CLASSIFICATION PROBLEMS OF AFRICAN MURIDAE

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INTRODUCTION

In a paper presented at the first Symposium of this Society in 1961 on the distribution patterns in continental Africa of the species of Muridae occurring in southern Africa (Davis 1962), little was said about the procedures which were being followed in deciding which of the extralimital forms were conspecific, nor were the reasons for certain changes in nomenclature given in any detail. The purpose of the present paper is to outline the revisionary procedures and to establish the name changes.

In the past, mammal faunas of Africa have been studied on a regional basis and it is only in the last 20 years or so, stimulated by the principles developed by Rensch (1929), Huxley (1940), Mayr (1949, 1963) and others, that a beginning has been made by mammalogists working on African problems to try to allocate the many described forms to their correct species on a pan-African basis.

Thomas (1915, 1920 and 1926) contributed to a better understanding of African *Rattus* by allocating certain *Rattus*-like species to new genera and subgenera. In his treatment of African *Rattus*-like rats, Ellerman (1941) retained the genera *Aethomys* Thomas, *Rattus* Linnaeus and *Thallomys* Thomas, relegating *Dephomys* Thomas, *Hylomyscus* Thomas, *Mastomys* Thomas, *Micaelamys* Ellerman, *Myomys* Thomas, *Ochromys* Thomas, *Praomys* Thomas and *Stochomys* Thomas to subgenera of *Rattus*. His listings of the described forms by genus or subgenus paved the way for future revision on a pan-African basis at the species level. This task has been attempted by a number of subsequent workers who found, however, that there was still much to be done at the generic and subgeneric level (e.g. Lundholm 1955, Setzer 1956, Petter 1957, Ansell 1960). Suffice it to say that none of these authors was able to reach a satisfactory solution, though each made useful contributions towards one. Lundholm (1955), especially, discovered a number of cranial and dental characters of diagnostic importance which have been of the utmost value in reaching a clearer idea of the affinities, not only of southern African Murinae, but also of the species of the subfamily in the rest of Africa. He also discovered a character in the bulla to distinguish some members of South African Otomyinae (Lundholm in Davis 1962) which makes it possible to allot *Otomys* forms to one of two species-groups.

METHODS AND MATERIAL

The procedure has been to list the taxa in Allen's "Checklist of African mammals" (1939) according to provisional "species", together with other forms described since 1938, taking as a starting point Ellerman's contributions as well as such general revisions as those of

Bohmann (1942, 1952) on *Dendromus* and *Otomys*, Davis (1949) on *Tatera* etc. Checklists of "described forms" are arranged in order of priority with their type localities. A collection of original descriptions has been gradually built up, mostly photocopies, and these are arranged in order of priority under each species in a loose-leaf catalogue now consisting of 30 volumes. Distribution data from museum specimens, the literature and unpublished survey reports are indexed and mapped on the degree-square system (Davis 1958, de Meillon, Davis and Hardy 1961) and finally listed by degree-squares from north to south. These lists give exact locality, its co-ordinates to the nearest minute, the source of the record and the name applied by the author or museum. Thus amendments, alterations and adjustments can easily be made when new information comes to hand. Much time has been devoted to building up a cumulative gazetteer of type and collecting localities of African Mammalia. This has been built up from published gazetteers such as those of Chapin (1954) for the Congo (and other parts of Africa), Swynnerton & Hayman (1951) for Tanganyika and Setzer (1956) for the Sudan, supplemented by searching available maps. The gazetteers published for some African territories by the American Board on Geographic Names have been particularly useful.

Photomicrographs of molars and alveoli are taken on 35 mm. film and enlarged 10 times so that all are directly comparable and measurements can be taken from the photographs. The convention has been adopted of photographing the molars of the right upper and left lower, and the alveoli of the left upper and right lower, jaws. Features (e.g. bulla region, incisors etc.) are taken from the left side.

Preparation of specimens for examination

The teeth are removed from the jaws after 12–24 hours' soaking in water. Extreme care has to be exercised so as not to break the roots or damage the bone. If gentle rocking and traction fail to release the tooth the jaws are soaked again. If this fails, then another specimen is selected, rather than risk damage. When the teeth are out, the jaws are carefully cleaned of tissue and allowed to dry. The teeth are mounted, roots up in a row, using Glyptal cement (diluted with one or two parts Thinner), on to a strip of black paper and labelled. Owl pellet material needs no soaking as a rule and after mounting the teeth it is usually best to mount the remains on strips of paper after dipping in a dilute (1 : 3) Glyptal solution to keep them from disintegrating.

Alveolar-molar root notation

The alveolar-molar root formula (AMF) notation has been devised to indicate the number of alveoli (disregarding whether a division is visible below jaw level), the number of roots [in square brackets] and the number of rootlets, short or long. The rootlets are indicated by arabic numerals and if short or very short the figure is enclosed in round brackets. Thus AMF 5-4-3: 2[3]+ii—3[4]—3+(i) means that the upper molar series, M.$^{1\text{-}3}$/, has 5, 4 and 3 alveoli and the same number of roots; and the lower molar series has M./$\overline{1}$ with 2 alveoli but 3 roots, and 2 intermediate rootlets; M./$\overline{2}$ has 3 alveoli and 4 roots and M./$\overline{3}$ has 3 alveoli, 3 roots and one small rootlet. When a root is broad and obviously derived from two elements and with

some indication of a division into two it is recorded as 2-rooted. Since there is uniform intergradation between two completely fused roots and two with the tips separated or forked it is not always easy to decide whether to call a root 1- or 2-rooted. In some the shape of the alveolus suggests a double root, yet the root itself is not divided distally, though it is clear that it consists of two elements.

THE ALVEOLAR-MOLAR ROOT PATTERN IN GROUPING AFRICAN MURIDAE

For convenience the taxonomic arrangement adopted by Ellerman, Morrison-Scott and Hayman (1953) is followed, which divides the southern African Muridae into the subfamilies Murinae, Dendromurinae, Cricetinae, Otomyinae and Gerbillinae, even though the last four should now more properly be considered cricetids.

The subdivision of the Murinae into two main groups on the basis of the alveolar-molar root formula (AMF) is not, at this stage, discussed from the phylogenetic viewpoint, although much of interest may transpire (cf. Herold and Niethammer 1963, for the Gerbillinae). For the present it is a practical device for clarifying the affinities of a number of controversial genera, subgenera and species. Many of the external, cranial and dental characters employed in the past would lead to a somewhat similar grouping, but it has been found that the present simple approach gives additional information and lends some support to conclusions reached on other grounds, including chromosome studies (Matthey 1954, 1955, 1958, 1959, 1963).

For simplicity the two groups are referred to as the "complex" *Rattus*-type and the "simple" *Mus*-type. Reduced to its simplest form the division can be made on the root and alveolar pattern of the cheek teeth of the lower jaw alone as follows:—

First lower molar with at least 3 main roots; AMF of mandible of the form 2[3]+0 to iii,–3[4]–3 but often with more roots and/or rootlets . . . "Complex" *Rattus*-type (Plate II).

First lower molar with 2 main roots; AMF of the form 2–2–1/2 or 2–3–1/?2 . . . "Simple" *Mus*-type (Plates III–V). The results of the above grouping are given in Table I.

The salient points to notice in Table I are (1) *Grammomys* is placed as a synonym of *Thamnomys*, but is retained as a subgenus, (2) *Rattus sensu* Ellerman *et al.* (1953) is divided between the *Rattus*- and *Mus*-groups, (3) *Leggada* (op. cit.) is revived as a subgenus of *Mus* and (4) the remaining genera (and subgenera) are divided between the two groups without change of status, although further study may well show that there are reasonable grounds for making some changes.

THE GENERA *Aethomys*, *Thallomys* AND *Thamnomys*

(Plate I, fig. 7, Plate II, figs. 1–12)

The species of these genera are long-tailed, rock, arboreal or bush rats and are of medium to large size. They are often confused with each other. For example "*Thamnomys ruddi*" Thomas proved to be a *Thallomys* (Lawrence and Loveridge 1953). "*Mus*" *namaquensis* A. Smith has been variously placed in the genera *Aethomys*, *Praomys*, *Rattus* and *Thallomys*; it now

TABLE 1: CLASSIFICATION OF THE GENERA AND SUBGENERA OF AFRICAN MURINAE* ACCORDING TO THE ALVEOLAR-MOLAR ROOT FORMULA (AMF)

Former classification	Genera and subgenera (present classification) *Rattus*-type	*Mus*-type
Genera *Thamnomys* and *Grammomys sensu* Ellerman (1941)	*Thamnomys* (*Grammomys*)	—
Genus *Rattus sensu* Ellerman *et al.* (1953)§	*Aethomys* [*Micaelamys*, *Stochomys* (*Dephomys* a syn.)]	*Praomys* (*Hylomyscus*, *Mastomys*, *Myomyscus*†)
	Thallomys	*Zelotomys* (*Ochromys* a syn.)
Genus *Mus sensu* Ellerman *et al.* (1953)§	—	*Mus* (*Hylenomys*‡, *Leggada*)
Other genera and subgenera as in Ellerman (1941)	*Arvicanthis*	*Acomys*
	Dasymys	*Beamys*‡
	Hybomys	*Colomys*
	Lemniscomys	*Cricetomys*
	Mylomys	*Lophuromys*
	Oenomys	*Malacomys*
	Pelomys (*Desmomys*‡, *Komemys*‡	*Muriculus*‡
		Nilopegamys‡
		Saccostomus
		Stenocephalemys‡
		Uranomys

* The AMF of the subfamilies Cricetinae and Dendromurinae fall into the *Mus*-type group (*Deomys*, *Prionomys*, *Delanymys* not seen).

† In place of *Myomys*, type species "*Mus*" *colonus* Brants unidentifiable (Ellerman *et al.* 1953).

‡ Not examined.

§ *Rattus rattus* (Linnaeus), *R. norvegicus* (Berkenhout) and *Mus musculus* Linnaeus, being non-indigenous, were not dealt with in this work. Their status, of course, remains unchanged.

finds its place as *Aethomys* (*Micaelamys*) *namaquensis* along with *A.* (*M.*) *granti*. "*Mus granti*" Wroughton was described in 1908 as "probably" having a mammary formula of 3–2=10 and to be related to "*Mus colonus*" Brants on account of this number of mammae and other characters. Ellerman (1941) erected a new subgenus (*Micaelamys*) of *Rattus* for it and gave its mammary formula as 3–2=10. Lundholm (1955) pointed out its close relationship to *A. namaquensis* and that it had 6 mammae. On examining the Type series at the British Museum (Nat. Hist.) in 1958 I discovered that although two specimens (BM 2.9.1.84, 85) were labelled 3–2=10 the mammae could not be detected on the skins; two pairs of mammae, however, could be detected in the Type specimen (ser. no. 86). In the long series of this species in the Kaffrarian Museum several specimens bear a note in Shortridge's handwriting "pect. mammae more often than not absent or underdeveloped". The mammary formula is unquestionably 0–2=4 or 1–2=6, as in *A. namaquensis*, and not 3–2=10 as in the original description.

There has been uncertainty about the relationship between *Thamnomys* Thomas *sensu stricto* and *Grammomys* Thomas, largely on account of the degree of development of the postero-internal cusp (t.7) in the first and second upper molars. It is proposed to regard *Grammomys* as a subgenus of *Thamnomys* and to allocate all but *T. venustus* to *Grammomys* since no clear dividing line seems to exist dentally at least, between *T. cometes*, *T. dolichurus* and *T. rutilans*.

There appears to be more in common between *Thamnomys* and *Thallomys* than between either of them and *Aethomys*. However since their mode of life has something in common, and they are often confused with each other an attempt will be made to provide a key, based on cranial and dental characters as far as possible.

KEY TO *Aethomys*, *Thallomys* AND *Thamnomys*

1 Postero-internal cusp (t.7) in first and second upper molars as large as t.4 and t.1; t.9 reduced .. .. subgenus *Thamnomys*

Postero-internal cusp (t.7) smaller than t.4 and t.1, reduced to a connecting ridge between t.8 and t.4, or absent 2

2 Postero-internal cusp (t.7) absent; no trace of metastyle behind t.9; terminal heel smaller in M./$\overline{1}$ than in M./$\overline{2}$.. .. .. (genus *Aethomys*) 4

Postero-internal cusp (t.7) either present or represented by a short connecting ridge between t.8 and t.4; metastyle commonly present behind t.9; terminal heel about as well-developed in M./$\overline{1}$ as in M./$\overline{2}$ 3

3 Bullae relatively large, more than 6.0 mm.; accessory median cusp in L.1 of M./$\overline{1}$ absent .. .. *Thallomys*

Bullae smaller, less than 6.0 mm.; acc. med. cusp in L.1 of M./$\overline{1}$ present subgenus *Grammomys*

4 M.1/ four- or 5-rooted; with two strong medial intermediate roots (as in *Rattus* s.s.); 5

Intermediate roots reduced to one (outer, labial) not strong; M.1/ four-rooted subgenus *Micaelamys*

5 Pelage bristly, even spiny; acc. med. cusp in L.1 of M./1 prominent subgenus *Stochomys*

Pelage soft, not bristly, acc. med. cusp small or absent .. .. subgenus *Aethomys*

Genus *Thamnomys* Thomas

1907 *Thamnomys* Thomas, Ann. Mag. nat. Hist. (7) 19: 121. Type species: *Thamnomys venustus* Thomas.
1915 *Grammomys* Thomas, Ann. Mag. nat. Hist. (8) 16: 150. Type species: *Mus dolichurus* Smuts. Valid as a subgenus.
1940 *Thamnomys*, Hatt, Bull. Amer. Mus. nat. Hist. 76: 537. (*Grammomys* a subgenus, as here.)
1941 *Thamnomys*, Ellerman, Fam. Gen. lvg. Rodents, 2: 103.
1941 *Grammomys*, Ellerman, ibid, 2: 104.

Status of the genus Thamnomys

Davis (1962) refers to *Thamnomys dolichurus*, implying that *Grammomys* had been dropped as a generic name. As noted in the above synonomy, Hatt's view that *Grammomys* should be a subgenus and not a separate genus is followed. He also allocated the species to the two subgenera as is done here, thus differing from Thomas' arrangement.

Species of the subgenus Thamnomys

T. venustus Thomas (with the forms *kempi* Dollman, *schoutedeni* Hatt, *major* Hatt and *kivuensis* Allen and Loveridge). *T. venustus* is distinguishable from all other species of the genus by its strongly developed postero-internal cusp (t.7) which dominates t.9 and the characteristic prominent cusps resembling those of *Oenomys hypoxanthus* (Ellerman 1941). Some individuals of *T. rutilans* seen have a well-developed t.7, but t.9 is larger—the opposite to *T. venustus*. Further, t.7 is not always a cusp but a ridge (e.g. Tervuren Mus. no. 10713). *T. rutilans* is therefore placed under the subgenus *Grammomys*, but it must be understood that an exhaustive examination has not been made.

Species of the subgenus Grammomys

Three (possibly four, if *T. gigas* is kept separate); *T. rutilans* Peters (with the forms *kuru* Thomas and Wroughton, and *centralis* Dollman); *T. dolichurus* Smuts (with the forms *dryas*

Thomas, *macmillani* Wroughton, *surdaster* Thomas and Wroughton, and about 18 others described since 1910); *T. cometes* Thomas and Wroughton (with the forms *ibeanus* Osgood, *lutosus* Dollman and *selindensis* Roberts) and *T. gigas* Dollman. The affinities of *T. gigas* are not clear, though it may perhaps be regarded as a large *T. cometes*.

Genus *Thallomys* Thomas

1920 *Thallomys* Thomas. Ann. Mag. nat. Hist. (9), 5: 141. Type species: *Mus nigricauda* Thomas.
1941 *Thallomys*, Ellerman. Fam. Gen. lvg Rodents 2: 145 (part).
1953 *Rattus*, Ellerman *et al.*, Sn Afr. Mamm. 264 (part, i.e. *R. paedulcus* Sundevall, subgenus *Aethomys*).
1955 *Thallomys*, Lundholm. Ann. Transv. Mus. 22: 321–9. (Relationship to other S. African *Rattus*-like genera.)

Status of the genus Thallomys

There is an indication of t.7 in the form of a short ridge between t.8 and t.4 as in some forms of subgenus *Grammomys* and a metastyle (Barrett-Hamilton and Hinton 1914) is often detectable behind t.9 as in the genus *Thamnomys* as a whole. This suggests a closer relationship to *Thamnomys* than to *Aethomys* and gives added support to Lundholm's conclusions (see diagram in Lundholm 1955a, p. 328).

The genus is apparently monotypic, since none of the described forms is sympatric. The prior name of *paedulcus* was correctly applied by Ellerman *et al.* (1953) and through the good offices of Dr. Per Brinck it has now been established that the type locality was in the Magaliesberg area and has been provisionally fixed as Crocodile Drift, Brits, Transvaal (SE 25–27 Db). This makes "*Mus*" *moggi* Roberts a synonym of the nominate form.

Intraspecific variation

This highly variable species may be divided provisionally into five "subspecies" groups as follows: (1) *paedulcus* Sundevall, *moggi* Roberts (a syn.), *acaciae* Roberts, *lebomboensis* Roberts, and *molopensis* Roberts; (2) *nigricauda* Thomas, *kalaharicus* Dollman, *nitela* Thomas and Hinton, *leuconoe* Thomas, *bradfieldi* Roberts (name revived on transfer from *Rattus*), and *davisi* Lundholm; (3) *damarensis* de Winton, *ruddi* Thomas and Wroughton, *herero* Thomas, *stevensoni* Roberts, *zambesiana* Lundholm and *quissamae* Petter and de Beaufort; (4) *loringi* Heller and *scotti* Thomas and Hinton, and (5) *shortridgei* Thomas and Hinton (*fide* van Rooyen unpub.).

Genus *Aethomys* Thomas

1915 *Aethomys* Thomas, Ann. Mag. nat. Hist. (8), 16: 477. Type species: *Epimys hindei* Thomas.

1926 *Stochomys* Thomas, Ann. Mag. nat. Hist. (9), 17: 176. Type species: *Dasymys longicaudatus* Tullberg.
1926 *Aethomys*, Thomas, ibid, p. 177. (Definition of the genus.)
1926 *Dephomys* Thomas, ibid, p. 177. Type species: *Mus defua* Miller.
1941 *Aethomys*, Ellerman, Fam. Gen. lvg Rodents, 2: 142.
1941 *Thallomys*, Ellerman, ibid, p. 145 (part, i.e. *A. namaquensis*).
1941 *Rattus*, Ellerman, ibid, p. 148 (part, i.e. subgenera *Stochomys*, p. 208, *Dephomys*, p. 210, *Micaelamys*, p. 213 (see also next entry).
1941 *Micaelamys* Ellerman, ibid, p. 169. Type species: *Mus granti* Wroughton (subgenus of *Rattus*).
1953 *Rattus*, Ellerman *et al.* Sn Afr. Mamm. p. 264 (part, viz. *Aethomys*, *Stochomys*, *Dephomys* and *Micaelamys*).
1955 *Aethomys*, Lundholm, Ann. Transv. Mus. 22: 321–9 (determines S. African *Aethomys* species-group as *A. chrysophilus*, *granti* and *namaquensis*).

The genus Aethomys

What has been done in effect is to go back to Thomas (1926) and to place *Stochomys* (with *Dephomys* as a synonym) under *Aethomys* and to add *Micaelamys* as the subgenus for *A. namaquensis* and *A. granti* following Lundholm (1955a). The genus *Aethomys* as defined by Thomas (1926) with minor exceptions applies to the present concept. To include *Stochomys* it is necessary to substitute "sometimes with" for "without" bristles in describing the character of the fur and to note that M.1/ is 4- or 5-rooted. (The 5-rooted species are *A.* (*S.*) *longicaudatus*, *A.* (*A.*) *bocagei* and *A.* (*A.*) *selindensis*, the last two being little known.)

Species of the subgenus Aethomys

A. chrysophilus de Winton (with *ineptus* Thomas and Wroughton, *acticola* Thomas and Wroughton, *tzaneenensis* Jameson, *voi* Osgood and about nine others described since 1910). These include *dollmani* Hatt whose status as a *chrysophilus* has not been personally verified (but see Ansell 1960 p. 92). There are approximately 16 forms of *A. kaiseri sensu lato* amongst which appear to be at least two species, possibly more, but they have not yet been sorted out satisfactorily. Apart from noting that *hindei* Thomas, *medicatus* Wroughton and about nine others seem to be *A. kaiseri* s.s. and that *walambae* Wroughton (with *pedester* Thomas, *amalae* Dollman and two others) appears to be a second species, nothing can be said at present.

Species of the subgenus Micaelamys

Two: the monotypic *A. granti* and the polytypic *A. namaquensis*. Compared with sympatric *A. namaquensis* from the zone of overlap, *A. granti* has a greyer belly, a shorter and more bristly

tail. The molars appear to be a trifle stouter and the accessory cusps better developed, but a critical biometrical analysis has not yet been done. So far no evidence of hybridisation has been obtained and the interpretation is a coming together of two forms which reached species status in isolation at some time during the Pleistocene. *A. namaquensis* is widely distributed in southern Africa (Davis 1962) and is known at a few points north of the lower Zambesi. The forms are correctly listed in Ellerman *et al.* (1953) but it is considered that *phippsi* Hill and Carter belongs to *A. namaquensis* rather than to *A. chrysophilus*. The form "*Rattus namaquensis longicaudatus*" described by von Lehmann (1955) would appear to be a synonym of *A. n. siccatus* Thomas: in any event the name "*longicaudatus*" is unavailable (see synonomy).

Species of the subgenus Stochomys

Two: *A. longicaudatus* Tullberg (with *ituricus* Thomas) and *A. defua* Miller. As pointed out by Heim de Balsac and Lamotte (1958) *A. defua* has some resemblance to *A. granti* and also to *A. longicaudatus*. It differs from *A. longicaudatus* in having 4-rooted instead of 5-rooted M.1/, in having less bristly fur and in certain minor molar cusp and cranial features; these do not seem great enough for the two species not to be placed in the same subgenus.

THE GENERA *Praomys* AND *Zelotomys*

Genus *Praomys* Thomas

(Plates I, figs. 5–6; IV, figs. 1–12.)

1915 *Praomys* Thomas, Ann. Mag. nat. Hist. (8) 16: 477. Type species: *Mus tullbergi* Thomas.
1915 *Myomys* Thomas, ibid, p. 477. Type species: *Mus colonus* Brants [See below, Ellerman *et al.* 1953.]
1915 *Mastomys* Thomas, ibid, p. 477. Type species: *Mus coucha* A. Smith. Valid as a subgenus.
1926 *Praomys*, Thomas, Ann. Mag. nat. Hist. (9) 17: 178 (diagnosis of the genus).
1926 *Hylomyscus* Thomas, ibid, p. 178. Type species: *Epimys aeta* Thomas. Valid as a subgenus.
1941 *Rattus*, Ellerman, Fam. Gen. Lvg Rodents 2: 208–213 (part, i.e. subgenera *Praomys*, *Hylomyscus*, *Myomys*, *Mastomys*).
1942 *Myomyscus* Shortridge, Ann. S. Afr. Mus. 36, 93. Type species: *Mus verreauxi:* A. Smith. ("*Myomys*" *granti* included in error: an *Aethomys*, see present paper.) Valid as a subgenus.
1953 *Rattus*, Ellerman *et al.* S. Afr. Mamm. 264 (part, viz. *Praomys*, *Myomys*, *Mastomys*, *Hylomyscus*, *Myomyscus*. Type species "*Mus*" *colonus* of *Myomys* not certainly identifiable and name rejected).
1955 *Mastomys*, Lundholm, Ann. Transv. Mus. 22: 329 (treated as a genus with the South African species *natalensis* A. Smith and *verreauxi* A. Smith on basis of cranial and dental similarities).

1956 *Mastomys*, Setzer, Proc. U.S. nat. Mus. 106: 515 (given generic status).
1956 *Praomys*, Setzer, ibid, p. 515 (a genus with *Myomys* and *Hylomyscus* as synonyms, not valid as subgenera).
1957 *Rattus*, Petter, Mammalia, 21: 125 (part, i.e. the subgenera *Mastomys*, *Praomys*, *Hylomyscus* and "*Myomys*", whose interrelations are discussed.)
1962 *Praomys*, Davis, Ann. Cape prov. Mus. 2: 62 (*Praomys* used as generic name for S. African species *natalensis* and *verreauxi*).

Distinctive characters of the genus

Size small to medium: fur soft; tail equally clothed with short hairs, not penicillate, but sometimes a small tuft at tip; post-tympanic hook of squamosal with divided mastoid process or "strut", the downward trending strut dividing the post-glenoid fossa, leaving a vacuity (as a rule*) behind; massetter knob slightly or only moderately developed; t.1 of M.$\underline{1}$/ moderately backwardly displaced; terminal heel about equally developed in M./$\overline{1}$ and $\overline{2}$; AMF 3–3–2/3:2–2–2; accessory med. cusp absent in L.1 of M./$\overline{1}$; choanae varying from narrow to wide; supraorbital ridges smooth or lightly to moderately beaded; mammary formula 0–2=4, 1–2=6, 2–2=8, 3–2=10, or five pairs or more in a continuous row.

KEY TO THE SUBGENERA OF *Praomys* (PROVISIONAL)

1 Choanae wider than the width of M.$\underline{1}$/; anterior palatal foramina not, or just reaching anterior root of M.$\underline{1}$/; incisors orthodont, tending to pro-odont *Hylomyscus*

Choanae about as wide, a little wider, or much narrower than width of M.$\underline{1}$/; ant. pal. foramina penetrating between the first upper molars; incisors moderately opisthodont 2

2 Choanae very narrow, less than the width of M.$\underline{1}$/; ant. pal. foramina penetrating deeply between molars, often extending to back of alveolus of inner root of M.$\underline{1}$/; tail about the same length as head and body; mammae 5 or more pairs, not sharply separated into pectoral and inguinal sets .. .. *Mastomys*

Choanae about the width of M.$\underline{1}$/; or a little narrower (*P.* (*M.*) *verreauxi* only); ant. pal. foramina penetrating less deeply between molars, usually to back of ant. root but occasionally deeper; tail longer than head and body or subequal (*P.* (*M.*) *angolensis* only); mammae divided into pectoral and inguinal sets 3

3 Mammae 3–2=10 .. .. *Myomyscus*

Mammae 1–2=6 or 2–2=8 .. .. *Praomys*

* *P. denniae* is an exception in having only a slight indentation (rather as in *Acomys ignitus* Pl. 1, fig. 3)

N.B. There are deficiencies in the above key, since it is still necessary to rely on the mammary formula. Furthermore the author has not yet had the opportunity of examining long enough series to be sure that the cranial features are as indicated for all forms of the subgenera or that other characters cannot be brought into make the key more exact.

Species of the subgenus Praomys

At least two, possibly three or even more. *P. morio* Trouessart (with *tullbergi* Thomas, *jacksoni* de Winton, *rostratus* Miller, *peromyscus* Heller, *montis* Thomas, *viator* Thomas, *lukolelae* Hatt (?), *sudanensis* Setzer and possibly others); *P. delectorum* Thomas (with *taitae* Heller, *melanotus* G. M. Allen and Loveridge, and *octomastis* Hatt).

P. delectorum may be distinguished from the *morio* group by its smaller size (condylobasal length up to c. 27 mm. as against c.31 mm. in *morio*) by its sleeker pelage, shiny tail and by its mammary formula of 2–2=8 (1–2=6 in *morio*). There are strong indications from chromosome studies that "*jacksoni*" (2N=28) and "*tullbergi*" (2N=34) are different (Matthey 1958, 1959); furthermore Heim de Balsac and Lamotte (1958) report the two "species" from the Ivory Coast. However much remains to be done to arrive at a valid grouping of the described forms; for the present attention is drawn to the distinctness of *P. delectorum*, often treated as a form of *morio* (e.g. see Vesey-FitzGerald 1962).

Species of the subgenus Mastomys

Two in southern Africa, three or four, even more, in Africa as a whole. *P. natalensis* (with *marikquensis* A. Smith (*coucha* A. Smith a syn.), *silaceus* Wagner, *macrolepis* Sundevall, *microdon* Peters, *erythroleucus* Temminck and at least 27 other described forms); *P. shortridgei* St Leger (*legerae* nom. nov. Ellerman *et al.* reverts to *shortridgei* on transfer to *Praomys* from *Rattus*).

P. natalensis is probably a "composite" of two or more species since chromosome studies have revealed marked differences (Matthey 1954, 1955, 1958), and two species co-existing in the same area have been reported (e.g. Setzer 1956). It is too early to attempt to allocate the numerous forms to separate species. *P. shortridgei* closely resembles *P. natalensis*, differing in having only five pairs of mammae which are arranged, as in *P. natalensis*, in a continuous row without clear separation into pectoral and inguinal sets.

Species of the subgenus Myomyscus

Four, possibly more. *P. verreauxi* A. Smith; *P. albipes* Rüppel [with *fuscirostris* Wagner (?), *rufidorsalis* Heuglin (?), *alettensis* Frick, *ankoberensis* Frick (Frick's forms are regarded as synonyms of the nominate ssp. by Osgood 1936)]; *P. fumatus* Peters (with *tana* True, *brockmani* Thomas, *butleri* Wroughton (?), *subfuscus* Osgood, *yemeni* Sanborn and Hoogstraal (?), *oweni* Setzer and *allisoni* Hayman; *P. daltoni* Thomas (with *ingoldbyi* Ellerman); *P. angolensis* Bocage.

These "*Myomys*" have not been examined in any great detail and the above allocations are tentative. It would appear that *butleri* may be intermediate between *P. daltoni* and

P. fumatus, which raises the question whether these two are conspecific. In any event it is relevant to note that *P. daltoni* has white- and grey-bellied forms (as has *P. fumatus*), but while the one is semi-commensal the other (*P. fumatus*) occupies a similar niche in rocky places in E. Africa to *Aethomys namaquensis* in S. Africa.

Genus *Zelotomys* Osgood

(Plate III, figs. 1–4)

1910 *Zelotomys* Osgood, Publ. Field Mus. Zool. 10: 7. Type species: *Mus hildegardeae* Thomas.

1920 *Ochromys* Thomas, Ann. Mag. nat. Hist. (9), 5: 142. Type species: *Mus woosnami* Schwann.

1941 *Ochromys*, Ellerman, Fam. gen. Lvg Rodents 2: 171 (subgenus of *Rattus*—noted as resembling *Zelotomys*).

1955 *Ochromys*, Lundholm, Ann. Transv. Mus., 22: 321–329. (Most aberrant of South African *Rattus sensu* Ellerman.)

Distinctive characters of the genus Zelotomys

Tail shorter than head and body; M.F. 3–2=10; upper incisors strongly pro-odont (*hildegardeae*) or orthodont (*woosnami*); AMF 3–3–2:2–2–2; M.3 in upper and lower jaw reduced; post-tympanic hook of squamosal triangular, truncate, slightly emarginate, but no vacuity; junction between posterior border of maxilla and palatine at level of last upper molars and well behind the post. palatal foramina (see Lundholm 1955 p. 327, fig. 4A for *Z. woosnami*).

Number of species

Two: *Z. hildegardeae* Thomas (with *vinaceus* Heller, *instans* Thomas, *shortridgei* Hinton, *kuvelaiensis* St Leger and *lillyana* Bohmann; *Z. woosnami* Schwann. The two species approach each other in the South West Africa/southern Angola border region, but have not yet been found together.

CONCLUSION

It has not been possible to do more than establish the name changes introduced in Davis (1962) and to indicate (Table I and Plates I–V) the framework within which an attempt is being made to arrive at an acceptable classification of African Muridae. It is hoped that the captions to the Plates I–V will help to clarify the status of some of the non-*Rattus*-like taxa of the Murinae and of the genus *Otomys* of the Otomyinae. Space precludes further discussion of these groups and also of the Cricetinae and Dendromurinae and Gerbillinae. It should be noted, however, that the Dendromurinae so far examined possess the simple *Mus*-type of alveolar-molar root pattern (AMF). It is tempting to suggest that those African Murinae

with the simple AMF are closer to the cricetids than those with the more complex *Rattus*-type formula. It is strange that the largest and smallest African rodent, viz. the giant rat *Cricetomys gambianus* and the dwarf mouse *Mus* (*Leggada*) *minutoides*, should both show the simple pattern. It is similarly interesting that the rather specialised *Malacomys* and *Colomys* belong to this group. However, without a much wider study on these lines of related taxa outside Africa it would be foolhardy to speculate at this stage on possible phylogenetic implications.

It is perhaps premature to list the "described forms" of the "biological species" of *Aethomys*, *Praomys*, *Thallomys*, *Thamnomys* and *Zelotomys* since there is uncertainty about the status of a number of them; it is furthermore by no means certain that all the "species" will stand up to a more critical assessment than has been possible to date, especially those extra-limital to southern Africa. Some may be shown to have passed beyond the species stage. In the final analysis it is anticipated that the cytotaxonomic studies being conducted by Matthey (see references) in particular, which have given many invaluable pointers already, will resolve many puzzles of nomenclature and identity and result in a much clearer picture of African Muridae systematics.

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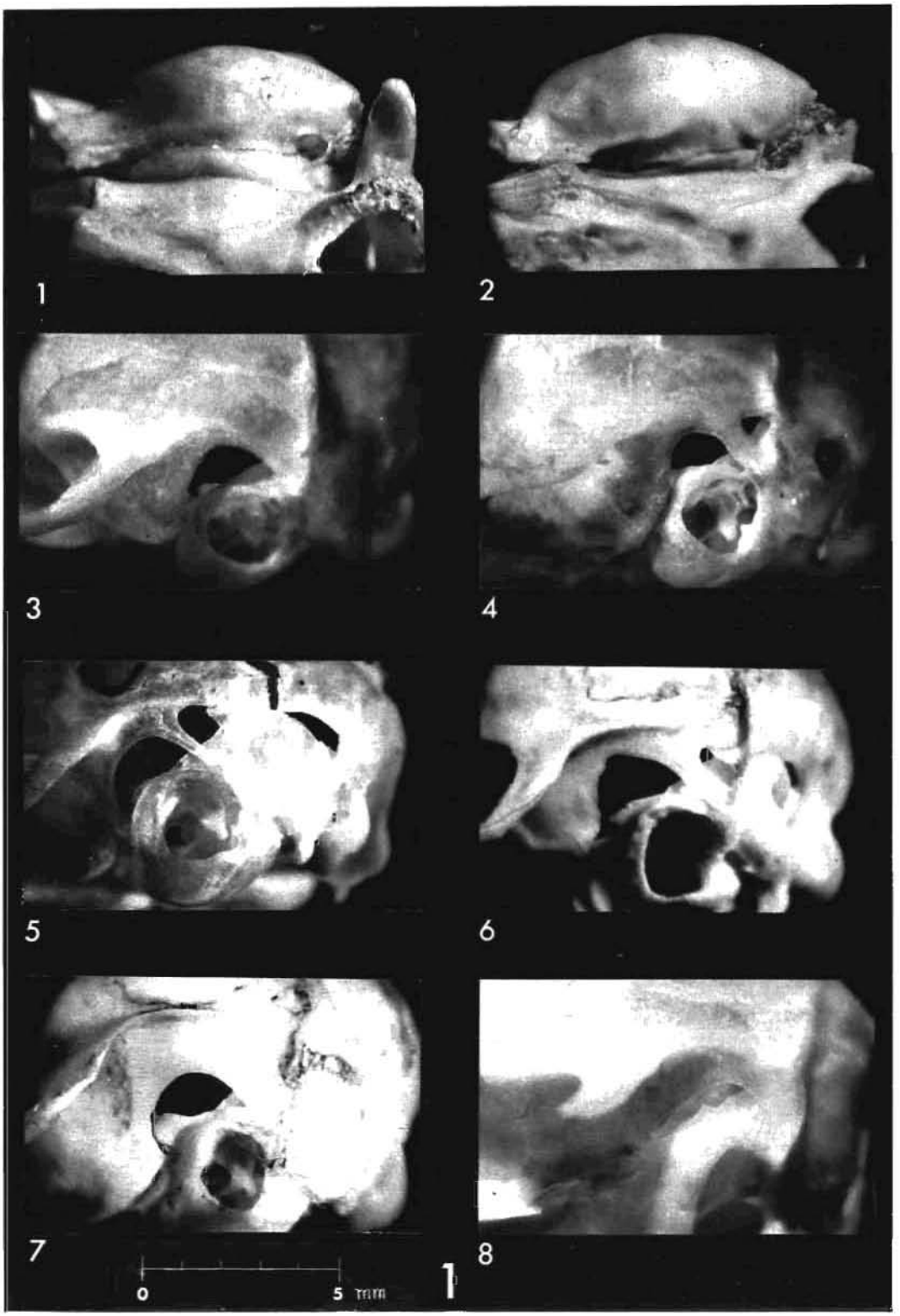

PLATE I

DIAGNOSTIC CHARACTERS IN THE TYMPANIC BULLA (OTOMYINAE) AND POST-TYMPANIC HOOK OF THE SQUAMOSAL (MURINAE)

FIGURES 1–2. Ventral tangential view of the inner aspect of the left bulla of specimens of *Otomys* belonging to the two main groups of species to show the difference in size of the posterior petrotympanic foramen (see Greene 1955, Rowlett 1957), for the passage of the pterygopalatine branch of the int. carotid artery.

FIGURE 1. *Otomys irroratus irroratus* (Brants). La Plaisante, Wolseley, C.P.: SE 33–19 Ac. PL 55.20:2, coll. C. J. Muller. A near topotype. Note the large foramen or "hole" character of Lundholm (in Davis 1962) which is common to *irroratus*, *tropicalis*, *unisulcatus* and some other *Otomys* spp.

FIGURE 2. *O. angoniensis mashona* Thomas. Chisawasha, Salisbury, S.R.: SE 17–31 Cc. (SAM 13767 A). PL 61.48:14, coll. C. M. Daignault. Note the small foramen and the shallow depression or "slit" running obliquely antero-ventrally, a character typical of *angoniensis*.

FIGURES 3–8. Side view of the left bulla region of some species of Murinae to show the varied structure of the posterior portion (proc. supramastoideus of the post-tympanic hook of the squamosal, see Lundholm 1955).

FIGURE 3. *Acomys ignitus kempi* Dollman. Mtowamba, Manyara, Tanganyika: SE 03–35 Dd. PL 63.33:22, coll. L. D. Vesey-FitzGerald (no. 15252). Identification provisional. Note small emargination of process in comparison with the next species (Figure 4). See also Figures 7–8.

FIGURE 4. *A. dimidiatus spinosissimus* (Peters). Abercorn, N.R.: SE 08–31 Dc. PL 63.33:3, coll. L. D. Vesey-FitzGerald (no. 12322). Identification provisional. Note well-developed "strut" lying across the postglenoid foramen leaving a post-vacuity. See also Plate V, Figures 9–10.

FIGURE 5. *Praomys* (*P.*) *delectorum taitae* (Heller). Amani, Tanganyika: SE 05–38 Ba. PL 62.4:14, coll. C. A. Hubbard (no. 345). Note long slender strut. See also Plate IV Figures 3–4.

FIGURE 6. *P.* (*Mastomys*) *natalensis marikquensis* (A. Smith). The Willows, Sterkfontein, Tvl.: SE 26–27 Ba. PL 55.4:3 coll. C. J. Muller. Note relatively broad strut lying across post-glenoid foramen. See also Plate IV, Figures 5–6.

FIGURE 7. *Aethomys* (*Stochomys*) *defua* (Thomas). Kenema, Sierra Leone: NW 07–11 Ca. PL 63.46:11 (BM 36.8.14.7) coll. D. H. S. Davis (no. A195). Note truncate posterior end to post-tympanic hook with no opening into the post-glenoid foramen a feature common to the genera *Aethomys*, *Rattus* s.s., *Thallomys*, *Thamnomys* and others of the *Rattus*-type group with "complex" alveolar-molar formulae (AMF), see Plate II.

FIGURE 8. *Saccostomus campestris hildae* Schwann. Olifantshoek, Postmasburg, C.P.: SE 27–22 Dc. PL 55.9:13, coll. C. J. Muller. Note the truncate process as seen in *Aethomys* etc. (see Figure 7 above). The AMF, however, is of the "simple" *Mus*-type see Plate III, Figures 7–8.

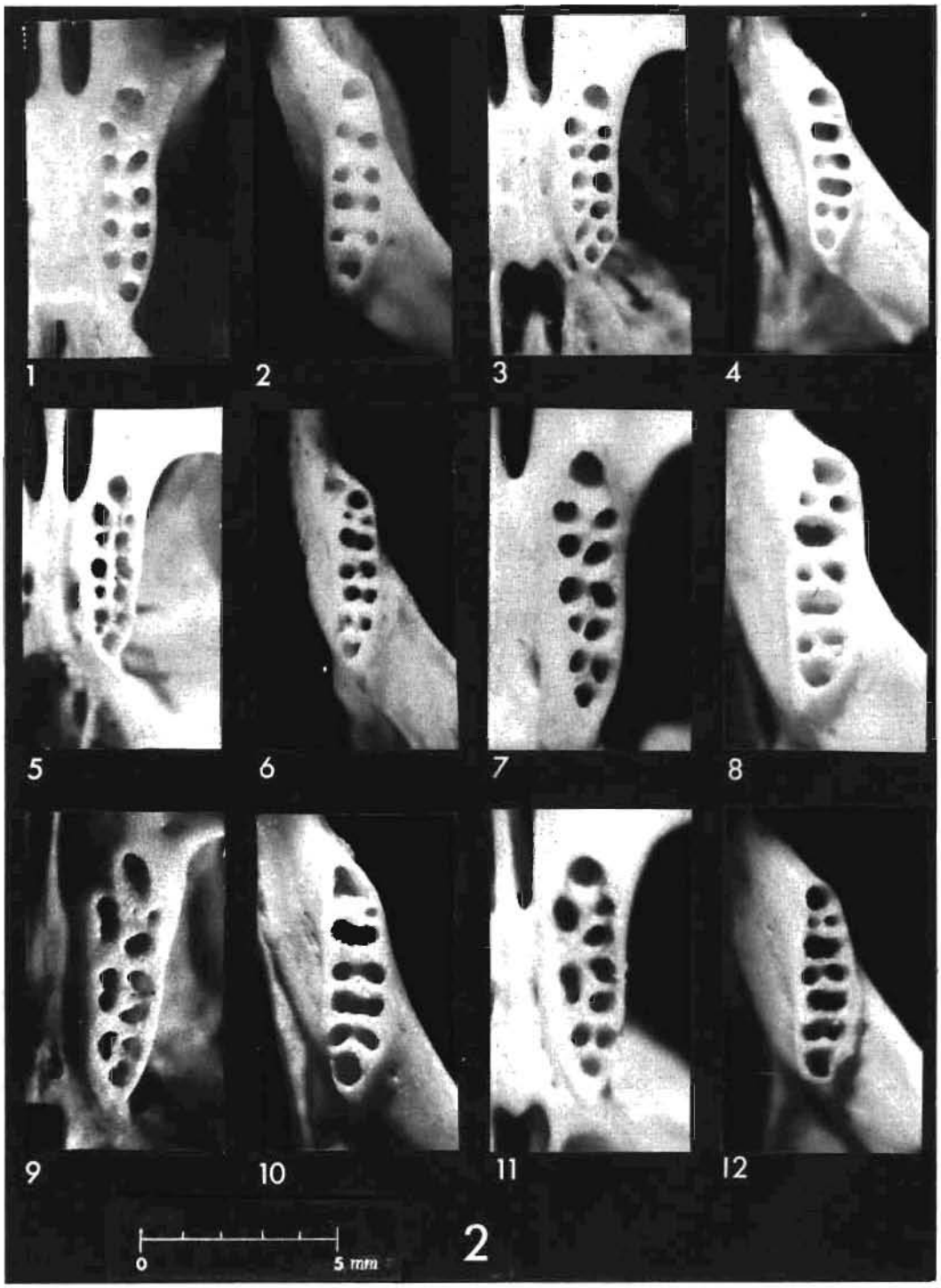

PLATE II

SPECIES WITH "COMPLEX" RATTUS-TYPE ALVEOLAR-MOLAR ROOT FORMULAE
Genera *Aethomys*, *Rattus* s.s., *Thallomys* and *Thamnomys*

FIGURES 1–2. *Thamnomys* (*Grammomys*) *rutilans centralis* Dollman. Zika Forest, Entebbe: NE 00–32 Ba. PL 59.82:165, coll. H. N. Southern (no. 165). AMF 4+(?i)–4–3:3–4–3. Lacks (?) medial outer root (rootlet) in M.1/ and intermediate rootlets in M./1. This is the only specimen of *rutilans* examined, hence may be a variant of the "normal" AMF for the genus *Thamnomys*.

FIGURES 3–4. *Thamnomys* (*Grammomys*) *dolichurus dryas* Thomas. Bwamba, Uganda: NE 00–30 Cc. PL 57.35:1, coll. W. F. R. Lumsden (No. 2: det. *dryas* at B.M.) AMF 5–4–3:2[3]+ i–2 [4]–3. Note the single outer medial rootlet in M./1, poorly developed in comparison with *Thallomys* (Figure 6) and *R. rattus* (Figure 8) and resembling *Aethomys namaquensis* (Figure 10).

FIGURES 5–6. *Thallomys paedulcus paedulcus* (Sundevall). 13 mi. Brits-Rustenburg road, Tvl.: SE 25–27 Da. PL 49.46:2, coll. R. Rose Innes & P. J. Geldenhuys. Near topotype. AMF 5–4[5]–3[4]: 2[3]+ii–2[4]–3[4]. The two moderately strong intermediate rootlets in M./1 are closest to *R. rattus* (Figure 8) of all the species on this plate. Note tendency for development of "extra" roots and rootlets.

FIGURES 7–8. *Rattus rattus* (Linnaeus). Niombe, C. Rukwa, Tanganyika: SE 08–31 Bb. PL 55.36:39, coll. I. A. D. Robertson. AMF 5–4–3+(i):2+ii–3–3. Note the well-separated inner roots in M.1–2/ and the strong intermediate roots in M./1. The 2 elements of the posterior root of M./1 are fused into a single root in spite of the large size of the alveolus whose outline is suggestive of 2 roots.

FIGURES 9–10. *Aethomys* (*Micaelamys*) *namaquensis drakensbergi* (Roberts).* Mlanje Plateau, Nyasaland: SE 15–34 Cc. PL 61.52:74, coll. G. C. Shortridge (KM 12043). AMF 4–3[4[–3:2[3]+i–2[4–2[3]. *A. namaquensis* is hardly known north of the Zambezi and it is of importance that the AMF of this specimen is almost identical to that of a specimen of *A. n. centralis* (Schwann). Venterstad, C.P.: SE 30–25 Da. PL 45.23:64 (KM 11069) AMF 4–3[4]–3:2[3]+i–2[4]–2[3]. There is also very little difference between *namaquensis* and the closely related *granti*.

*or a new subspecies

FIGURES 11–12. *Aethomys* (*Aethomys*) *chrysophilus pretoriae* Roberts, Hennops River, Pretoria: SE 25–27 Dd. PL 55.4:89, coll. C. J. Muller. AMF 4–3[4]–3:2[3]+ii–3–2[3]. Note the two strong intermediate rootlets in M./1, resembling those in *R. rattus*, these distinguish *chrysophilus* from *namaquensis*. *A. chrysophilus* shows variability in the degree of separation of the inner roots of M./2, and often have the roots completely separate; so far this has not been seen to affect M.1/. With the exception of the fused inner roots in M.1 & 2/, the AMF of this species comes very close to *R. rattus* (Figure 7–8).

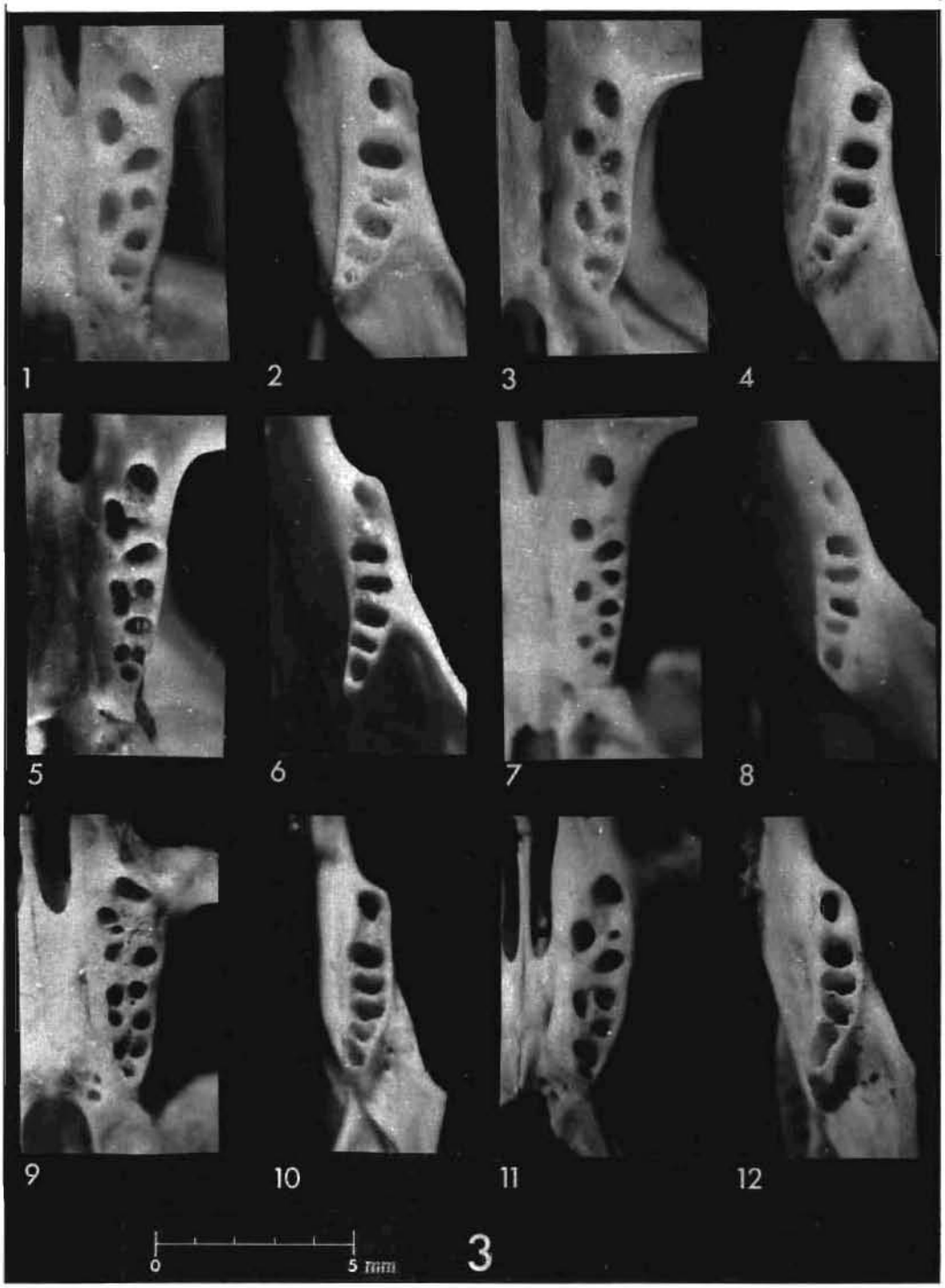

PLATE III

SPECIES WITH THE "SIMPLE" MUS-TYPE OF ALVEOLAR-MOLAR ROOT FORMULAE
Genera *Colomys, Lophuromys, Saccostomus, Uranomys* and *Zelotomys*

FIGURES 1–2. *Zelotomys hildegardeae hildegardeae* (Thomas). Nanyuki, Kenya: NE 00–37 Aa. PL 59.82:57 coll. H. N. Southern (no. 67). AMF 3–3–2:2–2–2. Note the reduced third upper molar (M.3/) in this and in *Z. woosnami* (Figure 3).

FIGURES 3–4. *Z. woosnami* (Schwann). 8 mi. W. Ukualuthi, Ovamboland, S.W.A.: SE 17–14 Dd. PL 51.27:182, coll. R. Rose Innes & P. J. Geldenhuys. AMF 3–3–2:2–2–2. Apart from its slightly smaller size there is nothing to distinguish *woosnami* from *hildegardeae* in these photographs. Externally body proportions are similar, but the tail of *woosnami* is whiter and the upper incisors are orthodont instead of being strongly pro-odont (as in *hildegardeae* and all its "forms"). End of post-tympanic hook truncate as in *Z. hildegardeae* (see Lundholm 1955 for this feature in "*Ochromys*" *woosnami*).

FIGURES 5–6. *Colomys goslingi goslingi* Thomas & Wroughton. Tshibati, Lwiro, Kivu, Congo: SE 02–28 Bb. PL 63.1:4, coll. U. Rahm (no. L 11180). AMF 3+(i)–3–3:2–2–2. This very distinct species (externally), showing some resemblance in its AMF to *Zelotomys* but M.3/ not as reduced, possesses a strut (post-tympanic hook), while this is absent in *Zelotomys*.

FIGURES 7–8. *Saccostomus campestris hildae* Schwann. Same specimen as Plate I, Figure 8. AMF 3+(i)–3–3:2–2–2. Lacks the strut (see Plate I Figure 8) but from its alveolar pattern alone might be confused with *Colomys* or *Praomys* spp., but mandible immediately separable by its relatively greater depth and if teeth present in a maxilla, by the 2-cusped first lamina in M.1/.

FIGURES 9–10. *Lophuromys woosnami prittei* Thomas. Nr. Uinka, Rwanda: SE 02–29 Ac. PL 63.1:3, coll. U. Rahm (no. E 612). AMF 4+i–4+(i)–3:2–2–2. The 4–4–3:2–2–2 formula applies to the other two species *L. flavopunctatus* and *L. sikapusi*, though from the specimens so far seen, *flavopunctatus* has fewer and *sikapusi* more rootlets. It is thus possible that the AMF may provide interspecies differences which may prove useful in localities where the two species occur together and may be difficult to separate (e.g. see Setzer 1956).

FIGURE 11–12. *Uranomys ruddi tenebrosus* Hinton. Mkhoma, Dowa. Nyasaland: SE 13–33 Db. PL 61.48:18, coll. J. M. Gericke (SAM 15792). Paratype. AMF 3+i–3+(ii)–2[3]:2–2–1[2]. Possesses a well-developed strut resembling that of *Colomys. Lophuromys* etc. but differing from *Zelotomys*. The last lower molar (M./3) is reduced slightly.

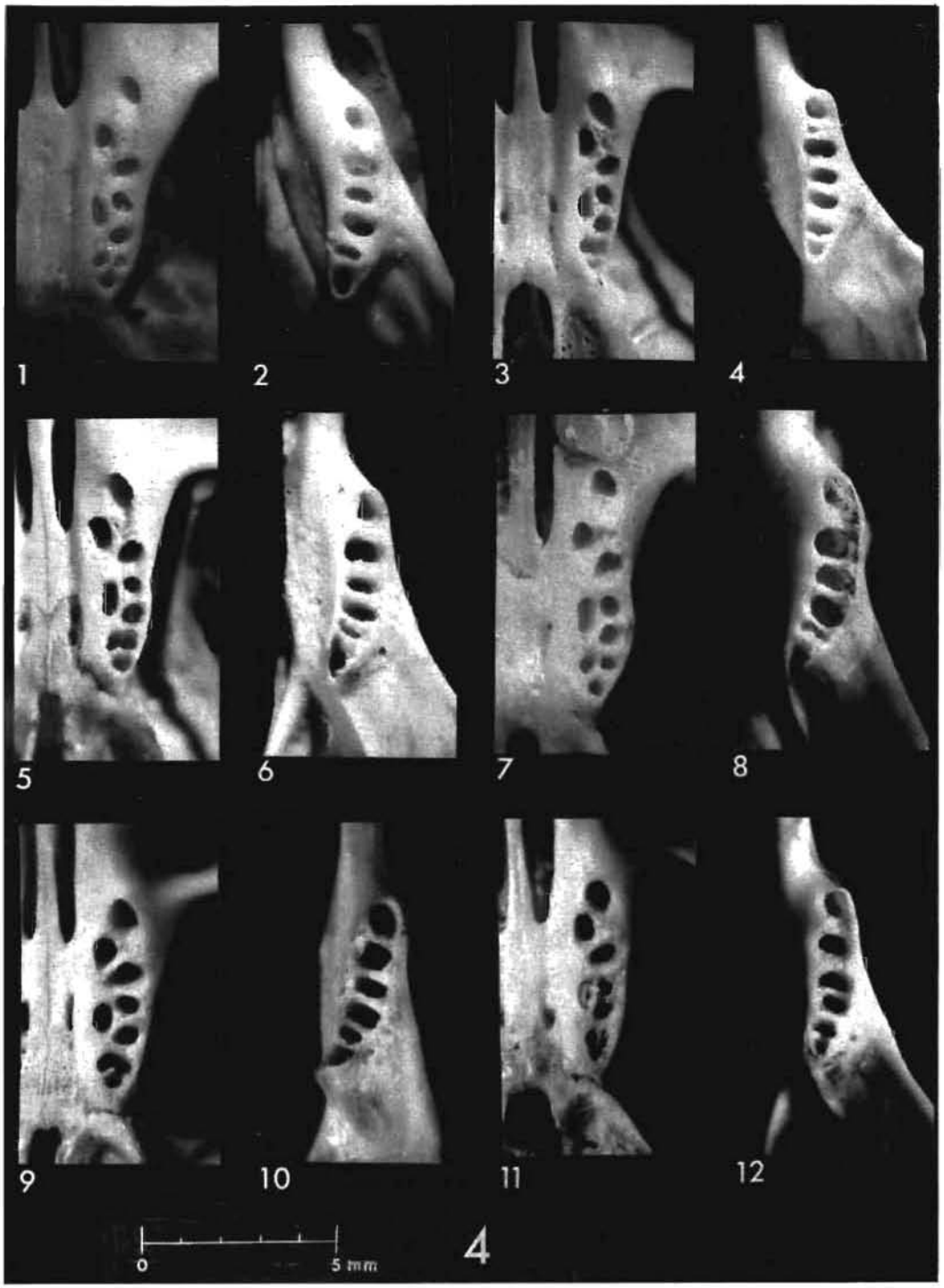

PLATE IV

SPECIES WITH "SIMPLE" MUS-TYPE ALVEOLAR-MOLAR ROOT FORMULAE
Genus *Praomys*

FIGURE 1–2. *Praomys* (*Praomys*) *morio jacksoni* (de Winton). Mbanga Forest, Entebbe: NE 00–32 Aa. PL 59.82:33, coll. H. N. Southern (no. 33). Topotypical. AMF 3–3–3:2–2–2. The ant. pal. foramina reach the back of the ant. root of M.1/ and the choanae are about as wide as the width of M.1/.

FIGURES 3–4. *P.* (*P.*) *delectorum taitae* (Heller). Same specimen as Plate I Figure 5. AMF 3+(i)–3–2[3]: 2+(i)–2–2. Very small rootlets in upper and lower first molars; ant. pal. foramina reaching about the middle of ant. root of M.1/; choanae a trifle wider than width of M.1/. Size smaller than *P. m. jacksoni* (Figures 1–2).

FIGURES 5–6. *P.* (*Mastomys*) *natalensis* (A. Smith). Same specimen as Plate I Figure 6. AMF 3–3–2[3]: 2–2–2. Ant. pal. foramina nearly reaching middle of the inner root of M.1/ (normally even further). Inner roots of M.1 & 2/ oblong (as in subgenus *Praomys* above) suggestive of two elements (some specimens seen in owl pellet material coll. A. J. Prinsloo have had divided roots, though never separate alveoli). Choanae extremely narrow, even narrower than *P. verreauxi* (Figure 9).

FIGURES 7–8. *P.* (*Mastomys*) *shortridgei* (St. Leger). Diwai, W. Caprivi Strip: SE 18–21 Bb. PL 54.18:2 (KM 4129). AMF 3–3–3:2–2–2. Note choanae narrower than width of M.1/ and that the ant. pal. foramina penetrate to the back of the inner root of M.1/. as in *P. natalensis*. *P. shortridgei* is 5-mammate (seen in the Type specimen in B.M.), but the mammae are not sharply divided into pectoral and inguinal sets as, for example, in *P. verreauxi*. Status uncertain.

FIGURES 9–10. *P.* (*Myomyscus*) *verreauxi* (A. Smith). Modderfontein, Citrusdal, C.P.: SE 32–18 Db. PL 54.48:14, coll. C. J. Muller. AMF 3–3–2[3]:2–2–2. Note that ant. pal. foramina reach the anterior margin of the inner root of M.1/ and the choanae are narrower than the width of M1./ as in *P. natalensis* and *P. shortridgei*.

FIGURES 11–12. *P.* (*M.*) *fumatus fumatus* (Peters). Kisigau Mt. (summit), Kenya: SE 03–38 Dc. PL 61.18A:3 (CMM 2941), coll. A. B. Percival. AMF 3–3–2[3]:2–2–2. Ant. pal. foramina reaching a trifle beyond the anterior margin of inner root of M.1/ as in the *P. natalensis* specimen (Figure 5) and *P. verreauxi* (Figure 9), but choanae about as wide as width of M.1/. Both *P. verreauxi* and *P. fumatus* have tails relatively longer than head and body and mammary formula of 3–2=10. and they share this and other characters with *P. daltoni* (W. Africa) and *P. albipes* (Ethiopia) (see Davis 1962).

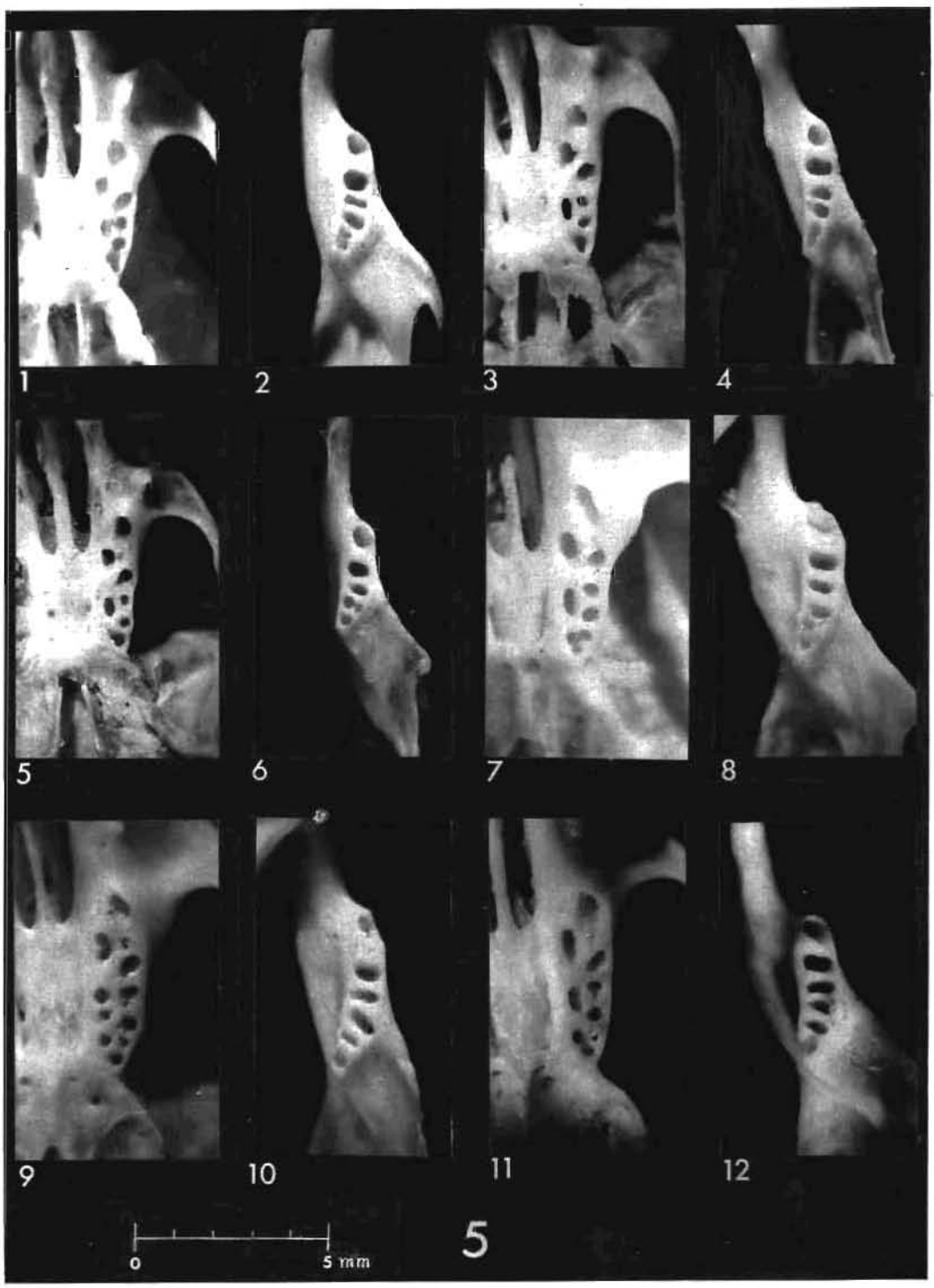

PLATE V

SPECIES WITH "SIMPLE" MUS-TYPE ALVEOLAR-MOLAR ROOT FORMULAE
Genera *Acomys* and *Mus*

NOTE: Both *Acomys* and *Mus* are "difficult" genera. The specimens selected for this plate reveal characters that may prove of value in making possible at least a preliminary grouping of the numerous "described forms". Of particular interest is the AMF of the mandible of "*Mus*" and "*Leggada*".

FIGURES 1–2. *Mus* (*Mus*) *musculus* Linnaeus. Forest Hill, Johannesburg, Tvl.: SE 26–28 Aa. PL 63.23:1, coll. A. J. Prinsloo. AMF 3–3–1[2]:2–2–1[2]. According to Herold (1963) this example would fall into his high frequency class and it may be taken as "normal" for *M. musculus*.

FIGURES 3–4. *M.* (*M.*) *triton murillus* (Thomas). Maxilla*: Mbizi, Ufipa, Tanganyika: SE 07–31 Dc. PL 63.33:5, coll. L. D. Vesey-FitzGerald (no. 12419). Mandible*: Ngorongoro Crater, Tanganyika: SE 03–35 Ba. PL 62.44:3, coll. C. A. Hubbard. AMF 3–3–2:2–2–1 (the alveoli of M3/3 suggest a double root, but neither root is divided at its distal end). Pattern similar to *M. musculus*, but upper and lower M.3 more reduced. *M. triton* is placed in the subgenus *Mus* with much reservation since it is based solely on the different root arrangement found in other "*Leggada*" (see *M. minutoides* Figures 5–6).

* The best photos chosen, there being no difference in the AMF in the 2 specimens.

FIGURES 5–6. *M.* (*Leggada*) *minutoides umbratus* (Thomas). Nottingham Road, Natal: SE 29–29 Bd. PL 48.17:96, coll. P. J. Geldenhuys & W. Fourie. AMF 3+(i)–3–1[2]:2–3–1. Note the difference in *M. minutoides* and *M. musculus* and *M. triton* between the root formula af the lower jaw. Before coming to study *M. minutoides* T. N. Pocock and A. J. Prinsloo were fully familiar with this character and drew my attention to it. Provisionally it is taken here as indicating membership of the subgenus *Leggada*. It has been noted in a specimen of *M. bufo* from Ngorongoro Crater, coll. C. A. Hubbard.

FIGURES 7–8. *Acomys ignitus kempi* Dollman. Same specimen as Plate I, Figure 3. AMF 3[4]+(i)–3–3: 2–2–2. Note that the small median rootlet in M.1/ is merely represented by a scar. It is stronger in the *A. d. spinosissimus* specimen (Figure 9). Herold (1963) notes several variants in *Acomys* spp. so that in all probability the AMF is unlikely to be of diagnostic importance interspecifically. Of evident importance is the depth to which the ant. pal. foramina penetrate between the molars. In the present form they extend to the middle of the inner root of M.1/ (cf. Figures 9 & 11).

FIGURES 9–10. *A. dimidiatus spinosissimus* (Peters). Same specimen as Plate I, Figure 4. AMF 3[4]+i–4+i–3:2+(i)–2–2. Note the two well separated inner roots in M.2/ and that the intermediate rootlet in M./1 is a mere scar. The ant. pal. foramina only reach the back of the anterior root of M.1/ in strong contrast to its position in *A. ignitus* (Figure 7).

FIGURES 11–12. *A. dimidiatus selousi* de Winton. West Nicholson, S.R.: SE 21–29 Ab. PL 46.86:189, coll. D. H. S. Davis & B. de Meillon. A near topotype. AMF 3[74]–3[74]+(i):2–2–2. Note smaller size, but general resemblance to the Abercorn specimen (Figures 9–10). In distinguishing owl pellet or fossil material, the consistently greater reduction in upper and lower M.3 in *Mus* seems a "good" character to distinguish the genus.