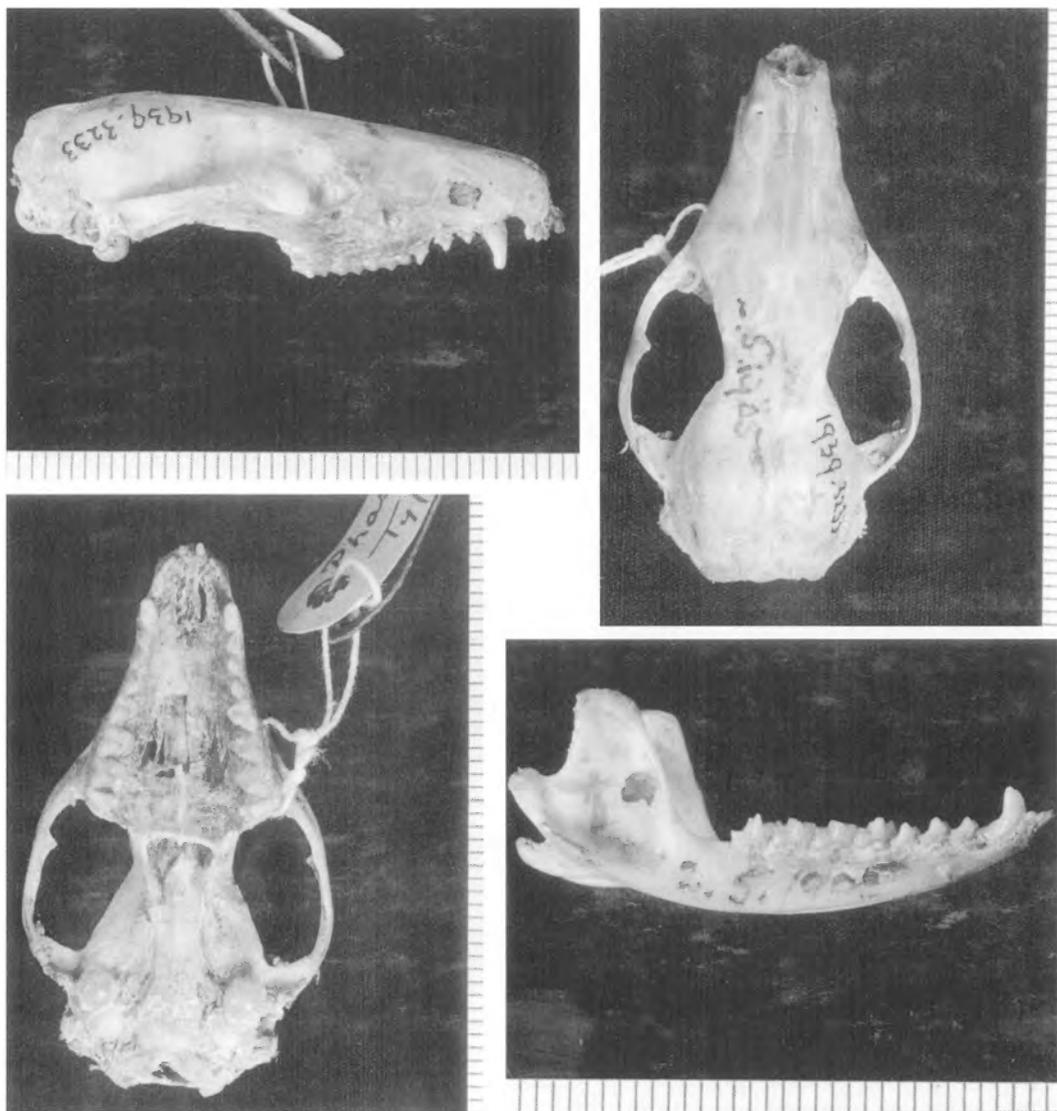
FIG. 31. Holotype of *Paramurexia rothschildi* Tate, 1938. BMNH 1939.3233, cranium and dentary. Sex = m; BL = 40.12; ZW = 24.63; IO = 8.00; OBW = 14.69; IBW = 8.11; R-LC^1 = 7.88; R-LM^1 = 12.72; R-LM^2 = 14.86; R-LM^3 = 19.39; R-LM^{1}T = 11.32; M^{2}W = 2.69; I^1-M^4 = 21.31; P$^{1-3}$ = 5.15; M$^{1-4}$ = 9.27; Dent = 32.15; I$_1$-M$_4$ = 18.65; P$_{1-3}$ = 5.30; M$_{1-4}$ = 9.61; M$_2$W = 1.72.

almost contacts the third interdigital pad, and highly developed, striate post-metatarsal and calcaneal pads rather than unspecialised.

REMARKS. *Taxonomic History.* Predictably, the history of this beautiful species is uneventful. Since its collection by A.S. Meek in 1905, institutional holdings of *rothschildi* have been bolstered only by the collections of F. Shaw

Mayer (in 1940), W. Hitchcock and R. Schodde (in 1969) and A. Engilis/R.E. Cole (in 1985). Such holdings are even now represented by no more than approximately 16 specimens.

Its distinctive, consistent physical attributes combined with its poor representation in reference collections has conferred on it a stable taxonomic history.
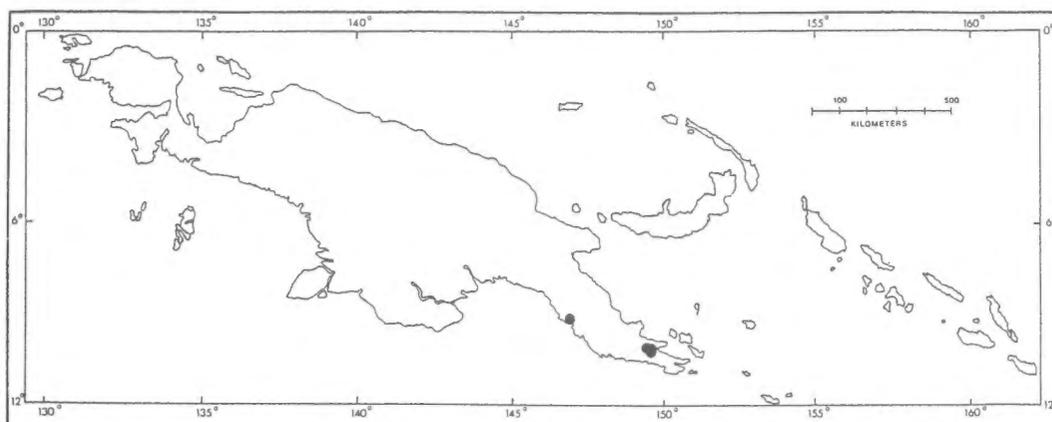
FIG. 32. Distribution of *Paramurexia rothschildi*.

The most interesting feature in the history of *rothschildi* is its anonymity from the time of its collection (1905) until Tate 'came across two specimens' (Tate, 1938) in the Tring Museum in the summer of 1937. Through the Director of the Tring Museum, Karl Jordan, Tate obtained the consent of Lord Rothschild to borrow the material for description. Tate retained the other specimen (paratype) for the American Museum of Natural History and described the species the following year. Rothschild died 27 August 1937, soon after Tate's visit, and before the description was published.

By 1938 Thomas had described species such as *flavipes adusta* (1923), *godmani* (1923), *bella* (1923), *swainsonii mimetes* (1924), *minutissima sinualis* (1926), *mimulus* (1906), *murex* (1913), *murex aspera* (1913), *melanura* (1899), *melanura modesta* (1912), *lorentzi venusta* (1921), *venusta rubrata* (1922), *doriae* (1886) and *daemonellus* (1904), all from the collecting efforts of Sherrin, Tunney, Wilkins, Stalker, Fritsche, the Pratt brothers, Kloss, Loria, and Meek. Some of these inveterate collectors were funded by Rothschild, and it was an established practice from the earlist days of the Tring Museum's *Novitates Zoologicae* until around 1921, for Lord Rothschild to invite Oldfield Thomas from the British Museum to describe the small mammals from such collecting trips. Rothschild's generosity in respect of such opportunities, and the subsequent donation of specimens to the British Museum, was always acknowledged by Thomas (Thomas, 1903a; 1903b; 1904; 1912; 1913; Thomas & Martin, 1920). The reason Thomas missed such an

extraordinary and distinct marsupial as *P. rothschildi* is unknown.

DISTRIBUTION (Fig. 32). From 6, near-coastal localities in the SE tip of PNG, all between 09°56'S - 10°02'S and 147°00'E - 149°43'E.

Heron (1975) suggested that during the 1904-5 expedition that collected the holotype and paratype of *rothschildi*, A.S. Meek collected along the Dilava River and not the Aroa. Both the Dilava and the Aroa Rivers have their headwaters just south of Mt Tafa and both join about 10km from the coast. Heron argues that collections made at 'the head of the Aroa (= Dilava) River' would have been made at an altitude above 1200m which agrees with Tate's (1947) estimate of 'probably ± 4000 feet'.

Apparently occuring between 600-1400m.

REPRODUCTION. Two lactating females were available (BBM 109489, BMNH 50.1110). The former, collected 13 March 1985, had 3 lactating nipples. Three well-grown, fully furred young were taken from the nest occupied by this female. The latter, collected 21 December 1940 was labelled 'with 2 embryos attached to the teats'. It is possible that the normal nipple number in *M. rothschildi* is 4, and that the 3 and 2 seen here result from small litters or are aberrant.

DESCRIPTION. *Mean Measurements* (mm). External: Total length (head, body, tail) TL (δ) 325 ($\female$) 291; Hind Foot (δ) 27.25 ($\female$) 26.50; Ear (notch) (δ) 20.13 ($\female$) 19.50; Skull: basicranial length (δ) 36.78 ($\female$) 31.31; M^{1-4} (δ) 8.85 ($\female$) 8.29; M^2 width (δ) 2.46 ($\female$) 2.40. (Table 5).
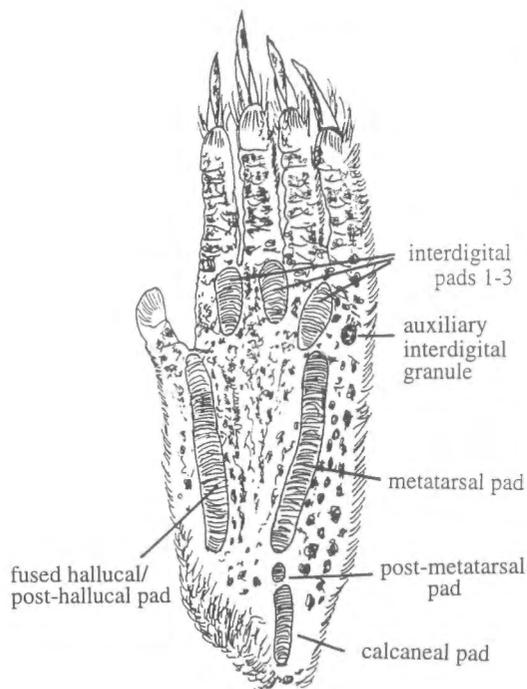
FIG. 33. Hindfoot padding in *Paramurexia rothschildi*.

labels on figure: interdigital pads 1-3; auxiliary interdigital granule; metatarsal pad; fused hallucal/ post-hallucal pad; post-metatarsal pad; calcaneal pad

Body Size. Although all but one ♂ (BMNH 50.1111) registered a basicranial length greater than that of the largest ♀, size difference between the sexes was not statistically significant (t = 0.42).

P4 Morphology. Three juveniles were available for P^4 assessment. In BBM 109485 both left and right P^4 were single-rooted, broad and premolariform with 2 cusps, one prominent anterior, the other a very weak posterior. Strong lingual cingulation was present on both. Left and right P_4 were single-rooted and premolariform, with a prominent anterior cusp which broadened posteriorly into a flat shelf.

In BBM 109481 left and right P^4 were single-rooted and more molariform than in BBM 190485. The metacone featured most prominently, but the paracone was present as a small, narrow spur. On both, stylar cusp E was well developed. The right P_4 was single-rooted, broad and premolariform with a small anterior cusp and the posterior, flat and peg-like. LP_4 was not present. In BMNH 50.1110 a right P^4 was present. Its morphology was simlar to that of BBM 109485.

Hind Foot Morphology (Fig. 33). Unique for its extraoardinary development of proximal pads of the hind foot. All specimens showed a greatly elongate metatarsal pad with close approximation to the third interdigital pad. Posterior to the metatarsal pad, a large striate postmetatarsal pad may be present (e.g., BBM 109841, BBM 109845, BBM 109489), or a small postmetatarsal pad may occur in close approximation with a very large striate calcaneal pad (e.g., AMNH 108106). All specimens examined exhibited an auxiliary pad outside the third interdigital pad of both left and right hind feet.

SPECIMENS EXAMINED. Agaun, 1km E. 1240m, 09°56'E 149°23'S (BBM 109481, BBM 109483, BBM 109485, BBM 109487); Agaun, 2.5km E., 1400m, 09°56'E 149°23'S (BBM 109489); Agaun at 4,500' (CM 12340); Aroa River (head of), 1220m, 08°57'E 147°00'S (BMNH 1939.3233, AMNH 108106); Boneno, 1220m, 09°54'E 149°25'S (BMNH 50.1111-12); Enaena, Mt Simpson, 1372m, 10°02'E 149°34'S (BMNH 50.1108-10); Ikara, Mt Simpson, 09°58'E 149°38'S (BMNH 50.1107); Opanabu (near Nowata), 610m, 10°01'S 149°43'E (CM 12287).

Murexechinus gen. nov.

Phascogale (in part), Temminck, 1824.
Antechinus (in part) Macleay, 1841.

TYPE AND ONLY SPECIES. *Phascogale melanura* Thomas, 1899.

GENERIC DIAGNOSIS. M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave. Tail longer than the head-body length.

It is distinguished from *Phascolosorex* and *Myoictis* by its lack of a dorsal body stripe and by its lack of reduced premolars, and from *Neophascogale* by its lack of reduced premolars and lack of a thickly-haired, white-tipped tail.

Murexechinus differs from *Micromurexia* as follows: ears with rich rufous to light fawn post-auricular patches rather than lacking post-auricular patches; pelage shows definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniform colour throughout; claws are thick and strongly curved rather than semi-straight and thin; tail thickly haired a uniform black (sometimes dark brown) rather than thinly haired and dorsoventrally bicoloured; I^1 broad, claw-like and heavily crowned rather than narrow, needle-like and minutely crowned; I^{2-4} strongly cingulated buccally and lingually, blade-like and robust rather than uncingulated,

TABLE 5. Absolute measurements for *Paramurexia rothschildi*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	Male	6	36.78±1.15	32.03-40.49	2.82	7.96	7.67
	Female	2	31.31±1.30	29.48-33.14	1.83	3.35	5.84
	Total	8	35.41±1.25	29.48-40.49	3.53	12.43	9.97
ZW	M	6	21.97±0.69	18.86-23.86	1.68	2.81	7.65
	F	2	19.23±0.97	17.86-20.60	1.37	1.88	7.12
	T	8	21.29±0.71	17.86-23.86	2.00	3.99	9.39
IOW	M	6	7.61±0.13	7.22-8.18	0.32	0.10	4.20
	F	2	7.84±0.23	7.53-8.16	0.32	0.10	4.08
	T	8	7.67±0.12	7.22-8.18	0.33	0.11	4.30
OBW	M	6	13.49±0.34	12.24-14.69	0.84	0.71	6.23
	F	2	12.38±0.28	11.98-12.78	0.40	0.16	3.23
	T	8	13.21±0.32	11.98-14.69	0.90	0.80	6.81
IBW	M	6	7.48±0.24	6.40-8.15	0.58	0.34	7.75
	F	2	6.65±0.18	6.39-6.91	0.26	0.07	3.91
	T	8	7.27±0.22	6.39-8.15	0.63	0.40	8.67
R-LC^1	M	6	7.56±0.24	6.26-8.09	0.60	0.36	7.94
	F	2	6.40±0.20	6.12-6.67	0.28	0.08	4.38
	T	8	7.72±0.26	6.12-8.09	0.74	0.55	9.59
R-LM^1	M	6	12.59±0.24	11.35-13.10	0.58	0.34	4.61
	F	2	11.02±0.24	10.68-11.36	0.34	0.12	3.09
	T	8	12.20±0.31	10.68-13.10	0.87	0.75	7.13
R-LM^2	M	6	15.13±0.27	13.85-15.87	0.66	0.43	4.36
	F	2	13.79±0.15	13.58-14.00	0.21	0.04	1.52
	T	8	14.79±0.29	13.58-15.87	0.82	0.67	5.54
R-LM^3	M	6	18.08±0.39	16.34-19.39	0.96	0.92	5.31
	F	2	16.35±0.35	15.86-16.84	0.49	0.24	3.00
	T	8	17.65±0.40	15.86-19.39	1.14	1.31	6.46
R-LM^{1}T	M	6	10.29±0.23	9.40-11.32	0.56	0.32	5.44
	F	2	9.44±0.17	9.20-9.68	0.24	0.06	2.54
	T	8	10.08±0.22	9.20-11.32	0.62	0.39	6.15
I^1-M^4	M	6	20.25±0.44	18.38-21.66	1.09	1.18	5.38
	F	2	17.97±0.16	17.75-18.19	0.22	0.05	1.22
	T	8	19.68±0.48	17.75-21.66	1.37	1.87	6.96
P$^{1-3}$	M	6	4.85±0.16	4.26-5.42	0.38	0.15	7.84
	F	2	4.51±0.21	4.21-4.80	0.30	0.09	6.65
	T	8	4.77±0.14	4.21-5.42	0.39	0.16	8.18
M$^{1-4}$	M	6	8.85±0.13	8.47-9.27	0.31	0.10	3.50
	F	2	8.29±0.09	8.16-8.41	0.13	0.02	1.57
	T	8	8.71±0.13	8.16-9.27	0.37	0.14	4.25
M^{2}W	M	6	2.46±0.05	2.32-2.69	0.13	0.02	5.28
	F	2	2.40±0.01	2.39-2.41	0.01	0.00	0.42
	T	8	2.45±0.04	2.32-2.69	0.11	0.01	4.49
Dent	M	6	29.39±0.98	25.35-32.32	2.40	5.78	8.17
	F	2	25.15±0.96	23.80-26.49	1.35	1.81	5.37
	T	8	28.33±1.01	23.80-32.32	2.86	8.17	10.10
I$_1$-M$_4$	M	6	17.86±0.29	16.91-18.79	0.72	0.52	4.03
	F	2	15.95±0.06	15.87-16.03	0.08	0.01	0.50
	T	8	17.39±0.37	15.87-18.79	1.04	1.08	5.98
P$_{1-3}$	M	6	5.23±0.15	4.68-5.75	0.36	0.13	6.88
	F	2	4.40±0.23	4.07-4.73	0.33	0.11	7.50
	T	8	5.03±0.18	4.07-5.75	0.51	0.26	10.14
M$_{1-4}$	M	6	9.56±0.07	9.29-9.70	0.18	0.03	1.88
	F	2	9.27±0.03	9.23-9.30	0.04	0.00	0.43
	T	8	9.48±0.07	9.23-9.76	0.20	0.04	2.11
M$_2$W	M	6	1.58±0.03	1.48-1.72	0.07	0.01	4.43
	F	2	1.48±0.01	1.46-1.50	0.02	0.00	1.35
	T	8	1.56±0.03	1.46-1.72	0.08	0.01	5.13
TL	M	5	325±9.85	295-350	22.03	485.32	6.78
	F	3	290.67±7.42	276-300	12.86	165.38	4.42
	T	8	312.63±9.05	276-350	25.60	655.36	8.19
T	M	4	172±4.50	162-184	9	90	5.23
	F	2	161±6.38	152-170	9	81	5.59
	T	6	168±4.08	152-184	10	112	5.95
HF	M	4	27.25±0.55	26-29	1.09	1.19	4.00
	F	2	26.50±1.06	25-28	1.50	2.25	5.66
	T	6	27.00±0.53	25-29	1.29	1.67	4.78
E	M	4	20.13±0.45	19-21.5	0.89	0.80	4.42
	F	2	19.50±0.35	19-20	0.50	0.25	2.56
	T	6	19.92±0.34	19-21.5	0.84	0.70	4.22
W	M	1	40				
	F	1	64				
	T	1	64				

narrow and lensate; $C^1/_1$ short and thick rather than extremely long and slender; upper premolar row short, with premolars crowded, wide and robust rather than premolar row long with premolars uncrowded and narrow; P^1 and P^2 in close contact rather than separate; lower molars with weak entoconids (i.e., M_3 entoconid shorter than paraconid) rather than very well developed entoconids; nasals flat rather than raised and fluted.

Murexechinus differs from *Phascomurexia* as follows: ears with rich rufous to light fawn post-auricular patches rather than lacking post-auricular patches; pelage shows definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniformly brown throughout; tail thickly haired a uniform black (sometimes dark brown) throughout, with ventral crest hairs long for entire tail length rather than semi-naked dorsally with weak ventral crest developing appreciably only toward distal end; I^1 broad and claw-like and heavily crowned rather than narrow and needle-like; I^{2-4} strongly cingulated rather than uncingulated; $C^1/_1$ short and thick, rather than long and slender; premolar row short with premolars crowded and broad, rather than long premolar row with uncrowded narrow premolars; P^1 and P^2 in close contact rather than separate.

Murexechinus is separable from *Murexia* by the shorter length of its upper and lower premolar rows P1-3.

Murexechinus is separable from *Paramurexia* by its smaller ears. *M. melanurus* also lacks a dark longitudinal dorsal body stripe.

Murexechinus melanurus (Thomas, 1899)
(Figs 34, 35, 36)

Phascogale melanura Thomas, 1899: 191.
Phascogale melanura modesta Thomas, 1912: 92.
Phascogale mayeri Dollman, 1930: 433, pl. 4.
Antechinus wilhelmina Tate, 1947: 130.

LECTOTYPE. CE 3915. Adult ♀ puppet skin, faded. Skull extracted but missing parietals, supraoccipitals and part of squamosal bones. PARALECTOTYPE. BMNH 1900.6.26.1, adult ♂ in ethanol, skull not extracted (lower jaw broken and skin badly faded).

TYPE LOCALITY. Moroka, headwaters of the Musgrave River, PNG, 9°24'S 147°32'E. At 1,300m. Coll L. Loria, 7 August 1893.

DIAGNOSIS. As for genus.

DESCRIPTION OF LECTOTYPE, PARA-LECTOTYPE AND DELEGATE. *Pelage* (Fig. 34). Both are very badly faded; lectotype is

overall a Buffy Brown on the shoulders which changes to Olive Brown over the rump. The belly is an overall Olive Buff and the tail is Olive Brown near the base, changing to Clove Brown nearer the tip. Post-auricular patches are a very faded Tawny Olive. There is no visible change in head to body colour. Paralectotype BMNH 0.6.26.1 (in ethanol) (Fig. 35) was not recorded for pelage colour.

To demonstrate typical colour patterns of *M. melanurus*, another specimen (AMNH 15704) has been selected (from a site as close as possible to the type locality) for pelage description. This will also serve as a basis upon which *A. wilhelmina* can be compared later. Little can be gained from a detailed pelage description of the lectotype and paralectotype.

AMNH 157074, adult ♂ study skin and skull, collected on Mt Dayman, Maneau Range (9°50'S 149°18'E): Fur above shoulders (6mm long) has basal 4mm Deep Mouse Gray, median 1mm Light Ochraceous Buff and apical 1mm black. The mid-back thereby appears a speckled agouti. Medially thickened guard hairs are interspersed thinly through the fur and are 8mm long on the rump and reduce to 3mm where they terminate at the crown of the head. Fur on the head is dominated by coarse black guard hairs giving the head a darker appearance than any other part of the body. Fur on, and above the shoulders, has a darkening of the median band to Ochraceous Tawny and black tips are gradually lost from guard hairs toward the sides of the body, leaving the mid-sides a soft Buckthorn Brown. There is no head-stripe or eye-ring.

A band of short, black, eyelash hairs completely encircles the eye. Coarse hairs (5.5mm long) around the anterior rim of the ear have expanded the pigmented median band to 2mm (Ochraceous Orange) giving a vague pre-auricular patch. Hairs immediately behind the ear have scarcely visible black tips but coarse guard hairs are absent. These soft hairs are coloured Ochraceous Orange and create a spectacular, soft post-auricular patch. From mid-shoulders to the rump the median colour band of hairs changes gradually from Light Ochraceous Buff through to Ochraceous Orange giving the rump, thighs and base of the tail a warm Ochraceous Tawny colour. The soft ventral fur (6.5mm long on the belly and 5mm long on the interramal region) is Light Mouse gray on the basal half and Warm Buff on the apical half and is interspersed by Warm Buff medially thickened

guard hairs 5mm long. The mid-belly is thus an overall Warm Buff.

Forefeet are covered thinly with Warm Buff hairs. Hindfeet are more thickly covered with darker Ochraceous Buff hairs. The tail is darkly coloured with Fuscous Black hairs averaging 2.5mm along its dorsal length and increasing to 3.5mm at the tip. Ventrally the hairs increase in length from 4mm at the base to 7mm at the tip giving a ventral crest which is slightly lighter (Clove Brown) than the dorsal surface.

Vibrissae (lectotype). Approximately 21 mystaceal vibrissae occur on each side and are up to 27mm long. The more dorsal mystaceal vibrissae are Fuscous Black while those lower have colourless tips. Supra-orbital vibrissae (Fuscous Black) number 2 (left) and 2 (right); genals (Fuscous Black and colourless) number 6 (left) and 6 (right), ulna-carpals (colourless) number 4 each side; submentals (colourless) number 3.

Tail (lectotype). The tail is much longer than head and body. It is thin and tapers toward the tip.

Hindfoot (lectotype). Interdigital pads are separate. The apical granule is greatly enlarged, elongate and striate. Hallucal and posthallucal pads are joined. The metatarsal pad is greatly enlarged, striate and extends forward almost touching the third interdigital pad.

Ears (lectotype). Pinnae are large with a complex supratragus which has a pronounced thickened posterior margin. The distal end is reflected ventrally. The reflected tip is slightly concave.

Dentition (lectotype) (Fig. 36). Upper Incisors: I^1 is broad, heavy and claw-like, procumbent and sharply curved posteriorly. It is taller crowned than all other upper incisors and is separated from I^2 by a diastema. Left and right I^1 are widely separate at their roots but the teeth touch almost halfway up the crown then to diverge away from each another. For I^{2-4} crown height and width, I^2 is greater than I^3 which is greater than I^4. All upper incisors show distinct buccal cingula but I^4 carries no anterior or posterior cusps. Roots of I^4 are narrow.

Upper Canines: C^1 is heavy and caniniform with very weak buccal and lingual cingula. A minute posterior cusp is present.

Upper Premolars: No diastemata occur in the premolar row which is short and crowded and characterised by the broad, heavy premolars. All carry strong buccal and weaker lingual cingula. P^1 is shorter than P^2 which is shorter than P^3. No clearly definable anterior or posterior cusps

occur on the upper premolars. P^1 is very broad with slight postero-lingual lobing, P^2 is broad, LP^3 is crushed obliquely between P^2 and M^1, RP^3 is missing in the lectotype skull.

Upper Molars: The posterior tip of P^3 is outside and slightly buccal to the parastylar corner of M^1. The anterior cingulum below stylar cusp B is very short and broad but complete. Stylar cusp B is unworn and reduced, and a minute protoconule is present at the base of the paracone apex. The paracone on M^1 is approximately half the length of the metacone. Stylar cusps C and E are not present in R or LM^1. M^1 has a strong posterior cingulum. There is an (?) abnormal spur of enamel directly below the preprotocrista. Stylar cusp D is reduced and narrow.

In M^2 a very broad anterior cingulum contacts the metastylar corner of M^1, tapers slowly as it progresses down and along the base of the paracrista and finally expands into the trigon basin. No protoconule is present. Stylar cusp D is high and narrow and there is a strong posterior cingulum. M^2 lacks stylar cusps A, C and E.

In M^3 the anterior cingulum is broad, strong and complete, as in M^2. Stylar cusp D is greatly reduced to a very small sharp peak. Stylar cusps E and C are absent as is the protoconule.

In M^4 the metastylar corner is weakly developed. The basal anterior cingulum is complete but narrower than in M^3. A posterior cingulum is weakly present. The protocone is broad but short. In occlusal view the angle made between the post-paracrista and the post-protocrista is 135°, indicating no metacone development.

Lower Incisors: The first lower incisor is much greater in crown height than I_2. I_1 and I_2 are oval in anterolateral view and gouge-like in occlusal view. I_2 is subequal in crown height to I_3 but narrower than I_3. I_3 is incisiform in lateral view with an inconspicuous posterior cusp at the base of the crest which descends posteriorly from the apex of the primary cusp. The lower canine rests against this posterior cusp. In occlusal view a gross notch separates this posterior cusp from the prominent posterolingual lobe.

Lower Canines: C_1 is short, heavy, broad and caniniform and charcterised by forward projection and slight curvature from root to crown. It has very weak buccal but strong lingual cingulation and a very weak cingular cusp.

Lower Premolars: The lower premolar row is short and crowded and P_{1-3} are broad and crushed, strongly cingulated buccally and lingually. In

crown height P_2 is taller than P_3 which is taller than P_1. All premolars are very broad and triangular. All possess small broad posterior cusps though none possesses an anterior cusp. P_3 is set very low as if not fully erupted. The bulk of each premolar mass is concentrated posterior to the line drawn transversely through the middle of the two premolar roots. P_1 is heavily lobed posterolingually.

Lower Molars: All the molars are broad and the molar row is relatively short. The M_1 talonid is much wider than the trigonid and an anterior cingulum is present but poorly developed. It terminates at the posterior base of the protoconid. A buccal cingulum is present. The M_1 paraconid is scarcely developed and appears in occlusal view as a minute spur, the linugal edge of which makes almost no appreciable swelling on the endoloph of M_1. The hypocristid and metacristid are roughly oblique to the long axis of the dentary. The cristid obliqua is long and extends from the hypoconid to the posterior wall of the trigonid intersecting the trigonid at a point slightly lingual to that point directly below the tip of the protoconid. The entoconid is high, long and blade-like. From the base of the metaconid posteriorly the talonid endoloph bulges lingually but returns with a buccal orientation to the hypoconulid.

In M_2 the talonid is slightly wider than the trigonid. The anterior cingulum is very well developed originating buccally in a weak parastylid notch into which the hypoconulid of M_1 is tucked. The buccal cingulum is strongly developed from the base of the protoconid to amalgamate with the posterior cingulum. The paraconid is well developed and is the smallest trigonid cusp. There is a minute metastylid and the entoconid is low but long. The cristid obliqua intersects the trigonid directly below the tip of the protoconid but well buccal to the metacristid fissure. The hypocristid extends from slightly anterior and buccal to the hypoconulid to the tip of the hypoconid. The endoloph of the trigonid follows the line of the dentary with no input from the entoconid.

In M_3 the trigonid is wider than the talonid. A small parastylid wraps around the hypoconulid of M_2 and there is a very strong anterior cingulum which terminates at the anterior base of the paraconid. Buccal and posterior cingula are as in M_2 but more poorly developed. The reduced cristid obliqua intersects the trigonid at a point well lingual to the longitudinal vertical midline drawn through the tip of the protoconid but

slightly buccal to the metacristid fissure. There is a low, poorly developed entoconid on M_3. The talonid endoloph makes a more buccal swing than that seen in M_2. Both the metacristid and hypocristid are oblique to the long axis of the dentary.

In M_4 the trigonid is wider than the talonid. The anterior cingulum is as in M_2. The posterior cingulum is weakly present. Of the three main trigonid cusps, the metaconid is slightly taller than the paraconid but both are dwarfed by the protoconid. A true hypoconid on M_4 is absent. Between the pseudo-hypoconid and the base of the metacristid, the cristid obliqua forms a very low, weak crest which degenerates before contacting the trigonid wall. A significant feature of M_4 morphology is the reduction of talonid crown enamel below the cristid obliqua (which could be regarded as M_4 buccal cingulum) which results in the talonid appearing (in occlusal view) as a narrow unsupported spur jutting off the trigonid wall. There is no entoconid on M_4.

Skull (Fig. 36). *M. melanurus* is a broad-faced dasyurid with a conspicuous concavity at the junction of the nasal and frontal bones, just anterior to the interorbital region. In the lectotype, the parietal, supraoccipital and part of the squamosal bones are missing and no fluting or inflation of the nasal bones is detectable. The left and right alisphenoid tymphanic bullae are widely separated and very small. The foramen pseudovale is very large and not bisected by the inner wing of the entocarotid canal. The eustachian canal opening is large, the posterior lacerate foramina are small and protected by a flange of the wing of the petrosal part of the periotic. The premaxillary vacuity extends from the level of the I^2 root back to the level of the edge of the anterior root of P^1. The small maxillary vacuities extend from the level of the protocone root of M^1 back to the level of the metastylar corner of M^2. Palatine vacuities are absent.

SYNONYMS

Phascogale melanura modesta Thomas, 1912
(Fig. 37)

HOLOTYPE. BMNH 11.11.29.11, adult ♂ (slightly faded skin, no skull in existence).

TYPE LOCALITY. Mt Goliath, Irian Jaya, 4°43'S 139°52'E.Coll. A.S. Meek.

ALTITUDE. Not quoted in type description (Tate, 1947 quotes 'from about 5,000 feet', [1,525m]).
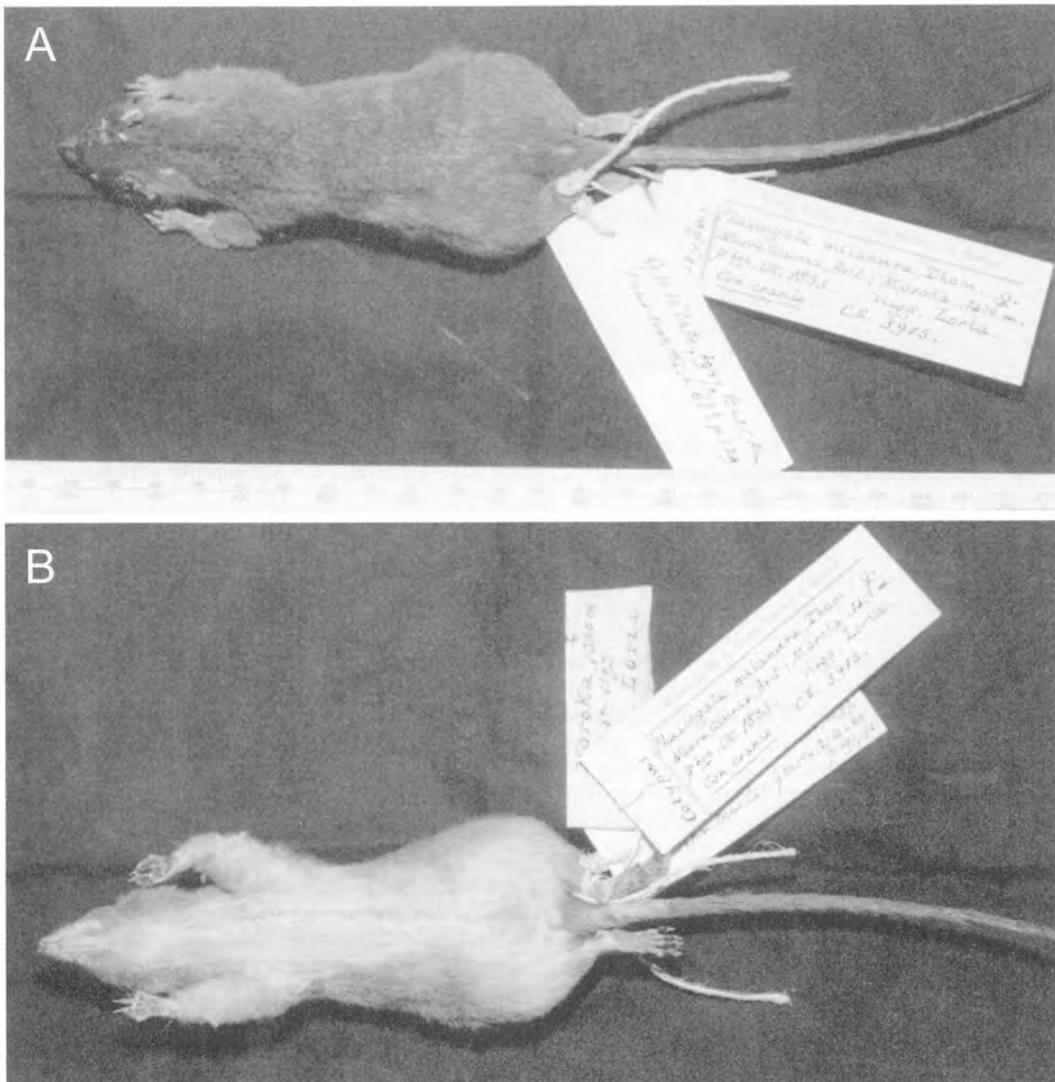
FIG. 34. Lectotype of *Phascogale melanura* Thomas, 1899 (now *Murexechinus melanurus*). CE 3915, study skin; A, dorsal view; B, ventral view. TL = 234mm; HB = 106mm; TV = 128mm; HF = 20mm.

DESCRIPTION. *Pelage* (Fig. 37). The skin shows a very small, relatively drab-looking animal with slipped belly fur and missing left fore-leg. The degree of fading is unassessable. Head colour is Sepia, mid-back Saccardo's Umber, rump Olive Brown. The thinly-haired tail is Bone Brown dorsally and Olive Brown ventrally. Dorsal manus and pes are Buffy Brown. The belly is Grayish Olive. Post-auricular patches are coloured Tawny Olive. Other external features are as in the lectotype.

Skull and Dentition. A skull does not accompany the study skin.

Phascogale mayeri Dollman, 1930
(Figs 38, 39)

HOLOTYPE. BMNH 29.5.27.57 (on label accompanying specimen), 'BM 29.5.37.57' (quoted in original description). Adult ♀ (skin and skull in good condition).

TYPE LOCALITY. Arfak Mountains, Irian Jaya, 1°09'S 134°00'E. At 1,000m. Coll. F. Shaw Mayer, 22 August 1921.
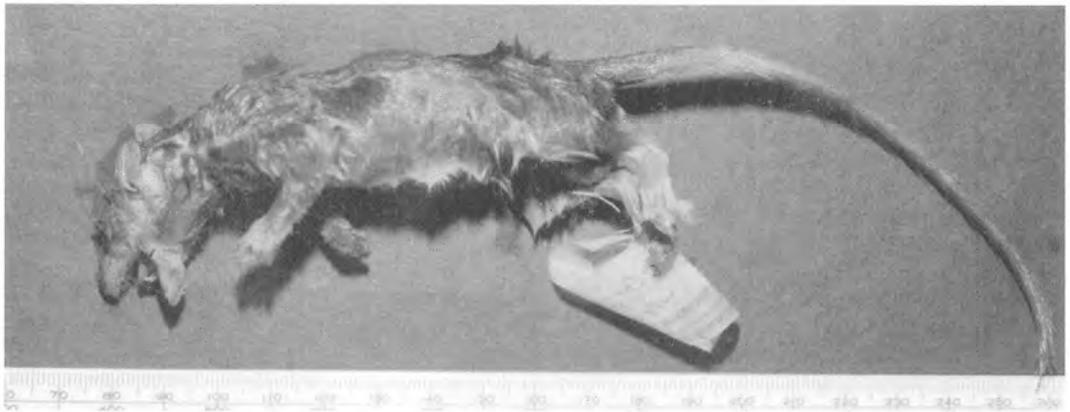
FIG. 35. Paralectotype of *Phascogale melanura* Thomas, 1899 (now *Murexechinus melanurus*). BMNH 1900.6.26.1, lateral view of alcoholic body. TL = 227mm; HB = 107mm; TV = 120mm; HF = 21mm.

DESCRIPTION. *Pelage* (Fig. 38). Typically drab representatives of the species at the western end of Irian Jaya. Head colour to mid-back is Sepia which warms on the rump, base of hind legs and tail to a Bister. Post-auricular patches are a dull Cinnamon Buff. The tail is well haired, and uniformly dark Olivaceous Black dorsally and Chaetura Drab ventrally. The overall impression of the dorsal pelage is of a dull agouti (green-brown with golden flecks) warming to a deeper brown-orange on the rump. The belly in *P. mayeri* is a very light Pale-Olive Buff and the fore and hind feet are Hair Brown. Other external features are as in the lectotype.

Dentition (Fig. 39). There are very few features in *P. mayeri* which differ from the lectotype dentition. *P. mayeri* teeth are heavily worn and RI^1 is lost as in RP_1. It is significant that crown height in incisor I^4 is greater than I^3 which is sub equal to I^2. There are clear, complete cingula on M_{1-4}.

Antechinus wilhelmina Tate, 1947
(Figs 40, 41)

HOLOTYPE. AMNH 109811, adult ♂ (skin and skull in excellent condition).

TYPE LOCALITY. 9km NE of Lake Habbema, Mt Wilhelmina, Irian Jaya, 4°05'S 138°50'E. At 2,800m. Coll. W.B. Richardson, 19 October 1938.

DESCRIPTION. *Pelage* (Fig. 40). Representative of the typically drab individuals of *melanurus* of Irian Jaya, but shows the very small size of adult animals from higher altitudes. The striking back tones seen in eastern animals are replaced with more sombre tones so that the head and tail are a muddy brown and post-auricular patches are unimpressive buff tones. With the strength of black in fur tips reduced throughout, the head and mid-back appear as a flecked Tawny Olive, the rump as a slightly warmer Saccardo's Umber, the tail a dull Bister. The belly is a Pale Cinnamon Pink (a dirty white) and post-auricular patches Cinnamon Buff.

Dentition (Fig. 41). I^1 is reasonably broad and slightly procumbent. It is a small replica of the typical broad, claw-like I^1 of *M. melanurus* where crown height $I^2 = I^3$ which is greater than I^4. C^1 is heavy and caniniform but lacks anterior and posterior cusps and buccal and lingual cingula, while the upper premolar row is short and crowded with no space separating the premolars. The premolars are more oval in occlusal view than in larger specimens. In M^1 stylar cusp B is greatly reduced and the preparacrista is extremely short. There is no protoconule. In M^2 and M^4 stylar cusp C is visible. There is no development of a metacone on M^4. The lower premolar row is short and crowded and is characterised by broad, retangular P_1 and P_2. Premolars contact or are closely approximated. In M_1 the paraconid is broader than in the lectotype of *P. melanura*. It appears as a broad flat spur, the lingual edge of which makes an appreciable swelling on the endoloph of M_1. Entoconids are reduced throughout.

Skull (Fig. 41). The skull lacks a concave depression at the nasal-frontal suture.

ADDITIONAL DIAGNOSTIC FEATURES

Murexechinus differs from all other dasyurids in: 1, I^1 only slightly procumbent but robustly
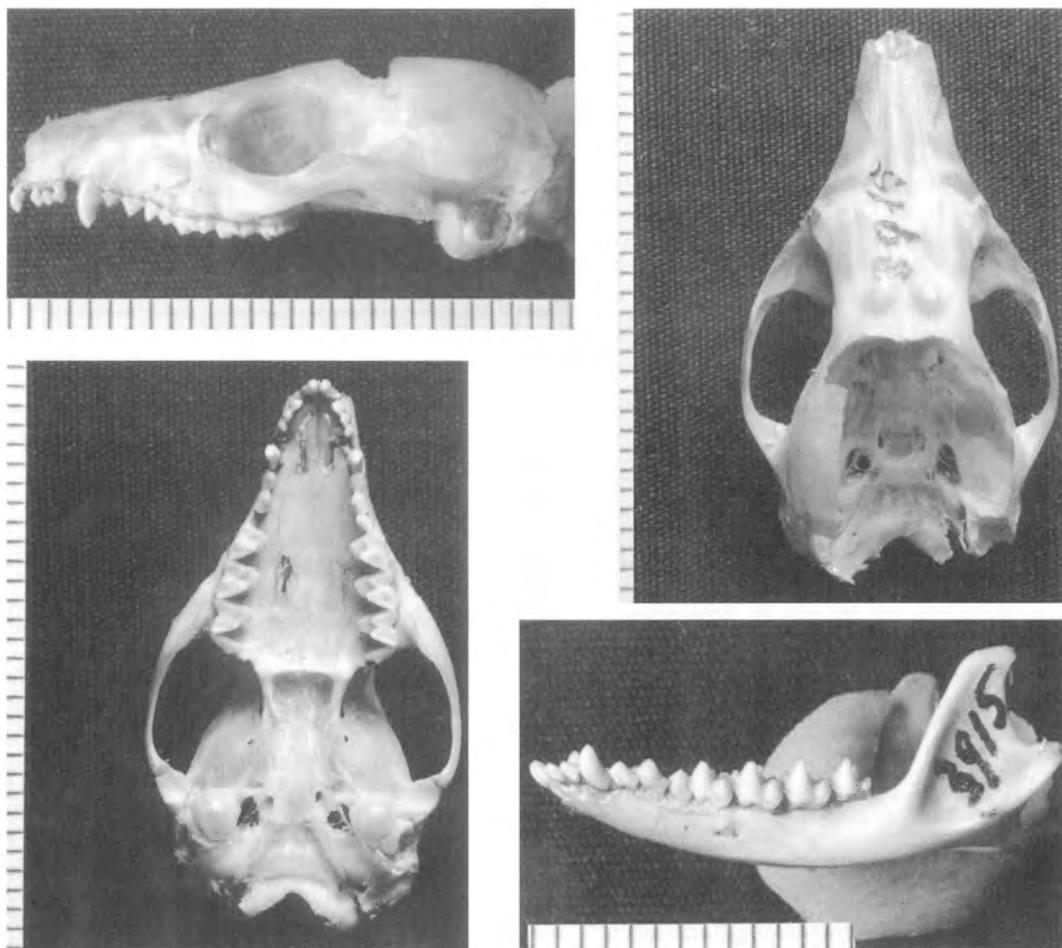
FIG. 36. Lectotype of *Phascogale melanura* Thomas, 1899. CE 3915, cranium and dentary. Sex = f; BL = 26.75; ZW = 16.73; IO = 6.93; OBW = 11.24; IBW = 5.52; R-LC^1 = 5.41; R-LM^1 = 9.81; R-LM^2 = 12.32; R-LM^3 = 14.47; R-LM^{1}T = -; M^{2}W = 2.13; I^1-M^4 = 14.69; P$^{1-3}$ = 3.19; M$^{1-4}$ = 6.85; Dent = 21.25; I$_1$-M$_4$ = -; P$_{1-3}$ = 3.28; M$_{1-4}$ = 7.46; M$_2$W = 1.37.

built, curved (claw-like), laterally compressed with much heavier crown and lower cingulum than *Micromurexia*, *Murexia*, *Phascomurexia* or *Paramurexia*; 2, I^1 and I^2 widely separated; 3, cingulated upper incisor row of broad-crowned teeth. Unlike in *Micromurexia*, *Murexia*, *Phascomurexia* and *Paramurexia*, I^2=I^3=I^4 and sometimes I^2>=I^3>I^4; 4, I^4 without a posterior cusp; 5, upper canines heavier and shorter than in *Micromurexia*, *Paramurexia*, and *Murexia*, but similar to *Paramurexia*. There is no posterior cusp; 6, an upper premolar row in which the more heavily cingulated teeth are uncrowded from C^1 to P^2, but where P^3 may touch P^2 and M^1; 7, P^1 are

P^2 are rounded and show slight postero-lingual lobing and there is no posterior cusp on P^3; 8, M^1 very broad, with wide protocone and complete anterior cingulum, the anterior margin of this tooth is straight or anteriorly convex, but not indented or concave; 9, M^1 and M^2 stylar cusp B large (smaller than stylar cusp D in M^1, subequal in M^2); 10, M^4 protocone more narrow than in *Micromurexia* but similar to *Paramurexia*, with anterior cingulum complete; 11, M^1 and M^2 stylar cusp D with tendency to be more conical than the low crest seen in *Micromurexia*, *Murexia* and *Phascomurexia*; 12, M^4 metacone reduced more than in *Micromurexia*, *Phascomurexia*, and

Murexia, similar to condition in *Paramurexia*; 13, M^3 ectoloph more heavily indented than in *Micromurexia, Murexia, Phascomurexia* or *Paramurexia*; 14, moderately heavily cingulated lower premolar row in which the rounded teeth are slightly crushed, and where P_3 is smaller than P_2; 15, cingulated P_3; 16, M_3 talonid subequal to the trigonid width; 17, paraconid on M_1 more reduced than in *Micromurexia, Phascomurexia* and *Murexia*, but similar reduction to that seen in *Paramurexia*; 18, three very reduced cusps on the M_4 talonid; 19, entoconid is more reduced than in *Micromurexia, Phascomurexia* and *Murexia* on M_2, similar reduction to that in *Paramurexia*; 20, metacristids and hypocristids are not transverse to the long axis of the dentary; 21, skull only slightly elongate and domed; 22, lightly fluted nasals; 23, poorly developed tympanic wing of the alisphoid with contrasting broad expansion of the pars mastoidea and adjacent squamosal; 24, tail thickly haired a uniform black (sometimes dark brown) throughout, with ventral crest hairs long for entire tail length; 25, polyoestrous and nipple number low (4); 26, penile morphology is simple.

In addition to those features noted in the generic diagnosis *M. melanurus* differs significantly (P<0.001) from *Micromurexia habbema* as follows (measurements are means, mm): broader zygomatic ZW (16.89:15.56); narrower interorbital width IOW (7.09:7.62); wider outside bullae OBW (10.99: 10.42); wider inside bullae IBW (5.12: 4.72); wider rostrum R-LC^1 (5.43: 5.00), R-LM^1 (9.71: 8.03), R-LM^2 (11.91: 10.49), R-LM^3 (14.12: 12.76); shorter upper premolar row P$^{1-3}$ (3.37: 3.85); longer upper molar row M$^{1-4}$ (6.78: 6.38); wider upper second molar M^{2}W (1.89: 1.73); shorter lower premolar row P$_{1-3}$ (3.45: 4.08); longer lower molar row M$_{1-4}$ (7.37: 6.86); wider lower second molar M$_2$W (1.22: 1.11); shorter ear E (15.83: 16.95); post-hallucal and hallucal pads of hind foot always fused, without accompanying auxiliary apical granules rather than the usual unfused hallucal and posthallucal pads, with accompanying auxillary granules.

M. melanurus also differs significantly (P<0.001) from *Phascomurexia naso* as follows: shorter basicranium BL (26.83:30.13); narrower interorbital width IOW (7.09:7.66); narrower inside bullae IBW (5.12:5.81); narrower rostrum R-LM^1 (9.71:10.57), R-LM^2 (11.91:12.97), R-LM^3 (14.12: 15.48); narrower maxillae R-LM^{1}T (7.69: 8.50); shorter upper tooth row I^1-M^4 (14.88: 17.32); shorter upper premolar row P$^{1-3}$ (3.37: 4.63); shorter upper molar row M$^{1-4}$ (6.78: 7.61); narrower second upper molar M^{2}W (1.89: 2.02); shorter dentary Dent (21.31:24.23); shorter lower tooth row I$_1$-M$_4$ (12.96:15.18); shorter lower premolar row P$_{1-3}$ (3.45:4.73); shorter lower molar row M$_{1-4}$ (7.37:8.32); narrower lower second molar M$_2$W (1.22:1.31); shorter total TL (247: 275); shorter tail T (133:149); shorter hind foot HF (22.27:25.35); shorter ear E (15.83: 18.40); tail usually black and never with white tip, rather than light coloured and often with white tip.

M. melanurus differs significantly (P<0.001) from *Murexia longicaudata* as follows: shorter basicranium BL (26.83:43.64); narrower zygomatic width ZW (16.89:25.33); narrower interorbital width IOW (7.09: 7.81); narrower basicranium outside bullae OBW (10.99: 14.59); narrower inside bullae IBW (5.12: 8.44); narrower rostrum R-LC^1 (5.43:8.40), R-LM^1 (9.71: 14.71), R-LM^2 (11.91: 17.80), R-LM^3 (14.12: 21.24); narrower maxillae R-LM^{1}T (7.69:11.95); shorter upper tooth row I^1-M^4 (14.88:25.01); shorter upper molar row M$^{1-4}$ (6.78: 7.49); narrower upper second molar M^{2}W (1.89:2.75); shorter dentary length Dent (21.31:36.17); shorter lower tooth row I$_1$-M$_4$ (12.96:22.73); shorter lower molar row M$_{1-4}$ (7.37: 10.90); narrower lower second molar width M$_2$W (1.22:1.71); shorter total TL (247: 398); shorter tail T (133: 197); shorter hind foot HF (22.27: 35.22); shorter ear E (15.83:20.50); ears with post-auricular patches rather than always lacking ear patches; pelage shows definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniformly brown throughout; pelage long and soft rather than short and harsh, tail thickly haired a uniform black (sometimes dark brown) with ventral crest hairs long through entire length, rather than tail almost naked brown with very weak ventral crest developing toward the distal end; I^1 broad and claw-like rather than narrow and needle-like; in overall crown size I^2 is greater than or equal to I^3 which is greater than or equal to I^4, rather than I^2 less than I^3 which is less than I^4; C^1/$_1$ is short and stout; premolar row short with premolars crowded and broad, rather than premolar row with uncrowded, narrow, widely spaced premolars; rostrum short and broad rather than elongate; nasals flat rather than raised and fluted.

M. melanurus differs significantly (P<0.001) from *Paramurexia rothschildi* as follows: Shorter basicranium BL (26.83:35.41); narrower
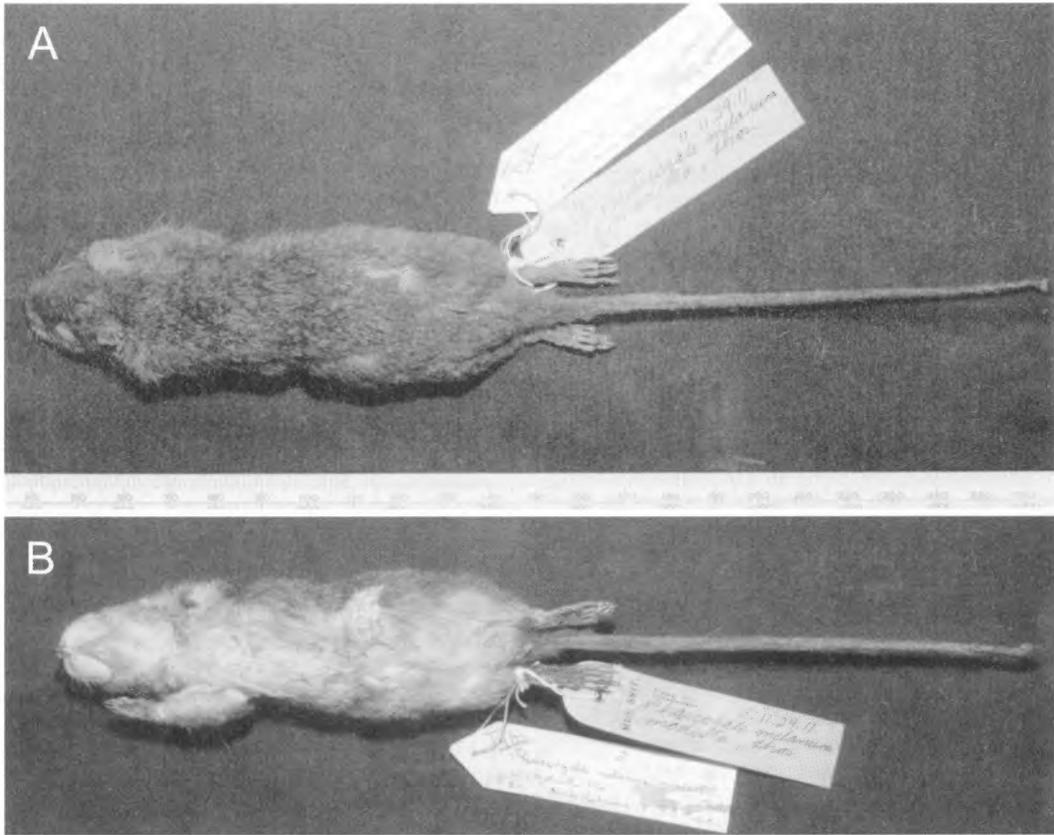
FIG. 37. Holotype of *Phascogale melanura modesta* Thomas, 1912 (now *Murexechinus melanurus*). BMNH 11.11.29.11, study skin; A, dorsal view; B, ventral view. TL = 232mm; HB = 106mm; TV = 126mm; HF = 20mm.

zygomatic width ZW (16.89:21.29); narrower basicranium outside bullae OBW (10.99:13.21); narrower inside bullae IBW (5.12: 7.27); narrower rostrum R-LC^1 (5.43: 7.72), R-LM^1 (9.71: 12.20), R-LM^2 (11.91: 14.79), R-LM^3 (14.12: 17.65); narrower maxillae R-LM^{1}T (7.69:10.08); shorter upper tooth row I^1-M^4 (14.88:19.68); shorter upper premolar row P$^{1-3}$ (3.37:4.77); shorter upper molar row M$^{1-4}$ (6.78:8.71); narrower upper second molar M^{2}W (1.89:2.45); shorter dentary Dent (21.31:28.33); shorter lower tooth row I$_1$-M$_4$ (12.96:17.39); sorter lower premolar row P$_{1-3}$ (3.45:5.03); shorter lower molar row M$_{1-4}$ (7.37:9.48); narrower lower second molar M$_2$W (1.22:1.56); ears with post-auricular patches rather than a black mask; pelage shows a warming colour change toward the rump, rather than a dorsal longitudinal stripe; tail thickly haired a uniform black (sometimes dark brown) with ventral crest hairs long throughout entire length, rather than tail thinly haired with short hairs and weak, lighter coloured ventral crest developing at the distal end.

REMARKS. *Taxonomic History*. *Murexechinus melanurus*, like no other species of New Guinean 'antechinus' has stood the test of time since its original description by Thomas in 1899. But it is not only its taxonomic longevity for which it is unique; it is unrivalled for its extraordinary range in colour, distribution and size. These factors have all contributed to the tangled fabric of its taxonomic history.

The original description was based on syntypes in Genoa and London. van der Feen, 1962 designated a lectotype. Later Thomas (1912), impressed by lack of bright auricular patches in an Irian Jayan specimen, proposed *P. melanura modesta*. While Thomas had few other spec-

imens to compare, later collections revealed specimens from the W which were drabber than *modesta* by the same degree that *modesta* was drabber than the nominate form; and specimens in the E which were more brightly coloured.

In 1930 Dollman (not 'Rothschild & Dollman', Tate 1947: 129) described a large, paler specimen from the far northwest of Irian Jaya (Arfak Mountains) which was later to be the bane of New Guinea dasyurid taxonomy. *Phascogale mayeri* was described for its large size and light colour, and Dollman was quick to point out its close affinity with *melanura* though it is doubtful that Dollman compared the skull of *mayeri* with the types of *melanura* despite his comments '... skull larger and more heavily built than in *P. melanura* ...' (Dollman, 1930: 433). In The Natural History Museum, London, Dollman had access to only three or four specimens of *melanura*; a small, subadult male collected by N.S. Meek from the Aroa River, a specimen collected by W. Stalker from the Marribore River, and Thomas' two types, *melanura* and *melanura modesta*. The study skin of *melanura modesta* was never accompanied by a skull and the paralectotype had never had the skull removed (it is still in the body today). Unless Dollman had access to the lectotype it is probably fair to assume that Dollman's comparison was based on the 5 cranial and dental measurements provided by Thomas in his *melanura* description.

With little British Museum comparitive material (where the paralectotype of *melanura* and specimens of Meek and Stalker were relatively brightly coloured, and where the type of *melanura modesta* was such a small adult), it is not surprising that Dollman chose to label as *mayeri* a new series of large, brownish coloured animals with light-orange post-auricular patches collected by F. Shaw Mayer in the Weyland Range, Irian Jaya.

This decision however, led to the eventual undoing of *mayeri*. One of the specimens of this Weyland Range series, identified by Dollman as *mayeri*, eventually found its way into the Archbold Collection of the American Museum of Natural History (AMNH 101978) where Tate noticed that dental, cranial and external features were similar to his series of *melanura*. In 1937, Tate formalised his suspicions surrounding the identity of *mayeri* by reducing it to subspecific status as *Phascogale* (*Antechinus*) *melanurus mayeri*, 'the close likeness of both skin and skull

of *mayeri* to *melanura* is undeniable' (Tate 1937: 339).

During the decade following 1937, New Guinean specimens collected by F. Shaw Mayer and W. B. Richardson greatly enhanced the marsupial holdings of the British and American Museums of Natural History. Tate took advantage of this swelling comparative collection and, after examining type material in major European museums, made significant revision (1947) to the taxonomy of *melanurus* (as it was then). He retreated from his earlier assertion that *mayeri* was but a subspecies of *melanurus* and instead assigned Dollman's *mayeri* full specific status as the senior synonym of his and Archbold's *tafa* (= *naso*).

Reasons for this backtrack are inexplicable, especially when *mayeri* fulfilled all the criteria (dental, cranial and external) nominated by Tate himself (1947: 128) to diagnose specimens of *A. melanurus* (the skull of *mayeri* displayed the typically thick, heavy, first upper incisor, broad I^{2-4} and small palatal foramina, and the skin showed the bases of the ears coloured chestnut (to a reduced degree). The tail was black. These features never appeared in any of Tate & Archbold's *P. tafa* types or in any of the series associated with them). While, in retrospect, there was little justification in Tate's erecting separate subspecies for *centralis*, *tafa* and *misim*, it is little wonder that the subspecies *mayeri mayeri* had to exist to accommodate this one specimen (from unusually low altitude (1,000m) and with rufous ear-patches) about which Tate still felt uncomfortable, 'A good series is needed for comparison with *centralis*' (1947: 129). Even more pessimism regarding the future of the *mayeri* group was expressed by Tate, 'All four of these races stand so close to one another that later reviewers may decide that they should be merged together' (Tate 1947: 129). Despite this prediction, the epithet *mayeri* has been persistently and erroneously included with the *tafa, centralis, misim* group (= *naso*) e.g., Laurie (1952), Ziegler (1977), Van Dyck (1982a), Archer (1982a). Jenkins & Knutson (1983) assigned the *mayeri* holotype to *naso*.

Regarding the synonymy of *modestus*, Tate (1947: 128) summarised the characteristics of his three proposed groups of Antechinus in New Guinea and included *modestus* not in Group 1 with *melanurus* but in group 2 with *tafa, tafa centralis* and *mayeri* (group 3 was *wilhelmina*). The following page (p. 129) saw Tate
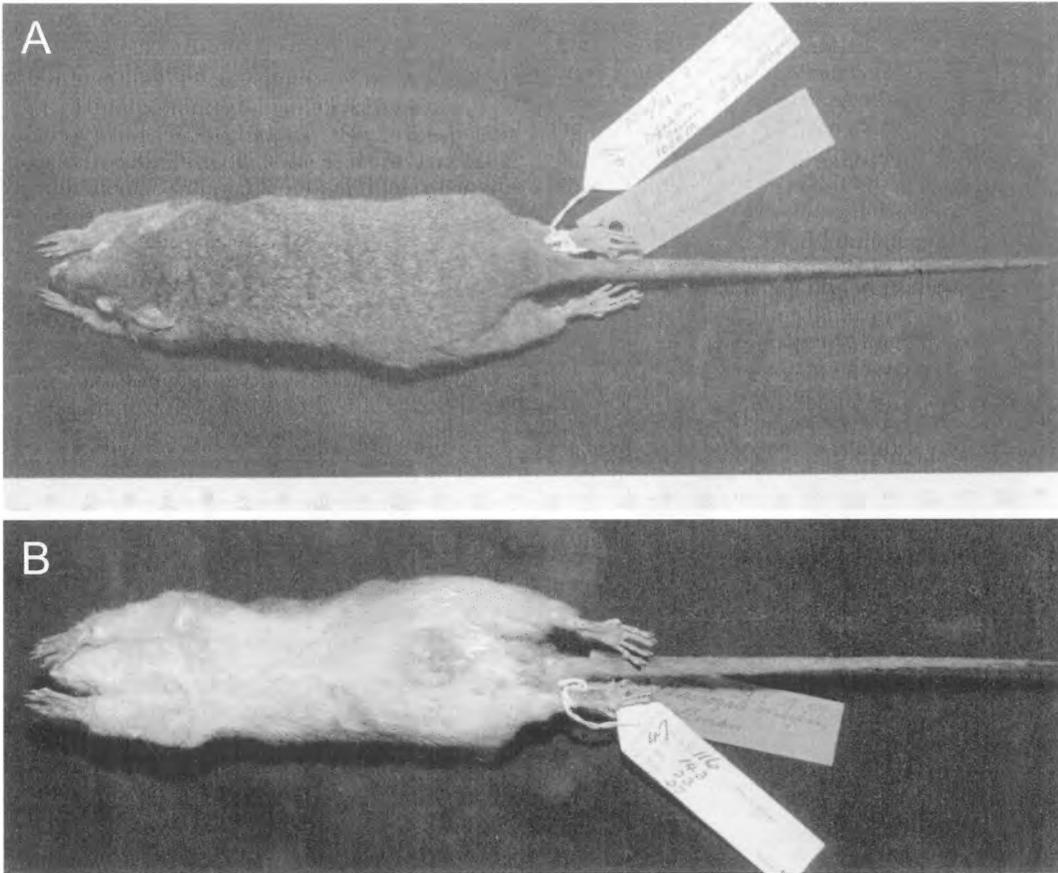
FIG. 38. Holotype of *Phascogale mayeri* Dollman, 1930 (now *Murexechinus melanurus*) BMNH 29.5.27.57, study skin; A, dorsal view; B, ventral view. TL = 259mm; HB = 116mm; TV = 143mm; HF = 23mm.

synonymise *modestus* with Thomas' *melanurus* (i.e., back to group 1). The reason for this is inexplicable (though some suggestions are made under 'Taxonomic History' in the account of *naso*.

Tate (1947) proposed *wilhelmina* to cater for not only the 'small replica(s) of *melanurus*' (p. 130) but to act as a sponge for what he considered an inadvertant taxonomic blunder associated with an earlier named species *habbema* (Tate & Archbold, 1941). The 'blunder' and its implications are discussed in detail under 'Taxonomic History' in the account of *habbema* and will only be summarised here.

Tate considered that *habbema* had been described from a mismatched skin and skull. In rectifying the problem he proposed to restrict use of the name *habbema* to the skin of the type

(which be considered to be an example of *mayeri* (=*naso*) and the skull he considered to be identical with another species which he named *wilhelmina* (=melanurus). The argument presented earlier here concludes that no mismatch had occurred and that the epithet *habbema* should still apply to the small, primitive, high-altitude dasyurid which constitutes the third and final New Guinea 'antechinus' after *naso* and *melanurus*. The type of *wilhelmina* represents no more than that which Tate had originally described it as 'a small replica of *melanurus*' (p. 130), and a junior synonym of that species.

Characters Tate then ascribed to *wilhelmina* became a composite of the characters of two different species which Tate considered the same. 'Furthermore the skull which was associated with
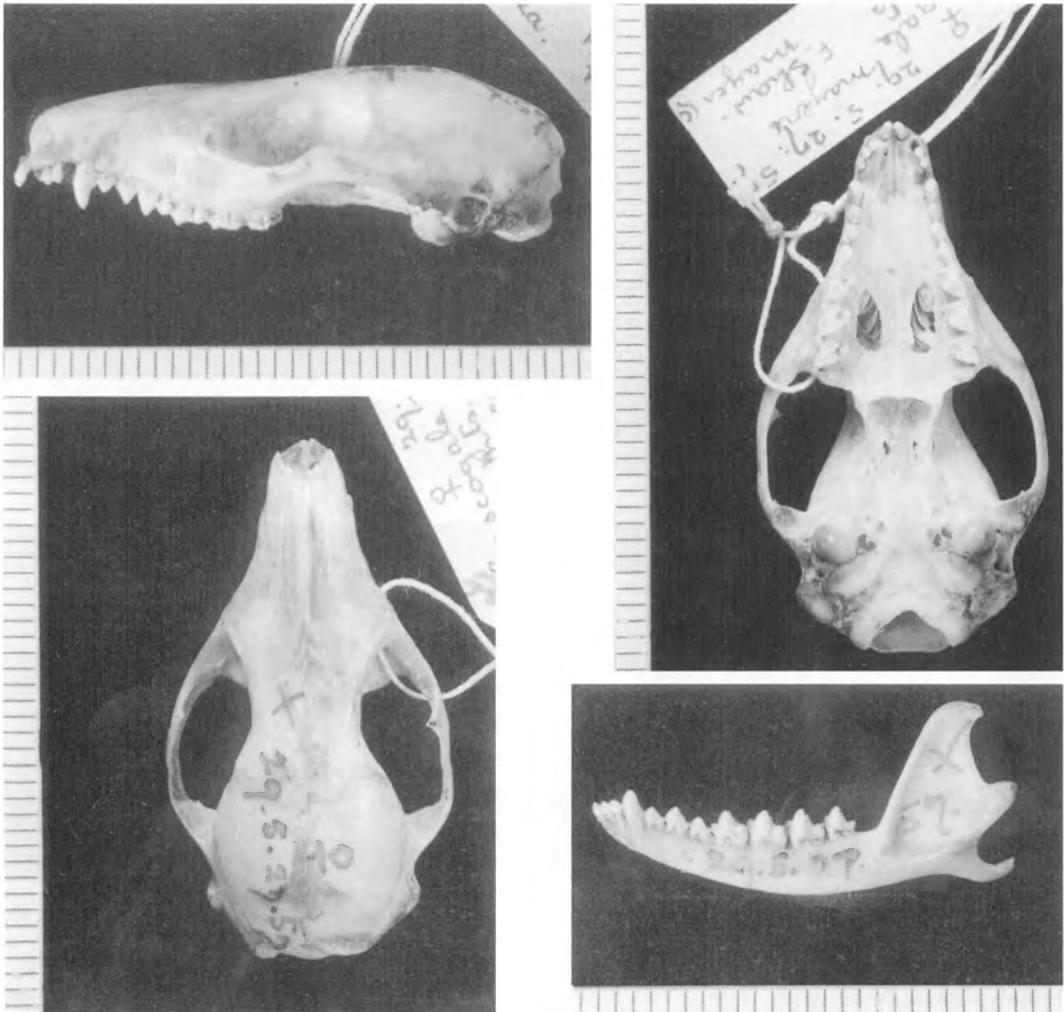
FIG. 39. Holotype of *Phascogale mayeri* Dollman, 1930, BMNH 29.5.27.57, cranium and dentary. Sex = f; BL = 30.12; ZW = 18.44; IO = 6.86; OBW = 11.79; IBW = 5.97; R-LC^1 = 6.28; R-LM^1 = 11.17; R-LM^2 = 13.66; R-LM^3 = 15.78; R-LM^{1}T = 8.85; M^{2}W = 2.15; I^1-M^4 = 16.81; P$^{1-3}$ = 4.05; M$^{1-4}$ = 7.41; Dent = 24.53; I$_1$-M$_4$ = 14.28; P$_{1-3}$ = 4.08; M$_{1-4}$ = 8.29; M$_2$W = 1.37.

the type skin of *A. habbema* exactly matches the skulls of *wilhelmina*' (Tate 1947: 131)! For example, features noted for *wilhelmina* included: 'bases of the ears faintly chestnut; tail black above and below. Body color gray brown, the hairs strongly washed with rufous' (all features of *melanurus*), '... first incisors very slender, other incisors narrow and slender; premolars small' (all features of *M. habbema*) '... mp^4 single-rooted' (a variable feature of *M. melanurus*) '... molars very small' p.128 (a *habbema* feature).

Laurie (1952) diagnosed the significance of a series of specimens from Mt Tomba, NE PNG (Shaw Mayer, 1947). She drew attention to basic differences from *wilhelmina* — their uniform brownish grey body colour, the rump not contrastingly reddish, the lack of ear patches, the tail being brown above and pale buffy below, and she described the species as *A. hageni* (= *habbema*). However, two years later she synonymised her *A. hageni* with the very species (*wilhelmina*) in which she had previously recognised so many conflicting characters.
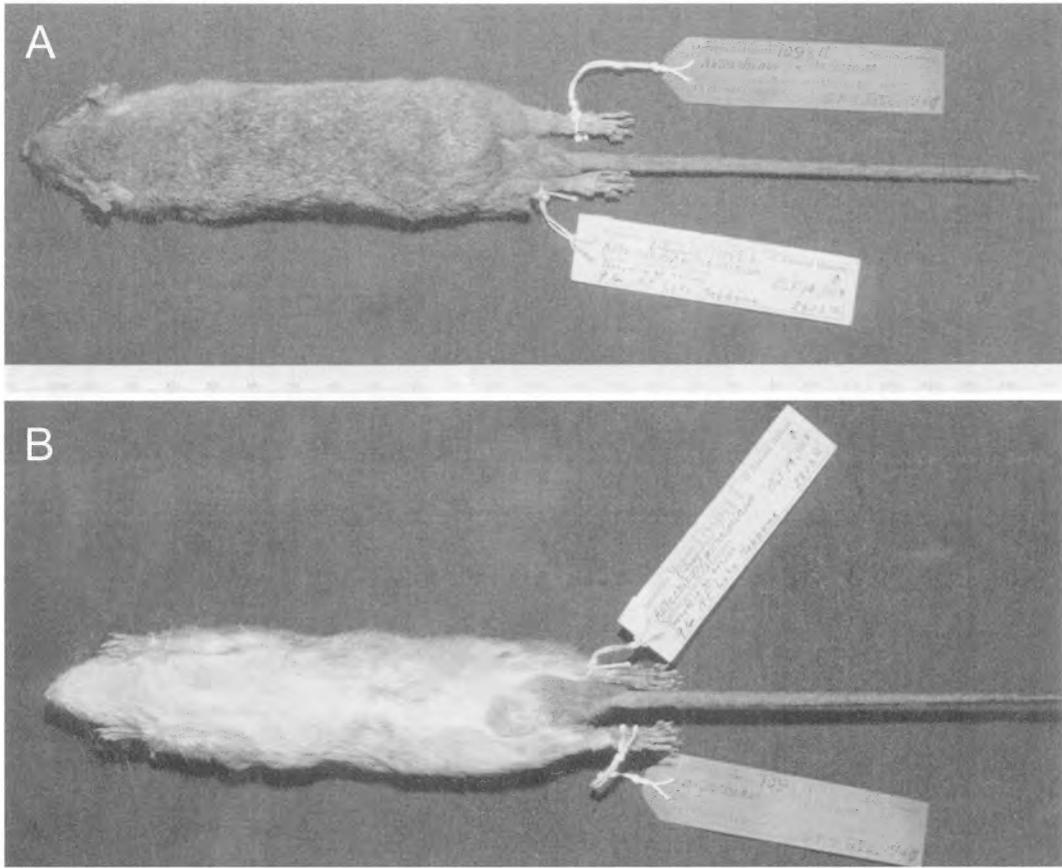
FIG. 40. Holotype of *Antechinus wilhelmina* Tate, 1947 *(now Murexechinus melanurus)*. AMNH 109811, study skin; A, dorsal view; B, ventral view. TL = 238mm; HB = 108mm; TV = 130mm; HF = 20mm.

In light of the mixture of Tate's descriptive features for *habbema* and Laurie's new species *(hageni)* it is strange that the name *wilhelmina* should have persisted as the third species of New Guinean 'antechinus' (with *naso* and *melanurus*) to the present day e.g., Laurie & Hill (1954), Ziegler (1977), Ziegler (1982), Kirsch & Calaby (1977), Corbet & Hill (1980), Honacki et al. (1982), Baverstock et al. (1990). Archer (1982a), preferred to refer to the specimens of *wilhelmina* by collection locality (Mt Wilhelm) and museum accession number. Jenkins & Knutson (1983) assigned the *hageni* holotype to *wilhelmina*, while Westerman & Woolley (1993), Woolley (1994), Krajewski et al. (1996) and Armstrong et al. (1998) recognised *wilhelmina* and *habbema* as specifically distinct.

DISTRIBUTION (Fig. 42). From sea level to mid-montane areas of the central cordillera (up to 2,800m). Between 134°00'E in W Irian Jaya to 151°01'E (Normanby Island). It has been collected in rainforest, mid-montane forest, beech forest, pandanus forest and mossy forest. Full floristic details of collection localities appear in Archbold et al. (1942: 258), Brass (1964: 109) and Brass (1959: 41, where the largest recorded specimen was collected [and refered to as *longicaudata*]). Menzies (1972) recorded 2 maxillary fragments of *melanurus* from sparsely wooded *Eucalyptus* savannah near Port Moresby.

REPRODUCTION. All pouches examined had 4 teats. Lactating females were collected in (dates included in parentheses), January (1), August (17,22,26), September (12, 19), October (13, 20), November (10), December (16). Dwyer (1977) noted the capture of lactating females in April (7, 17), September (13, 21) and December (8).
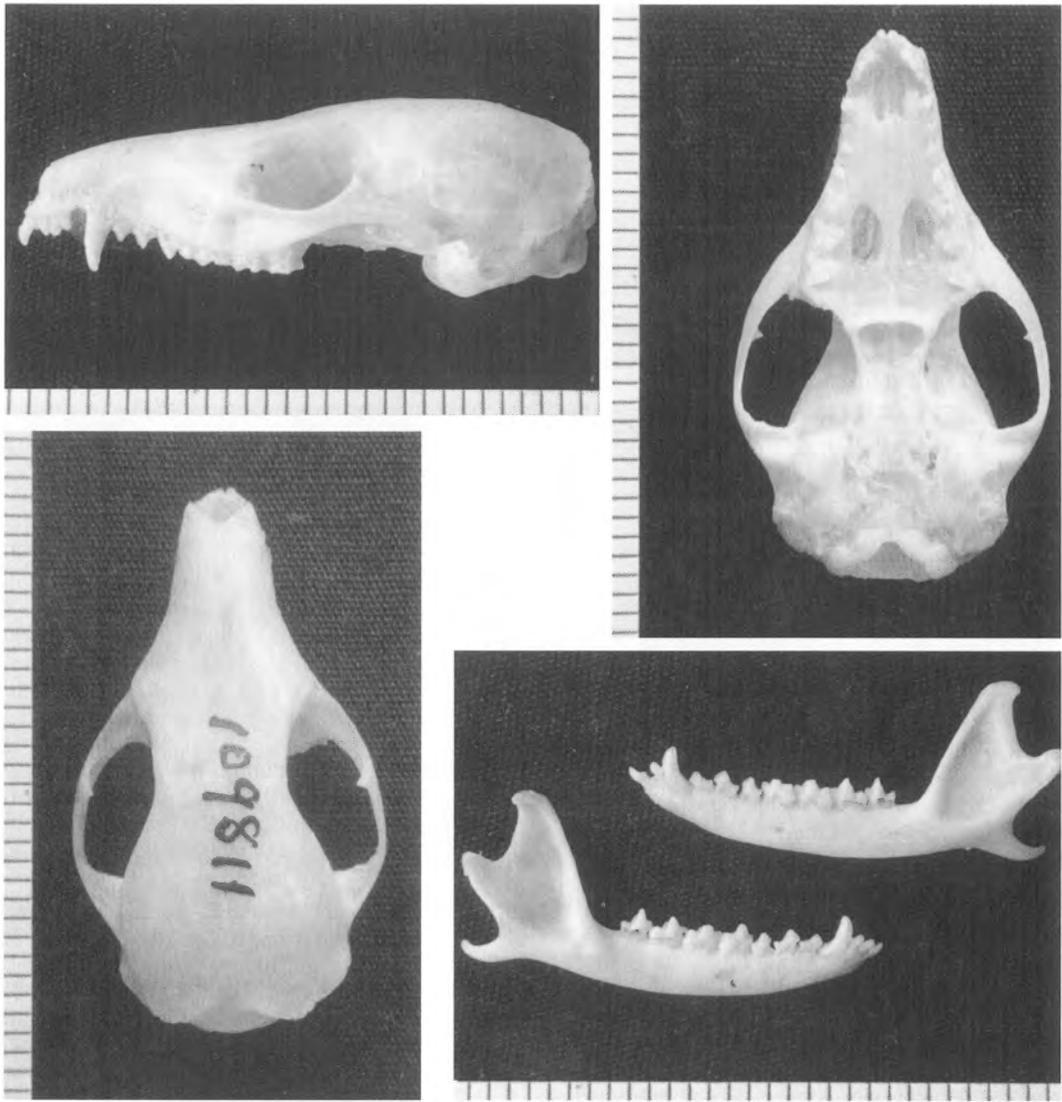
FIG. 41. Holotype of *Antechinus wilhelmina* Tate, 1947. AMNH109811, cranium and dentary. Sex = m; BL = 26.64; ZW = 16.90; IO = 6.91; OBW = 10.61; IBW = 4.79; R-LC^1 = 5.29; R-LM^1 = 9.47; R-LM^2 = 11.75; R-LM^3 = 14.00; R-LM^{1}T = 7.48; M^{2}W = 1.75; I^1-M^4 = 14.76; P$^{1-3}$ = 3.72; M$^{1-4}$ = 6.33; Dent = 21.44; I$_1$-M$_4$ = 12.72; P$_{1-3}$ = 3.44; M$_{1-4}$ = 6.67; M$_2$W = 1.18.

DESCRIPTION. *Mean Measurements*. External (mm): total length (head, body, tail) ($\male$) 256, ($\female$) 230; tail (to cloaca) ($\male$) 135, ($\female$) 130; hind foot (su) ($\male$) 22.55, ($\female$) 21.44; ear (notch) ($\male$) 15.92, ($\female$) 15.65. Skull: basicranial length ($\male$) 27.30, ($\female$) 25.99; M$^{1-4}$ length ($\male$) 6.81, ($\female$) 6.72; M^2 width ($\male$) 1.90 ($\female$) 1.89. (Table 6).

P4 Morphology. P^4 may be single, or double-rooted (of 9 pairs of P^4 examined, 4 pairs were single-rooted, 5 pairs double-rooted) but all crowns were molariform, the most significant cusp being the metacone. Other features include a small cusp homologous to a paracone. P$_4$ was always single-rooted as either a peg-like spur, or premolariform and relatively bulky. When heavily built, this tooth was often oriented obliquely in the dentary.

SIZE. In *M. melanurus* body size decreases significantly with increasing altitude. Using basicranial length BL as a reflector of overall body size, its average value in adult specimens of both sexes collected lower than 1,000m a.s.l. mean=32.52mm (R=29.29-36.83, N=6, SD= 2.50), at altitudes greater than 1,000m a.s.l. but less than or equal to 2,000m a.s.l. BL mean= 26.85mm (R=23.11-30.33, N=23, SD=1.86), and at altitudes greater than 2,000m a.s.l. but less than or equal to 3,000m a.s.l. BL mean=25.75mm (R=22.23-28.32, N=32, SD=1.24).

The pattern is similar for males and females if treated separately. The largest individual examined was ♂ AMNH 159473 (BL = 36.83mm) from Mt Pabinama, Normanby Island (10°06'S 151°01'E) at 820m.

The smallest adult examined was ♀ AMNH 109815 (BL=22.23mm) from 9km NE Lake Habbema (04°05'S, 138°50'E) at 2,200m. Largest specimens have come from the NW-SE extremities of the island.

COLOUR (Fig. 43). The intensity of fur colour in *M. melanurus* is highly variable, and individuals of all colour forms, from drab to brilliant can be found from sea level through to 2,500m a.s.l. A significant trend of colour enhancement occurs, however, from the north west through to the south eastern tip of the island. All study skins examined were assigned a subjective colour rating (C), 1 (for extremely drab) through to 5 (for very brightly coloured individuals with rich tones). The trend can be further demonstrated by dividing the island into longitudinal blocks. For specimens collected west of longitude 140°00'E the average colour rating C = 2.03 (R = 1.0-3.5, N = 19, SD = 0.90), for specimens collected between 140°01'E and 146°00'E C = 2.98 (R = 2.01-4.0, N=24, SD=0.73), and for those between 146°01'E and 150°00'E C=3.7 (R=2.0-5.0, N=21, SD=0.73).

SPECIMENS EXAMINED. Araboe-bivak, 1750m, 03°51'S 136°26'E (RMNH 1839, RMNH 1936); Arau, Kratke Mts., 1400m, 06°20'S 146°05'E (AMNH 190868); Arfak Mts., 1000m, 01°09'S 134°00'E (BMNH 29.52757); Aroa River, 09°05'S 146°48'E (BMNH 1939.3239); Baiyanka, 2287m, 05°35'S 144°51'E (BMNH 50.1100); Baiyanka, 2440m, 05°35'S 144°51'E (BMNH 50.1101); Bernhard Camp 4km SW, 850m, 03°30'S 139°12'E (AMNH 152034); Bialon, Morobe, 686m, (MCZ 29337); Boneno, 1220m, 09°54'S 149°25'E (BMNH 50.1106); Boobiari Mt. (base), (FN 80); Bulolo 10km W., 780m, 07°11'S 146°39'E (BBM 51268, BMNH 54045); Collin's Sawmill, Mt Otto, 2660m, 05°59'S 145°25'E (AMNH 190866); Daviumbu Lake, 25m, 07°36'S 141°17'E (AMNH 105795); Dayman Mt., 1540m, 09°49'S 149°16'E (AMNH 157075); Derimapa Mt., 1220m, 03°50'S 135°43'E (AMNH 101978, BMNH 33.6168); Derimapa Mt., 1525m, 03°50'S 135°43'E (BMNH 33.6169); Enaena, 1220m, 10°03'S 149°38'E (BMNH 50.1102); Enaena, 1372m, 10°03'S 149°38'E (BMNH 50.1104-50.1105), Enaena, 1525m, 10°03'S 149°38'E (BMNH 50.1103); Erimbari Mt., 2500m, 06°12'S 145°20'E (QM JM 1093-1094); Fermain, 1372m, 05°14'S 141°40'E (BBM 22905); Fly River, 80m, 05°20'S 147°57'E (AMNH 105037); Giluwe Mt., 2400-2745m, 06°03'S 143°53'E (BMNH 53.202-53.203); Giluwe Mt. W slopes, 2684m, 06°03'S 143°53'E (CM 14); Gwariu River, 200m, 09°40'S 149°17'E (AMNH 157075); Habbema Lake 18km N, 2200m, 04°05'S 138°42'E (AMNH 157075, AMNH 109794, AMNH 109805, AMNH 109828, AMNH 150988, AMNH 109821); Habbema Lake 9km NE, 2200m, 04°05'S 138°50'E (AMNH 109815, AMNH 109811, AMNH 109819); Hagen Govt. Stn 25km N, 1525m, 05°49'S 144°07'E (BMNH 50.1839); Hagen Mt., 2134-2440m, 05°54'S 144°09'E (AMNH 156357, AMNH 156362-156363, AMNH 156365-156366); Hagen Mt., 2135-2440m, 05°54'S 144°09'E (AMNH 156371, AMNH 156379, AMNH 156381-156387, AMNH 156390, AMNH 156401); Hagen Mt., 2501m, 05°54'S 144°09'E (AMNH 156356); Hagen Mt., 2592m, 05°54'S 144°09'E (AMNH 156358, AMNH 156360, AMNH 156369, AMNH 156377); Idenberg R., 50m, 03°31'S 139°11'E (AMNH 152026); Idenberg R., 1200m, 03°31'S 139°11'E (AMNH 152032); Idenberg R., 03°31'S 139°12'E (AMNH 152033); Itiki, 350m, 10°35'S 150°00'E (AMNH 108559); Java Rarre, 20km E Sogeri, 600m, 09°25'S 147°26'E (BBM 60276); Kratke Mts., 1350m, 06°13'S 146°01'E (AMNH 190871); Kratke Mts Arau, 1400m, 06°20'S 146°05'E (AMNH 190869); Kratke Mts Arau, 06°20'S 146°05'E (AMNH 190870); Madang, Atitau, 1159m, 04°48'S 145°20'E (AMNH 198722); Mafulu, 1255m, 08°31'S 147°00'E (AMNH 104051); Matsika, 980m, 08°35'S 146°54'E (AMNH 104052); Minj, 1830m, 05°50'S 144°39'E (BMNH 53.199); Misim Mt., 1738m, 07°13'S 146°50'E (MCZ 29920); Mola-Kokoda Road, 900m (AMNH 108562); Moroka, 1300m, 09°24'S 147°32'E (MCSNCE 3915); Mur Mur Pass, 2700m, 05°45'S 145°56'E (BBM 97458); Mur Mur Pass, 2800m, 05°45'S 143°56'E (BBM 60674); Nondugl, 1900m, 05°52'S 144°45'E (AMNH 183817); Oksapmin, 1800m, 05°15'S 14214 (BMNH 99905); Oksapmin, 1900m, 05°12'S 141°38'E (BBM 55431); Oransbari, 3m, 01°21'S 134°18'E (AMNH 221628); Otto Mt., 2200m, 05°59'S 145°25'E (AMNH 190867); Pabinama Mt. Normanby I., 280m, 10°06'S 151°01'E (AMNH 159473); Schrader Mts, 2440m, 05°10'S 144°26'E (BMNH 69.297); Shungol Mt., 2000m, 06°51'S 146°44'E (BBM 98282); Sibil Valley, 1250m, 05°00'S 141°00'E (BBM 222, RMNH 16932); Stuart I. (opposite), (AMNH 105854); Tambul 10km NNE, 2700m, 05°45'S 143°56'E (BBM 97406); Telefomin, 1525m, 05°12'S 141°38'E (BBM 99733, JM 6170, JM 6171); The Gebroeders, 1525m, 03°50'S 135°43'S (BMNH 1939.3238); Tomba Mt., 2501m, 05°50'S 144°02'E (BMNH 50.1836); Tomba Mt., 2592m, 05°50'S 144°02'E (BMNH 50.1834-50.1835); Tomba Mt., 05°50'S 144°02'E (M 9560); Utakwa River, 1661m, 04°11'S 137°12'E (BMNH 13.61889) Wanuma 5km N, 1200m,

04°48'S 146°19'E (BBM 103798); Welya, 2592m, 05°44'S 143°56'E (BMNH 53200); Wilhelm Mt., 2500-2370m, 05°46'S 144°59'E (AMNH 190895); Wilhelm Mt. E slopes, 2770m, 05°46'S 05°46'S 144°59'E (AMNH 190865).

PHYLOGENETICS

CHARACTER ANALYSIS. Although Nixon & Carpenter (1993) assert that one does not need to know 'primitive' and 'derived' states before attempting analysis, I have included here a short evaluation of the determination of polarity of characters used to assess relationships among 'antechinuses' and 'murexias'. Although phylogenies of identical topology will naturally be produced from analyses with reversed polarity (i.e., without prior appreciation of polarity) the weight of palaeontological evidence suggesting overall trends of derivation in dasyuroids and didelphoids makes analysis of phylogenies based on reversed polarities untenable (i.e., defending such character transformations as possession of P_3, widely spaced premolars, upper incisor number 8, large 3-cusped M_4 talonid etc, as derived conditions).

The decisions of polarity expressed in the matrix that follows have relied heavily on the discussions of Archer (1976b, 1981, 1982a, 1982b), Kirsch & Archer (1982) and Reig et al. (1987) and their interpretation of the fossil record.

Incisors. Incisors are commonly absent in the fossil record, however, Archer (1976b) considered the following conditions of upper incisor morphology to be plesiomorphic in dasyurids: V- or U-shaped upper incisor rows (Character 1); I^1 and I^2 separated by a small diastema (Ch. 7); hypsodont condition of I^1 relative to I^2 correlated to a diastema between I^1 and I^2 and crowns non-spatulate (Chs 8, 9); I^4 longer-crowned than I^3 (Chs 11, 15) (Archer found this condition clouded in *Antechinus* because the then broader interpretation of the genus included New Guinea taxa). While in the present analysis variation in crown size in lower incisors did not provide a usable transformation series, the relative size of the lingual incisor heel did. I could find no prior polarity assessment of this feature, and on the basis of the upper incisor trends noted above, have treated a greatly reduced lower incisor heel as derived (Ch. 39). Peg-like morphology in upper and lower incisors has also been postulated as the plesiomorphic condition for didelphoids, any increased spatulation or reduction/enlargement in size representing a derivation (Reig et al., 1987). The polarity assigned to

characters 3, 4, 6, 8, 10, 12, 13 and 15 is an extension of this opinion and incorporates similar polarity decisions made by Kirsch & Archer (1982) for characters 4, 8, 9, 11 and 14 in particular. Procumbency of upper incisors (Ch. 2) and prostration of lowers (Ch. 38) are regarded here as derived features, decisions based on comments on specialisation by Archer (1976b) and the condition in the majority of didelphoids (Reig et al., 1987).

Canines. Caniniform canines are regarded to represent the primitive state in didelphoids and dasyuroids (Archer, 1976b, 1981). Characters 16, 17, 18, 19 and 20 are polarised accordingly, and incorporate putative derived conditions of root/crown definition and presence of a posterior cusp on C^1 from comparison with the didelphoid record (Reig et al., 1987).

Premolars. Archer (1976b) proposed that narrow premolars in uncrowded premolar rows represent the primitive premolar condition in didelphoids and hence dasyuroids (Chs 21, 22, 23, 43, 48). He noted a direct correlation between the development of shorter and wider premolars with extreme shortening of the premolar row (Ch. 25). Elsewhere he noted (Archer, 1981) that reduction of P3, widening of the premolars and crowding of the premolar tooth row are derived states within the genus *Sminthopsis* as well as within dasyurids as a whole. Tate (1947) noted short muzzles and short palates accompanying short, crowded tooth rows in more derived vertebrate-killing dasyurids. Reig et al. (1987: 12) concluded that the primitive condition in didelphoids for upper premolars was one of 'well-developed, trenchant, narrow teeth increasing in size from the first to the third' (Chs 40, 41, 42, 44, 45, 47). They also considered bulbousness in P^3 a derived condition. Given the absence of lingual and buccal cingula from ancestral forms, cingulation of lower premolars (Ch. 46) was assumed to represent the derived condition. The presence/absence of a posterior cusp on P^3 (Ch. 24) was a condition for which there was little comment in recent literature, and one which exhibited great variability within the didelphoids. Given that the development of a strong posterior cusp on P^3 appeared to be associated with an increase of buccal cingulation, I have treated pronounced cusping of P^3 as derived, but concede that this decision may be ill-advised.

Molars. Archer (1976b) and Wroe (1999) noted that the anterior cingulum of upper molars was complete in ancestral didelphids and is regarded
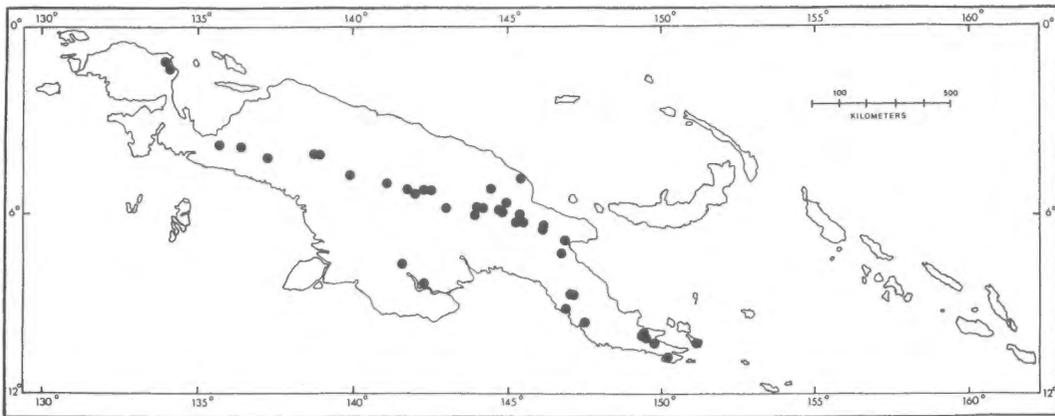
FIG. 42. Distribution of *Murexechinus melanurus*.

as representing the primitive state in dasyuroids (Ch. 26). Cingulum width is inversely related to the width of molars according to Archer. Reig et al. (1987) added that a bulbous, non-compressed protocone on the upper molars (Chs 27, 31) was representative of the primitive condition along with the length of M^2 being longer or subequal in length to M^3 (Ch. 28). Support for regarding the presence of stylar cusp B as plesiomorphic and its reduction or loss as apomorphic is presented by Archer (1976b) and Muirhead & Archer (1990). The close proximity of the paracone to stylar cusp B (Ch. 37) is regarded as an apomorphic condition (Kirsch & Archer, 1982). Archer (1976b) did not use the condition of stylar cusp D in his analysis given that stylar cusp pattern did not appear to distinguish between genera. Reig et al. (1987: 11) addressed the ancestral condition of stylar cusp D thus 'the anatomy of the molar teeth in Lower Cretaceous therians and in *Alphadon* and *Peradectes* indicates that a well-developed stylar shelf with a complete series of stylar cusps ['stylar shelf with usually five regular-sized stylar cusps' p.13], but without enlargement of the metastylar area is the primitive condition' (Ch. 33). Well-developed ectoflexus in the ectoloph of upper molars (Ch. 34) is considered apomorphic for dasyurids (Muirhead & Archer, 1990), as is reduction or loss of the M^4 metacone (Ch. 35) (Archer, 1976b), loss of upper molar posterior cingulum (Ch. 36) and reduction or loss of M_1 paraconid (Chs 49, 53) (Kirsch & Archer, 1982). Tall, well-developed entoconids are regarded as an ancestral condition and are known from all Cretaceous didelphids (Archer, 1976b; Kirsch & Archer, 1982; Muirhead & Archer, 1990:

Muirhead, 1994, Wroe, 1999). Archer (1981) commented concerning entoconids in dasyurids, that species occupying higher rainfall areas such as those of highland New Guinea had well developed entoconids while many Australian arid-adapted dasyurids lack them, and that the absence of entoconids in Australian dasyurids is a derived condition. Any reduction of M_4 talonid cusps below 3 (Ch. 51) is regarded as a derivation as well as reduction of the M_3 talonid width (Ch. 50) (Archer, 1976b; Kirsch & Archer, 1982). Transverse metacristids (Ch. 54) are considered structurally primitive (Archer, 1976b) among dasyurids and the condition is thought to reflect a more insectivorous diet. The orientation of the M^4 preparacrista (Ch. 32) is here assumed to be in the primitive condition when it is transverse to the long axis of the skull. This notion receives support from examination of the condition in a number of microbiotheroids and didelphoids (*Dromiciops, Pediomys, Glironia, Caluromys, Philander, Metachirus, Micoures, Marmosa, Monodelphis, Thylatheridium, Lutreolina, Thylophorops, Sparassocynus, Didelphis, Chironectes*). Orientation in highly derived dasyurids (e.g. *Sarcophilus, Thylacinus*) is more oblique, maximising the shearing capacity of the M_4 postprotcristid.

A picture of relative rostral width (and, ultimately an index of brachycephaly) (Ch. 55) is given by comparing skull width across the lachrymal canals against rostral length measured from I^1 to the lachrymal canal. In the suite of taxa I have reviewed for this study, values varied from approximately 67% (in *Thylacinus*) to approximately 104% (in *Sarcophilus*). While the primitiveness of *Thylacinus* is debatable, I have

assumed that because short muzzles are a direct result of shortened check-tooth rows, that brachycephalic skulls can be regarded as representing the derived condition. Archer (1981) interpreted brachycephaly as a derived condition. The convexity or fluting of nasals (Ch. 56) was considered a primitive condition after examining the range of variation in a number of didelphoids for which specimens or figures (e.g., Reig et al., 1987) were available (*Dromiciops*, *Caluromys*, *Philander*, *Metachirus*, *Marmosa*, *Monodelphis*, *Lestodelphys*, *Lutreolina*, *Didelphis*, *Chironectes*). Expansion of the tympanic wing of the alisphenoid (Ch. 57), and that of the pars mastoidea (Ch. 58) are both considered derived states (Kirsch & Archer, 1982) as are squamosal-frontal contact (Ch. 61) and possession of palatine vacuities (Ch. 62) (Archer, 1981). (Given the division of opinion regarding the assignment of polarity to the condition of maxillary vacuities (Marshall, 1977 vs Archer, 1982b vs Reig et al., 1987) I opted not to use this character in the data analysis).

While Archer (1981) regarded narrow nasals (Ch. 59) in *Sminthopsis* to represent a derived condition, I have broadened the concept of 'narrowness' to include gentle flaring posteriorly inasmuch as the boundary of the nasal remains reasonably straight along its longitudinal length. This state represents the nasal condition in the majority of didelphoids. Greater posterior expansion of the nasals I have regarded as derived. 'Doming' of the skull (Ch. 60) also is interpreted differently to Archer's (1981) concept of it, where he sought to describe the swelling of the nasal-frontal sutures ('Roman-nosing') in *Sminthopsis virginiae* and *S. douglasi*. Here, I am attempting to distinguish between the gentle flex in the antero-posterior profile of the skull seen in didelphoids and the extreme dolichocephalic condition found in *Planigale*. Accordingly I have regarded the 'gentle dome' as the plesiomorphic condition and extreme dorso-ventral flattening as derived. The morphology of the supratragus (Ch. 63) has been useful in distinguishing species of *Antechinus* (Van Dyck, 1980), however assigning correct polarity to the various states of the supratragus is subjective. Here I regard the more simple paddle-like condition as plesiomorphic, while the more florid, twisted and corpulent structures I have treated as derived. Tail length (Ch. 64) is also polarised subjectively, but guided by Archer's (1981) decision that long tails probably represent a derived condition. I have extended

this to include very short tails. The decision on tail length polarity, however, was ultimately based on the condition found in living microbiotheriods such as *Dromiciops* which is similar, dentally and cranially, to Late Oligocene-Early Miocene *Microbiotherium* (Marshall, 1982; Segall, 1969 cited in Reig et al., 1987). I have therefore regarded a tail length of slightly less than head-body length as representative of the primitive condition.

The development of striated calcaneal pads (Ch. 65) is an extraordinary development confined to two New Guinea taxa. I have treated this condition as derived as also I have the condition of extremely long claws (Ch. 66) (seen in *Antechinus swainsonii* and *A. minimus*), longitudinal body stripes (Ch. 67) and brushed tails (Ch. 69). These subjectively polarised derivations are very rare within the study group and amount more to autapomorphies useful in describing the taxa in which they occur.

I have assigned polarities to pouch condition (Ch. 68) after the argument of Reig et al. (1987) who concluded that the presence of a pouch was the derived condition, and that pouch evolution occurred repeatedly within Didelphoidea. Small body size is regarded as the plesiomorphic condition (Ch. 70).

Penile morphology is difficult to polarise with confidence. Reig et al. (1987: 38) conclude on the basis of commonality and outgroup comparison with reptiles, monotremes and placentals that 'the bifid glans is thus considered the plesiomorphic condition in didelphimorphs and in marsupials as a whole'. Woolley (1987), however, concluded that the simple, non-bifid penises of *Dasyuroides byrnei*, *Dasycercus cristicauda* and *Dasykaluta rosamondae* suggested primitive anatomy. Reig et al. (1987; 38) cite Barbour (1977: 241) in suggesting that in *Didelphis marsupialis*, *Philander opposum*, *Marmosa mexicana* and *Caluromys derbianus* '... as in all other marsupials except the macropodids, *Tarsipes* and *Notoryctes*, the glans penis is cleft, bifid and divided ...', but much earlier, Woolley & Webb (1977: 309) had noted 'in others [marsupials] the tip is undivided, and either tapered or blunt' and later Woolley (1982) demonstrated non-bifid penis anatomy and accessory structures in a suite of species (*D. rosamondae*, *Pseudantechinus macdonnellensis*, *P. ningbing*, *Parantechinus bilarni* and *P. apicalis*). In looking for the plesiomorphic dasyurid condition I have (rightly or wrongly)

TABLE 6. Absolute measurements for *Murexechinus melanurus*. See 'Methods' for limits of measured dimensions and Table 1 (caption) for abbreviations.

Measurement		N	mean±r	OR	SD	V	CV
BL	M	41	27.30±0.43	22.93-36.83	2.72	7.38	9.96
	F	22	25.99±0.41	22.23-30.12	1.94	3.77	7.46
	T	64	26.83±0.32	22.23-36.83	2.53	6.41	9.43
ZW	M	42	17.16±0.25	14.58-21.83	1.61	2.58	9.38
	F	20	16.34±0.31	13.81-18.55	1.37	1.86	8.38
	T	63	16.89±0.20	13.81-21.83	1.57	2.46	9.30
IOW	M	43	7.09±0.04	6.51-8.14	0.28	0.08	3.95
	F	21	7.06±0.07	6.50-7.67	0.32	0.10	4.53
	T	65	7.09±0.04	6.50-8.14	0.30	0.09	4.23
OBW	M	40	11.05±0.11	10.26-13.73	0.71	0.50	6.43
	F	19	10.86±0.16	9.92-12.02	0.69	0.48	6.35
	T	60	10.99±0.09	9.92-13.73	0.70	0.49	6.37
IBW	M	41	5.11±0.10	4.23-7.15	0.63	0.39	12.33
	F	19	5.13±0.14	4.30-6.25	0.60	0.36	11.70
	T	61	5.12±0.08	4.23-7.15	0.61	0.38	11.91
R-LC^1	M	43	5.53±0.09	4.93-7.80	0.60	0.36	10.85
	F	22	5.24±0.11	4.40-6.28	0.53	0.29	10.10
	T	66	5.43±0.07	4.40-7.80	0.59	0.35	10.87
R-LM^1	M	43	9.80±0.11	8.97-12.69	0.73	0.53	7.45
	F	22	9.53±0.19	8.35-11.17	0.87	0.75	9.13
	T	66	9.71±0.10	8.35-12.69	0.78	0.61	8.03
R-LM^2	M	34	11.96±0.16	10.78-15.62	0.96	0.91	8.03
	F	16	11.83±0.26	10.09-13.66	1.05	1.10	8.88
	T	51	11.91±0.14	10.09-15.62	0.98	0.96	8.23
R-LM^3	M	39	14.26±0.11	12.73-18.50	1.20	1.44	8.42
	F	18	13.87±0.24	12.03-15.78	1.03	1.05	7.43
	T	58	14.12±0.15	12.03-18.50	1.16	1.34	8.22
R-LM^{1}T	M	42	7.72±0.10	6.97-10.42	0.68	0.47	8.81
	F	19	7.65±0.12	6.83-8.85	0.54	0.29	7.06
	T	62	7.69±0.08	6.83-10.42	0.64	0.41	8.32
I^1-M^4	M	43	15.06±0.20	13.85-20.04	1.32	1.74	8.76
	F	22	14.55±0.23	13.17-16.81	1.10	1.20	7.56
	T	66	14.88±0.16	13.17-20.04	1.26	1.60	8.47
P$^{1-3}$	M	43	3.39±0.05	2.95-4.70	0.33	0.11	9.73
	F	22	3.34±-.08	2.90-4.09	0.37	0.13	11.08
	T	66	3.37±0.04	2.90-4.70	0.34	0.12	10.09
M$^{1-4}$	M	43	6.81±0.08	6.29-8.67	0.51	0.26	7.49
	F	22	6.72±0.09	6.20-7.49	0.40	0.16	5.95
	T	66	6.78±0.06	6.20-8.67	0.47	0.22	6.93
M^{2}W	M	44	1.90±0.06	1.75-2.41	0.41	0.02	21.58
	F	22	1.89±0.03	1.70-2.15	0.15	0.02	7.94
	T	67	1.89±0.02	1.70-2.41	0.15	0.02	7.94
Dent	M	44	21.63±0.32	18.55-29.40	2.11	4.45	9.75
	F	22	20.69±0.36	17.55-24.53	1.69	2.86	8.17
	T	66	21.31±0.25	17.55-29.40	2.01	4.05	9.43
I$_1$-M$_4$	M	44	13.14±0.17	12.10-17.62	1.15	1.33	8.75
	F	21	12.62±0.19	11.41-14.38	0.85	0.71	6.74
	T	66	12.96±0.13	11.41-17.62	1.09	1.18	8.41
P$_{1-3}$	M	44	3.47±0.06	2.97-4.80	0.37	0.14	10.66
	F	22	3.41±0.06	3.00-4.08	0.30	0.09	8.80
	T	67	3.45±0.04	2.97-4.80	0.35	0.12	10.14
M$_{1-4}$	M	44	7.42±0.09	6.67-9.65	0.63	0.39	8.49
	F	22	7.30±0.12	6.50-8.40	0.54	0.29	7.40
	T	67	7.37±0.07	6.50-9.65	0.60	0.01	8.14
M$_2$W	M	44	1.23±0.02	1.07-1.61	0.11	0.01	8.94
	F	22	1.20±0.02	1.05-1.37	0.09	0.01	7.50
	T	67	1.22±0.01	1.05-1.61	0.10	0.01	8.20
TL	M	16	256±8.50	192-330	34	1171	13.28
	F	9	230±4.67	205-248	14	209	6.09
	T	25	247±6.20	192-330	31	981	12.55
T	M	31	135±2.87	101-165	16	271	11.85
	F	18	130±2.36	110-143	10	106	7.69
	T	49	133±2.00	101-165	14	216	10.53
HF	M	30	22.55±0.47	16-31	2.55	6.49	11.31
	F	18	21.44±0.34	19-23.5	1.46	2.14	6.81
	T	48	22.27±0.31	19-31	2.12	4.48	9.52
E	M	25	15.92±0.20	15-18	1.01	1.01	6.34
	F	13	15.65±0.27	14-18	0.97	0.97	6.20
	T	38	15.83±0.16	14-18	1.00	1.00	6.32
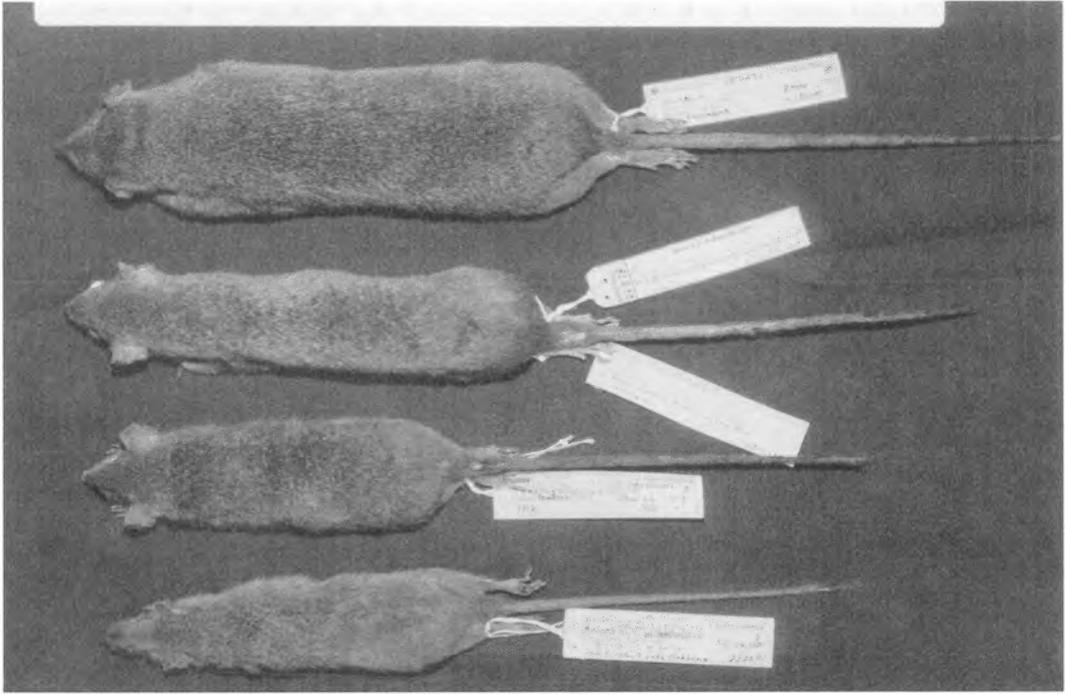
FIG. 43. Size and colour variation in *Murexechinus melanurus*. From the top AMNH 159473 Mt Pabinama, Normanby I. (m); AMNH 221628 Geelvink Bay, Oransbari (m); AMNH 108559 Itiki (m), AMNH 109828 Bele R. 18km N Lake Habbema (f).

assigned the simplest condition (the urethra terminating at the end of a simple non-bifid glans as in *D. rosamondae)* as the plesiomorphic condition; other forms of the penis (bifid glans, deeply cleft and divided penis, acquisition of corpora cavernosa and/or a penile appendage) are considered derivations.

Semelparity (Ch. 72) is treated here as a derived condition (Strategy 1 of Lee et al., 1982) on the arguments of Braithwaite (1973) and Lee & Cockburn (1985). Polarity assignment to nipple number (Ch. 73) can only be made subjectively, but for dasyurids, the plesiomorphic nipple number should correlate with the plesiomorphic reproductive strategy and not that of Strategy 1 species (monoestrous or facultative monoestrous taxa confined to predictable, highly seasonal geographic regions and dominated by 'pouches' with high nipple numbers). This is a departure from the argument of Reig et al. (1987) who consider that for didelphoids (which are polyoestrous, polytocous and seasonal breeders (Lee & Cockburn, 1985) frequently sporting a high and variable number of nipples (4-27) in

both abdominal and inguinal concentrations), fewer than nine nipples represents the derived state. Instead I would suggest that for primitive dasyurids lower nipple number represented by the Strategy IV-VI species (polyoestrous, breeding all year round) most closely expresses the primitive condition. This decision is also partly influenced by the nipple condition found in *Dromiciops*, which is four (Mann, 1958 cited in Reig et al., 1987).

PHYLOGENETIC ANALYSIS. The distribution of character states used to help resolve the affinities of *Antechinus* and *Murexia* is presented in Table 7. The first 37 characters relate to the upper dentition (15 features of the upper incisors, 5 of the upper canines, 5 of the upper premolars) while the following 17 relate to the lower dentition (2 for lower incisors, 9 for lower premolars, 6 for lower molars). Eight cranial characters were scored along with 11 external features. Character 73 relates to post-mating mortality in males. The transition series is not completely comprehensive and includes some characters whose polarities have

been determined by subjective criteria, but at the least, the characters used are compatible with earlier studies thereby enabling comparison of the results of analysis.

The phylogenetic analysis associated with this study was aimed primarily at resolving the affinities of the New Guinea taxa with Australian *Antechinus*. The distribution of character states for 73 characters (Table 7) among 33 taxa (with the addition of a hypothetical ancestor) is listed in Table 8. The analyses were run with characters unweighted and unordered (although successive weighting and ordered runs produced basically the same results). Ordered (unweighted) analysis produced one most parsimonious tree. Unordered (unweighted) analysis produced 15 trees of length 511, Consistency Index (Kluge & Farris, 1969) 0.46, and Retention Index (Farris, 1989) 0.69. The analysis was repeated using PAUP with 10 random addition sequences with identical results. The strict concensus of the most parsimonious trees (Fig. 44) shows (among other things) that the relationships between *M. habbema*, *M. longicaudata* and *P. naso* cannot be satisfactorily resolved. Synapomorphic character changes defining major clades are as follows: Dasyuridae, node 54: 8 (0>1), 14 (0>1), 31 (0>1), 46 (0>1), 51 (0>1); 54 (0>1); Australian taxa, node 51: 26 (0>1), 27 (0>1), 30 (0>1), 37 (0>1), 56 (2>3); the Planigalinae, node 50: 60 (2>3), 68 (1>2), 73 (3>4); the Phascogalinae, node 42: 71 (0>1); *Phascogale* node 34:8 (4>5), 11 (3>4); the Dasyurinae, node 47:53 (0>1); the Sminth-opsinae, node 49:26 (1>2), 62 (0>1).

The *Antechinus* clade of Fig. 44 is defined, at node 42, by Character 71 (penis with a bifid tip); node 40 (the *A. swainsonii-A. minimus* clade) by Character 66 (claws very long); node 39 is defined by Characters 17 (C^1 root and crown clearly differentiated and 73 (nipple number high and variable). Nodes 41, 36 and 38 are not defined by synapomorphies but described by a series of homoplasious forward changes. Node 37 is described by Character 8 (I^{2-4} crowns broader than roots), and node 35, the root of the *A. adustus*, *Phascogale* clade, is defined by 4 synapomorphies, Characters 2 (markedly procumbent incisors, 3 (I^1 crown much heavier than root), 12 (I^{1-4} heavily cingulated) and 15 (I^2 greatly enlarged). *Phascogale* (node 34) is defined by synapomorphies of Characters 8 (I^{2-4} crowns much heavier than roots) and 11 ($I^2>I^3>I^4$).

The morphological comparisons presented here suggest that the New Guinea taxa *M.*

habbema, *M. longicaudata*, *P. naso*, *P. rothschildi* and *M. melanurus* represent a suite of related but morphologically primitive taxa that lack clear signs of close relationship to each other but which have minor autapomorphies to serve to distinguish them from oneanother. They are largely plesiomorphic in their teeth and skulls relative to Australian *Antechinus* and other dasyurid genera. *Micromurexia*, *Phascomurexia* and *Murexia* are the most plesiomorphic and recognised by their common possession of the following: a spur or peg-like I^1 with its crown extremely high; I^{2-4} with narrow crowns and unfolded cusps; $I^4>I^3>=I^2$; long, fine, needle-like C^1; an uncrowded upper premolar row where P^3 does not possess a posterior cusp; broad upper molars with complete anterior cingula; M^1 whose anterior margin is convex or straight; broad protocone on M^{1-3}; $M^{1,2}$ with stylar cusp D a low crest; slight indentation on the $M^{2,3}$ ectoloph; $I_{1,2}$ almost perpendicular; P_3 larger than, or slightly smaller than P_2; uncrushed premolar row and uncingulated P_3; well developed M_1 paraconid; M_4 talonid with 3 cusps; large entoconids; elongate rostrum with fluted nasals and domed skulls; poorly developed tympanic wings of the alisphenoid; simple penis morphology; rudimentary pouch and low nipple number (4).

Each, however possesses characters that might be considered more derived than the others. *M. habbema*, for example, has slightly cingulated I^{1-4}, upper premolars that are more rounded in occlusal view, $P_{1,2}$ that show postero-lingual lobing and a skull that is slightly less elongate. *M. longicaudata* has widely spaced upper first incisors, a more reduced M^4 protocone, heavier cingulation on P_3, M_4 talonid on which the 3 cusps are much more reduced and hind foot pads more strongly and extensively developed. *P. naso* has markedly procumbent I^1 which is slightly more bulky and less needle-like than that seen in *M. habbema* and *M. longicaudata*. Its canines are shorter and thicker with root and crown becoming more differentiated, M^4 protocone is reduced as are the 3 cusps on M_4, and it often has a white-tipped tail.

P. rothschildi is clearly more derived than either *M. habbema* or *P. naso* and shares no specially close relationship with *M. longicaudata*. Although possessing the following primitive features: M^1 very broad, with a wide protocone and complete anterior cingulum, the anterior margin of this tooth being straight or anteriorly convex, but not indented or concave; a slightly cingulated upper incisor row where

$I^2 < I^3 < I^4$; I^4 without a posterior cusp; M^1 and M^2 stylar cusp D a relatively low crest rather than a tall cone, skull elongate and domed; fluted nasals; poorly developed tympanic wing of the alisphenoid with contrasting expansion of the pars mastoidea and adjacent squamosal, the following represent derivations on that plesiomorphic frame: I^1 lightly built but curved (more claw-like) and slightly laterally compressed with heavier crown than *Micromurexia*, *Murexia* or *Phascomurexia*; I^1 and I^2 widely separated; upper canines long, thin (but bulkier and shorter than in *Micromurexia*, *Paramurexia* and *Murexia*), the root and crown being more differentiated than in any of those genera; an upper premolar row in which P^3 usually touches P^2 and M^1; P^1 are P^2 are rounded and show postero-lingual lobing; M^1 and M^2 stylar cusp B large (slightly smaller than stylar cusp D in M^1, subequal in M^2); M^4 metacone reduced more than in *Micromurexia*, *Paramurexia* and *Murexia*; a lower premolar row in which the more rounded teeth are slightly crushed, and where P_3 is smaller than P_2, cingulated P_3; paraconid on M_1 more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; three very poorly developed cusps on the M_4 talonid; entoconid of M_2 more reduced than in *Micromurexia*, *Paramurexia* and *Murexia*; long postmetarsal pad and large heel pad on hind foot.

M. melanurus is the most derived member of the New Guinea taxa discussed here and it shares a closer relationship with Australian dasyurids than other New Guinea taxa. Superficially, *M. melanurus* is remarkably antechinus-like. Although, like other New Guinea taxa it possesses a very broad M1 with a wide protocone and complete anterior cingulum with a straight or convex anterior margin, an I^4 without a posterior cusp, a relatively unreduced M^1 stylar cusp B, I_1 relatively perpendicular to the line of the dentary, an elongate and domed skull, poorly developed tympanic wing of the alisphenoid with expanded pars mastoidea and adjacent squamosal, the following represent major derivations seen commonly in the Dasyuridae: I^1 broad, claw-like and heavily crowned; I^{2-4} strongly cingulated buccally and lingually, blade-like and robust; $I^2 = I^3 = I^4$; $C^1/_1$ short and thick; upper premolar row short, with premolars crowded, wide and robust; P^1 and P^2 in close contact; M^2 and M^3 with a more heavily indented ectoloph; lower premolars almost circular in occlusal view; lower molars

with weak entoconids and nasals flat rather than raised and fluted.

Externally, *M. melanurus* shares pelage colouration often found in Australian taxa, with rich rufous to light fawn post auricular patches and a definite change in colour from head to rump (usually agouti changing to warm russet) rather than uniform colour.

With respect to the Australian *Antechinus*, there is little doubt about the plesiomorphic nature of *A. godmani*, however my early contention (Van Dyck 1982a) that *A. godmani* was more closely related to New Guinea 'antechinuses' (in particular *A. mayeri* [= *P. naso*]) than it was to Australian antechinuses, is clearly wrong, that opinion being based on a comparison of too few New Guinean specimens and an embarrassingly rich suite of symplesiomorphies. The impression of the primitiveness of *A. godmani*, however, remains, with its relatively poorly developed upper incisors with their broad roots and slight cingulation, the incisor 'gradient' $I^4 = I^3 = I^2$, needle-like upper canines, narrow uncrowded upper and lower premolar row, relatively low stylar cusp D of $M^{1,2}$, slight metacone of M^4 and less reduction in the M_4 talonid.

These features are highly refined in the sister pair *A. swainsonii* and *A. minimus*. While they retain those primitive features found in *A. godmani*, there is great specialisation of the upper incisors (I^1 being laterally compressed and spade-like with no diastema between I^1 and I^2, I^{2-4} are lenticular), upper premolars (lensate, P^3 with pronounced cusp), upper molars (stylar cusp D of $M^{1,2}$ tall and conical), lower incisors (almost prostrate in *A. swainsonii*, slightly more erect in *A. minimus*) and lower premolars (widely spaced, lenticular). The tail is relatively shorter than in other antechinuses and the claws are longer. Given the high degree of derivation in these two species I favour the suggestion that *A. swainsonii* and *A. minimus* are sister species to *A. godmani*. (Having said that, I admit to a suspicion that we simply do not know with any real confidence whether the features seen in *A. swainsonii* and *A. minimus* are highly derived on an *A. godmani* frame, or the features seen in *A. godmani* are derivations on a primitive *A. swainsonii*/*A. minimus* frame.)

Antechinuses more derived than the *A. godmani*/*A. swainsonii*/*A. minimus* group display more typical dasyurid derivations such as a sharp incisor gradient ($I^2 > I^3 > I^4$); I^{1-4} heavily

cingulated; bulky, non needle-like C^1 with root and crown clearly differentiated and a small cusp present; a more rounded P^1, a greatly reduced M^4 metacone; slightly crushed lower premolars; a broad P_3 and a less elongate skull,

The *A. flavipes* group (as per Baverstock et al. (1982)), consists of *A. leo* and *A. bellus* as sister species to *A. flavipes*. There has been little confusion with the identity of *bellus* in the past. Such features as its pale grey pelage, narrow interorbital width, broad zygomata, broad rostral width, narrow upper incisors, relatively short canine, lack of posterior nasal expansion and expanded alisphenoid bullae have always served to make its identity clear. The identity of *leo*, however (in spite of its more club-shaped and widely separate L and RI^1, relatively massive upper canines, very bulbous, crushed upper premolars and greatly reduced M^4 talonid), has long been masked by *flavipes* with which it has consistently been confused. Nonetheless, on the wider scale, the *bellus*/*leo* relationship is defined by very broad I^{2-4} crowns, and the two species share pronounced lingual lobing on $P^{1,2}$; a large posterior cusp on P^3, absence of a posterior cingulum on M^x and simple supratragus of the ear.

A. adustus, *Phascogale tapoatafa* and *calura* share very procumbent, heavily crowned I^1, heavily cingulated I^{1-4} and an enlarged I^2, a suite of derived features which, along with a shared reproductive strategy (see Lee & Cockburn, 1985) supports the notion that phascogales might simply be highly derived antechinuses.

There is no doubt that the morphological comparison of New Guinea taxa presented in this study result in a phylogeny vastly different to those generated by recent genetic studies (e.g., Kirsch et al., 1990, Krajewski et al., 1993, Krajewski et al., 1994, Retief 1995, Krajewski et al., 1996, Krajewski et al., 1997, Armstrong et al., 1998). There is, however, some congruence between the morphology-based phylogeny of this work and that resulting from albumin immunology (Baverstock et al., 1990), particularly with respect to relationship between *Antechinus*, *Phascogale* and *Murexia*.

It is difficult to interpret these differences. The recommendation to reassign New Guinea 'antechinuses' to *Murexia* (Krajewski et al., 1996) was based on the resolution of the 'murexia' clade (*rothschildi*, *longicaudata*, *naso*, *melanurus*, *habbema*) achieved through analysis of cytochrome *b* sequences using *Planigale*

ingrami as its outgroup. The choice of *Planigale* as an outgroup might be criticised as inappropriate given its inclusion in the Dasyuridae. Morphology-based analysis selecting from Table 8 the same taxa as Krajewski et al. (1996) (*P. calura*, *P. tapoatafa*, *M. rothschildi*, *M. longicaudata*, *A. naso*, *A. melanurus*, *A. habbema*, *A. flavipes*, *A. swainsonii*, *A. stuartii*) and employing *Planigale* as the outgroup, results in a similar monophyletic New Guinea clade (*M. rothschildi*, *M. longicaudata*, *A. naso*, *A. melanurus*, *A. habbema*) but it is defined by 7 reversals (Characters 27, 29, 30, 37, 51, 60, 73), with 6 homoplasious reversals and 3 homoplasious forwards steps. (The node underpinning the Australian and New Guinean taxa is similarly defined by 14 reversals (Characters 11, 13, 31, 39, 40, 44, 48, 50, 51, 52, 55, 60, 68, 73) with 4 homoplasious reversals.

Armstrong et al. (1998) echoed the Krajewski et al. (1996) suggestion to reassign the New Guinea antechinuses to *Murexia* on the basis of their phylogeny of antechinuses and murexias drawn from cytochrome-*b*, 12S-rRNA, protamine-P1 genes. The same criticism of invalid outgroup choice could apply, however, to their use of *Phascogale*. A morphology-based phylogeny of similar topology to Armstrong et al. (1998) is produced using taxa from Table 8 and employing *Phascogale* as the outgroup. The New Guinea clade (*M. rothschildi*, *M. longicaudata*, *A. naso*, *A. melanurus*, *A. habbema*) however, is defined by one synapomorphy (Character 58) and 9 reversals (Characters 27, 29, 30, 37, 50, 60, 71, 72, 73), with 1 homoplasious reversals and 3 homoplasious forwards step. (The node underpinning Australian and New Guinean taxa is defined by 1 synapomorphy (Character 5), 14 reversals (Characters 2, 3, 6, 8, 10, 11, 15, 32, 33, 39, 40, 52, 57, 69) and 4 homoplasious reversals.

If the fossil record and outgroup comparisons can be trusted to correctly polarise characters for the dasyurid ancestor, rooting the tree on a derived member of the dasyuridae can reverse polarity of the tree, forcing plesiomorphic taxa into clades based on their most derived members with subsequent branches being occupied by progressively more primitive taxa. Then, of course the nodes are defined by reversals.

Subsequent genetic studies, however, using non-dasyurid outgroups (*Myrmecobius*, Krajewski et al., 1993; *Peroryctes*, Kirsch et al., 1990; *Homo*, *Mus*, *Ornithorhynchus*, Krajewski
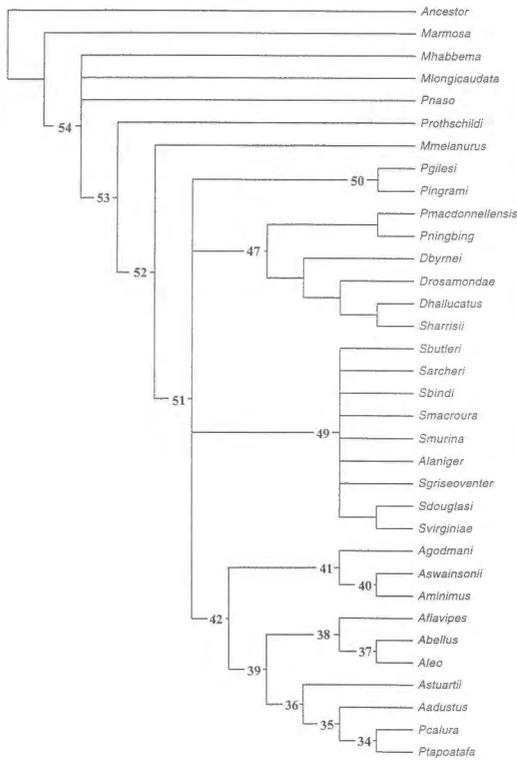
FIG. 44. Strict concensus of 15 most parsimonious trees generated by PAUP and Hennig '86.

et al., 1997) have supported the monophyly of the New Guinea 'murexias' and the dissociation of *Phascogale* from the Australian *Antechinus* clade. Manual production of a monophyly in the New Guinea taxa from Fig. 44 takes a minimum of an extra 15 steps, which is roughly equivalent to embedding *A. godmani* in the Sminthopsinae as the sister species of *A. laniger*. When such an artificial monophyly is achieved in the New Guinea taxa, the PNG clade is no longer defined by synapomorphies.

In contrast to the morphological picture, genetic phylogenies would suggest New Guinea 'murexias' have undergone massive and successive reversals and losses, and that *Phascogale* and *Antechinus* have accrued derived states in parallel. They might also suggest that incorrect polarities have resulted from the palaeontological and outgroup comparisons. Phascogalines and 'murexias' might share a similar base-composition that, in phylogenetic analyses of sequences or DNA hybridisation distances, causes their branches to attract oneanother. One thing is clear, that regardless of whether the New Guinea 'murexias' form a molophyletic group or not, genetic analyses have yet to give a united resolution of relationships *within* the 'murexia' group. While aspects of morphology discussed in this paper do not provide strong evidence for phylogenetic relationships between the most plesiomorphic New Guinea taxa (*M. habbema*, *P. naso* and *M. longicaudata*), they do indicate the following: a gulf between the New Guinea 'murexias' and Australian *Antechinus*; distant relationships between *M. longicaudata* and *P. rothschildi*; distant relationships between *M. melanurus* and *habbema/naso*; and the more derived nature of *rothschildi* and *melanurus* relative to the others. I consider these reasons sufficient to warrant the revision at the generic levels I have proposed here. The putative relationship between *Phascogale* with *Murexia* as revealed by genetic studies, however, will continue to constitute one of the most bitter pills for dasyurid morphologists to swallow.

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TABLE 7. Character states (defined in derived state) used to resolve affinities of *Murexia* and *Antechinus*.

UPPER INCISORS: **1**. Incisor row transverse. 0 = V or U-shaped; 1 = transverse.

2. Incisors procumbent. 0 = not procumbent; 1 = slightly procumbent; 2 = more than 1; 3 = procumbent.

3. I^1 crown relatively bulky with cingulum low. 0 = crown of I1 a thin spur; 1 = more bulky than 0; 2 = bulkier than 1; 3 = bulkier than 2; 4 = bulkier than 3; 5 = bulkier than 4; 6 = crown heavy.

4. I^1 laterally compressed, elongate. 0 = I^1 needle or peg-like; 1 = more compressed than 0; 2 = more compressed than 1; 3 = pade-like.

5. R and L I^1 separated by wide diastema. 0 = touching; 1 = narrowly spaced; 2 = widely spaced.

6. I^1 non-needle-like. 0 = I^1 needle-like; 1 = less needle-like than 0; 2= less needle-like than 1; 3 = less needle-like than 2; 4 = less needle-like than 3; 5 = less needle-like than 4; 6 = spatulate or club-shaped.

7. I^1 and I^2 juxtaposed. 0 = I^1 and I^2 widely spaced; 1 = spacing less than 0; 2 = spacing less than 1; 3 = spacing less than 2; 4 = spacing less than 3; 5 = crushed.

8. I^{2-4} crowns broader than roots. 0 = crown-root width equal; 1 = crown slightly broader; 2 = broader than 1; 3 = broader than 2; 4 = broader than 3; 5 = crown much broader than root.

9. I^{2-4} lensate, elongate. 0 = I^{2-4} peg-like; 1 = more elongate than 0; 2 = more than 1; 3 = more than 2; 4 = lensate.

10. I^{2-4} crowns broad (occlusal) and cusps folded lingually. 0 = crowns narrow and cusps unfolded; 1 = crowns broader and slightly folded; 2 = more than 1; 3 = more than 2; 4 = crowns broad and folded.

11. $I^2 >= I^3 > I^4$. 0 = $I^4 > I^3 >= I^2$; 1 = $I^4 = I^3 = I^2$; 2 = $I^2 >= I^3 > I^4$; 3 = $I^2 > I^3 > I^4$; 4 = $I^2 > I^3 > I^4$.

12. I^{1-4} cingulated. 0 = no cingulation; 1 = slight cingulation; 2 = more than 1; 3 = more than 2; 4 = heavily cingulated.

13. I^4 with posterior cusp. 0 = No posterior cusp; 1 = posterior cusp present.

14. Total upper incisors = 8. 0 = 10; 1 = 8.

15. I^2 greatly enlarged. 0 = no; 1 = yes.

UPPER CANINES: **16**. C^1 relatively short. 0 = very long; 1 = shorter than 0; 2 = shorter than 1; 3 = short.

17. C^1 root and crown clearly differentiated. 0 = no differentiation 1 = differentiated; 2 = more than 1; 3 = more than 2.

18. C^1 bulky, non needle-like. 0 = needle-like; 1 = less than 0; 2 = less than 1; 3 = less than 2; 4 = cone-shaped.

19. C^1 non-caniniform. 0 = caniniform; 1 = less than 0; 2 = premolariform.

20. C^1 with posterior cusp. 0 = cusp absent; 1 = small cusp present.

UPPER PREMOLARS: **21**. P^1 circular in occlusal view. 0 = elongate; 1 = More rounded than 0; 2 = more rounded than 1; 3 = more rounded than 2.

22. P^1 and P^2 touching or crushed. 0 = wide space between P^1 and P^2; 1 = small space between P^1 and P^2; 2 = P^1 and P^2 touch or crushed.

23. P^1 and P^2 with postero-lingual lobing. 0 = no lobing; 1 = slight lobing; 2 = pronounced lobing; 3 = very pronounced lobing.

24. P^3 with large posterior cusp. 0 = no cusp; 1 = slight cusp; 2 = pronounced cusp.

25. P^3 greatly reduced or lost. 0 = no; 1 = yes.

UPPER MOLARS: **26**. M^{1-3} narrow with incomplete anterior cingulum. 0 = M^{1-3} broad, cingulum complete; 1 = narrow, cingulum incomplete or nearly so; 2 = narrow, cingulum; incomplete, molars very narrow.

27. M^1 anterior margin (protocone to stylar cusp A) indented or concave. 0 = convex or straight; 1 = indented or concave.

28. M^2 shorter than M^3. 0 = no, $M^2 => M^3$; 1 = yes.

29. M^{2-4} protocone width greatly reduced. 0 = protocone broad; 1 = protocone narrower than 0; 2 = narrower than 1; 3 = narrower than 2.

30. M^1 stylar cusp B greatly reduced. 0 = no reduction, almost coplanar with D; 1 = reduced; 2 = greatly reduced.

31. M^4 protocone reduced. 0 = protocone large; 1 = protocone slightly reduced; 2 = reduction greater than 1; 3 = reduction greater than 2; 4 = reduction greater than 3; 5 = reduction greater than 4; 6 = reduction greater than 5; 7 = reduction greater than 6.

32. M^4 preparacrista orients obliquely to longitudinal axis of skull. 0 = orientation transverse to longitudinal; 1 = slightly oblique; 2 = oblique.

33. M^1, M^2 stylar cusp D greatly enlarged. 0 = stylar cusp D a low crest; 1 = taller than 0; 2 = taller than 1; 3 = stylar cusp D tall and conical.

34. M^2, M^3 ectoloph greatly indented. 0 = no; 1 = slight indent; 2 = more than 1; 3 = greatly indented.

35. M^4 metacone loss. 0 = metacone small; 1 = metacone more reduced than 0; 2 = more than 1; 3 = more than 2; 4 = metacone lost.

36. M^x posterior cingulum absent. 0 = present; 1 = absent.

37. M^1 paracone and stylar cusp B fused. 0 = no, widely separated; 1 = approximated; 2 = greater approximation than 1; 3 = fused.

TABLE 7 (*Cont.*).

LOWER INCISORS: **38**. I_1, I_2 prostrate. *0* = I_1, I_2 almost perpendicular to dentary axis. *1* = more prostrate than 0; *2* = almost horizontal.

39. I_3 heel narrower than than heel of I_1. *0* = I_3 heel wider than heel of I_1 heel; *1* = heels equal width; *2* = I_3 heel slightly narrower; *3* = narrower than 2; *4* = narrower than 3.

LOWER PREMOLARS: **40**. $P_3 < P_2$. *0* = $P_3 > P_2$; *1* = $P_3 <= P_2$; *2* = $P_3 < P_2$.

41. Lower premolars crushed. *0* = premolars widely spaced; *1* = nearly touching; *2* = slightly crushed; *3* = more than 2; *4* = more than 3.

42. P_1, P_2 in contact. *0* = widely spaced; *1* = just contacting; *2* = crushed.

43. P_3 broad or oriented transversely. *0* = P_3 longitudinal with dentary axis; *1* = broad; *2* = transverse to dentary axis.

44. P_{1-3} almost circular in occlusal view. *0* = premolars elongate; *1* = premolars oval; *2* = premolars almost round.

45. P_2, or P_3 lenticular. *0* = not lenticular; *1* = very narrow; *2* = lenticular.

46. P_3 cingulated. *0* = not cingulated (or P_3 absent); *1* = cingulated.

47. P_1, P_2 with posterio-lingual lobing. *0* = no lobing; *1* = slight lobing; *2* = heavily lobed.

48. P_3 single-rooted or absent. *0* = neither; *1* = yes, single-rooted or absent.

LOWER MOLARS: **49**. M_1 paraconid reduced. *0* = paraconid well developed; *1* = paraconid more reduced than 0; *2* = paraconid more reduced than 1.

50. M_3 talonid much narrower than trigonid. *0* = no; *1* = yes.

51. M_4 talonid with reduced cusp. *0* = 3 cusps, well developed; *1* = 3 cusps, poorly developed; *2* = 2 cusps; *3* = 1 cusp; *4* = loss of talonid.

52. M_2 entoconid reduced. *0* = entoconid tall; *1* = reduced; *2* = greatly reduced; *3* = absent.

53. M_1 paraconid absent. *0* = present; *1* = absent.

54. M_{1-3} metacristids and hypocristids not transverse to long axis of dentary. *0* = transverse; *1* = not transverse.

CRANIAL FEATURES: **55**. Skull brachycephalic (ratio skull width between lachrymal canals to length I_1-lachrymal canal). *0* = elongate (67-75%); *1* = less elongate than 0 (76-84%); *2* = less elongate than 1 (85-93%); *3* = less elongate than 2 (94-102%); *4* = skull brachycephalic (103-111%).

56. Nasals non-fluted. *0* = fluted; *1* = less fluted than 0; *2* = less fluted than 1; *3* = flat.

57. Tympanic wing of the alisphenoid greatly expanded. *0* = tympanic wing small; *1* = tympanic wing greatly expanded.

58. Expansion of the pars mastoidea and adjacent squamosal. *0* = no expansion; *1* = expansion.

59. Nasals expanded posteriorly. *0* = not expanded; *1* = expanded.

60. Skull flat, not domed. *0* = domed; *1* = less than 0; *2* = flat or concave; *3* = dorso-ventrally flattened.

61. Squamosal-frontal contact. *0* = no; *1* = yes.

62. Palatine vacuities. *0* = not present; *1* = present.

EXTERNAL FEATURES: **63**. Supratragus folded. *0* = simple; *1* = folded.

64. Tail very short or very long. *0* = slightly shorter than head-body; *1* = much shorter or much longer than head-body.

65. Hind foot pads highly developed and striated post-metatarsal pads present. *0* = no; *1* = yes: *2* = well developed.

66. Claws very long. *0* = no; *1* = yes.

67. Body with longitudinal stripe. *0* = no; *1* = yes.

68. Backward-opening pouch. *0* = no, rudimentary; *1* = pouch; *2* = yes, backward-opening.

69. Tail with terminal brush. *0* = no; *1* = yes.

70. Body size large. *0* = very small; *1* = larger than 0; *2* = larger than 1; *3* = large.

71. Penile morphology complex. *0* = simple, non-bifid glans; *1* = small bifurcation of glans; *2* = deeply cleft and divided penis; *3* = acquisition of accessory corpora cavernosa or penis appendage.

72. Males die soon after mating. *0* = no; *1* = yes.

73. Nipple number high and variable. *0* = 4; *1* = 6; *2* = 8; *3* = 10; *4* = 12; *5* = variable.

TABLE 8. Distribution of character states (defined in derived state) used to resolve affinities of *Murexia* and *Antechinus*.

Taxon	Character states
Ancestor	00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 00000 000
Marmosa sp.	00000 00000 00000 00000 00000 00100 00010 10001 00000 00000 00001 00000 00010 00001 205
M. habbema	01001 00110 01010 00000 10100 00000 11111 00001 00000 00000 00012 00100 00110 00001 000
M. longicaudata	01002 00110 00010 00000 00000 00000 21111 00000 00000 10001 10011 00000 00111 00002 000
P. naso	02100 10110 00010 11100 10000 00000 21111 00001 00000 10001 10011 00100 00110 00001 000
P. rothschildi	01202 20111 01010 11100 10110 00000 21112 00001 21110 10010 11012 10100 00112 01001 000
M. melanurus	01302 30202 12010 21200 11100 00000 21122 00001 21120 11010 11012 20100 00110 00001 000
A. bellus	02420 30432 22010 21200 21220 11011 41223 11121 32210 12010 22013 30001 00100 00001 113
A. leo	01412 40413 33010 12301 32220 11011 41221 11111 32210 12010 32012 20012 00100 00001 113
A. flavipes	02211 20332 33010 22201 21110 11011 42323 01011 32220 12010 32012 30012 00000 00001 115
A. adustus	03500 52313 34011 22311 22310 01011 32223 01301 31210 11010 21013 30012 00000 00001 111
A. stuartii	01320 31331 33010 22211 21110 01011 31313 01201 21110 11010 21012 30012 00000 00001 115
A. swainsonii	01430 53340 12010 21001 01020 01011 22311 01201 00002 10010 21011 30011 00010 10001 115
A. minimus	00421 42330 12010 21100 01020 11011 32221 11111 11001 10010 21011 30011 00010 10001 115
A. godmani	01221 20231 12010 21100 11120 11011 31121 11101 10010 11010 21011 30012 00100 00001 111
P. calura	03510 40513 44011 31211 11100 01011 32232 01142 21210 11021 22013 31011 00100 00011 112
P. tapoatafa	03600 62514 44011 22201 11210 01011 22222 01142 31120 12010 32013 31011 00100 00011 112
P. macdonnellensis	01012 00101 02010 21101 11101 11012 52232 1303- 22-10 11120 33113 31002 00101 00001 301
D. rosamondae	02001 00101 30010 00300 111-1 11011 52233 1203- 32-10 12120 33014 21111 00111 00001 001
D. byrnei	02002 00101 00010 00300 21101 11012 62223 1301- 11-10 10120 33113 21001 00100 01111 001
P. ningbing	01002 01100 01110 21001 01001 11022 62222 1203- 22-00 11120 33113 31002 00100 00001 301
D. hallucatus	01001 10000 01010 00000 101-1 11001 52211 1302- 00-00 10120 31112 20011 00100 00003 315
S. harrisii	10000 15001 00010 00400 323-1 11032 72414 1303- 42-30 03120 43114 10011 00110 00004 300
P. ingrami	01202 30211 23110 21210 31210 11011 72122 02142 11220 11111 33013 30113 10000 00200 004
P. gilesi	02202 30211 22110 21301 313-1 11022 62233 0324- 22-10 12111 33002 30113 00010 00200 004
S. douglasi	01111 20101 00010 11200 22110 21011 31323 11010 21010 11000 30003 30101 11100 00101 002
S. virginiae	01112 10121 00010 10100 11120 21021 40321 11000 10010 12010 30003 20101 11100 00101 005
S. butleri	00002 10100 01010 20100 11110 21021 31222 11010 11010 10001 33003 30101 11100 00101 002
S. archeri	00002 00100 00010 21101 10100 21021 41323 11011 10010 10001 33003 30101 11100 00101 005
S. bindi	00002 00100 00010 21110 11100 21021 41322 11011 21010 11001 32003 30101 11100 00101 002
S. macroura	00002 00110 00010 20110 11000 21021 30322 11001 21010 11000 31002 30101 11100 00101 001
S. murina	00100 00110 00010 20010 11110 21021 40322 11121 11010 10000 33001 30101 11100 00101 005
S. griseoventer	00111 00110 00010 21121 11010 21011 40322 11111 11000 10000 32001 30101 11100 00101 002
A. laniger	01212 30130 00010 33221 00010 21011 51222 11100 00001 00111 33002 31100 11110 00111 005

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