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A SYSTEMATIC REVISION OF SOUTHERN AFRICAN *AETHOMYS* THOMAS, 1915 (RODENTIA: MURIDAE)

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A SYSTEMATIC REVISION OF SOUTHERN AFRICAN *AETHOMYS* THOMAS, 1915 (RODENTIA: MURIDAE)

by

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A systematic revision of southern African *Aethomys* Thomas, 1915 (Rodentia: Muridae)

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ABSTRACT

Five species of African rock rats of the genus *Aethomys*, *A. namaquensis*, *A. granti*, *A. silindensis*, *A. chrysophilus* and *A. ineptus*, are recognized in southern Africa. Morphometric analyses indicated that *A. namaquensis*, *A. granti* and *A. silindensis* differ markedly in cranial size and/or shape. Morphometric analyses involving cytogenetically known specimens of *A. chrysophilus* revealed the presence of two sympatric, morphologically similar species, *A. chrysophilus* and *A. ineptus*. This is in agreement with observations on cranial morphology and earlier investigations involving cytogenetics, protein electrophoresis and sperm morphology. Contrary to published

reports, the morphometric data show that the Central African *A. nyikae* does not occur in southern Africa, and the single previous record from eastern Zimbabwe is probably based on a misidentification.

Four subspecies, *A. n. namaquensis*, *A. n. lehocla*, *A. n. alborarius* and *A. n. monticularis*, which broadly coincide with major biomes of southern Africa, are recognized within *A. namaquensis*. Two subspecies, *A. c. chrysophilus* and *A. c. imago*, which broadly coincide with altitudinal limits of the eastern part of southern Africa, are recognized within *A. chrysophilus*. Intraspecific variation in *A. ineptus* is clinal, with size positively and significantly correlated with longitude. Variation within the geographically restricted *A. granti* suggests a southwesterly-northeasterly cline.

A cladistic appraisal of phylogenetic relationships among the 11 recognized species of *Aethomys* in Africa, based on qualitative cranial characters, suggests the retention of *Micaelamys* and *Aethomys* as subgenera.

Key words: *Aethomys*, systematics, nomenclature, morphometrics, cranial morphology, cytogenetics, distribution, geographic variation

For my family with love and gratitude

"Systematics is just as essential to modern biology as algebra is to an aspect of mathematics and quantum theory is to a part of physics."

M. N. Bruton

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Figure 2.1*a-k* Reference points of cranial measurements. Asterisks indicate measurements used in original descriptions, while broad arrows denote the 11 basic characters selected for the revision (see text).

a. ***1-GLS** - Greatest length of skull, from anterior edge of nasals to posterior edge of occipital condyle, along longitudinal axis of skull; **2-GLN** - Greatest length of nasals, from longest posterior projection of nasal wings to anteriormost edge of nasal bones; ***3-FRO** - Greatest length of frontals; ***4-PAR** - Greatest length of parietals; ***5-INT** - Interparietal length, from intersection of sagittal suture and posterior end of parietal, perpendicular to posterior end of interparietal; **6-NPP** - Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch; **7-NPO** - Distance from anterior edge of nasals to posterior edge of postorbital bar; **8-ZAL** - Zygomatic arch length, from posterior-most part of anterior part of zygomatic arch to anterior-most part of posterior part of zygomatic arch; ***9-BBC** - Breadth of braincase--width at dorsal root of squamosals; ***10-ZYW** - Greatest zygomatic width, between outer margins of zygomatic arches, perpendicular to longitudinal axis of skull; ***11-IOB** - Least breadth of interorbital constriction--least distance dorsally between orbits; ***12-NAS** -

Nasal width, at anterior-most point where nasals join premaxillae.

b. **13-CBL** - Condylobasal length of skull, from posterior-most projection of occipital condyles to anterior edge of premaxillae; ***14-PIC** - Incisor to condyle length, from posterior surface of I^1 at alveolus to posterior-most projection of occipital condyle; ***15-BSL** - Basal length of skull, from anterior-most point of lower border of foramen magnum to anterior edge of premaxilla; ***16-PPL** - Post-palatal length, from anterior-most edge of hard palate to anterior-most point on lower border of foramen magnum; ***17-PAL** - Palatal length, from posterior edge of I^1 alveolus to posterior edge of hard palate; **18-TRL** - Toothrow length, from anterior alveolus to posterior surface of M^3 alveolus; ***19-LPF** - Greatest length of longest palatal foramen; ***20-MAW** - Greatest maxillary width between labial crown edges of M^1; ***21-PWM** - Hard palate width at M^1 measured on lingual side of teeth at alveolus; **22-PAC** - Hard palate width at point of constriction immediately posterior to M^3; **23-VCW** - Vidian canal width at foramen lateral to pterygoid processes; **24-FJW** - Least distance between foramina jugulare on posterior edge of bullae; ***25-BUL** - Greatest bulla length at 45° angle to skull axis; ***26-BUW** - Greatest bulla width at 45° angle to skull axis.

c. ***27-ITC** - Incisor to condyle length, from anterior surface of I^1 at alveolus to posterior-most projection of the occipital condyle; ***28-LOD** - Length of diastema, from posterior base of I^1 alveolus to anterior base of M^1 alveolus; **29-HOR** - Height of rostrum, perpendicularly from a point directly behind incisors; **30-IOE** - Distance from anterior base of zygomatic plate

to anterior edge of ear opening; **31-IZD** - Infraorbital-zygomatic plate distance, from dorsal edge of infraorbital foramen to anterior base of zygomatic plate; **32-MPO** - Foramen magnum-postorbital bar length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of postorbital bar; **33-MPZ** - Foramen magnum-zygomatic arch length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of posterior part of zygomatic arch; **34-FME** - Foramen magnum-external auditory meatus length, from lateral edge of foramen magnum (at notch in lateral view) to posterodorsal edge of external auditory meatus.

d. ***35-GHS** - Greatest height of skull perpendicular to horizontal plane through bullae; **36-BCH** - Brain case height, from dorsal surface of sagittal crest to mid-ventral surface of basioccipital between anterior bullae; **37-FMH** - Foramen magnum height--widest part of foramen in vertical plane; **38-FMW** - Foramen magnum width--widest part of foramen magnum in a horizontal plane; **39-CNW** - Greatest occipital condyle width perpendicular to skull axis; **40-WAB** - Width at bullae on ear openings perpendicular to skull axis.

e. **41-FIB** - I^1 breadth--breadth of principal upper incisor at level of median edge of alveolus.

f. **42-UTR** - Crown length of maxillary toothrow, from anterior edge of M^1 at alveolus to posterior edge of M^3 at alveolus; **43-LFM** - Length of M^1 along cingulum; **44-LSM** - Length of M^2 along cingulum; **45-LTM** - Length of M^3 along cingulum.

g. **46-WFM** - Greatest cross-sectional crown width of M^1; **47-WSM** - Greatest cross-sectional crown width of M^2; **48-WTM** - Greatest cross-sectional crown width of M^3.

h. ***49-GML** - Greatest mandible length, in a straight line, from anterior edge of I_1 alveolus to posterior surface of angular process; ***50-MDL** - Greatest length of mandible (excluding teeth), from posterior surface of condylar process to anteroventral edge of incisor alveolus; **51-AFA** - Angular process-mandibular condyle length, in straight line from ventral edge of angular process to middorsal ridge of mandibular condyle; **52-MRH** - Mandible-ramus height, from dorsal edge of coronoid process to ventral edge of angular process; **53-MCA** - Mandibular condyle-angular process distance, in straight line from dorsal edge of mandibular condyle to ventral edge of angular process.

i. **54-LMH** - Least mandible height, perpendicularly from between posterior M_1 alveolus and anterior M_2 alveolus; **55-MFA** - Mandibular foramen-angular process length, from anterior edge of mandibular foramen to posterior edge of angular process; **56-MAF** - Mandibular foramen-articular facet length, from ventral edge of mandibular foramen to midposterodorsal edge of articulating facet; ***57-CMH** - Coronoid mandible height, from dorsal edge of coronoid process to ventral edge of mandible in line with mandibular foramen.

j. **58-MTL** - Mandibular toothrow, from anterior edge of I_1 alveolus to posterior edge of M_3 alveolus; **59-IML** - Posterior incisor-M_3 length, in a straight line from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus; **60-MTR** - Mandibular toothrow length, from anterior edge of M_1 alveolus to posterior edge of M_3 alveolus; **61-LLM** - Length of M_1, along cingulum; **62-LMS** - Length of M_2, along cingulum; **63-LMT** - Length of M_3, along cingulum.

k. **64-WLM** - Greatest cross-sectional crown width of M_1;

CHAPTER 1

GENERAL INTRODUCTION

1.1 BACKGROUND TO THE GENUS *AETHOMYS*

African rock rats of the genus *Aethomys* are long-tailed murid rodents of medium to large size (Meester *et al.* 1986; Skinner and Smithers 1990). The generic name is derived from the Greek *eithos*, meaning sunburnt, and *mys*, meaning a mouse (Rosevear 1969).

1.1.1 Distribution

As currently understood, the genus is a diverse group endemic to East, Central and southern Africa, but extending marginally into West Africa (Musser and Carleton 1993).

1.1.2 Habitat

Members of the genus are known to utilize a wide variety of substantially covered habitats, ranging from excavated burrows, rock crevices, rocky terrain and outcrops, tree trunks, to open savanna woodland (De Graaff 1981; Skinner and Smithers 1990). While not generally commensal, they occasionally associate with man, particularly in agriculturally developed areas (Skinner and Smithers 1990).

1.1.3 Habits

They are nocturnal, terrestrial and to some extent arboreal rodents that are either gregarious or form small family units. Some species are known to be well adapted to hot, arid environments and to aestivate in dry, summer months (Withers *et al.* 1980).

1.1.4 Food

Although few data are available, all species currently included in the genus are generally regarded to be omnivorous, with a preference for seed and grain (Watson 1987; Woodall and Mackie 1987).

1.1.5 Reproduction

African rock rats are generally thought to produce an average of three offspring per litter (Rautenbach 1978). Some species breed throughout the year, while others show no evidence of breeding during colder months (Skinner and Smithers 1990). There is, however, a tendency for unstable population cycles associated with high mortality and high reproductive potential (Withers *et al.* 1980). Population explosions may result in epidemiological problems, such as in the transmission of plague (Hallet *et al.* 1970), Rift Valley fever (Swanepoel *et al.* 1978) and schistosomiasis (Gear *et al.* 1966). This may also cause extensive damage to agricultural crops (Wilson 1970, 1975; Smithers 1971; De Graaff 1981).

1.1.6 Generic Classification

The genus has undergone a number of nomenclatural changes (Rosevear 1969). Some species currently assigned to *Aethomys* were originally ascribed to *Gerbillus*, *Praomys*, *Mus* and *Epimys* (De Graaff 1981). For simplicity, Thomas (1915*a*) proposed *Aethomys* as a subgenus and later accorded it a full generic rank (Thomas 1915*b*). This view was accepted by Ellerman (1941) in his review of the genus, in which one of the currently recognized species, *A. namaquensis*, was referred to the genus *Thallomys*.

1.1.7 Subgeneric Classification

Ellerman *et al.* (1953) relegated *Aethomys* to a subgenus of *Rattus*. Based on dental (Lundholm 1955; Meester *et al.* 1964; Davis 1965, 1968, 1975) and karyological (Matthey 1954, 1958, 1964) characteristics, however, it was subsequently reinstated as a genus, but this treatment was broadened to include *Stochomys* (with *Dephomys* as a synonym) and *Micaelamys* as subgenera (Davis 1965, 1968). Shortly thereafter, Davis (1975) considered *Dephomys* as generically distinct from *Stochomys* and removed the latter from *Aethomys*. He subdivided the genus into two subgenera, *Micaelamys* and the nominate subgenus *Aethomys*.

1.1.8 Species Level Systematics

Following Davis (1975), *A. namaquensis* and *A. granti* have traditionally been ascribed to *Micaelamys*. He allocated the remaining species to the nominate subgenus *Aethomys* which was

further subdivided into the "*kaiseri*" and "*hindei*" groups. The "*kaiseri*" group comprised *A. kaiseri*, while the "*hindei*" group included *A. bocagei*, *A. chrysophilus*, *A. nyikae*, *A. silindensis*, and *A. thomasi*. The West African endemic, *A. stannarius*, was regarded as a race of *A. hindei* (Ellerman 1941; Rosevear 1969; Hutterer and Joger 1982). More recently (Musser and Carleton 1993), the ten species recognized by Davis (1975) are still considered valid.

1.1.9 Infraspecific Systematics

Over the years, 44 subspecies have been attributed to the ten currently recognized species (Musser and Carleton 1993), but the status of some forms remains largely unknown (Denys and Tranier 1992; Denys 1995; C. Denys *pers. comm.*[1]).

1.1.10 Phylogeny

There is uncertainty about phylogenetic relationships between *Aethomys* and other African murines (Musser and Carleton 1993). Ellerman (1941) considered characteristics of the genus to overlap to some extent with *Rattus* and *Arvicanthis*. The genus has also been considered to be closely related to *Mus* (De Winton 1897), *Praomys* (= *Mastomys*), *Thallomys*, *Zelotomys* (Roberts 1951; Misonne 1969; De Graaff 1981), *Stochomys*, *Dephomys*, *Dasymys* and *Pelomys* (Davis 1965, 1968, 1975; Misonne 1969; Bonhomme *et al.*

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[1] C. Denys, Laboratoire de Mammifères et Oiseaux, Museum National d'Histoire Naturelle, Paris, France.

1985; Denys 1990*a*, 1990*b*).

Little is also known about evolutionary relationships among the currently recognized species of *Aethomys*. Apart from Davis (1975), who attempted an inclusive interpretation of species' relationships, no evolutionary study has considered all currently recognized species simultaneously. The available information has been confined to comparisons between few taxa, such as *A. bocagei*, *A. thomasi*, *A. silindensis* and *A. kaiseri* (Ellerman 1941; Musser and Carleton 1993).

Palaeontological data have been recorded from South Africa (De Graaff 1960, 1961; Avery 1981, 1982, 1995; Hendey 1981; Pocock 1987; C. Denys *pers. comm.*[1]; J. F. Thackeray *pers. comm.*[2]). Recently, two Pliocene fossil species, *A. adamanticola* and *A. modernis*, the oldest known representatives of the genus in Africa, have been described from South Africa. The former has characteristics that have been interpreted as plesiomorphic for the genus, whereas the latter is very similar to some extant southern African species (Denys 1990*a*).

Other palaeontological records include two East African Plio-Pleistocene fossil species, *A. lavocati* (Jaeger 1976, 1979) and *A. deheinzelini* (Wesselman 1984; Black and Krishtalka 1986; Denys 1987). There is no indication of any close relationship between these fossil species and those from South Africa (Denys 1990*a*, 1990*b*).

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[1] C. Denys, Laboratoire de Mammifères et Oiseaux, Museum National d'Histoire Naturelle, Paris, France.
[2] J. F. Thackeray, Department of Palaeontology, Transvaal Museum, Pretoria, South Africa.

1.2 TAXONOMIC STATUS OF *AETHOMYS* IN SOUTHERN AFRICA

Several pan-African (Ellerman 1941; Ellerman *et al.* 1953; Davis 1975; Musser and Carleton 1993) and regional (Rosevear 1969; Meester *et al.* 1986; Skinner and Smithers 1990) reviews of the genus *Aethomys* have been undertaken, but it has not been revised since its original description by Thomas in 1915. Ever since the genus was proposed, the erection of subgenera, the taxonomic placement of species, and the subsequent descriptions of numerous subspecies have led to a systematic uncertainty that requires a revision. At the very least, this should encompass the southern African taxa where the uncertainty is equally prevalent (Schlitter 1978).

1.2.1 Subgeneric Classification

Although the genus is traditionally divided in two subgenera, *Micaelamys* and *Aethomys* in southern Africa, the characters separating them are regarded as taxonomically insignificant (Musser and Carleton 1993).

1.2.2 Species Level Systematics

Following Ellerman *et al.* (1953), five species, *A. namaquensis*, *A. granti* (both in the subgenus *Micaelamys*), *A. chrysophilus*, *A. silindensis* and *A. nyikae* (subgenus *Aethomys*), are currently recognized in southern Africa (Meester *et al.* 1986; Skinner and Smithers 1990; Musser and Carleton 1993). While *A. namaquensis* and *A. chrysophilus* are widely distributed in the

subregion, *A. silindensis* and *A. granti* are relatively rare and geographically restricted. This has resulted in lack of representative material in study collections, therefore confounding reliable taxonomic allocations. In addition, the reported occurrence of *A. nyikae* in the subregion, based on a single juvenile specimen, has been accepted with reservation (Skinner and Smithers 1990).

Despite the current distinction between species, members of the genus are morphologically similar, and yet form a cytogenetically diverse group. The prevailing confusion has been exacerbated by recent chromosomal, protein electrophoretic, and spermatozoan morphology studies, which suggest the presence of two cryptic species within the currently recognized *A. chrysophilus* (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker *et al.* 1988; Breed *et al.* 1988).

1.2.3 Infraspecific Systematics

Over the years, 30 subspecies have been attributed to species of *Aethomys* in southern Africa. Although currently regarded as synonyms of nominate species, it is not clear whether the remarkable geographic variation in body size and other parameters reflects either a complex of species or subspecies (Smithers 1971; De Graaff 1981; Musser and Carleton 1993).

1.3 AIM OF STUDY

Ever since the genus *Aethomys* was proposed, the erection of

subgenera, the taxonomic allocations of species and the description of numerous subspecies have been the source of systematic uncertainty. This uncertainty largely emanates from the rarity and restricted nature of some species, questionable distributional records, general morphological similarities, high degrees of chromosomal diversity and remarkable phenotypic variation. There is, therefore, a need for a revision that will focus on the systematic status of subgenera, species, as well as subspecies.

1.3.1 Study Area

The revision encompasses taxa from the southern African subregion (south of the Zambezi and Kunene Rivers; Smithers 1983), and includes Botswana, Lesotho, Mozambique (south of the Zambezi River), Namibia, South Africa, Swaziland, and Zimbabwe (Figure 1.1). To retain a nomenclatural perspective, however, it was necessary to consider *Aethomys* from elsewhere in Africa.

1.4 OBJECTIVES OF STUDY

The main objectives of this study are:

1) To clarify the systematic status of *Aethomys* in southern Africa using a wider range of morphological techniques than has hitherto been applied to the group. In so doing, these data, in a broader sense, contribute to the increasing body of knowledge on small mammal systematics in Africa.

2) To provide a sound basis for making taxonomic judgements by undertaking an extensive assessment of geographic and non-geographic variation within species. To date, the nature and extent of geographic and non-geographic variation in this group of rodents has been virtually unknown, and is confounded by the fact that previous classifications have been based primarily on comparisons of type material.

3) To advance a hypothesis of phylogenetic relationships within the genus using all recognized species and a range of morphological traits, in an attempt to: a) elucidate phylogenetic relationships within the genus; b) derive a classification; c) assess supraspecific taxonomic implications, particularly with regard to the subgenera *Micaelamys* and *Aethomys* in southern Africa; and d) develop a biogeographical hypothesis in an attempt to explain the group's evolutionary relationships.

1.5 RELEVANCE OF STUDY

Apart from the contribution to small mammal systematics in Africa, this study may have implications in epidemiological and agricultural research associated with problem rodents. Some species have been implicated in the epidemiology of plague (Hallet *et al.* 1970), Rift Valley fever (Swanepoel *et al.* 1978) and schistosomiasis (Gear *et al.* 1966) while others may cause extensive damage to crops and stored grain (Wilson 1970, 1975; Smithers 1971; De Graaff 1981).

Members of the genus, however, are morphologically similar and yet form a cytogenetically diverse group. There is therefore

a need for a more fundamental understanding of the species identities based on morphology. Consequently, this study also attempts to devise simple and practical identification schemes that may assist health and agricultural authorities in the identification of these problem rodents in southern Africa.

1.6 APPROACH

1.6.1 Material Examined

This revision is based on museum specimens obtained from the following institutions (preceded by their standard acronyms; Genoways and Schlitter 1981):

AMNH: American Museum of Natural History, New York.
BMNH: The Natural History Museum, London.
DM: Durban Natural Science Museum, Durban.
KM: Kaffrarian Museum, King William's Town.
MM: Museums of Malawi, Blantyre.
MMKM: McGregor Museum, Kimberley.
NHMZ: Natural History Museum of Zimbabwe, Bulawayo.
NMB: National Museum, Bloemfontein.
TM: Transvaal Museum, Pretoria.
USNM: National Museum of Natural History, Smithsonian Institution, Washington D.C.

1.6.2 Procedure

1.6.2.1 Morphological Methodologies

The approach in this investigation has been to follow the biological species concept (Mayr 1942, 1969). In its simplest form, this states that species are "groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups" (Mayr 1942). Since the present study is dependent on museum specimens, disruption of gene flow was inferred from morphological evidence (Genoways and Choate 1972; Sneath and Sokal 1973; George *et al.* 1981; Wiley 1981; Dowling *et al.* 1989; Mayr and Ashlock 1991) by classical and numerical (multivariate morphometrics) taxonomic procedures.

1.6.2.1.1 An Overview of Multivariate Morphometric Methods Used

Multivariate morphometric techniques have been used to evaluate sources of variation (Straney 1978), allometry (Bookstein *et al.* 1985), ontogenetic patterns (Rohlf and Marcus 1993), morphological integration (Olson and Miller 1958; Cheverud 1982), and character associations (Taylor 1990; Taylor and Meester 1993). Most commonly, they have been used as a systematic tool to quantify differences in morphology both *within* and *among* Operational Taxonomic Units (OTUs; Sneath and Sokal 1973) (Zelditch *et al.* 1989). Joint relationships in character complexes, both *within* and *among* taxa, are simultaneously assessed through the reduction of large character sets to a few

dimensions (James and McCulloch 1990). This can be achieved by either "traditional morphometrics" that assess orthogonal distances (length, width, depth and oblique) or "new morphometric techniques" that rely on unit-free landmark/outline-based coordinates (Marcus 1990; Marcus *et al.* 1993; Rohlf and Marcus 1993).

The approach adopted in this study involves traditional morphometrics, in which linear dimensions were subjected to: 1) a class of morphometric analyses that identifies phenotypic groupings in which no *a priori* subdivision of samples into discrete units are presumed; and 2) *a posteriori* analyses that assess the integrity of the designated groups for the identification of specimens. In the former class of analyses, numerous algorithms are available (Crisp and Weston 1993) and, because they can yield substantially different results, several were employed. For example, different techniques are based on different indices, criteria, and assumptions. For this reason, two main classes of analytical techniques were used: ordination procedures and cluster analysis. Unless otherwise indicated, ordination was largely performed through principal components analysis (PCA). *A posteriori* analyses were accomplished by canonical variates (discriminant) analysis (CVA). These techniques are described briefly below. A more detailed discussion of these methods is provided by Blackith and Reyment (1971), Sneath and Sokal (1973), Neff and Marcus (1980), Wiley (1981), Bookstein *et al.* (1985), Rohlf (1990), James and McCulloch (1990), Rohlf and Bookstein (1990), Marcus *et al.* (1993), Rohlf and Marcus (1993), Sneath (1995), and references therein.

Ordination procedures reduce data to a few dimensions on the basis of distance or similarity matrices. Of the various ordination procedures, PCA assesses variation either between OTUs (Q-mode) or characters (R-mode) in an ungrouped sample by extracting linearly independent aspects of variation (linear combinations of original variables or principal components) with maximal variance (Sneath and Sokal 1973; Pimentel 1979; Gould 1984; Jolliffe 1986; Livezey 1989; James and McCulloch 1990). Graphically useful scores for each entity in the sample (principal component scores) and the relative contribution of each original variable to the principal components axes (character loadings), with their signs depending on programme used (Pimentel and Smith 1986*b*; Rohlf 1986), are generated. The proportion of variation accounted for by each character (percent variance contribution) and each principal component axis (percent trace) are also derived (Pimentel and Smith 1986*b*). If its assumptions are met, PCA has the advantage of being readily understood in geometric terms and may yield results superior to other algorithms (James and McCulloch 1990).

To complement the ordinations, minimally connected networks or minimum spanning trees (MST; Sneath and Sokal 1973) were always used in combination with PCA. The MST connects points with single links to form the tree of shortest length. When superimposed on ordinations it indicates nearest-neighbour relationships between OTUs and is useful in depicting local distortions inherent in graphs of low dimensionality (Rohlf 1970; Whiffin 1982; Marcus 1990).

In some of the analyses, correspondence analysis (CA) (or reciprocal averaging; James and McCulloch 1990), another ordination procedure, was also used to define groups *a priori*.

This class of analyses reduces a two-way contingency table of categorical data along principal axes on the basis of the chi-square statistic (*inertia*) (Hill 1973, 1974; Benzecri 1977; Greenacre 1984, 1986, 1990; James and McCulloch 1990; M. J. Greenacre *pers. comm.*[1]). Applications of correspondence analysis using continuous data have previously been made in systematics (Petit-Marie and Ponge 1979; Greenacre and Vrba 1984; M. J. Greenacre *pers. comm.*[1]).

For comparison, cluster analysis was always used in combination with PCA and MST. This approach generates phenograms (or dendrograms) which reflect a one-dimensional summary of relationships. It allows the classification of the phenetically most similar entities into hierarchical categories based on distance or similarity measures (Sneath and Sokal 1973; Mayr and Ashlock 1991). Unless otherwise indicated, the conventional unweighted pair-group method using arithmetic averages (UPGMA) clustering was used. This cross-averaging algorithm is favoured in systematics because by minimizing input and output distances (space conserving), it distributes OTUs into a reasonable number of groups (Belbin 1989; James and McCulloch 1990). To measure the goodness of fit of the phenogram to the original distances (distance phenogram) and correlations (correlation phenogram; see below), cophenetic correlation coefficients were computed (Pimentel and Smith 1986*b*).

A CVA defines mutually orthogonal multivariate axes

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[1] M. J. Greenacre, Department of Statistics, University of South Africa, Pretoria, South Africa.

All univariate and multivariate statistical procedures were accomplished using algorithms included in BIOΣTAT I and II Version 2.0 (Pimentel and Smith 1986*a*, 1986*b*), UNIVAR (FORTRAN programme developed by Power (1970) and recompiled for the IBM PC by N. J. Dippenaar[1]), NTSYS-pc Version 1.01 (Rohlf 1986), STATGRAPHICS Version 5 (STSC Inc., U.S.A. 1991) and SimCA (Greenacre 1990).

1.6.2.2 Phylogenetic Inference

Morphological and molecular data can yield congruent phylogenies (Mickevich and Johnson 1976; Mickevich and Farris 1981; Hillis 1985), and can also be complementary (Miyamoto 1981; Duellman and Hillis 1987; Hillis 1987). In spite of this, quantified morphological characters derived from commonly used morphometric methods are often considered inappropriate for phylogenetic analysis (Pimentel and Riggins 1987; Cranston and Humphries 1988; Fink and Zelditch 1995; Zelditch *et al.* 1995).

The reason is that singly or in combination, morphometric characters are generally regarded to be potentially influenced by: 1) non-genetic factors (McFarlane 1964; Hillis 1987); 2) intense natural selection pressures (Morton and Alexander 1982); 3) coding/transformation procedures that are notoriously difficult, largely theoretically unknown and/or unjustifiable (Pimentel and Riggins 1987; Cranston and Humphries 1988; Bookstein 1994; discussions on MorphMet, an INTERNET LISTserve);

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[1] N. J. Dippenaar, Department of Mammals, Transvaal Museum, Pretoria, South Africa.

4) size-related variation, which despite being adjusted for, may never be entirely removed (Creel 1986); 5) values of original characters that may be derived from small sample sizes; and 6) difficulties in discerning and/or testing for homology (Pimentel and Riggins 1987; Rohlf and Marcus 1993).

Recent studies suggest a landmark-based geometric morphometric approach, the thin-plate spline method (TPS; Swiderski 1993), as suitable for identifying characters that can, for example, be subjected to tests of homology (Fink and Zelditch 1995; Zelditch *et al.* 1995). This novel method has not been rigorously tested, however, particularly in mammalian taxa, is practically difficult to implement, and may also be subject to theoretically unknown underlying factors.

Generally, qualitative morphological data seem to be less prone to the problems cited above. Consequently, qualitative morphological traits form the basis of phylogenetic inference in the genus *Aethomys* elucidated in this study.

1.6.2.2.1 An Overview of Phylogenetic Methods Used

Approaches to, and views on the utility of various numerical methods of phylogenetic inference are diverse, and these are reviewed by Hennig (1966), Sneath and Sokal (1973), Wiley (1981), Felsenstein (1982), Brooks and Wiley (1985), Swofford and Olsen (1990), Mayr and Ashlock (1991), Wiley *et al.* (1991), Hillis (1995), Sneath (1995), and numerous recent publications in *Cladistics*, *Systematic Biology*, *Systematic Botany* and *Taxon*. Phenetic methods are unlikely to recover the true phylogeny when shared ancestral characters (symplesiomophies) derived through

convergence, parallelism or reversal (homoplasies) are unevenly distributed (Farris 1983; Hillis 1987). On the other hand, numerical cladistic methods attempt to avoid the problems inherent in phenetic methods.

Numerical cladistic analyses attempt to elucidate phylogenetic relationships on the basis of distance- or character-based methods (Mayr and Ashlock 1991). Distance-based methods, such as UPGMA cluster analysis and neighbour-joining are, however, criticized for assuming equal rates of evolutionary change in all lineages, and for not making full use of the available information because of data conversions (Farris 1983; Hillis 1987). Similarly, some character-based approaches, such as the compatibility and maximum-likelihood methods, are considered inaccurate in evolutionary models, and are computationally complicated (Hillis *et al.* 1993). In addition, some of the numerical cladistic methods cited above have been applied only to molecular data (Mayr and Ashlock 1991).

However, character-based methods based on the principle of maximum parsimony or minimum-evolution methods (Cavalli-Sforza and Edwards 1967), attempt to avoid the problems referred to above and are the most widely used numerical cladistic methods. Generally, their preferential use stems from 1) logical simplicity and ease of interpretation, as they give preference to simpler rather than complicated hypotheses, and where possible, tend to avoid *ad hoc* hypotheses; 2) prediction of both ancestral character-states and amount of change along branches; and 3) flexibility in maximizing weighting strategies and conducting character analyses (Swofford and Olsen 1990; Hillis *et al.* 1993). More importantly, a large array of efficient and powerful

analytical tools are readily available. Among numerous other options, these programs provide exact solutions through the exhaustive enumeration of all possible topologies and an exact branch-and-bound algorithm (Handy and Penny 1982). In cases of multiple, equally parsimonious trees, heuristic solutions can be obtained by consensus techniques (Adams 1972; Nelson 1979; Margush and McMorris 1981; Page 1989; Barrett *et al.* 1991). In addition, it is also possible to estimate the reliability of the inferred phylogeny and to assess phylogenetic and cladistic structure in the data through re-sampling and other statistical procedures (Faith 1991; Klassen *et al.* 1991; Hillis and Huelsenbeck 1992; Hillis and Bull 1993).

Under the criterion of maximum parsimony, hypotheses of phylogenetic relationships rely on minimizing the number of evolutionary steps from one character-state to another to unravel common ancestral relationships (Mayr and Ashlock 1991; Wiley *et al.* 1991). Evolutionary pathways are established and tested exclusively by the distribution of presumed shared-derived homologous characters (synapomorphies) (Wiley *et al.* 1991). However, when character conflicts occur, *ad hoc* hypotheses cannot be avoided. To ensure that such pathways lead to the characterization of monophyletic groups, the status of the characters needs to be delineated into derived (apomorphic) and ancestral (plesiomorphic) characters (taxic homology; Rieppel 1980; Patterson 1982; Smith 1990).

The distinction between apomorphic and plesiomorphic characters, however, is difficult to establish. This has led to many methods for assessing the evolutionary polarity of characters. These include the ingroup, palaeontological,

ontogenetic and outgroup methods (Maddison *et al.* 1984). Although their relative merits are subject to debate (cf. Lundberg 1973; Nelson 1978; Patterson 1982, 1983 versus Waltrous and Wheeler 1981; Voorzanger and van der Steen 1982; Maddison *et al.* 1984), the last two methods are possibly the most widely accepted. Since they are independent of each other, the ideal is to use both ontogenetic evidence and outgroup comparison, as each would serve as a test for the validity of the other (Mayr and Ashlock 1991). The general lack of ontogenetic evidence, however, often precludes its use. Character polarization in the present investigation was therefore established by outgroup comparison. Apart from practical considerations, this method has merit because in considering character-states and relationships of outgroups, an estimate of ancestral character-states for the ingroup can be made, even when several character-states are found among the outgroups. The method also gives reliable means of converting networks into directed trees to approximate evolutionary pathways (Waltrous and Wheeler 1981; Farris 1982; Maddison *et al.* 1984; Hillis 1987).

The selection of an appropriate outgroup is often difficult and the subject of considerable debate (Waltrous and Wheeler 1981; Farris 1982; Hood and Smith 1982). Maddison *et al.* (1984) showed that outgroup analysis using a single outgroup, as commonly practiced, may not always give the most reliable solution. They further emphasized that while distant outgroups can provide a decision for phylogenetic reconstruction based on parsimony, the ancestral state assessment is more robust the closer and more comprehensive the outgroups are to the ingroups. For these reasons, the assessment of phylogenetic relationships

in this study are based on outgroup taxa that have been suggested to be relatively close to *Aethomys*, namely *Dasymys incomtus* and *Rattus rattus*.

All cladistic analyses were accomplished using algorithms included in Phylogenetic Analysis Using Parsimony (PAUP) version 3.1.2d5 (Swofford 1993) in combination with MacClade version 3.01 (Maddison and Maddison 1992), and Hennig86 version 1.5 (Farris 1988; Fitzhugh 1989).

1.6.2.3 Conversion of Inferred Phylogeny into a Classification

The reconstruction of a phylogeny and the derivation of a classification are two independent operations (Hull 1970; Felsenstein 1983). Although not all systematic studies may emphasize the derivation of a classification, inferences of phylogenetic relationships may not easily be comprehended without summary in the form of a classification (Simpson 1961).

However, the philosophical positions adopted by various systematists can conventionally be divided into three schools of Linnaean hierarchy-based classifications: phenetic (Sneath and Sokal 1973), cladistic (Hennig 1966; Wiley 1981; Wiley *et al.* 1991), and evolutionary (Simpson 1961; Mayr 1981; Mayr and Ashlock 1991). In its simplest form, the unresolved difference between them is largely concerned with how characters should be used to derive a balanced Linnaean hierarchical classification that reflects both similarity and descent.

Pheneticists advocate classifications based on overall similarity (Sneath and Sokal 1973). Cladists only consider the relative positions of the branching points in lines of descent

(Hennig 1966; Wiley 1981; Wiley *et al.* 1991). Evolutionary taxonomists rely on the amalgamation of phenetic and cladistic information. They also consider other criteria such as species richness, morphological gaps, equivalence in ranks, and adaptive zones (Mayr 1981; Mayr and Ashlock 1991).

The difference between cladistic and evolutionary classifications largely results from the reliance by cladists on monophyletic (holophyletic; *sensu* Ashlock 1971) groups (clades) (Wiley 1981; Wiley *et al.* 1991). Evolutionary taxonomists accept and feel justified in ranking paraphyletic groups (grades) (Mayr 1981; Mayr and Ashlock 1991).

The controversy between cladistic and phenetic classifications arises from the viewpoint of pheneticists that the degree of difference among organisms is measurable and therefore repeatable. They further consider that the division points in the lines of descent are either speculative or unknowable (Sneath and Sokal 1973). Cladists argue that the relative positions on the division points in the lines of descent can be determined by appropriate study of characters, and also believe that there is no satisfactory way to measure or use relative overall similarity among organisms (Wiley 1981).

Pheneticists consider evolutionary classifications to be based on best judgement (subjectivity) rather than a repeatable procedure (Sneath and Sokal 1973). The position of evolutionary taxonomists is that phenetic classifications are not sufficient to determine the probable phylogeny. They also consider the selection and weighting of characters by pheneticists not to be in accordance with their evolutionary significance, but with their numbers, magnitude, or some other purely morphological

criterion (Michener 1970; Mayr 1981).

More recently, other systematists have argued that Linnaean ranks do not contribute to the representation of phylogenetic relationships. They have made a controversial suggestion that the entire Linnaean classification system should be discarded, opting instead for an unranked system (de Queiroz and Gauthier 1990, 1992, 1994; Cannatella and Hillis 1993; Bryant 1996). They proposed and outlined basic principles of an alternative system, phylogenetic taxonomy, in which rules of nomenclature are based directly on the tenet of common descent. An emphasis is placed on the association between taxon names and monophyletic taxa as the most fundamental aspect of the meanings of those names. They consider their approach as a basis for developing a nomenclatural system with explicit, universal and stable evolutionary meaning to taxon names. While there may be merit in the new approach, the present investigation, nevertheless, adhered to the typological Linnaean hierarchical system for comparison with the majority of previous studies.

Consequently, the present investigation is only directed towards deriving a classification for *Aethomys* with reference to the three traditional philosophies of classification. The derived classification is used to summarize overall patterns of phylogenetic relationships. An emphasis is placed on supraspecific taxonomic problems, particularly with regard to the subgenera *Micaelamys* and *Aethomys* in southern Africa, and on biogeographical implications. Since phenetic classifications rely on overall similarity, without regard for phylogeny, only cladistic and evolutionary classifications were considered. Where applicable, however, phenetic information was incorporated in the

derived classification.

1.6.3. Morphological Terminology

Throughout the study, morphological cranial terminology follows Thomas (1905), Hill (1935), Hall (1946), Rosevear (1969), Hebel and Stromberg (1976), De Blase and Martin (1981) and De Graaff (1981).

1.7 THESIS OUTLINE

The first part of this study (Chapter 2) is directed towards selecting meaningful taxonomic characters for use in a revision of *Aethomys* in southern Africa. This includes a morphometric assessment of functional units of the cranium which attempts to conform with the morphological integration concept as advocated by Olson and Miller (1958).

Chapter 3 addresses questions relating to the evaluation of non-geographic variation in the group by using a series of univariate and multivariate procedures. This was undertaken with the primary objective of establishing: 1) whether sexes should be treated separately or together, and 2) which specimens had reached adult dimensions and were therefore suitable for measurement recording and analysis in subsequent morphometric studies of the genus.

Chapter 4 examines the taxonomic status of southern African species of *Aethomys* by univariate and multivariate morphometrics as well as qualitative morphology. These analyses also included some specimens of known cytogenetic affinity. To ascertain the

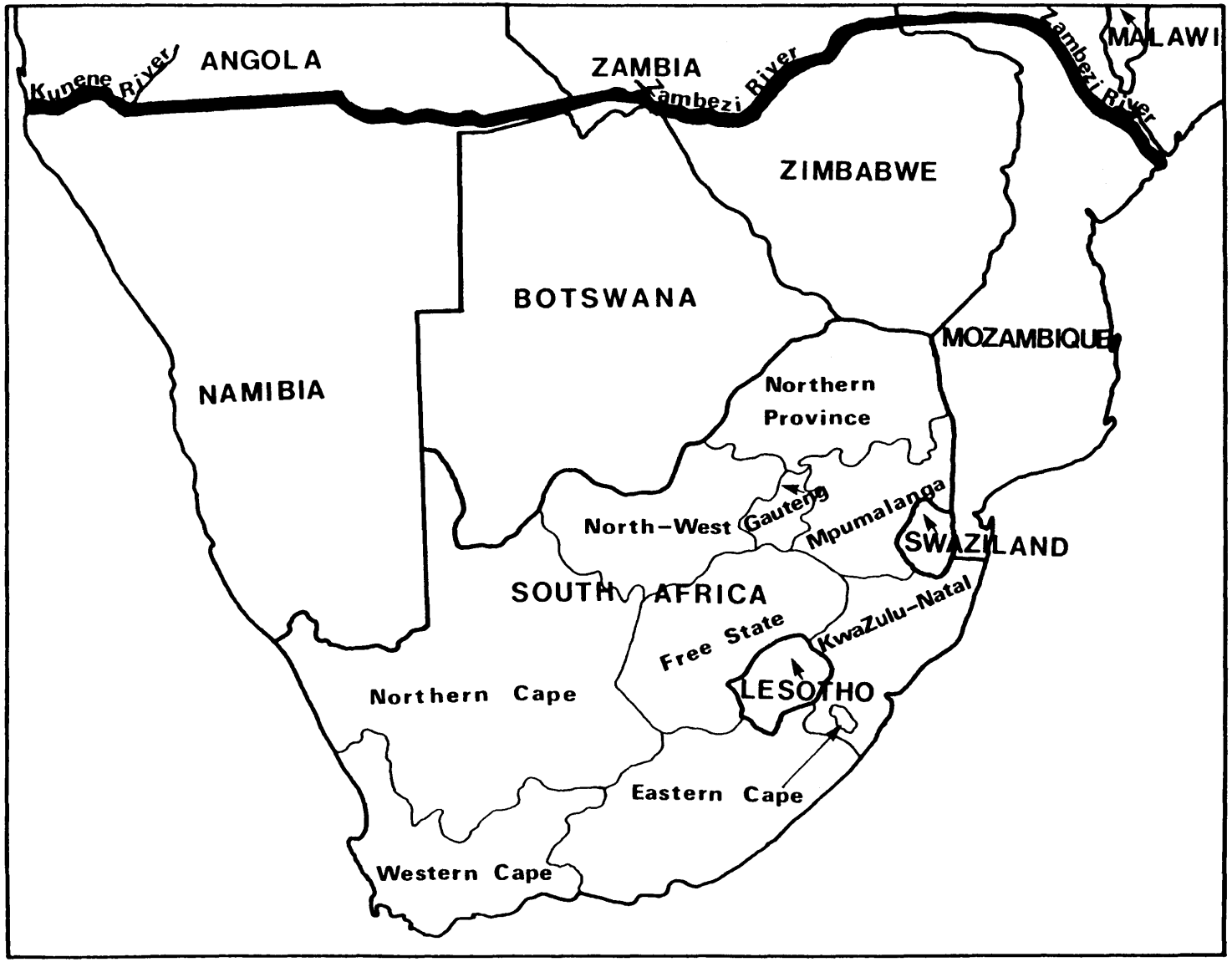
taxonomic position of some species, specimens of *Aethomys* from elsewhere in Africa were included in some of the analyses. An identification key and a formal taxonomic synthesis of species is subsequently presented together with notes on their distribution and diagnostic characters. The latter includes aspects of sperm, bacular and cuticular hair morphology summarized from previously published data.

Chapters 5 to 8 examine patterns of geographic variation in four of the five recognized species (*A. namaquensis*, *A. chrysophilus*, *A. ineptus* and *A. granti*, respectively) by univariate and multivariate morphometric procedures as well as qualitative cranial morphology. Too little material precluded the analysis of geographic variation in *A. silindensis*. Where applicable, subspecies accounts are presented.

Chapter 9 addresses questions relating to phylogenetic relationships of species within the genus by cladistic analyses of all recognized species in Africa based on qualitative morphological data. A classification for the genus is derived, and its taxonomic and biogeographical implications are discussed.

The final chapter provides a synthesis and general discussion of the major findings of the study and includes a revised classification for the genus.

Figure 1.1 Southern African political boundaries, south of the Zambezi and Kunene Rivers, indicating the geographical limits of the present revision. South African provinces referred to in the text are also indicated.



CHAPTER 2

THE SELECTION OF TAXONOMIC CHARACTERS FOR MORPHOMETRIC ANALYSIS[1]

2.1 INTRODUCTION

The present chapter examines the selection of quantitative taxonomic characters for use in the revision of *Aethomys* from southern Africa. Character selection is a critical but often neglected step in many systematic studies (Strauss and Bookstein 1982; Rohlf 1990). In small mammals, no established procedure is available for selecting appropriate character sets. Approaches used to date generally fall into four categories: 1) selection of character sets that have been used in the past, often with the *ad hoc* addition or deletion of characters after elementary correlation analysis (Power 1971; Chapman *et al.* 1992); 2) selection of as many measurements as practicable (Watson and Dippenaar 1987; Chimimba and Kitchener 1991), reflecting the influence of numerical taxonomy as advocated by Sneath and Sokal (1973); 3) selection based on an assessment of functional units of the cranium (Taylor 1990; Taylor and Meester 1993); and 4) selection of landmarks as suggested by the most recent developments in morphometrics (Strauss and Bookstein 1982; Bookstein *et al.* 1985; Zelditch *et al.* 1989; Rohlf and Bookstein

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[1] This chapter is essentially the text of the paper in Appendix IX entitled: CHIMIMBA, C. T., AND DIPPENAAR, N. J. 1995. The selection of taxonomic characters for morphometric analysis: A case study based on southern African *Aethomys* (Mammalia: Rodentia: Muridae). *Ann. Carnegie Mus. Nat. Hist.* 64:197-217.

1990; Marcus *et al.* 1993; Rohlf and Marcus 1993).

Although characters selected on the basis of the first two categories can perform well, it is important to assess character redundancy in morphometric studies (Blackith and Reyment 1971; Sneath and Sokal 1973; Thorpe 1976; James and McCulloch 1990; Rohlf 1990). Nevertheless, apart from a few studies (Thomas 1968; Best 1978; Taylor 1990; Taylor and Meester 1993), this has been rarely considered in practice. The utilization of unevaluated characters could have a profound effect on analyses (Pimentel and Smith 1986*b*), ranging from distortion of inter-OTU relationships (Blackith and Reyment 1971) to an increase in analysis time that often results in analytical problems while processing large data matrices (Chimimba and Kitchener 1991). Some studies have shown that after the assessment of linear dependence (redundancy) and colinearity, sets of many quantitative characters can be reduced to a few and still contain equivalent information (Mahalanobis *et al.* 1949; Albrecht and Blackith 1957).

Various approaches that have been used to screen for reliable characters include either ANOVA or correlations between characters (Pimentel and Smith 1986*b*). The former procedure is restricted to multigroup studies in which character redundancy is sometimes ignored (Pimentel and Smith 1986*b*). The latter approach summarizes correlations between characters by PCA, factor (Thomas 1968; Johnston 1973; Gould *et al.* 1974) and cluster analyses (Power 1971; Taylor 1990; Taylor and Meester 1993) with the selection of characters from within highly correlated subsets of characters. Another strategy has been to employ Mahalanobis' (1936) D^2 statistic (Thorpe 1976), a similarity coefficient that

takes into account the degree of information redundancy in each character as summarized by the within-group covariance. However, owing to the instability of correlation coefficients for sample sizes smaller than 20, Van Valen (1974) considered this an oversimplification (Thorpe 1976).

The approach used in the present study stems from current theory of evolutionary change which emphasizes the unity of the genotype (Mayr 1963, 1976; Lewontin 1974; Wright 1978, 1980) in which organisms are the integrated functional units that evolve (Waddington 1957; Riedl 1978; Gould and Lewontin 1979; Selzer 1993; Borgia 1994). Embryological studies have, for instance, demonstrated that the cranium represents an interacting functional character suite that has a common ontogenetic origin (Noden 1978, 1983; Gans and Northcutt 1983; Zelditch *et al.* 1993). Moreover, Olson and Miller (1958) hypothesized, and subsequently demonstrated, that the degree of cranial integration can be measured by the intensity of statistical associations in the phenotype. Therefore, developmentally and functionally related traits ought to be relatively highly correlated in the phenotype. On both empirical and theoretical grounds these authors placed developmentally and functionally interdependent morphological characters into "Functional sets" ("F-sets"). Empirically derived sets of characters that were relatively highly correlated were placed into "Phenotypic sets" ("P-sets"). Other studies support the *a priori*-defined morphologically integrated functional units of Olson and Miller (1958) (Moss and Young 1960; Cheverud 1982; Cheverud *et al.* 1989; Cane 1993). Taylor (1990) and Taylor and Meester (1993) extended the morphological integration concept into a character selection

protocol.

The present chapter is aimed at selecting meaningful morphometric characters for use in a revision of southern African *Aethomys*. Accordingly, the procedure of Taylor (1990) and Taylor and Meester (1993), which summarized character correlations in the yellow mongoose (*Cynictis penicillata*, Viverridae) by cluster analysis, is expanded upon to meet three important requirements: 1) "comprehensiveness" (i.e., the consideration of adequate coverage of the phenotype), 2) "economy" (by the removal of redundant characters), and 3) "pattern summary" (of relationships between characters consistent with the morphological integration concept of Olson and Miller 1958). *Aethomys* from southern Africa is here used as a case study for this character selection protocol that could find wider application in morphometric studies of other taxa.

Recent developments in landmark-based methods (Mousseau 1991; Rohlf and Marcus 1993), especially their extension to three-dimensional space, suggest a modification of the morphological integration concept. This would involve a more rigorous morphometric assessment of functional units (Van der Klaauw 1948-1952) based on landmarks (rather than measuring points) and a closer integration with more recent advances in ontogenetic cranial development (Thorogood and Tickle 1988).

2.2 MATERIAL AND METHODS

The present chapter is based almost exclusively on a single homogeneous sample, representing an island population of *Aethomys namaquensis* (21 males, 13 females) from Keimoes Island, Orange

River, Northern Cape Province. However, additional samples of *A. granti* (7 males, 7 females) from Sutherland, Northern Cape Province, and *A. chrysophilus* (6 males, 10 females) from Al-te-ver Farm, 1 km SSE Maasstroom, Northern Province, South Africa, were used to develop criteria for the selection of the final set of measurements. The material examined is listed in Appendix I, and a gazetteer is presented in Appendix VI.

Specimens were assigned to seven toothwear classes (following Verheyen and Bracke 1966; Morris 1972; Perrin 1982; Dippenaar and Rautenbach 1986), but to reduce the effect of age variation, only adult, toothwear class VI (Chapter 3; Chimimba and Dippenaar 1994) specimens with complete data sets were considered.

An initial set of 66 linear cranial (40 skull, nine mandible, and 17 dental) measurements (Figure 2.1*a-k*) were recorded to the nearest 0.05 mm using a pair of Fowler digital callipers, a Fowler Interface and EASYCAL program developed by S. Reig[1] for direct data input to rBase (Ashton-Tate Software, U.S.A.). While the character set reflects an attempt to distribute measurements across functional units of the skull, this was not always possible because of constraints imposed by the use of callipers and the taxonomic need to include traditional characters not selected on the basis of the morphological integration concept. Owing to the unreliability of external characters, only cranial characters were considered.

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[1] S. Reig, Museo Nacionale de Ciencias Naturales, Consejo Superior de Investigaciones Cientificas, Madrid, Spain.

Univariate and multivariate data screening (Pimentel and Smith 1986*a*, 1986*b*; Reig 1989) revealed two male specimens with outlier values not consistent with toothwear class VI. One was exceptionally large (USNM 451966) in most measurements and the other (USNM 452055) had an abnormally small greatest cross-sectional crown width of M_3 (66-WMT). To avoid the introduction of bias in the sample, the two specimens were considered not representative of the population, and excluded from subsequent analyses.

Homoscedasticity was tested for by Hartley's (1950) F_{max}-test (Sokal and Rohlf 1981) and a one-way ANOVA was used to assess sexual dimorphism. Skewness (g_1), kurtosis (g_2) and normality (Chi-square test) of the data were also examined (Zar 1974; Sokal and Rohlf 1981; Pimentel and Smith 1986*a*, 1986*b*).

Following Cheverud (1982), character associations were investigated by the cluster analysis of PCA scores generated from standardized, statistically problem-free characters. Results of three Q-mode PCAs (sexes pooled and separate) of correlations among all OTUs were similar so that only the pooled sample is considered below. The first 14 components (explaining 99.98% of the sample variance) were retained and Euclidean distances between each pair of characters subjected to Ward's (1963) hierarchical clustering algorithm to generate phenotypic sets (P-sets). This algorithm produces homogeneous clusters by minimizing the squared positional variation of elements in a cluster independently at each step (Cheverud 1982).

Selection of characters from within the cluster analysis-generated subclusters depended on six ancillary criteria in the following order of priority: (1) relative weightings of

characters in R-mode PCA and correspondence analysis of three known species, *A. chrysophilus*, *A. granti* and *A. namaquensis*; (2) consideration of coefficients of variation (CV) incorporating Haldane's (1955) correction (Sokal and Rohlf 1981); (3) measurement error (ME) (Ostle and Mensing 1975; Pankakoski *et al.* 1987; Bailey and Byrnes 1990; Lougheed *et al.* 1991) expressed as percentage of total variability due to *within*-individual variation (percent measurement error; % ME), based on three independent sets of repeated measurements recorded on separate occasions for *A. namaquensis*; (4) relative ease of measurement; (5) measuring points associated with frequently damaged areas of the skull (with reference to analyses that require complete data sets; Kim 1975; Klecka 1975); (6) previous use, particularly in original descriptions.

2.3 RESULTS

2.3.1 Univariate Screening of Measurements[1,2]

Hartley's (1950) F_{max}-test for homogeneity of variances between males and females of *A. namaquensis* indicated significant ($P < 0.05$) heteroscedasticity in four measurements, 19-LPF, 20-MAW, 38-FMW, and 50-MDL (see Figure 2.1*a-k* for measurements).

Descriptive statistics and results of a one-way ANOVA

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[1] Univariate statistics are available from the Transvaal Museum Library.
[2] Because of large numbers of characters involved, all characters are abbreviated in this chapter but fully expressed in subsequent chapters.

indicated a generally low level of sexual dimorphism in *A. namaquensis*, with significant differences in only six of the 66 characters: 4-PAR ($P < 0.05$), 21-PWM ($P < 0.05$), 31-IZD ($P < 0.01$), 51-AFA ($P < 0.01$), 53-MCA ($P < 0.01$), and 57-CMH ($P < 0.01$). This finding justified the pooling of sexes in subsequent analyses.

Results of tests for skewness and kurtosis based on the pooled male and female sample of *A. namaquensis* showed three of the 66 characters to be both skewed and kurtotic: 34-FME (both $P < 0.01$), 38-FMW ($P < 0.05$ and $P < 0.001$, respectively), and 50-MDL (both $P < 0.05$). One character, 65-WMS, was skewed only ($P < 0.05$). Three characters were kurtotic only: 49-GML ($P < 0.01$), 55-MFA ($P < 0.05$), and 62-LMS ($P < 0.001$).

Chi-square tests for normality in the pooled male and female sample of *A. namaquensis* showed that 26 of the 66 characters were non-normally distributed: 2-GLN ($P < 0.01$), 4-PAR ($P < 0.05$), 7-NPO ($P < 0.05$), 9-BBC ($P < 0.05$), 11-IOB ($P < 0.05$), 12-NAS ($P < 0.01$), 16-PPL ($P < 0.05$), 17-PAL ($P < 0.01$), 23-VCW ($P < 0.001$), 26-BUW ($P < 0.05$), 28-LOD ($P < 0.01$), 29-HOR ($P < 0.001$), 31-IZD ($P < 0.05$), 34-FME ($P < 0.05$), 38-FMW ($P < 0.001$), 40-WAB ($P < 0.05$), 41-FIB ($P < 0.001$), 47-WSM ($P < 0.05$), 49-GML ($P < 0.001$), 51-AFA ($P < 0.05$), 55-MFA ($P < 0.05$), 56-MAF ($P < 0.05$), 57-CMH ($P < 0.05$), 61-LLM ($P < 0.01$), 62-LMS ($P < 0.001$), 66-WMT ($P < 0.01$). These results may reflect the instability of this class of tests when sample sizes are small, but also draw attention to potentially problematic characters.

After the assumptions tests, the following highly conservative criteria were used to either reject or retain a character: (1) a character was rejected if it differed

significantly at the 5% level in more than one test; (2) a character was rejected if it was significant in one or more tests at the 1% level of significance; and (3) a character was retained if test statistics for sexual dimorphism, homoscedasticity, and normality did not differ significantly, or were significant in one of the three tests but only at the 5% level of significance. As a consequence, 15 potentially problematic characters were rejected (2-GLN, *12-NAS, *17-PAL, 23-VCW, *28-LOD, 29-HOR, 34-FME, 38-FMW, 41-FIB, *49-GML, *50-MDL, 55-MFA, 61-LLM, 62-LMS, 66-WMT, which included the five traditional characters indicated by asterisks). Although sample sizes were small for this class of tests, reconsideration of the 15 characters indicated that most were problematic with respect to one or more of the following: (1) vaguely defined recording points, which made the placement of calliper tips difficult and therefore subject to error; (2) high variability between specimens; and (3) an association with frequently damaged parts of the skull.

2.3.2 Analysis of Character Associations

In the phenogram derived from Ward's (1963) cluster analysis of the 51 remaining characters, three relatively discrete character groupings are apparent (Figure 2.2). The three major clusters, designated I, II, and III, are summarized in Table 2.1. Although some characters are apparently not related to the majority of characters within a given subset (indicated by question marks in Table 2.1), subclusters at both the 4- and 8-cluster stages in general form logical subsets. Major cluster I relates mainly to what may be termed a "Mixed"

Neurocranial/Orofacial functional set (F-set). Characters in this major cluster reflect size-related measurements that span the major functional units of the skull, if not the entire length of the skull. This cluster of characters is further subdivided into a subcluster comprising "Longitudinal distances" (1) and the other comprising "Oblique distances" (2).

Major cluster II relates mainly to the Neurocranial functional set. Although there are no clear demarcations at the 8-cluster stage in terms of three partially independent submatrices (frontal, parietal, and occipital; Cheverud 1982) of the Neurocranial functional set, characters in subcluster 3 include measurements of the dorsal side of the cranium and various measurements related to the configuration of the braincase itself, the exception being 8-ZAL which belongs to the orbital submatrix of the Orofacial functional set. Subcluster 4 also includes two measurements related to the configuration of the braincase, as well as upper toothrow length (18-TRL), which belongs to the dental phenotypic set in the Orofacial functional set, and distance from anterior base of zygomatic plate to anterior edge of ear opening (30-IOE) of "Mixed" Orofacial/Neurocranial origin.

Major cluster III relates mainly to the Orofacial functional set. Most characters (23 of 33) collectively fit into orbital/oral/masticatory phenotypic set in the Orofacial functional set. In cluster C, subcluster 5 includes measurements of the lateral region of the rostrum, the orbital and post-palatal regions and the toothrows, and one mandibular measurement, whereas almost all mandibular measurements appear in subclusters 6 and 7. Of interest is that almost all measurements

related to the bullae and the foramen magnum also appear in cluster C.

Most prominent at the 8-cluster stage is subcluster 8, which, with the exception of hard palate width at M^1 (21-PWM), are masticatory characters joining up at relatively low distances, suggestive of a tightly integrated dental submatrix.

2.3.3 Selection of Measurements

One of the criteria developed to select measurements from within subclusters relied on ordinations, both principal component (Figure 2.3) and correspondence (Figure 2.4) analyses, of known taxa (*A. namaquensis*, *A. chrysophilus*, and *A. granti*). The first two axes from the PCA show *A. granti* to separate from both *A. chrysophilus* and *A. namaquensis* along the second axis, whereas the latter two species are separated from each other along the first axis; there was little or no differentiation between the three taxa along components 3 to 14. Principal component I generally has high and negative loadings on all measurements (Table 2.1), with generally high percent variances associated with each character's component contribution (in brackets in Table 2.1). This suggests that the separation between *A. chrysophilus* and *A. namaquensis* is primarily size-related. The second axis, which is instrumental in separating *A. granti* from both *A. chrysophilus* and *A. namaquensis*, has character loadings and percent variances of different magnitudes (the former with different signs), suggesting shape-related variation. The important characters with relatively high loadings (regardless of sign) on the second axis are: 3-FRO, 4-PAR, 5-INT, 6-NPP, 26-BUW,

31-IZD, 37-FMH, 47-WSM, 53-MCA, 56-MAF, 58-MTL, 59-IML, and 65-WMS.

Figure 2.4 shows the two-dimensional symmetric profiles from correspondence analysis, with specimens from the same taxon enclosed in polygons. There is clear separation among the three species along both principal axes I (Inertia = 25.27% and λ_1 = 0.0004) and II (20.59%; λ_2 = 0.0003). A plot of individual characters, which allows examination of the level of association between rows (specimens in this case) and columns (characters), is superimposed on the same figure. The scattergram shows that separation of the three taxa can be explained in terms of the corresponding apposition of the following characters in the planes of separation: 3-FRO, 4-PAR, 5-INT, 6-NPP, 26-BUW, 31-IZD, 37-FMH, 43-LFM, 44-LSM, 45-LTM, 46-WFM, 47-WSM, 51-AFA, 53-MCA, 56-MAF, 58-MTL, 59-IML, and 65-WMS. Characters important in the separation of the three taxa are shown by their relatively high loadings in the first and second principal coordinates (Table 2.1) which, for ease of interpretation, are presented in permills (thousandths).

The results of the PCA and correspondence analysis are largely congruent in that the 13 shape-related characters generated by the second principal component were also generated by the two principal coordinates in correspondence analysis. The following characters also featured prominently in correspondence analysis: 43-LFM, 44-LSM, 45-LTM, 46-WFM, and 51-AFA.

Table 2.1, in which characters are arranged according to cluster analysis-derived phenotypic sets, summarizes the data used in character selection. This includes CVs, % ME values, character loadings on the first and second axes of principal

component and correspondence analyses. Other criteria invoked were relative ease of measurement, potential for non-missing values, previous use and cranial configuration. Based on the premise that most subclusters represent distinct submatrices of either the Neurocranial or the Orofacial functional unit, one or more characters were selected as representative of the configuration of a particular unit. More than one character was often selected, particularly if the characters were consistently found to be relevant in both the principal component and correspondence analyses, and these included obviously misplaced characters with regard to functional units of the cranium.

The rationale for the selection of characters within a subcluster (with subcluster numbering corresponding to the 8-cluster stage in Figure 2.2 and Table 2.1) and is presented below:

Subcluster 1.-- The notion that shape is more heritable than size (Humphries *et al.* 1981) has been criticized by Leamy and Thorpe (1984). Size is certainly important in infraspecific studies. For example, in a PCA of different populations of *C. penicillata*, Taylor (1990) and Taylor and Meester (1993) found that virtually all the significant variation was in the first size-related axis. Consequently one character from subcluster 1, comprising size-related measurements, was selected for inclusion in the basic data suite. High loadings on the first principal component axis (> 0.90) indicate that all characters in this major cluster qualify as good predictors of general size. In addition, all the characters have low coefficients of variation and percent measurement error values. The greatest length of the skull (1-GLS) was, however, selected because of its relatively

high loading on the first principal coordinate in correspondence analysis, relative ease of measurement, and the fact that it features prominently in rodent systematics. This character, in combination with cranial width and depth measurements (see below), also captures descriptive information relating to gross cranial configuration.

Subcluster 2.-- Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (6-NPP) was selected because it featured prominently in the first principal coordinate in correspondence analysis. It has relatively low CV and % ME values and being an "oblique" measurement, may capture different configurations of the skull.

Subcluster 3.-- Of the seven characters in this subcluster, greatest length of frontals (3-FRO) is the only character selected. In addition to having low CV and % ME values, it was consistently highlighted as important by both axes in the correspondence analysis as well as the second component of PCA. It is also a measurement that features prominently in original descriptions.

Subcluster 4.-- None of the four characters in this subcluster was shown to be of particular relevance (but see discussion on the selection of descriptive characters below).

Subcluster 5.-- The following three characters in this subcluster were selected: greatest bulla width (26-BUW), foramen magnum height (37-FMH), and mandibular foramen-articular facet length (56-MAF), all of which were shown to be of importance, either independently or in combination, by both principal coordinates in the correspondence analysis and principal component II in the PCA. These characters also have low CVs and %

ME values. Collectively, the three characters capture different configurations of the skull, as suggested by the negative and positive loadings, respectively, of foramen magnum height (37-FMH) and mandibular foramen-articular facet length (56-MAF) on the second principal component. Greatest bulla width (26-BUW) features prominently in original descriptions.

Subcluster 6.-- Angular process-mandibular condyle length (51-AFA), one of the eight characters in this subcluster, was selected because of its importance in principal coordinate I in correspondence analysis, and low CV and % ME values. Mandibular toothrow (58-MTL) is another character shown to be of importance (but see discussion of subcluster 7).

Subcluster 7.-- Of the four characters comprising this subcluster, posterior incisor-M_3 length (59-IML) was selected because of its low CV and % ME values, and its importance in both correspondence (coordinate I) and principal component (component II) analyses. This character, as well as mandibular toothrow (58-MTL) in subcluster 6, although placed in different subsets, seem to encapsulate the same information, but since the latter measurement is relatively difficult to score, 59-IML was selected.

Subcluster 8.-- Three characters in this subcluster were selected because of their low CVs, % ME values, and their importance (either individually or in combination) in principal coordinates I and II of the correspondence analysis, and principal component II of the PCA. These were: length of M^1 (43-LFM), and greatest cross-sectional crown widths of M^2 (47-WSM) and M_2 (65-WMS). The combination of an upper jaw tooth length (43-LFM) and width (47-WSM) and lower jaw tooth width

(65-WMS) may improve the information content associated with different tooth configurations.

Overall, three of the 11 selected characters, 1-GLS, 3-FRO, and 26-BUW (indicated by asterisks in Table 2.1 and broad arrows in Figures 2.1*a-k*), feature prominently in original descriptions.

The underlined characters in Table 2.1 were selected for descriptive purposes only, and include breadth of braincase (9-BBC), greatest height of skull (35-GHS), interorbital constriction (11-IOB), and greatest bulla length (25-BUL). These characters, in combination with greatest length of skull (1-GLS), capture gross cranial configuration. For ease of reference in subsequent chapters, the 15 cranial measurements are summarized in Figure 2.5. Other descriptive characters incorporated into the data set were the standard external measurements, head and body length, tail length, hind foot length, and ear length, all recorded from specimen labels.

Given the three groupings of characters (11 basic cranial, four descriptive cranial, and four standard descriptive external), their selective use (independently or in combination) will depend on the choice of analyses to be used in the revision. Since multivariate procedures involve the assessment of joint relationships among intercorrelated variables to evaluate overall inter-OTU differences (James and McCulloch 1990), all subsequent multivariate analyses will be based on the 11 basic cranial characters, and will form the basis of taxonomic conclusions in the revision. The four descriptive cranial characters, in combination with the 11 basic cranial characters (Figure 2.5), could be used for exploratory multivariate analyses. Univariate analyses, which evaluate the equality of means for each variable

independently, and ignore correlations among variables (Willig *et al.* 1986), could be based on all three groupings of characters, and only used for descriptive and comparative purposes.

2.4 DISCUSSION

The approach to character selection adopted in the present paper is an extension of the procedure suggested by Taylor (1990) and Taylor and Meester (1993) who summarized character correlations in *C. penicillata* by means of cluster analysis. Representative characters were then selected on the basis on low coefficients of variation, previous use, and ease of measurement, and the results interpreted in terms of the morphological integration concept of Olson and Miller (1958).

In the case of *Aethomys*, the approach mirrored that of Taylor (1990) and Taylor and Meester (1993), but was expanded to include potentially useful characters from various regions of the skull (including characters used previously) in a single homogeneous sample. The data set was screened for outliers and all characters subjected to univariate assumptions tests (normality, equality of variances and sexual dimorphism). These were followed by the analysis of statistical associations between characters, using PCA and cluster analysis, with reference to a morphometric assessment of functional units of the cranium. This approach is consistent with the morphological integration concept of Olson and Miller (1958). The analyses also included samples drawn from various taxa in the current classification as an aid in the selection of characters from identified phenotypic sets and their subsets, while considering

criteria such as the CV, % ME, ease of recording and previous use.

The procedures followed by Taylor (1990), Taylor and Meester (1993) and the present study are more objective than using untested, previously used characters or simply recording as many characters as possible in the hope of assessing relationships between OTUs. These approaches could have wider application in morphometrics, particularly in organisms in which cranial ontogenetic origins and interactions, structural components, evolution and adaptive functional potential of organismic form can be determined (Noden 1978, 1983; Gans and Northcutt 1983; Zelditch *et al.* 1993). This has already been tentatively demonstrated in some mammalian (Olson and Miller 1958; Moss and Young 1960; Moore 1981; Cheverud 1982) and avian groups (Noden 1978, 1983; Cane 1993).

Analysis of the largest available sample of southern African *Aethomys* from a single locality (an island population of *A. namaquensis*) identified two outliers that were considered not representative of the population and were excluded from the data set. The assumptions tests (Zar 1974; Sokal and Rohlf 1981; Pimentel and Smith 1986*a*, 1986*b*) identified 15 characters as statistically problematic due to significant sexually dimorphism, heteroscedasticity, and/or were non-normally distributed. These results could be related *a posteriori* to difficulties experienced in their recording, ambiguously defined measuring points in some specimens, high variability of characters among specimens, and characters associated with frequently damaged parts of the skull.

Interestingly, nasal width (12-NAS), palatal length (17-PAL), length of diastema (28-LOD), greatest mandible length

(from anterior edge of I_1 alveolus to posterior surface of angular process) (49-GML), and from anteroventral edge of I_1 alveolus to posterior surface of condylar process (50-MDL) which were problematic have been used extensively in previous studies (Smith 1834; Roberts 1951; Ellerman *et al.* 1953; Meester *et al.* 1986; Skinner and Smithers 1990). The data screening procedures underscore Pimentel and Smith's (1986*b*) remarks that test statistics are particularly useful in the earliest phases of data analysis in taxonomic studies.

The results of the cluster analysis of character associations were encouraging in as much as the major Neurocranial and Orofacial functional units were identified. In this respect, the results are similar to those obtained by Cheverud (1982), Taylor (1990) and Taylor and Meester (1993). Apart from these functional units, some measurements, particularly the length measurements traditionally used by taxonomists such as condylobasal length, failed to fit into these units and formed a major cluster comprising "Mixed" Neurocranial/Orofacial characters. In *C. penicillata*, these "Mixed" measurements were grouped in the Neurocranial functional set (Taylor 1990; Taylor and Meester 1993) rather than in a separate major cluster as in *Aethomys*.

The primary objective of the study was to evaluate new and previously used characters in order to identify a reduced set of measurements that would summarize the most important variation present in the cranial configuration. Since many of the measurements spanned the major functional units of the cranium, it was not surprising that the classification of measurements was equivocal. However, the analysis did generate highly correlated

subsets of measurements, particularly in the case of dental characters. Strong indications of logical subsets were also evident in the configuration of the braincase and dorsal aspect of the skull, and the orbital/oral/masticatory functional submatrices with which characters related to the bullae and foramen magnum were also associated.

Ancillary to the analysis of character associations, analysis of known taxa was undertaken to develop criteria for the selection of representative characters from within the phenotypic sets generated by the cluster analysis. This step was considered necessary since the analysis of character associations did not produce unequivocal groupings of characters, and because it was not clear how tightly specific functional units are integrated in the phenotype. The final selection of the 11 basic measurements to be used for the revision of southern African *Aethomys* was also made with reference to coefficients of variation, measurement error, likelihood of damage, and use by previous authors. The 11 measurements are: greatest length of skull (1-GLS), greatest length of frontals (3-FRO), distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (6-NPP), greatest bulla width (26-BUW), foramen magnum height (37-FMH), length of M^1 (43-LFM), greatest cross-sectional crown width of M^1 (47-WSM), angular process-mandibular condyle length (51-AFA), mandibular foramen-articular facet length (56-MAF), posterior incisor-M_3 (59-IML) and greatest cross-sectional crown width of M_2 (65-WMS). All characters had low coefficients of variation except greatest length of parietals (4-PAR), interparietal length (5-INT), hard palate width at M^1 (21-PWM), infraorbital-zygomatic plate distance (31-IZD), length of M^2 (44-LSM) and M^3 (45-LTM),

greatest cross-sectional crown width of M^3 (48-WTM), and length of M_3 (63-LMT) (Table 2.1). The percent measurement error showed this parameter to be negligible in all characters recorded (Table 2.1). In contrast, percent measurement error values of over 50% have been recorded in recent studies on birds and mussels (Bailey and Byrnes 1990).

The PCA and correspondence analysis were used to develop criteria for the selection of representative characters with good agreement on characters shown to be of relevance. The CVA (Pimentel 1979; Campbell and Atchley 1981; Livezey 1989, 1990; Livezey and Storer 1992) was also considered but in an analysis of the 51-character data set, a singular dispersion matrix precluded further analysis (Pimentel and Smith 1986*b*). Similar computational difficulties were encountered by Taylor (1990) and Taylor and Meester (1993) using a 48-variable matrix.

In these circumstances, a stepwise discriminant analysis is recommended (Livezey *in litt*[1].), in part because the multivariate discrimination is based on a subset of original variables that maximally contrast groups and cannot produce a singular covariance matrix. Furthermore, in performing the stepwise selection procedure (either forward or backward stepping), an additional multivariate assessment of the relative (combined) importance and redundancy of variables in separating groups is performed. Unfortunately, the stepwise procedure, available in Statistical Packages for Social Sciences (SPSS; Nie *et al.* 1975),

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Statistical Analysis System (SAS; SAS Institute, Inc. 1990), and Biomedical Computer Programmes (BMDP; Dixon 1985), were not available for this study.

It is likely that the computational problems encountered are related to: 1) large numbers of linearly and colinearly constrained variables (Pimentel and Smith 1986*b*); 2) the presence of ipsative variables (Pimentel 1979); and 3) the sample size being much smaller relative to number of variables (Williams and Titus 1988). These results emphasize the dangers of encountering analytical problems when using many unscreened variables in morphometric studies (Blackith and Reyment 1971).

Recently, sophisticated three-dimensional measuring equipment and advances in unit-free, landmark-based morphometric methods (Strauss and Bookstein 1982; Rohlf and Bookstein 1990, and references therein; Marcus *et al.* 1993; Rohlf and Marcus 1993) have been introduced. Future development of character selection protocols should therefore focus on a clearer demarcation of the functional units of the cranium in relation to the individual cranial elements. Additionally, there should be a synergism between landmark selection and the objectives of both species delineation and higher classification. In the present study the emphasis was on the former, while a different set of qualitative data will be used for phylogenetic analysis. The emphasis should also shift to a rigorous assessment of traditional characters. This is already apparent in the present investigation where some of these characters were included simply for descriptive purposes and for comparison with previous studies, particularly with reference to their utility in relating morphometric results to the nomenclature.

2.5 CONCLUSIONS

Prior to a systematic revision of southern African rock rats of the genus *Aethomys*, statistical procedures were used to select morphometric characters for recording and subsequent use in a revision of the group. The procedure advocated herein could have wider application in morphometric studies. An initial set of 66 cranial characters was reduced to 51 after the data set was subjected to routine assumptions tests. The remaining 51 characters, considered to be statistically problem-free, were reduced to a final set of 11 characters. This followed the use of cluster and ordination procedures to summarize patterns of correlations between characters, develop criteria for the selection of representative measurements within cluster analysis-generated subclusters, and the subsequent removal of redundant variables. The procedure attempts to economize while at the same time adequately represent the phenotype, an approach consistent with the concept of morphological integration. Four additional cranial and four standard external characters, to be used for descriptive and comparative purposes only, were also included in the final data set.

Figure 2.1*a-k* Reference points of cranial measurements. Asterisks indicate measurements used in original descriptions, while broad arrows denote the 11 basic characters selected for the revision (see text).

a. ***1-GLS** - Greatest length of skull, from anterior edge of nasals to posterior edge of occipital condyle, along longitudinal axis of skull; **2-GLN** - Greatest length of nasals, from longest posterior projection of nasal wings to anteriormost edge of nasal bones; ***3-FRO** - Greatest length of frontals; ***4-PAR** - Greatest length of parietals; ***5-INT** - Interparietal length, from intersection of sagittal suture and posterior end of parietal, perpendicular to posterior end of interparietal; **6-NPP** - Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch; **7-NPO** - Distance from anterior edge of nasals to posterior edge of postorbital bar; **8-ZAL** - Zygomatic arch length, from posterior-most part of anterior part of zygomatic arch to anterior-most part of posterior part of zygomatic arch; ***9-BBC** - Breadth of braincase--width at dorsal root of squamosals; ***10-ZYW** - Greatest zygomatic width, between outer margins of zygomatic arches, perpendicular to longitudinal axis of skull; ***11-IOB** - Least breadth of interorbital constriction--least distance dorsally between orbits; ***12-NAS** - Nasal width, at anterior-most point where nasals join premaxillae.

b. **13-CBL** - Condylobasal length of skull, from posterior-most projection of occipital condyles to anterior edge of premaxillae; ***14-PIC** - Incisor to condyle length, from posterior surface of I^1 at alveolus to posterior-most projection of occipital condyle; ***15-BSL** - Basal length of skull, from

anterior-most point of lower border of foramen magnum to anterior edge of premaxilla; ***16-PPL** - Post-palatal length, from anterior-most edge of hard palate to anterior-most point on lower border of foramen magnum; ***17-PAL** - Palatal length, from posterior edge of I^1 alveolus to posterior edge of hard palate; **18-TRL** - Toothrow length, from anterior alveolus to posterior surface of M^3 alveolus; ***19-LPF** - Greatest length of longest palatal foramen; ***20-MAW** - Greatest maxillary width between labial crown edges of M^1; ***21-PWM** - Hard palate width at M^1 measured on lingual side of teeth at alveolus; **22-PAC** - Hard palate width at point of constriction immediately posterior to M^3; **23-VCW** - Vidian canal width at foramen lateral to pterygoid processes; **24-FJW** - Least distance between foramina jugulare on posterior edge of bullae; ***25-BUL** - Greatest bulla length at 45° angle to skull axis; ***26-BUW** - Greatest bulla width at 45° angle to skull axis.

c. ***27-ITC** - Incisor to condyle length, from anterior surface of I^1 at alveolus to posterior-most projection of the occipital condyle; ***28-LOD** - Length of diastema, from posterior base of I^1 alveolus to anterior base of M^1 alveolus; **29-HOR** - Height of rostrum, perpendicularly from a point directly behind incisors; **30-IOE** - Distance from anterior base of zygomatic plate to anterior edge of ear opening; **31-IZD** - Infraorbital-zygomatic plate distance, from dorsal edge of infraorbital foramen to anterior base of zygomatic plate; **32-MPO** - Foramen magnum-postorbital bar length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of postorbital bar; **33-MPZ** - Foramen magnum-zygomatic arch length, from lateral edge of foramen magnum (at notch in lateral view) to anterior

edge of posterior part of zygomatic arch; **34-FME** - Foramen magnum-external auditory meatus length, from lateral edge of foramen magnum (at notch in lateral view) to posterodorsal edge of external auditory meatus.

d. ***35-GHS** - Greatest height of skull perpendicular to horizontal plane through bullae; **36-BCH** - Brain case height, from dorsal surface of sagittal crest to mid-ventral surface of basioccipital between anterior bullae; **37-FMH** - Foramen magnum height--widest part of foramen in vertical plane; **38-FMW** - Foramen magnum width--widest part of foramen magnum in a horizontal plane; **39-CNW** - Greatest occipital condyle width perpendicular to skull axis; **40-WAB** - Width at bullae on ear openings perpendicular to skull axis.

e. **41-FIB** - I^1 breadth--breadth of principal upper incisor at level of median edge of alveolus.

f. **42-UTR** - Crown length of maxillary toothrow, from anterior edge of M^1 at alveolus to posterior edge of M^3 at alveolus; **43-LFM** - Length of M^1 along cingulum; **44-LSM** - Length of M^2 along cingulum; **45-LTM** - Length of M^3 along cingulum.

g. **46-WFM** - Greatest cross-sectional crown width of M^1; **47-WSM** - Greatest cross-sectional crown width of M^2; **48-WTM** - Greatest cross-sectional crown width of M^3.

h. ***49-GML** - Greatest mandible length, in a straight line, from anterior edge of I_1 alveolus to posterior surface of angular process; ***50-MDL** - Greatest length of mandible (excluding teeth), from posterior surface of condylar process to anteroventral edge of incisor alveolus; **51-AFA** - Angular process-mandibular condyle length, in straight line from ventral edge of angular process to middorsal ridge of mandibular condyle; **52-MRH** - Mandible-ramus

height, from dorsal edge of coronoid process to ventral edge of angular process; **53-MCA** - Mandibular condyle-angular process distance, in straight line from dorsal edge of mandibular condyle to ventral edge of angular process.

i. **54-LMH** - Least mandible height, perpendicularly from between posterior M_1 alveolus and anterior M_2 alveolus; **55-MFA** - Mandibular foramen-angular process length, from anterior edge of mandibular foramen to posterior edge of angular process; **56-MAF** - Mandibular foramen-articular facet length, from ventral edge of mandibular foramen to midposterodorsal edge of articulating facet; ***57-CMH** - Coronoid mandible height, from dorsal edge of coronoid process to ventral edge of mandible in line with mandibular foramen.

j. **58-MTL** - Mandibular toothrow, from anterior edge of I_1 alveolus to posterior edge of M_3 alveolus; **59-IML** - Posterior incisor-M_3 length, in a straight line from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus; **60-MTR** - Mandibular toothrow length, from anterior edge of M_1 alveolus to posterior edge of M_3 alveolus; **61-LLM** - Length of M_1, along cingulum; **62-LMS** - Length of M_2, along cingulum; **63-LMT** - Length of M_3, along cingulum.

k. **64-WLM** - Greatest cross-sectional crown width of M_1; **65-WMS** - Greatest cross-sectional crown width of M_2; **66-WMT** - Greatest cross-sectional crown width of M_3.

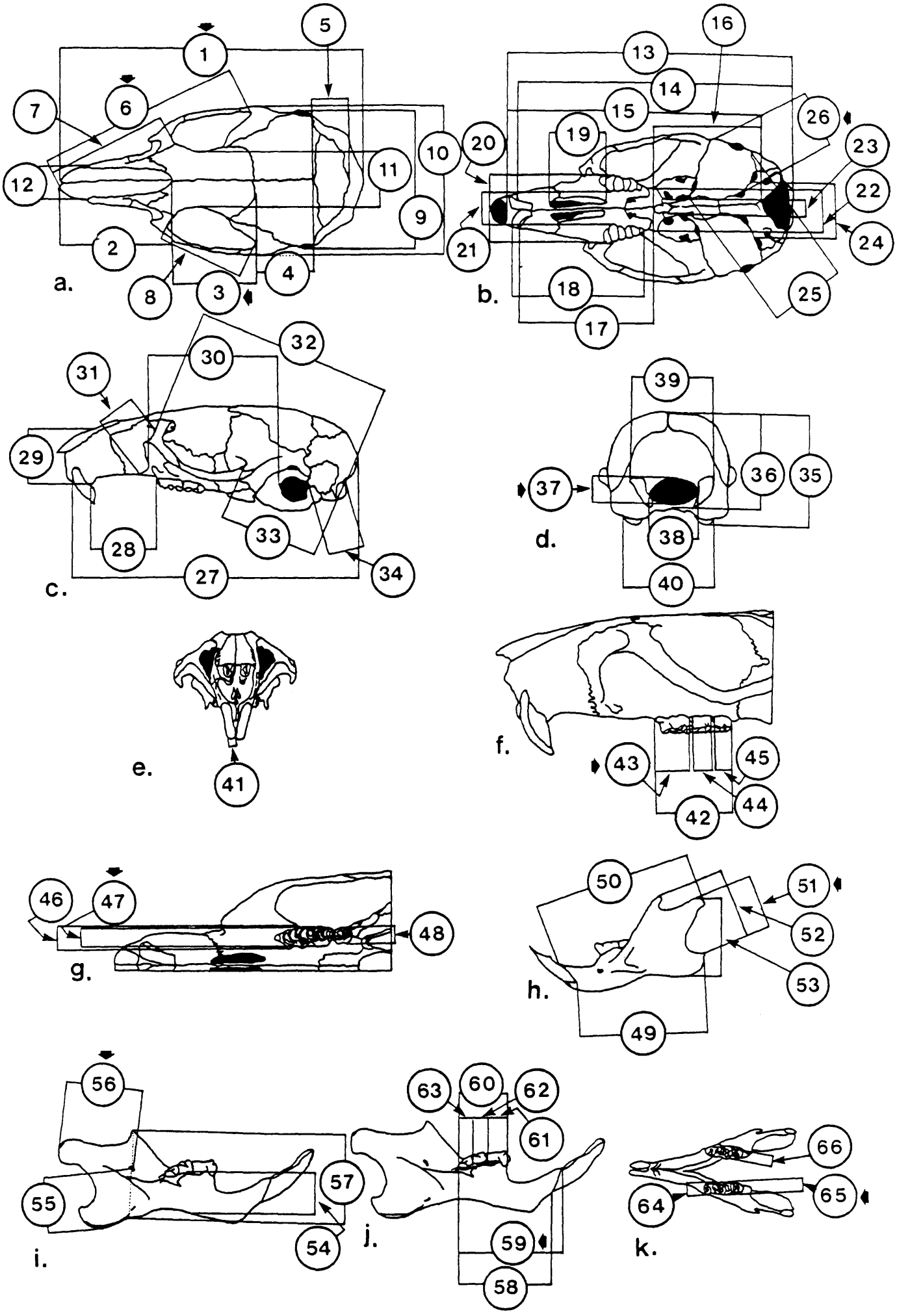

Figure 2.2 Phenogram depicting relationships between cranial measurements in *Aethomys namaquensis*. Clusters formed at the three-, four- and eight-cluster stages are indicated by enclosed letters and numbers. Characters are defined in Figures 2.1*a-k*. Cophenetic correlation coefficient = 0.81.

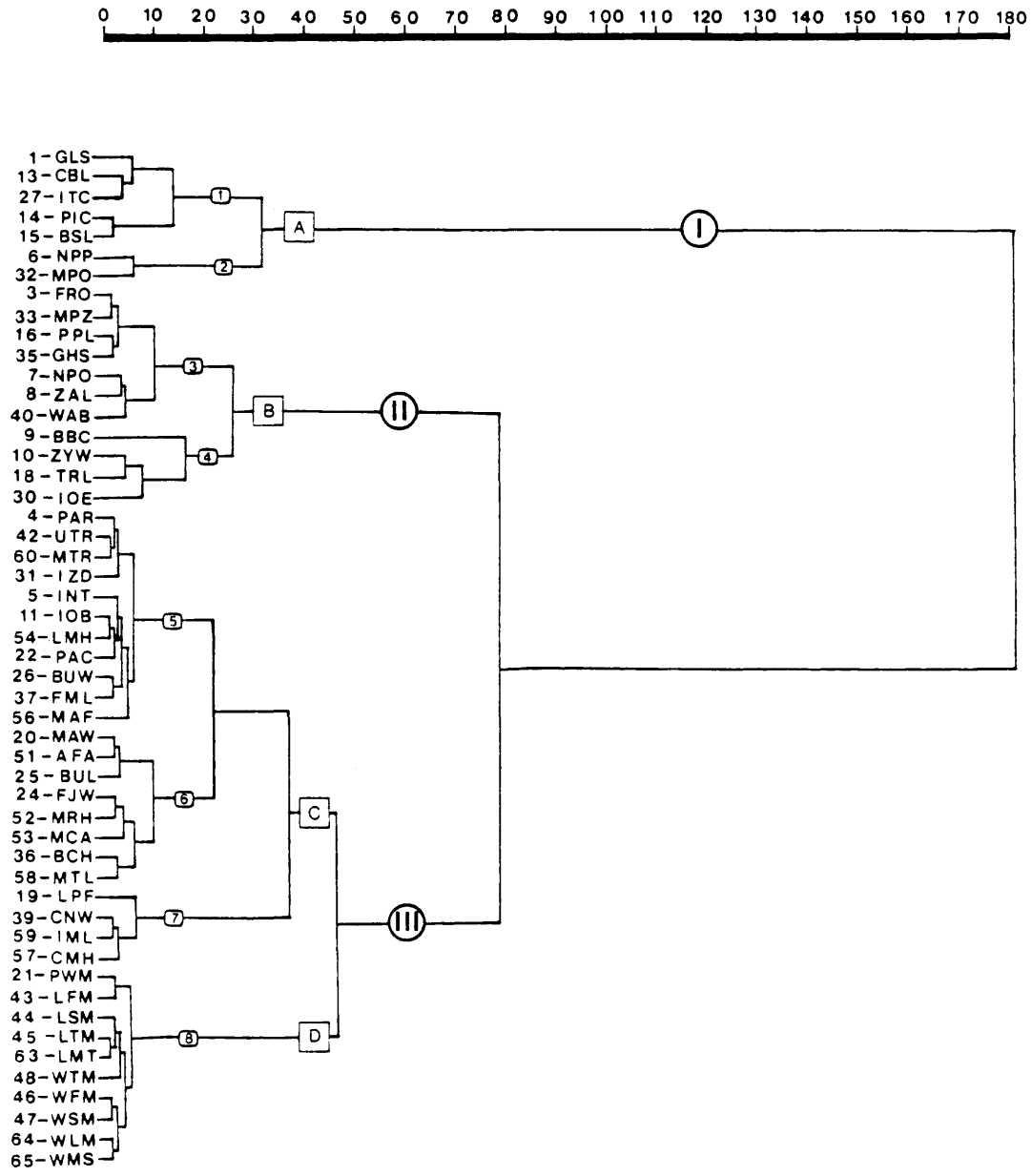

Figure 2.3 First two components from a principal components analysis of specimens of *Aethomys chrysophilus*, open triangle; *A. granti*, open circle; and *A. namaquensis*, open square. Polygons include specimens from the same taxon.

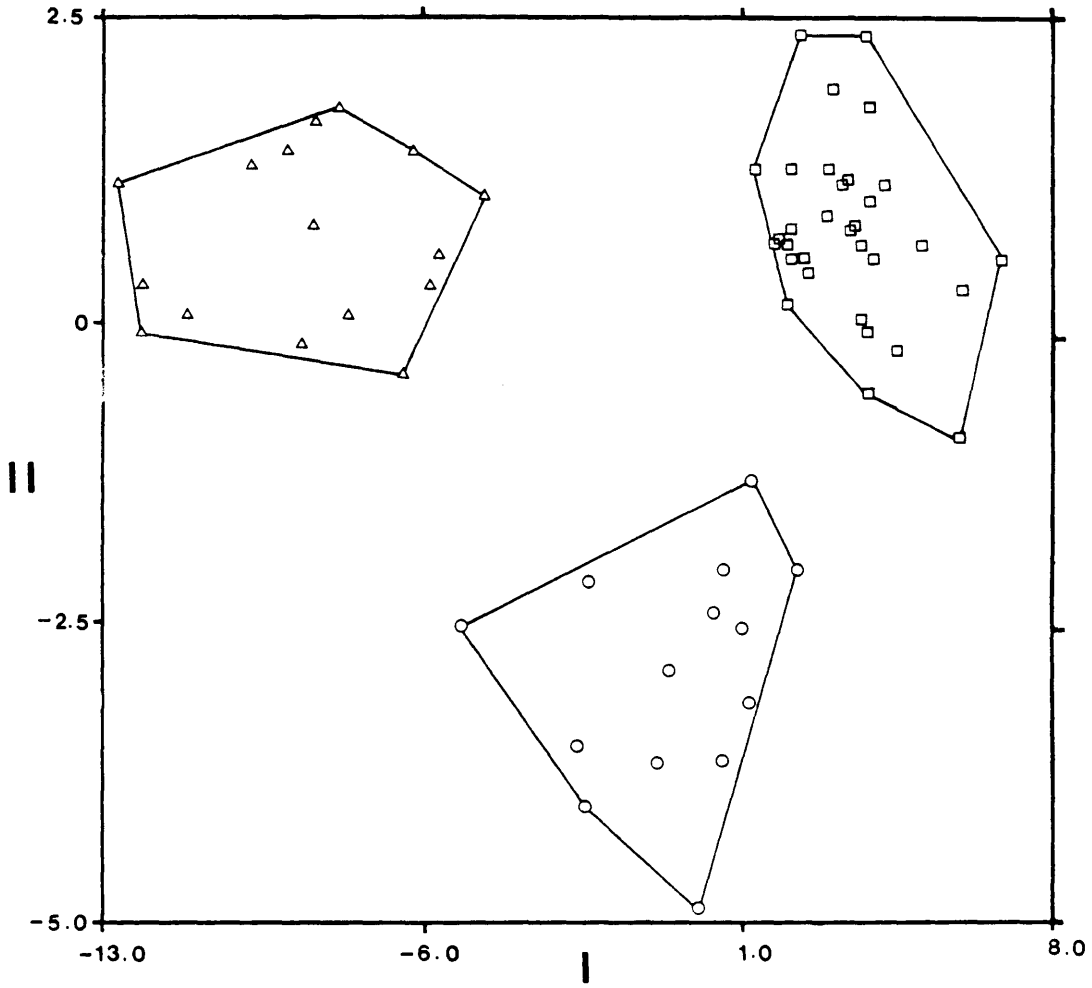

Figure 2.4 Optimal two-dimensional symmetrical map of characters and specimens generated by correspondence analysis of *Aethomys chrysophilus*, open triangle; *A. granti*, open circle; and *A. namaquensis*, open square. Polygons include specimens from the same taxon. Characters are defined in Figure 2*a-k*.

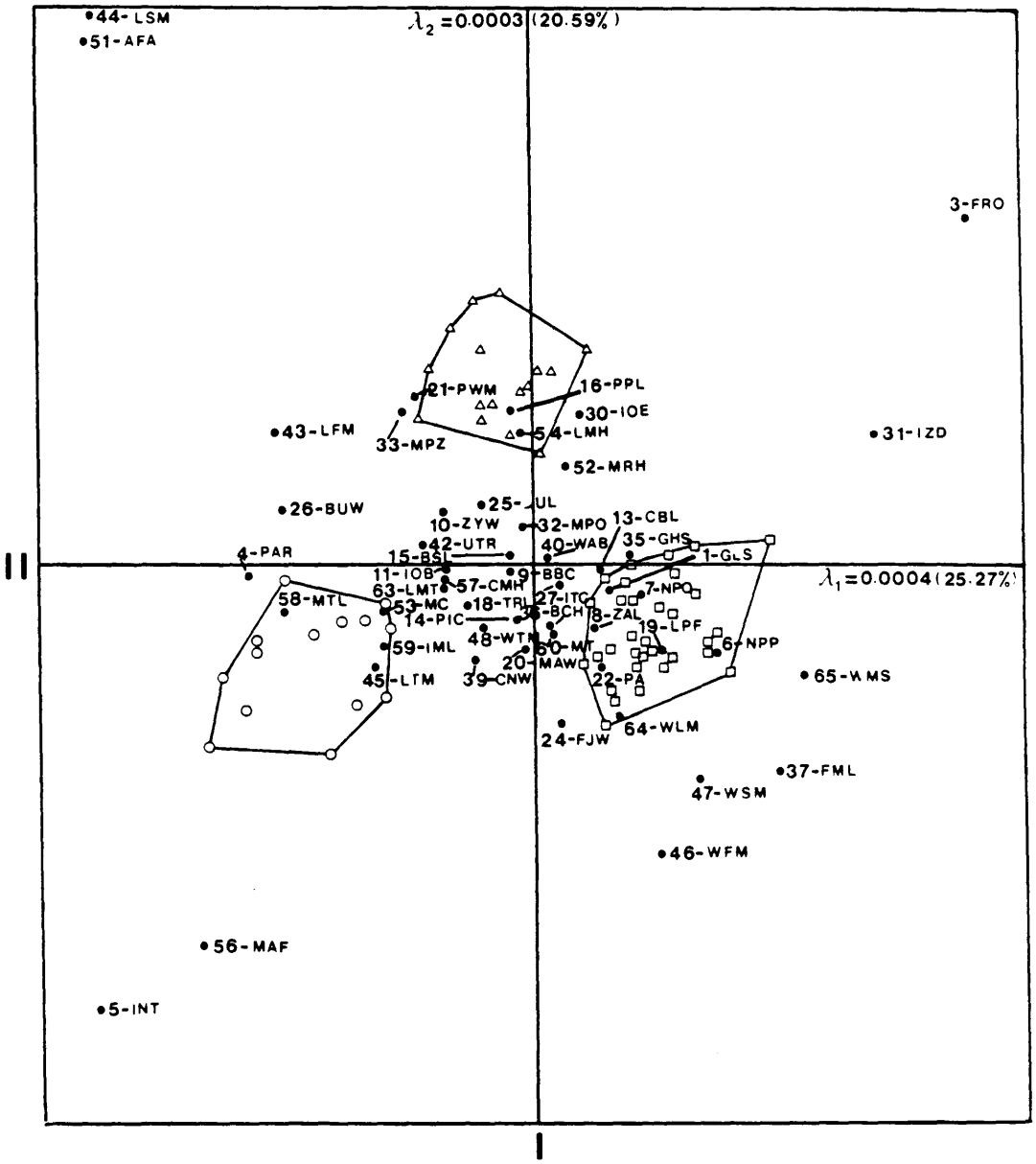

Figure 2.5 A summary of measurements selected from the character selection procedure to be used in a systematic revision of *Aethomys* from southern Africa. Measurement reference points are defined in Figure 2.1*a-k*: **1-GLS**: greatest length of skull; **2-FRO**: greatest length of frontals; **3-NPP**: length of nasals to zygomatic arch; **4-BBC**: breadth of braincase; **5-IOB**: interorbital breadth; **6-BUL**: greatest length of bulla; **7-BUW**: greatest width of bulla; **8-GHS**: greatest height of skull; **9-FMH**: foramen magnum height; **10-LFM**: length of M^1; **11-WSM**: width of M^2; **12-AFA**: length of angular process to mandibular condyle; **13-MAF**: length of mandibular foramen to condyle; **14-IML**: length of I_1 to M_3; **15-WMS**: width of M_2.

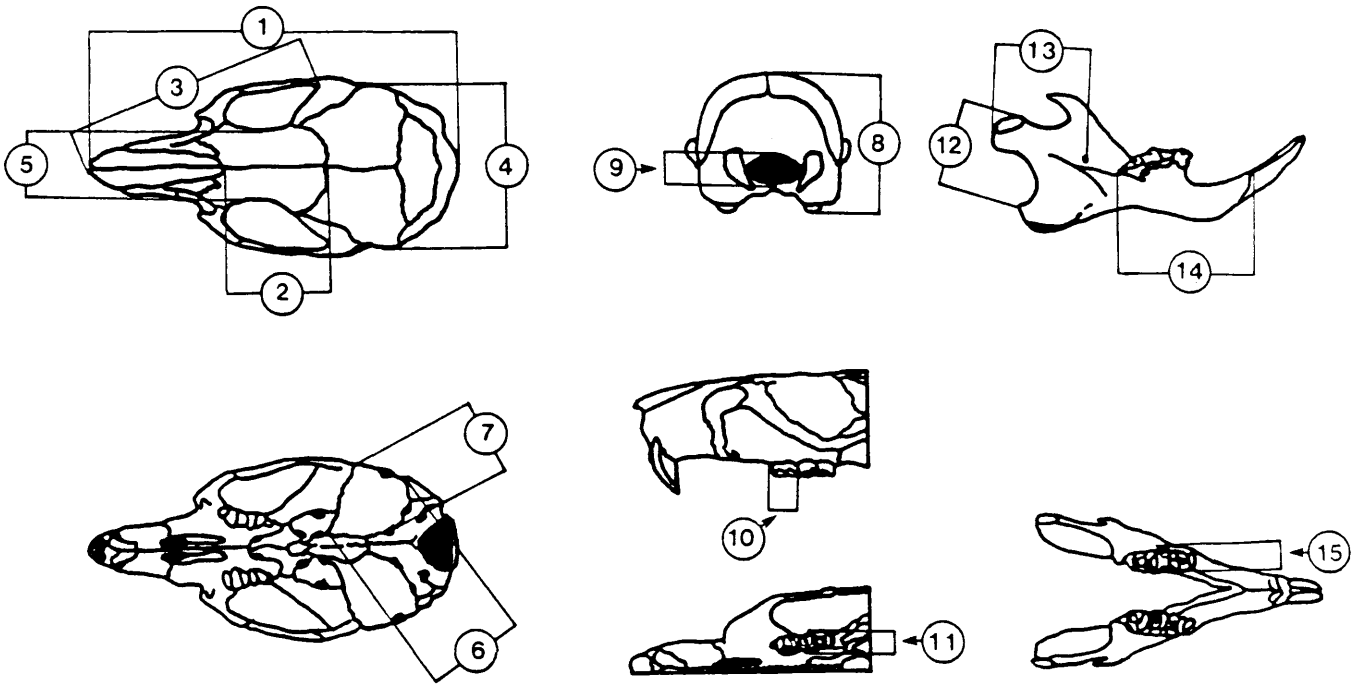

Table 2.1 Principal component (PCA) (including percent variance contributions, in brackets) and principal coordinate (CA) (in permills) loadings for the first two axes, coefficients of variation (CV) and percent measurement error (% ME) for each character. Letters and numbers to the left indicate clusters formed at the three-, four- and eight-cluster stages of the cluster analysis. Characters followed by a question mark do not belong in the particular functional (F-set) or phenotypic (P-set) set. Characters in brackets were important in principal components and correspondence analyses. Underlined characters were selected for descriptive and comparative purposes only. Characters preceded by an asterisk were selected for use in subsequent morphometric analyses. Characters are defined in Figures 1*a-k*.

Character/F-set	PCA I	PCA II	CA I	CA II	CV	% ME
I."MIXED" NEUROCRANIAL/OROFACIAL F-SET						
1."Incisor-condyle distances"						
*1-GLS	-0.957 (91.65)	0.130 (1.69)	11	-3	1.93	0.013
13-CBL	-0.959 (91.93)	0.130 (1.68)	10	-1	2.02	0.014
27-ITC	-0.973 (94.71)	0.049 (0.24)	4	-3	1.05	0.015
14-PIC	-0.974 (94.84)	-0.074 (0.55)	-2	-8	2.02	0.008
15-BSL	-0.968 (93.63)	-0.026 (0.07)	-3	1	2.53	0.014
2."Oblique distances"						
*(6-NPP)	-0.856 (73.23)	0.294 (8.66)	26	-13	2.18	0.014
32-MPO	-0.857 (97.50)	0.026 (0.07)	-1	5	1.91	0.014
II. NEUROCRANIAL F-SET						
B. (Braincase and dorsal part of skull)						
3. *(3-FRO)	-0.668 (44.60)	0.594 (35.23)	63	50	4.44	0.006
33-MPZ	-0.973 (94.60)	-0.050 (0.25)	-18	22	2.49	0.013
16-PPL	-0.947 (89.61)	0.061 (0.37)	-3	22	3.08	0.012
35-GHS	-0.892 (79.59)	0.239 (5.71)	14	1	2.71	0.010
7-NPO	-0.888 (78.89)	0.154 (2.38)	16	-4	3.32	0.015
8-ZAL ?	-0.941 (88.47)	0.085 (0.73)	9	-9	2.14	0.012
40-WAB	-0.941 (88.64)	0.033 (0.11)	2	1	2.55	0.014
4. 9-BBC	-0.952 (90.60)	-0.010 (0.01)	-3	-1	2.91	0.008
10-ZYW	-0.977 (95.43)	-0.070 (0.49)	-12	8	2.34	0.015
18-TRL ?	-0.971 (94.25)	-0.134 (1.81)	-9	-6	2.11	0.014
30-IOE ?	-0.959 (91.91)	0.177 (3.13)	7	22	1.82	0.014
III. OROFACIAL F-SET						
C. (Oral and orbital cavities, exoccipital bullae)						
5. (4-PAR ?)	-0.797 (63.53)	-0.301 (9.06)	-40	-1	7.34	0.008
42-UTR	-0.905 (81.89)	-0.040 (0.16)	-15	3	3.71	0.013
60-MTR	-0.827 (68.39)	0.061 (0.37)	3	-10	2.43	0.006
(31-IZD)	-0.615 (37.85)	0.500 (24.97)	49	19	6.65	0.014
(5-INT ?)	-0.345 (11.92)	-0.714 (51.00)	-62	-64	9.55	0.007
11-IOB	-0.898 (80.70)	-0.142 (2.02)	-12	0	2.81	0.013
54-LMH	-0.904 (81.74)	0.106 (1.12)	-2	19	5.44	0.009
22-PAC	-0.720 (51.90)	0.105 (1.11)	10	-15	5.55	0.015
*(26-BUW ?)	-0.865 (74.76)	-0.250 (6.25)	-35	8	3.73	0.001
*(37-FMH ?)	-0.436 (19.03)	0.437 (19.07)	36	-30	4.90	0.012
*(56-MAF)	-0.421 (17.73)	-0.662 (43.77)	-48	-55	5.60	0.013

Table 2.1.--*Continued.*

Character/F-set	PCA I	PCA II	CA I	CA II	CV	% ME
6. 20-MAW	-0.943 (88.21)	-0.047 (0.22)	-1	-12	2.98	0.013
*(51-AFA)	-0.934 (87.22)	-0.147 (2.17)	-63	75	5.52	0.010
25-BUL ?	-0.855 (73.17)	0.003 (0.01)	-7	9	4.64	0.012
24-FJW ?	-0.718 (51.58)	-0.050 (0.25)	4	-23	5.45	0.008
52-MRH	-0.781 (60.93)	0.113 (1.28)	5	14	5.87	0.011
(53-MCA)	-0.850 (72.32)	-0.254 (6.43)	-21	-5	4.36	0.006
36-BCH ?	-0.900 (80.91)	0.035 (0.12)	3	-8	2.93	0.013
(58-MTL)	-0.866 (75.06)	-0.374 (14.00)	-35	-7	3.89	0.008
7. 19-LPF ?	-0.722 (52.10)	0.152 (2.31)	18	-13	5.00	0.013
39-CNW ?	-0.886 (78.43)	-0.190 (3.60)	36	-14	3.82	0.013
*(59-IML)	-0.905 (81.93)	-0.314 (9.86)	-21	-12	3.01	0.011
57-CMH	-0.887 (78.74)	-0.133 (1.78)	-12	-1	3.56	0.006
D. (Dental)						
8. 21-PWM ?	-0.787 (61.91)	-0.099 (0.98)	-16	24	7.98	0.013
*(43-LFM)	-0.896 (75.48)	-0.126 (1.58)	-37	19	6.12	0.013
(44-LSM)	-0.736 (54.13)	-0.048 (0.23)	-62	94	12.99	0.005
(45-LTM)	-0.665 (44.27)	-0.202 (4.08)	-22	-15	7.10	0.007
63-LMT	-0.644 (41.45)	-0.129 (1.67)	-12	-3	6.98	0.005
48-WTM	-0.670 (44.87)	-0.044 (0.19)	-7	-9	6.52	0.013
(46-WFM)	-0.478 (22.90)	0.184 (3.38)	18	-42	5.19	0.014
*(47-WSM)	-0.475 (22.59)	0.339 (11.48)	24	-31	5.78	0.011
64-WLM	-0.704 (49.51)	0.208 (4.34)	12	-22	5.39	0.010
*(65-WMS)	-0.501 (25.11)	0.580 (33.68)	39	-16	4.62	0.012

% Trace: 68.4% (PC Axis I); 6.4% (PC Axis II)
Inertia: 25.3% (λ_1=0.0004) (CA Axis I); 20.6% (λ_2=0.0003) (CA Axis II)

CHAPTER 3

NON-GEOGRAPHIC VARIATION IN *AETHOMYS* FROM SOUTHERN AFRICA[1]

3.1 INTRODUCTION

The present chapter examines non-geographic variation in *Aethomys* from southern Africa based on four relatively large samples of *A. namaquensis* and *A. chrysophilus*. The prior assessment of non-geographic variation is critical in morphometric studies of geographic variation, and in the morphometric delineation of taxa (Thorpe 1976; Van der Straeten and Dieterlen 1992). Of fundamental importance are decisions regarding the components of variation to consider for statistical evaluation (Straney 1978). While some authors such as Leamy and Bader (1968) and Mayr (1969) consider non-geographic variation to comprise a genetic and non-genetic component, most workers view it as a function of differences in, for example, sex, age, season, cohort and individuals within populations (Thorpe 1976; Straney 1978; Leamy 1983; Webster and Jones 1985; Dippenaar and Rautenbach 1986; Van der Straeten and Dieterlen 1992).

Non-geographic variation has in the past been assessed by a variety of univariate statistics and procedures such as the coefficient of variation (Genoways and Jones 1972), multiple *t*-tests (Straney 1978), and two-way ANOVA (Robbins 1973), but

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[1] This chapter is essentially the text of the paper in Appendix IX entitled: CHIMIMBA, C. T., AND DIPPENAAR, N. J. 1994. Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa. *S. Afr. J. Zool.* 29:107-117.

their application has been criticized (Straney 1978; Leamy 1983). Two novel methods that rely either on the partitioning of variance components (Straney 1978) or the percent contribution of the sum of squares (% *SSQ*) of each source of variation to the total *SSQ* (Leamy 1983), have been proposed more recently. The former method is computationally involved, but yields results that are generally comparable to the latter which can be computed directly from a conventional two-way ANOVA table. Willig *et al.* (1986) expressed reservations about the univariate approach. They argued that significance tests for equality of means used for each variable independently present the dilemma of having to consider the number of characters that must exhibit significance before overall significance is declared. They recommended the use of multivariate analysis of variance for evaluating overall group differences since it utilizes rather than ignores correlations among variables.

Some workers such as Cheverud (1982) have attempted to adjust for sexually dimorphic and age-influenced characters by regression analyses of transformed characters (Thorpe 1976; Reist 1985) or by PCA (Leamy and Thorpe 1984; Somers 1986). Such adjustments, however, require adequate samples from throughout the area under study (Thorpe 1976; Dippenaar and Rautenbach 1986), a requirement hardly ever met by small mammal data sets. As an alternative to the sampling problem, other workers have attempted to pool geographic samples, but this is a dubious practice (Dippenaar and Rautenbach 1986).

The present study evaluates non-geographic variation at the level of sexual dimorphism and age variation. It uses the *SSQ* approach (and for comparison Model I two-way ANOVA), and a series

of multivariate procedures, with the objective of establishing criteria for the selection of specimens for the revision of the genus in southern Africa.

3.2 MATERIAL AND METHODS

The present chapter is based on relatively large samples of *A. namaquensis* from Boekenhoutkloof, Gauteng (25 males, 23 females), and Narap Farm, 28 km SSE Springbok, Northern Cape Province (15 males, 17 females), and *A. chrysophilus* from Al-te-ver Farm, 1 km SSE Maasstroom, Northern Province (9 males, 13 females), and Olifantspoort Farm 328, 19.2 km S Rustenburg, North-West Province (13 males, 8 females), South Africa. Specimens examined are listed in Appendix II and a gazetteer presented in Appendix VI. The homogeneity of the samples of *A. chrysophilus* (*sensu lato*), which is apparently composed of two sibling species (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker *et al.* 1988; Breed *et al.* 1988), was confirmed by preliminary analyses of cytogenetically known specimens (see Chapter 4).

Examination of the maxillary toothrow (following Verheyen and Bracke 1966; Morris 1972; Perrin 1982; and Dippenaar and Rautenbach 1986), led to the recognition of seven toothwear classes (Figure 3.1).

The basic set of 11 linear cranial measurements selected in the preceeding chapter (Chimimba and Dippenaar 1995; Figure 2.5) were used. These were recorded to the nearest 0.05 mm using a

pair of digital callipers and DataQ developed by D. L. Schultz[1] for direct data input into Quattro (Borland International Inc. 1987). The data set also included four descriptive cranial measurements (breadth of braincase, interorbital breadth, greatest length of bulla, and greatest height of skull), and four external measurements (length of head and body, length of tail, length of hind foot, and length of ear) recorded from specimen labels. These variables were not included in multivariate analyses.

After data screening, which resulted in the exclusion of one outlier from Boekenhoutkloof (TM 30432), the four samples were independently subjected to Model I two-way ANOVA. From the ANOVA tables, estimates of % *SSQ* of four sources of variation (sex, age, sex-age interaction and error (= residual)) were computed by the division of the *SSQ* associated with each source of variation by the total *SSQ*. Analysis also included *a posteriori* Student-Newman-Keuls (SNK) tests for maximally non-significant subsets ($P > 0.05$; Sokal and Rohlf 1969, 1981). Haldane's (1955) correction was used in the computation of the CV.

All univariate analyses were performed on the 11 basic and four descriptive characters. The material available was characterized by small sample sizes, particularly of toothwear classes I and VII, so that not all (and in some cases not consecutive) toothwear classes were represented. This led to univariate analyses of either *three* (Narap: II, III and VI; Olifantspoort: II, III and IV, and Al-te-ver: III, IV and V) or

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[1] D. L. Schultz, Aiken, Southern Carolina, U. S. A.

four (Boekenhoutkloof: III, IV, V, VI) toothwear classes.

Variation due to sex and age was also examined by PCA and UPGMA cluster analysis. Unlike the univariate analyses, PCA and UPGMA cluster analyses allowed the analysis of a wider range of toothwear classes that also included the poorly represented toothwear classes I and VII. A CVA of toothwear classes (excluding those with too few observations) were also undertaken. A MANOVA was used to test for significant differences between group centroids. All multivariate analyses were based on the basic set of 11 cranial measurements.

3.3 RESULTS

3.3.1 Univariate assessment

Univariate results for the four samples analysed were broadly congruent over the 11 basic and four descriptive measurements. Consequently, the univariate assessment is largely based on *A. namaquensis* from Boekenhoutkloof and *A. chrysophilus* from Olifantspoort. The former comprised the largest single sample and also included the widest range of consecutive toothwear classes (III-VI), whereas the latter sample included toothwear classes (II-IV). *F*-values from a Model I two-way ANOVA and % *SSQ* for the two samples (Table 3.1) show that more measurements have significant ($P < 0.01$) *F*-values for age than for sex. Similarly, age generally gave higher % *SSQ* values (range % *SSQ* = 1.57-45.56 for *A. namaquensis*; 7.41-83.59 for *A. chrysophilus*) than sex (0.00-9.99 for *A. namaquensis*; 0.05-40.00 for *A. chrysophilus*). Length of nasals to zygomatic arch, length

of angular process to mandibular condyle, length of mandibular foramen to condyle showed significant age variation in both samples. The importance of these measurements was also apparent in the *A. namaquensis* sample from Narap and the *A. chrysophilus* sample from Al-te-ver. Generally, these measurements also contributed relatively more to the total variance attributed to age.

Only one measurement, interorbital breadth in the Boekenhoutkloof sample, and two measurements, greatest height of skull and width of M^2 in the *A. chrysophilus* sample from Olifantspoort, showed significant sexual dimorphism. These measurements also show the largest percent contribution to the total variance due to sex (Table 3.1).

Only one measurement from each sample (length of nasals to zygomatic arch and width of M_2) showed significant interaction between age and sex. The negligible contribution due sex-age interaction was also shown by the relatively small % *SSQ* means in both samples (mean % *SSQ* = 6.39 in *A. namaquensis*; 10.67 in *A. chrysophilus*). In both samples, the largest percent contribution to the total variance was due to error (mean % *SSQ* = 79.54, range % *SSQ* = 44.11-92.00, in *A. namaquensis*; 45.45, 14.07-73.65 in *A. chrysophilus*).

Despite the concordance in univariate results, the % *SSQ* contributions generally showed a much higher degree of congruence between 'three toothwear class'-group analyses in samples of *A. chrysophilus* from Olifantspoort (mean % *SSQ* contributions for sex = 7.48; age = 36.40; interaction = 10.67; error = 45.45) and Al-te-ver (sex = 8.75; age = 32.76; interaction = 13.43; error = 45.06), and *A. namaquensis* from Farm Narap (sex = 2.70; age =

43.42; interaction = 7.23; error = 46.65) than the 'four toothwear class'-group analysis in the *A. namaquensis* sample from Boekenhoutkloof (sex = 1.71; age = 12.36; interaction = 6.39; error = 79.54). Except for the error component, the 'three toothwear class'-group analyses showed higher % *SSQ* values than the 'four toothwear class'-group analysis.

In the SNK tests, a large number of measurements from all samples showed no significant differences between toothwear classes analysed: Boekenhoutkloof (10; classes III-VI), Narap (6; II, III, VI), Olifantspoort (6; II-IV), and Al-te-ver (8; III-V), the highest numbers being recorded in the first and last samples which included only toothwear class III and older specimens. (Representative results for the four samples are presented in Table 3.2.). Conversely, in the samples that included toothwear class II and older specimens (Olifantspoort and Narap), most measurements (9 of 15 in each sample) showed significant variation between toothwear classes. In instances in which significance was recorded, either all toothwear classes differed significantly in a few measurements (Olifantspoort and Narap 3 measurements, and Al-te-ver 4), or were variously grouped into non-significant subsets: in *A. namaquensis* from 1) Boekenhoutkloof (which represented the widest range of consecutive toothwear classes) classes V and VI were mostly grouped in non-significant subsets, and sometimes IV and VI, and III and IV; 2) from Narap, toothwear classes II and III were consistently grouped into the same non-significant subset, with both differing significantly from toothwear class VI. In *A. chrysophilus* from both Olifantspoort and Al-te-ver, toothwear classes III and IV were consistently grouped in the same

non-significant subset. The pattern that emerges from the SNK analyses is that the inclusion of toothwear class II specimens with toothwear class III and older specimens leads to an increase in the number of measurements showing significant age variation, and that analysis of only toothwear class III and older specimens also show a large proportion of measurements with significant differences. Toothwear class III specimens either fall in the same non-significant subset as those of toothwear class II or toothwear class IV. The SNK results suggest, therefore, that specimens of toothwear classes II and III should be excluded from the final data set, and that an argument could possibly be made for the exclusion of toothwear class IV specimens.

Descriptive statistics of all samples show a direct relationship between the magnitude of a character and age, as exemplified by samples from Boekenhoutkloof and Olifantspoort (Table 3.3).

3.3.2 Multivariate assessment

The multivariate assessment is restricted largely to the relatively large samples of *A. namaquensis* from Boekenhoutkloof and Narap, with reference to the samples of *A. chrysophilus* from Olifantspoort and Al-te-ver. The Narap sample is of particular interest since it includes specimens that represent all seven toothwear classes. Because of insufficient cell sizes for a combined CVA of males, females and toothwear classes, the data were initially subjected to PCA and UPGMA cluster analyses.

The first two principal components resulting from analyses of the Boekenhoutkloof and Narap samples are shown in Figure 3.2.

Both scattergrams reflect age, rather than sex, as the major source of variation. Toothwear class III specimens from Boekenhoutkloof tend to separate from those of toothwear classes IV-VII at an oblique angle. There is no clear separation between toothwear classes IV-VII along either axis. In the PCA of the Narap sample, there is clear separation between toothwear classes IV-VII and toothwear classes I-III, especially along the first axis.

An examination of the remaining axes (3 to 14) for both samples did not reveal any separation of toothwear classes. In both samples, the first principal component generally had high, negative loadings for most measurements (Table 3.4), with a trend towards high percent variances associated with each measurement's component contribution (in brackets in Table 3.4). The important measurements with relatively high loadings on the first axis (35.4% of the total variance) in the Boekenhoutkloof sample (Table 3.4*a*) are: greatest length of skull, length of nasals to zygomatic arch, length of angular process to mandibular condyle, length of I_1 to M_3. In addition to these measurements, greatest length of frontals, greatest width of bulla and width of M_2 are important in the first axis (64.9%) of the Narap sample (Table 3.4*b*).

Important measurements on the second axis (16.1%) of the Boekenhoutkloof sample are: greatest length of frontals, widths of M^2 and M_2 (Table 3.4*a*). In the Narap sample, foramen magnum height was important on the second axis (11.5%) (Table 3.4*b*). Collectively, most of these measurements also feature either as significantly different or contribute highly towards the total % *SSQ*s in the univariate statistics. Results for *A. chrysophilus*

from Olifantspoort reflected those for the Boekenhoutkloof sample in that there was some overlap between toothwear classes III and IV but in the *A. chrysophilus* sample from Al-te-ver, the overlap was greater. Both these samples included toothwear class II specimens (and in the case of Al-te-ver a single toothwear class I specimen) and their positions in the PCA graphs closely reflected the pattern observed in the Narap sample. In all PCA graphs there was little, if any, indication of sexual dimorphism.

Because of the relatively low level of variation explained by successive components such as the first three axes for *A. namaquensis*: Boekenhoutkloof (62.3%), Narap (86.3%); *A. chrysophilus*: Al-te-ver (84.5%), Olifantspoort (76.4 %)), the samples were also examined by cluster analyses. In the Boekenhoutkloof sample, a distance phenogram showed no discrete groupings in respect of sexes or toothwear classes. The only exceptions were three specimens of toothwear class III and one specimen each of toothwear classes IV and V which form a subcluster, a result consistent with the PCA (Figure 3.3*a*).

In the Narap sample, two major clusters were apparent: one comprising all specimens of toothwear classes I-III, with a subcluster consisting of specimens of toothwear class I (except for one specimen in toothwear class II), and the other comprising all specimens of toothwear classes IV-VII (Figure 3.3*b*). Both samples failed to show partitioning of the sexes. Similar patterns were evident from the Olifantspoort and Al-te-ver populations (cophenetic correlation coefficients = 0.69 and 0.83 respectively) in that toothwear class I and II specimens formed distinct subclusters, but as with the PCA results, the distinction between toothwear class III and IV-VII was not as

marked as in the Narap sample.

The MANOVA of males and females, for which specimens of the toothwear classes indicated below had to be pooled to increase cell sizes, revealed no significant sexual differences in any of the samples (Boekenhoutkloof, pooled classes IV-VI: $F = 0.63$; $P > 0.05$; Olifantspoort IV-VI: $F = 0.97$, $P > 0.05$; Narap IV-VI: $F = 0.66$, $P > 0.05$; Al-te-ver IV and V: $F = 1.69$, $P > 0.05$). These results, together with those of the univariate analyses justified the pooling of sexes for the discriminant analyses of toothwear classes.

The results of the discriminant analyses are best exemplified by the 'four toothwear-class' (III-VI) analysis of the relatively large sample from Boekenhoutkloof (Figure 3.4). This resulted in a 71.0% overall *a posteriori* classification, and in the scattergram of canonical variates I and II, four of five toothwear class III specimens tend to separate from those of toothwear classes IV-VI along the first canonical variate (54.9% variance). Specimens of toothwear class III are maximally separated along the second axis (38.9%) from those of toothwear class V. With the exception of greatest length of frontals, greatest width of bulla and width of M_2 (which loaded highly in the PCA's first axis of the Narap sample) those measurements that load highly in the PCA of the Boekenhoutkloof and Narap samples, also load highly in the CVA (Table 3.4). Length of I_1 to M_3, together with width of M_2, are the important measurements on the second canonical variate.

The MANOVA showed significant differences between the group centroids of the four toothwear classes ($F = 1.91$; $P = 0.01$). Except for the Olifantspoort sample that indicated no significant

differences between group centroids of the analysed toothwear classes (II-IV) (F = 1.76; P = 0.18), the remaining two samples showed significant differences between group centroids (Narap: F = 2.56, P = 0.01, toothwear classes II-IV and VI; Al-te-ver: F = 2.53, P = 0.04, toothwear classes III-V).

3.4 DISCUSSION

The primary objective of the present study was to examine age- and sex-related variation in *Aethomys* with a view to: 1) determine whether the sexes should be treated separately or combined, and 2) which subset of toothwear classes represent specimens that have reached adult dimensions and therefore are eligible for inclusion in subsequent morphometric studies of the genus.

Both univariate and multivariate results clearly showed a lack of sexual dimorphism in the two *Aethomys* species studied. With regard to age variation, however, the univariate SNK tests were equivocal as to which toothwear classes should be considered in subsequent studies. This was resolved when the univariate and multivariate results were considered together, showing that there is an increase in dimensions with progression from toothwear class I to at least IV.

The SNK results suggested that specimens of toothwear classes II and III should be excluded from the final data set and, possibly, an argument could even be made for the exclusion of toothwear class IV specimens. In the PCAs, both toothwear classes I and II (and in two instances toothwear class III) plotted well apart from the other toothwear classes.

Additionally, in two other instances there was some to extensive overlap between toothwear class III and some of the higher toothwear classes.

In so far as toothwear classes IV to VII were concerned, some of the SNK tests grouped the first toothwear class with toothwear class III in the same non-significant subset. However, in the PCA, and in the CVA of the largest sample from Boekenhoutkloof, specimens of toothwear classes IV to VII plotted close together.

If the toothwear classes are visualized as demarcating sections of variable and unknown length on a hypothetical growth curve, then specimens of toothwear class III seem to fall at a point on the curve just before it begins to stabilize. These results provide justification for pooling toothwear classes IV-VI for subsequent recording and analyses in the revision of the genus.

Toothwear class VII specimens are excluded from the final data set since: 1) very few examples of this toothwear class are encountered in collections, 2) extensive toothwear often renders measuring points on the teeth uncertain, and 3) there seems to be a higher incidence of age-related deformations in very old rodents in general (N. J. Dippenaar *pers. obs.*[1]).

The univariate % *SSQ* analysis of the four samples indicated that most measurements have relatively small sex and age components but a large error component. Similar patterns were

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observed in six of the seven species examined by Straney (1978). Apart from providing a realistic baseline for the subsequent interpretation of geographical and taxonomic trends, and the assessment of relative contributions of population factors, variance partitioning is also useful in determining the relative taxonomic value of characters (Straney 1978; Leamy 1983). If the aim of the study is to compare specimens across populations (as is usually the case), and eliminating or adjusting for extraneous sources of variation due to factors such as age or sex, then characters showing the least variances for these factors but with large error variances are the most appropriate. Characters utilized in the present study were selected on the basis of the morphological integration concept (Olson and Miller 1958; Moss and Young 1960; Moore 1981; Cheverud 1982; Taylor 1990; Taylor and Meester 1993; Chapter 2). In the % *SSQ* analyses, their generally large error components place confidence in the systematic usefulness of the selected characters.

Based on the 'four toothwear class' analyses in the present study, overall % *SSQ* values due to sex and age are generally lower than those reported by Leamy (1983), who used a similar approach, and Straney (1978), who used the variance components approach. Leamy (1983) suggested that such differences may be a function of the type of characters used. In contrast to the present study, these two investigations included appendicular characters. It has been demonstrated that appendicular characters exhibit higher growth rates than axial characters (Leamy and Bradley 1982). Although his conclusion was restricted to the age component, Leamy (1983) suggested the existence of a direct proportionality between characters with higher growth rates and

larger variance components. The % *SSQ* contributions in the current study are comparable to those found in *Cynictis penicillata* (Taylor and Meester 1993), a study restricted to axial characters.

In spite of relatively small sample sizes in the present study, a robust picture emerges from parallel univariate and multivariate analyses. The approach adopted here is useful as a preliminary step to any morphometric study, and the differentiation of some toothwear classes cautions against either arbitrary decisions or the superficial evaluation of non-geographic variation.

3.5 CONCLUSIONS

Prior to a systematic revision of African rock rats of the genus *Aethomys* in southern Africa, the nature and extent of non-geographic variation attributable to sex and age in two samples each of *A. chrysophilus* and *A. namaquensis* were examined using univariate and multivariate statistical procedures. Results of Model I two-way ANOVA, % *SSQ*, and a series of multivariate procedures were concordant and showed a lack of sexual dimorphism in all samples examined, but marked variation between seven age categories based on the degree of toothwear on the maxillary toothrow. When univariate and multivariate results were considered together, the pooling of sexes, as well as specimens of toothwear classes IV, V and VI, was justified. Very few toothwear class VII specimens were available and their exclusion was largely arbitrary. Few measurements showed sex-age interaction. The largest percent contribution to the total

variance was due to error. In general, variance partitioning indicated that if comparisons are to be made, caution needs to be exercised on the type of characters, number of factor levels and the methodology used

Figure 3.1 Right maxillary toothrow of *Aethomys namaquensis* illustrating seven toothwear classes. Toothwear class I: cheek-teeth not fully erupted, M^3 conspicuously below eruption level of M^1 and M^2 (TM 27832); toothwear class II: cheekteeth fully erupted, M^3 somewhat smaller, cusps conspicuous but with no or very little wear (TM 27842); toothwear class III: all cheekteeth in apposition, minimal cusp wear (TM 31258); toothwear class IV: cusp wear obvious, but not extensive (TM 30433); toothwear class V: cusp wear extensive, but most cusps still distinguishable (TM 30432); toothwear class VI: cusp wear extensive, but traces of cusps not completely lost (TM 30438); toothwear class VII: toothwear severe, occlusal surfaces worn smooth with no traces of cusps (TM 30428).

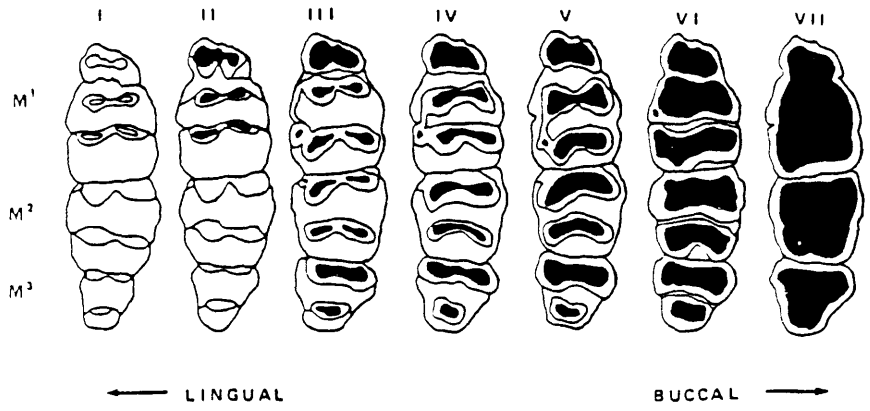

Figure 3.2 The first two axes from principal component analyses of *Aethomys namaquensis* from (**a**) Boekenhoutkloof and (**b**) Narap. The sex and toothwear classes [I (open square), II (solid square), III (open triangle), IV (solid circle), V (solid triangle), VI (open circle), VII (open diamond)] of all specimens are indicated. Polygons enclose specimens of each toothwear class.

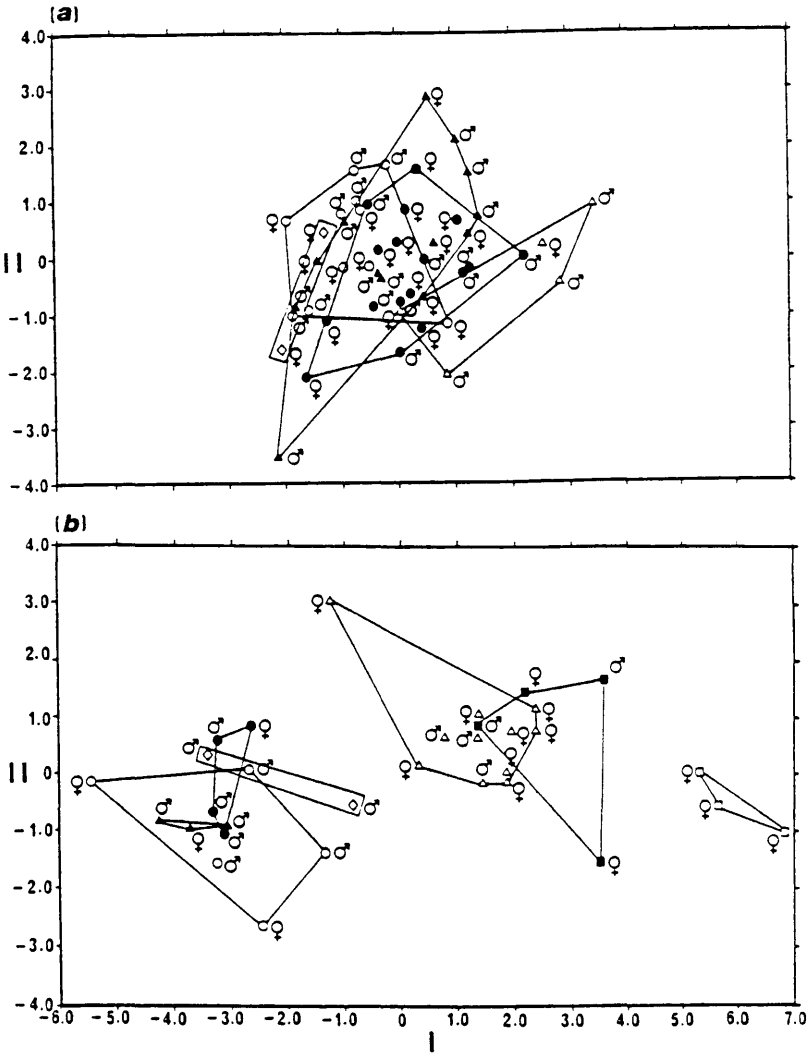

Figure 3.3 Distance phenograms from UPGMA cluster analyses of *Aethomys namaquensis* from (**a**) Boekenhoutkloof and (**b**) Narap. The sex and toothwear classes [I (open square), II (solid square), III (open triangle), IV (solid circle), V (solid triangle), VI (open circle), and VII (open diamond)] of all specimens are indicated. Cophenetic correlation coefficients = 0.66 and 0.73, respectively.

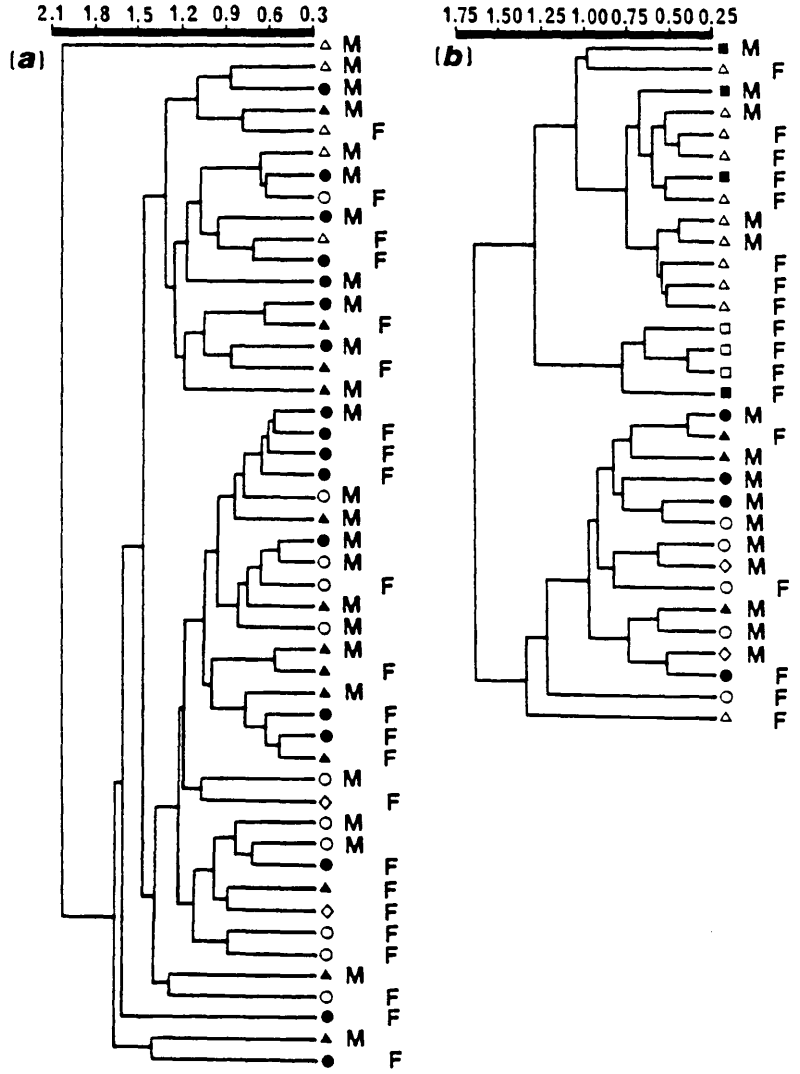

Figure 3.4 The first two axes from a canonical variates analysis of toothwear classes in *Aethomys namaquensis* from Boekenhoutkloof. The toothwear classes [III (open triangle), IV (solid circle), V (solid triangle), VI (open circle)] and sex of all specimens are indicated. Minimum convex polygons enclose specimens of each toothwear class. Group centroids are denoted by a star.

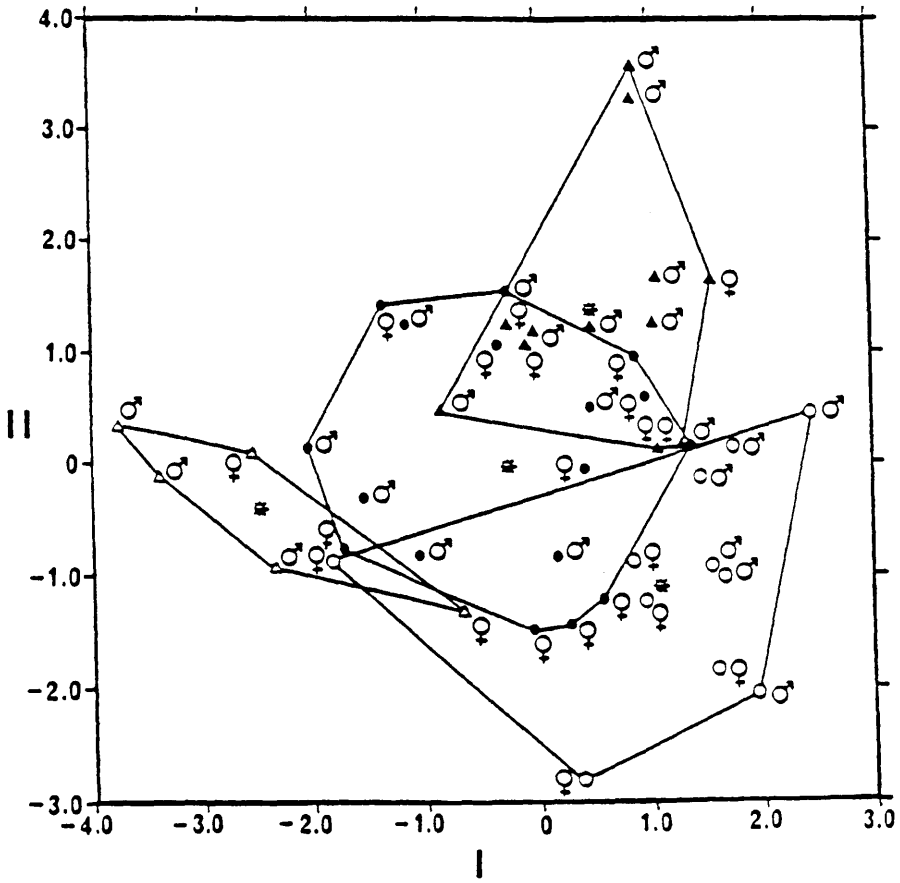

Table 3.1 *F*-values and % Sum of Squares (% *SSQ*) of each source of variation from a Model I two-way ANOVA of (**a**): four toothwear classes (III-VI) of male and female *Aethomys namaquensis* from Boekenhoutkloof and (**b**): three toothwear classes (II-IV) of male and female *Aethomys chrysophilus* from Olifantspoort. * = P < 0.05; ** = P < 0.001. Measurements are defined in Figure 2.5.

Variable	*F*-value			% *SSQ*			
	Sex (S)	Age(A)	S X A	Sex(S)	Age(A)	S X A	Error
(**a**)							
Greatest length of skull	1.26	0.56	0.31	3.00	4.04	2.23	90.73
Greatest length of frontals	0.96	0.75	0.13	2.31	5.40	0.94	91.35
Length of nasals to zygomatic arch	0.49	13.08***	2.80*	0.57	45.56	9.76	44.11
Breadth of braincase	0.00	0.66	1.52	0.00	4.43	10.26	85.31
Interorbital breadth	6.07*	2.87*	2.71	9.99	14.14	13.41	62.46
Greatest length of bulla	0.52	0.40	1.13	1.21	2.79	7.86	88.14
Greatest width of bulla	0.25	1.07	0.20	0.59	7.59	1.42	90.40
Greatest height of skull	0.05	1.15	1.02	0.11	7.76	6.86	85.27
Foramen magnum height	0.90	0.22	0.92	2.10	1.57	6.54	89.79
Length of M^1	0.45	1.59	1.94	0.94	9.74	11.85	77.47
Width of M^2	0.07	0.68	1.84	0.00	4.71	12.04	83.25
Length of angular process to mandibular condyle	0.03	5.04**	0.80	0.05	27.22	4.33	68.40
Length of mandibular foramen to condyle	0.15	4.21**	0.34	0.30	24.39	1.96	73.35
Length of I_1 to M_3	2.02	3.50*	0.99	3.78	19.61	5.55	71.06
Width of M_2	0.24	0.88	0.06	0.80	6.40	0.80	92.00
Mean				1.71	12.36	6.39	79.54
(**b**)							
Greatest length of skull	0.52	11.21**	0.43	1.44	62.62	2.41	33.53
Greatest length of frontals	0.14	6.03*	1.24	0.53	45.21	9.32	44.94
Length of nasals to zygomatic arch	0.95	5.04*	2.88	3.23	36.60	19.52	40.65
Breadth of braincase	0.21	6.17**	0.49	0.82	48.31	3.86	47.01
Interorbital breadth	2.22	2.00	0.45	11.57	21.00	4.71	62.72
Greatest length of bulla	1.48	35.66***	0.26	1.37	83.59	0.61	14.07
Greatest width of bulla	0.06	1.40	0.72	0.33	17.18	8.84	73.65
Greatest height of skull	7.95**	1.37	1.92	29.97	10.33	14.49	45.21
Foramen magnum height	2.30	1.82	0.05	12.79	20.23	0.57	66.41
Length of M^1	1.00	1.57	2.13	4.68	15.21	21.05	59.06
Width of M^2	11.26**	1.76	0.69	40.00	12.31	4.62	43.07
Length of angular process to mandibular condyle	0.02	18.35***	2.11	0.05	69.33	7.96	22.66
Length of mandibular foramen to condyle	0.50	12.96***	0.57	1.25	65.53	2.90	30.32
Length of I_1 to M_3	0.02	3.05	0.71	0.11	31.18	7.32	61.39
Width of M_2	1.38	1.07	8.50**	3.70	7.41	51.85	37.04
Mean				7.48	36.40	10.67	45.45

Table 3.2 Multiple-range SNK tests of toothwear classes in *Aethomys namaquensis* from: (**a**) Boekenhoutkloof (toothwear classes III-VI) and (**b**) Narap (II, III and VI), and *Aethomys chrysophilus* from: (**c**) Olifantspoort (II-IV) and (**d**) Al-te-ver (III-V). Non-significant subsets ($P > 0.05$) are indicated by vertical lines; NS = no significant differences; AS = all means significantly different; *n* = sample size; *SD* = standard deviation. Measurements and their abbreviations are defined in Figure 2.5.

Variable	Toothwear class (*n*)	*SD*	Mean		Variable	Toothwear class (*n*)	*SD*	Mean	
(**a**)									
GLS	III(5)	0.66	28.78		NPP	III(5)	0.56	20.34	
	VI(11)	0.80	29.57	NS		IV(17)	0.66	21.48	
	IV(17)	0.45	29.87			V(13)	0.65	22.01	|
	V(13)	0.68	30.28			VI(11)	0.68	22.27	|
AFA	III(5)	0.48	5.58		IML	III(5)	0.29	8.56	⊢
	IV(17)	0.33	6.07	⊢		V(13)	0.21	8.81	⊢
	V(13)	0.34	6.13	⊢		IV(17)	0.30	8.78	⊢
	VI(11)	0.18	6.23	⊢		VI(11)	0.29	9.01	⊢
(**b**)									
GLS	II(4)	0.93	27.19		BBC	II(4)	0.26	12.39	|
	III(11)	0.69	28.36	AS		III(11)	0.30	12.73	|
	VI(5)	0.93	31.80			VI(5)	0.35	13.25	
BUW	II(4)	0.10	4.73	|	WMS	II(4)	0.05	1.67	
	III(11)	0.19	4.89	|		III(11)	0.04	1.67	NS
	VI(5)	0.16	5.16			VI(5)	0.04	1.69	
(**c**)									
FRO	II(4)	0.38	9.71		BUL	II(4)	0.07	6.71	
	III(10)	0.48	10.31	|		III(10)	0.14	7.24	AS
	IV(4)	0.18	10.84	|		IV(4)	0.03	7.41	
FMH	II(4)	0.14	4.59		MAF	II(4)	0.17	3.89	
	III(10)	0.16	4.64	NS		III(10)	0.31	4.69	|
	IV(4)	0.19	4.80			IV(4)	0.23	4.81	|
(**d**)									
BBC	III(8)	0.30	14.03	|	IOB	III(8)	0.14	4.83	
	IV(7)	0.61	14.31	|		IV(7)	0.32	4.88	NS
	V(5)	0.46	14.89			V(5)	0.22	5.08	
LFM	IV(7)	0.12	2.80	|	AFA	III(8)	0.24	6.44	
	III(8)	0.11	2.83	|		IV(7)	0.30	6.87	AS
	V(5)	0.09	2.98			V(5)	0.45	7.51	

Table 3.3 Standard statistics of 15 measurements of males and females in **a**): five toothwear classes of *Aethomys namaquensis* from Boekenhoutkloof and (**b**): three toothwear classes of *Aethomys chrysophilus* from Olifantspoort. $\bar{Y}$ = arithmetic mean; 2*SE* = two standard errors; *CV* = coefficient of variation; *n* = sample size. See Figure 2.5 for abbreviations.

(**a**)

Sex	Toothwear class (*n*)		Variable							
			GLS	FRO	NPP	BBC	IOB	BUL	BUW	GHS
M	III(3)	$\bar{Y}$	28.44	9.35	20.08	12.72	4.36	6.47	4.78	9.60
A		2*SE*	0.26	0.16	0.26	0.17	0.04	0.21	0.21	0.22
L		*CV*	1.61	2.90	2.27	2.27	1.53	5.62	7.55	3.91
E	IV(8)	$\bar{Y}$	29.40	9.49	21.12	13.19	4.67	6.57	4.87	9.78
S		2*SE*	0.31	0.22	0.29	0.16	0.10	0.13	0.09	0.05
		CV	3.02	6.44	3.86	3.40	5.86	5.51	5.30	1.44
	V(7)	$\bar{Y}$	30.40	9.68	22.05	12.92	4.49	6.57	4.85	9.75
		2*SE*	0.24	0.12	0.23	0.12	0.03	0.07	0.10	0.10
		CV	2.26	3.59	2.96	2.71	1.78	3.20	5.75	2.82
	VI(6)	$\bar{Y}$	31.37	9.79	22.54	13.03	4.75	6.80	4.92	9.78
		2*SE*	0.10	0.13	0.10	0.16	0.04	0.08	0.04	0.08
		CV	0.77	3.36	1.05	2.96	2.29	2.78	1.81	1.99
F	III(2)	$\bar{Y}$	29.28	9.36	20.73	13.32	4.52	6.55	4.68	9.75
E		2*SE*	0.49	0.03	0.42	0.08	0.05	0.06	0.01	0.06
M		*CV*	2.37	0.46	2.83	0.80	1.56	1.30	0.30	0.80
A	IV(9)	$\bar{Y}$	30.29	9.42	21.80	13.01	4.44	6.62	4.92	9.86
L		2*SE*	0.14	0.20	0.08	0.12	0.05	0.08	0.04	0.08
E		*CV*	1.40	6.29	1.06	2.77	3.09	3.64	2.45	2.56
S	V(5)	$\bar{Y}$	30.28	9.40	21.94	12.92	4.48	6.51	4.88	9.54
		2*SE*	0.32	0.29	0.32	0.12	0.08	0.15	0.06	0.08
		CV	2.35	6.78	3.21	2.04	4.07	5.04	2.66	1.98
	VI(5)	$\bar{Y}$	30.54	9.60	21.95	13.00	4.53	6.47	4.94	9.68
		2*SE*	0.48	0.33	0.41	0.10	0.07	0.16	0.04	0.18
		CV	3.53	7.67	4.17	1.72	3.49	5.41	1.77	4.22
	VII(2)	$\bar{Y}$	31.17	9.46	22.53	13.01	4.98	6.91	4.90	9.86
		2*SE*	0.30	0.21	0.20	0.50	0.16	0.02	0.13	0.06
		CV	1.34	3.07	1.22	5.44	4.41	0.41	3.75	0.86

Table 3.3a.--*Continued.*

Sex	Toothwear class (*n*)		Variable						
			FMH	LFM	WSM	AFA	MAF	IML	WMS
M	III(3)	$\bar{Y}$	4.56	2.23	1.82	5.44	4.25	8.41	1.68
A		2*SE*	0.13	0.16	0.03	0.10	0.06	0.15	0.03
L		*CV*	4.94	12.63	2.77	3.11	2.27	3.14	3.09
E	IV(8)	$\bar{Y}$	4.53	2.49	1.76	6.12	4.51	8.72	1.67
S		2*SE*	0.08	0.03	0.02	0.09	0.08	0.08	0.02
		CV	4.78	3.53	2.87	4.30	4.82	2.50	3.42
	V(7)	$\bar{Y}$	4.46	2.56	1.80	6.10	4.59	8.81	1.65
		2*SE*	0.06	0.08	0.04	0.11	0.12	0.13	0.01
		CV	3.93	8.78	5.24	5.26	7.16	4.06	2.40
	VI(6)	$\bar{Y}$	4.49	2.53	1.74	6.33	4.71	8.99	1.68
		2*SE*	0.08	0.03	0.02	0.08	0.07	0.12	0.03
		CV	4.55	2.82	3.00	3.05	3.42	3.13	4.82
F	III(2)	$\bar{Y}$	4.34	2.47	1.80	5.78	4.11	8.79	1.69
E		2*SE*	0.03	0.08	0.04	0.60	0.35	0.12	0.04
M		*CV*	0.98	4.58	2.76	14.68	11.89	1.93	2.94
A	IV(9)	$\bar{Y}$	4.45	2.48	1.79	6.02	4.61	8.90	1.66
L		2*SE*	0.61	0.07	0.02	0.13	0.07	0.06	0.02
E		*CV*	4.12	8.02	3.50	6.53	4.53	2.05	3.16
S	V(5)	$\bar{Y}$	4.55	2.38	1.74	6.17	4.54	8.75	1.63
		2*SE*	0.08	0.06	0.02	0.18	0.18	0.08	0.01
		CV	4.08	5.30	3.10	6.67	8.94	2.16	1.76
	VI(5)	$\bar{Y}$	4.38	2.48	1.79	6.17	4.79	9.03	1.67
		2*SE*	0.07	0.02	0.02	0.05	0.19	0.15	0.03
		CV	3.79	2.07	2.55	1.83	8.75	3.72	3.74
	VII(2)	$\bar{Y}$	4.55	2.62	1.83	6.71	5.02	8.99	1.67
		2*SE*	0.16	0.21	0.01	0.25	0.11	0.08	0.09
		CV	4.82	11.34	0.77	5.27	3.10	1.18	7.22

(**b**)

Sex	Toothwear class (*n*)		Variable							
			GLS	FRO	NPP	BBC	IOB	BUL	BUW	GHS
M	II(2)	$\bar{Y}$	31.00	9.72	22.12	13.15	4.70	6.74	5.15	11.22
A		2*SE*	0.95	0.13	0.09	0.24	0.07	0.07	0.11	0.11
L		*CV*	4.31	1.88	1.43	2.53	1.96	1.47	2.89	1.32
E	III(7)	$\bar{Y}$	33.68	10.42	23.54	13.88	4.90	7.25	5.45	11.33
S		2*SE*	0.43	0.15	0.39	0.09	0.09	0.06	0.05	0.12
		CV	3.39	3.68	4.38	1.78	4.64	2.25	2.32	2.74
	IV(2)	$\bar{Y}$	33.87	10.58	23.73	13.99	4.84	7.41	5.38	10.98
		2*SE*	0.46	0.36	0.31	0.44	0.01	0.02	0.01	0.20
		CV	1.92	4.81	1.82	4.40	0.15	0.38	0.13	2.51
F	II(2)	$\bar{Y}$	30.97	9.67	21.56	13.32	4.55	6.69	5.33	10.64
E		2*SE*	0.08	0.45	0.03	0.32	0.07	0.03	0.06	0.29
M		*CV*	0.37	6.51	0.16	3.40	2.02	0.63	1.46	3.79
A	III(3)	$\bar{Y}$	33.14	10.06	23.30	13.69	4.71	7.20	5.36	10.86
L		2*SE*	0.41	0.40	0.42	0.22	0.15	0.04	0.22	0.15
E		*CV*	2.14	6.84	3.15	2.83	5.45	1.06	7.00	2.31
S	IV(2)	$\bar{Y}$	34.36	11.10	24.42	14.06	4.86	7.41	5.40	11.07
		2*SE*	0.92	0.08	0.92	0.10	0.06	0.03	0.15	0.04
		CV	3.77	1.02	5.30	1.01	1.75	0.57	3.93	0.51

Table 3.3b.--*Continued*.

Sex	Toothwear class (*n*)		Variable						
			FMH	LFM	WSM	AFA	MAF	IML	WMS
M	II(2)	$\bar{Y}$	4.74	2.67	1.85	5.55	4.03	9.13	1.80
A		2*SE*	0.20	0.02	0.04	0.22	0.05	0.27	0.03
L		*CV*	5.97	0.80	3.06	5.61	1.58	4.18	2.36
E	III(7)	$\bar{Y}$	4.60	2.59	1.85	6.60	4.67	9.86	1.68
S		2*SE*	0.06	0.03	0.02	0.12	0.13	0.15	0.02
		CV	3.67	3.49	2.68	4.81	7.62	4.10	2.62
	IV(2)	$\bar{Y}$	4.53	2.67	1.91	6.62	4.81	9.82	1.75
		2*SE*	0.10	0.04	0.05	0.22	0.19	0.38	0.01
		CV	2.97	2.12	3.70	4.60	5.59	5.40	0.41
F	II(2)	$\bar{Y}$	4.86	2.45	1.75	5.82	3.76	9.52	1.65
E		2*SE*	0.09	0.03	0.04	0.19	0.08	0.02	0.04
M		*CV*	2.62	1.73	2.84	4.50	3.01	0.22	3.43
A	III(3)	$\bar{Y}$	4.72	2.59	1.80	6.37	4.74	9.86	1.72
L		2*SE*	0.08	0.08	0.01	0.11	0.12	0.10	0.02
E		*CV*	2.85	5.14	0.85	3.03	4.19	1.71	2.42
S	IV(2)	$\bar{Y}$	4.65	2.67	1.81	7.00	4.81	9.64	1.68
		2*SE*	0.12	0.08	0.03	0.06	0.21	0.29	0.01
		CV	3.50	3.98	2.34	1.11	6.17	4.18	0.42

Table 3.4 Loadings of measurements on the first two components from principal components analyses of *Aethomys namaquensis* from (**a**) Boekenhoutkloof and (**b**) Narap. The percent variance contribution is given in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components	
	I	II
(**a**)		
Greatest length of skull	-0.882 (77.75)	0.298 (8.86)
Greatest length of frontals	-0.139 (1.94)	0.563 (31.67)
Length of nasals to zygomatic arch	-0.890 (79.18)	0.355 (12.63)
Greatest width of bulla	-0.379 (14.35)	-0.269 (7.26)
Foramen magnum height	0.067 (0.44)	-0.493 (24.31)
Length of M^1	-0.493 (24.26)	-0.288 (8.27)
Width of M^2	0.188 (3.53)	-0.654 (42.72)
Length of angular process to mandibular condyle	-0.749 (56.04)	-0.011 (0.01)
Length of mandibular foramen to condyle	-0.814 (66.31)	0.145 (2.11)
Length of I_1 to M_3	-0.768 (59.05)	-0.295 (8.70)
Width of M_2	-0.256 (6.54)	-0.551 (30.38)
% Trace:	Axis I = 35.4%;	Axis II = 16.1%
(**b**)		
Greatest length of skull	-0.977 (95.42)	-0.058 (0.33)
Greatest length of frontals	-0.772 (59.57)	-0.281 (7.91)
Length of nasals to zygomatic arch	-0.974 (94.81)	-0.071 (0.51)
Greatest width of bulla	-0.909 (82.65)	0.120 (1.43)
Foramen magnum height	-0.188 (3.52)	0.781 (60.94)
Length of M^1	-0.618 (38.21)	0.088 (0.78)
Width of M^2	-0.642 (41.27)	0.368 (13.56)
Length of angular process to mandibular condyle	-0.939 (88.15)	-0.208 (4.31)
Length of mandibular foramen to condyle	-0.903 (81.61)	-0.206 (4.23)
Length of I_1 to M_3	-0.887 (78.71)	-0.218 (4.77)
Width of M_2	-0.708 (50.15)	0.525 (27.52)
% Trace:	Axis I = 64.9%;	Axis II = 11.5%

Table 3.5 Loadings of measurements on the first two axes from a canonical variates analysis of *Aethomys namaquensis* from Boekenhoutkloof. The percent variance contribution is given in brackets. Measurements are defined in Figure 2.5.

Variable	Canonical Variates	
	I	II
Greatest length of skull	0.787 (1.97)	-0.180 (85.13)
Greatest length of frontals	0.211 (59.29)	-0.010 (39.69)
Length of nasals to zygomatic arch	0.824 (3.47)	0.023 (95.77)
Greatest width of bulla	0.218 (12.48)	-0.208 (1.87)
Foramen magnum height	-0.048 (9.72)	0.078 (89.16)
Length of M^1	0.281 (13.75)	0.039 (76.91)
Width of M^2	-0.264 (84.81)	-0.069 (14.57)
Length of angular process to mandibular condyle	0.549 (87.06)	-0.084 (10.39)
Length of mandibular foramen to condyle	0.497 (2.63)	-0.152 (80.11)
Length of I_1 to M_3	0.409 (1.48)	-0.365 (95.80)
Width of M_2	-0.113 (93.16)	-0.315 (0.23)
% Trace:	Axis I = 54.9%;	Axis II = 38.9%

CHAPTER 4

DELINEATION OF SOUTHERN AFRICAN SPECIES OF *AETHOMYS*

4.1 INTRODUCTION

African rock rats of the genus *Aethomys* are endemic to East, Central and southern Africa, and extend marginally into West Africa (Musser and Carleton 1993). Five of the ten species currently recognized in the genus (Musser and Carleton 1993), namely, *A. namaquensis*, *A. granti*, *A. chrysophilus*, *A. silindensis*, and *A. nyikae*, have been reported from southern Africa (Meester *et al.* 1986; Skinner and Smithers 1990). The southern African species are currently classified in two subgenera, *Micaelamys* that includes *A. namaquensis* and *A. granti*, and *Aethomys* that includes *A. chrysophilus*, *A. silindensis*, and *A. nyikae* (Meester *et al.* 1986).

Aethomys chrysophilus and *A. namaquensis* are widely distributed in the subregion whereas *A. granti* has only been recorded from the Karoo in the south-central parts of South Africa. *Aethomys silindensis* is known from three localities in eastern Zimbabwe (Meester *et al.* 1986; Skinner and Smithers 1990). Davis (1975) reported *A. nyikae* from eastern Zimbabwe on the basis of a single juvenile specimen whose identity is uncertain (Meester *et al.* 1986; Skinner and Smithers 1990).

Aethomys chrysophilus is composed of two electrophoretically distinct cytotypes (2n = 44 and 2n = 50; Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986; Baker *et al.* 1988), that also differ in sperm morphology (Gordon and

Watson 1986; Visser and Robinson 1987; Breed *et al.* 1988). The absence of hybrids in areas of sympatry is suggestive of reproductive isolation between the two cytotypes (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986).

The recognition of subgenera and the taxonomic allocations of species have been the source of systematic uncertainty (Davis 1975; Schlitter 1978; Meester *et al.* 1986; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Skinner and Smithers 1990; Musser and Carleton 1993). This uncertainty largely emanates from the rarity and restricted nature of some species, questionable distributional records, general morphological similarities, and high degrees of chromosomal diversity. This problem is exacerbated by remarkable intraspecific phenotypic variation that has led to the description of numerous subspecies.

The aim of this chapter is to examine the relationships and taxonomic status of southern African species of *Aethomys* by univariate and multivariate morphometrics as well as qualitative cranial morphology. In addition to resolving the taxonomic status of this group of rodents, the data has significance with regard to epidemiology and pest management. Some species have been implicated in the transmission of plague (Hallet *et al.* 1970), Rift Valley fever (Swanepoel *et al.* 1978) and schistosomiasis (Gear *et al.* 1966) while others may cause extensive damage to crops and stored grain (Wilson 1970, 1975; Smithers 1971; De Graaff 1981).

4.2 MATERIAL AND METHODS

The study is based on 3799 specimens, 19 of which had been karyotyped, from 801 localities in southern Africa. All cytogentically known specimens, type material, other specimens examined and their constituent localities, together with a gazetteer are given in Appendices III, IV, V, and VI, respectively. The same set of 11 basic cranial measurements selected on the basis of the procedure developed in Chapter 2 (Chimimba and Dippenaar 1995) were used. The data set also included four descriptive cranial and four external measurements but these were not included in multivariate analyses (Chapter 2; Chimimba and Dippenaar 1995).

Character recording and analyses were based on adult specimens of toothwear classes IV, V and VI (Chapter 3; Chimimba and Dippenaar 1994). This effectively reduced the influence of age variation. Similarly, the absence of sexual dimorphism in these species justified the pooling of sexes in the analyses (Chapter 3; Chimimba and Dippenaar 1994).

4.2.1 Analytical Procedure

All sample localities in southern Africa, irrespective of taxon, were mapped and grouped into 14 computationally manageable, geographical subsets from: Namibia, Botswana, northern and southern Zimbabwe, Mozambique south of the Zambezi River, Northern Province, North-West Province, Gauteng and Mpumalanga, Swaziland and KwaZulu-Natal, Lesotho and Orange Free State, northern, southern and western Northern Cape Province,

western and eastern Western Cape Province and Eastern Cape Province. Each subset was subjected to data screening using PCA, MST and UPGMA cluster analyses based on standardized variables. The UPGMA cluster analyses and MST were performed on both average taxonomic distances and product-moment correlation coefficients among OTUs, whereas PCA was computed from product-moment correlation coefficients among characters. All multivariate analyses were based on 11 basic cranial measurements selected in Chapter 2 (Chimimba and Dippenaar 1995).

The PCA, MST and UPGMA cluster analyses were subsequently used to identify phenetic groupings within each of the 14 subsets. This often involved the exclusion of well-delineated phena and re-analyses of the remaining specimens, leading eventually to the delineation of distinct phena from each of the 14 geographic areas. Collection localities of each phenon were mapped and, where necessary, samples pooled for the computation of standard statistics. Pooling of geographically contiguous localities was undertaken with reference to phytogeographic zones (Acocks 1988) and vegetation maps (Keay 1959). These geographic populations (OTUs) were subjected to PCA, MST, and UPGMA cluster analyses for the determination of species relationships. Some of the 278 OTUs comprised sample sizes of $n \leq 3$. To reduce potential statistical bias, and to comply with minimum sample size requirements of $n \geq 4$ for UNIVAR (Power 1970), small samples were excluded from analyses. The only exception was *A. silindensis* in which the only six available adult specimens were considered separate OTUs. As a consequence, 194 OTUs were subjected to multivariate statistical procedures. The allocation of specimens excluded from analyses because of small sample sizes was verified

by PCA, MST, and UPGMA cluster analyses of individual specimens.

The phena delineated by the above procedure correspond to four of the five species currently recognized in southern Africa: *A. namaquensis* (104 OTUs), *A. granti* (5), *A. silindensis* (6), and *A. chrysophilus* (79). To further define phenetic groupings within *A. chrysophilus*, additional PCA, MST, and UPGMA cluster analyses were undertaken. These analyses involved cytogenetically known specimens from Mpumalanga, Gauteng and the Northern Province (2n = 44, *n* = 4; 2n = 50, *n* = 15). This sample was bolstered by an additional 40 cytogenetically unknown specimens whose cytogenetic affiliation was inferred based on their collection at the karyotypically-sampled localities (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987). The phenetic groupings thus obtained were further examined using CVA and MANOVA. The specimens of known cytogenetic provenance were used in a diagnostic CVA to classify 979 specimens of unknown cytogenetic affinity from throughout southern Africa.

4.2.2 Qualitative Morphological Variation

After having delineated species morphometrically, representative samples (*n* = 2017) of each species (including type material) from the entire subregion were re-examined for qualitative morphological variation. This included the comparison of pelage colouration in natural light using the colour standards of Oyama *et al.* (1967).

4.2.3 Nomenclature

The nomenclature of southern African *Aethomys* was resolved by separate analyses that included the holotypes of *A. granti*, *A. chrysophilus* and its 10 described subspecies (*ineptus*, *acticola*, *tzaneenensis*, *pretoriae*, *magalakuini*, *capricornis*, *imago*, *tongensis*, *fouriei* and *harei*), the holotype and paratype of *A. silindensis*, and the holotypes of *A. namaquensis* and 13 of its 16 described subspecies (*lehocla*, *auricomis*, *centralis*, *avarillus*, *monticularis*, *grahami*, *calarius*, *siccatus*, *capensis*, *klaverensis*, *drakensbergi*, *lehochloides* and *waterbergensis*). The holotypes of *alborarius*, *albiventer* and *namibensis* were not available for examination. Separate analysis also included the holotype and nine specimens of *A. nyikae* from Malawi. To accommodate the damaged *A. namaquensis* holotype, some analyses were based on a subset of seven variables.

4.3 RESULTS

4.3.1 Delineation of Southern African Species of *Aethomys*

The results of a PCA of samples of *A. namaquensis* (104 OTUs), *A. granti* (5), *A. silindensis* (6), and *A. chrysophilus* (2n = 44, *n* = 48, and 2n = 50, *n* = 31) are given in Figure 4.1. *Aethomys silindensis* clusters well apart from other *Aethomys* species along both axis I and II (Figure 4.1*a*). The 2n = 44 and 2n = 50 cytotypes within *A. chrysophilus* are clearly separated in the two-dimensional space, while *A. namaquensis* and *A. granti* plot well apart along the fourth axis (Figure 4.1*b*). An MST based

on distance coefficients and superimposed on the PCA scattergram (not illustrated) also emphasized the five discrete phena.

Principal component I (83.3% of variance) had relatively high negative loadings on all measurements (Table 4.1). The generally high percent variance contributions of characters suggest that the separation of *A. silindensis* is primarily related to size.

The second PCA axis (9.2% of variance), along which there is some differentiation of the 2n = 44 and 2n = 50 cytotypes within *A. chrysophilus* and also emphasizes the marked differentiation of *A. silindensis*, has both positive and negative character loadings and percent variance contributions of different magnitudes (Table 4.1). This suggests shape-related variation between these taxa. Characters with relatively high loadings and percent variance contributions on this axis are greatest length of frontals, foramen magnum height, width of M^2 and width of M_2. The fourth PCA axis (1.5% of variance), along which *A. granti* is markedly separated from *A. namaquensis*, has character loadings and percent variance contributions of different magnitudes (Table 4.1) consistent with shape-related variation involving the posterior mandibular region.

These results indicate that apart from size, subtle shape differences in the frontal and foramen magnum regions of the skull and dental characteristics on both the upper jaw and the mandible delineate the southern African species of *Aethomys*.

The distance phenogram (Figure 4.2) shows five discrete clusters corresponding with the currently recognized species and the two cytotypes within *A. chrysophilus*.

4.3.2 Analysis of *A. chrysophilus* Species Complex in Southern Africa

The analysis of variation within the *A. chrysophilus* species complex in southern Africa focused on the 19 specimens of known cytogenetic provenance and 40 specimens from Mpumalanga, Gauteng and the Northern Province for which cytogenetic data are available. Both the PCA (Figure 4.3) and UPGMA cluster analysis based on correlation coefficients (Figure 4.4) reveal two distinct clusters which correspond with the 2n = 44 and 2n = 50 cytotypes. A close association exists between the cytogenetically known specimens and those for which a cytogenetic affiliation was inferred. An MST superimposed on the PCA scattergram (not illustrated) similarly delineated the two cytotypes. The two cytotypes co-exist at Thabazimbi (specimen 19, 2n = 50 with 23 - 30, 46 - 48, 2n = 44), the Tzaneen Estates (20, 2n = 50 with 49, 50, 2n = 44), and Soutpan (21, 2n = 50 with 52 - 55, 2n = 44).

The second PCA axis (20.1% of variance), along which the two cytotypes separate, has character loadings and percent variance contributions that suggest shape-related variation (Table 4.2). Variables with relatively high loadings (regardless of sign) and high percent variance contributions on the second axis are greatest length of frontals, length of nasals to zygomatic arch, foramen magnum height, width of M^2 and width of M_2.

A CVA of the two phena produced a 100% *a posteriori* classification (Table 4.3). The CVA scores presented as a histogram (Figure 4.5) show two distinct groups which correspond to the 2n = 44 and 2n = 50 cytotypes within *A. chrysophilus*. A MANOVA indicated a highly significant difference between the

group centroids (F = 20.33; P < 0.001; 2n = 44 group centroid = 1.59; score range: -0.07 - 4.11; 2n = 50: centroid = -2.88; range = -1.65 - -4.95).

A diagnostic CVA based on these results classified 37.3% of the 979 cytogenetically unknown specimens of *A. chrysophilus* (*sensu lato*) from throughout southern Africa as 2n = 50 and 62.5% as 2n = 44. Only two specimens, one from the North-West Province (TM 22285, Zeerust) and the other from the Northern Province (TM 25367, De Hoop Private Nature Reserve) had an equal probability (0.50) of belonging to either cytotype. Cytogenetically known specimens from outside Mpumalanga, Gauteng and the Northern Province were all correctly classified, including two specimens from the Hluhluwe Game Reserve (2n = 44), one from the Ngome Forest Area (2n = 44), and another from Pinetown (2n = 44), all from KwaZulu-Natal. Within the 2n = 50 group, 92.9% of the specimens had a probability of $\geq$ 0.70 of belonging to this cytotype (probability range = 0.51 - 1.00; n = 365). In the 2n = 44 group, the percentage was 95.9% (0.51 - 1.00; n = 612). These results suggest that the 2n = 50 and 2n = 44 cytotypes within *A. chrysophilus* are valid species which herein are referable to *A. chrysophilus* De Winton, 1897 and *A. ineptus* Thomas and Wroughton, 1908, respectively (see Nomenclature Section below).

4.3.3 Diagnostic Morphological and Morphometric Characters

Observations on diagnostic cranial and external morphology of the delineated species are summarized in the identification key and diagnoses below. Important features involve the configuration of the presphenoid, *canalis nervi pterygoidei* and

alisphenoid process of the squamosal, distortion of M^1 and its cusp alignment, shape of the posterior ascending ramus, and the extent of triangulation of t_8 on M^3 (Figure 4.7).

In contrast, the southern African species of *Aethomys* cannot reliably be distinguished on pelage colour. There is considerable geographic variation in pelage colour in *A. namaquensis*, *A. chrysophilus* and *A. ineptus* but in *A. silindensis* and *A. granti* it is less pronounced.

As an additional aid to species identification, a search was made for simple ratios from standard statistics of 11 basic cranial, four descriptive cranial and four external measurements (Table 4.4). Cranial ratios, using all specimens from the subregion, were computed for characters with high negative (width of M^2 and width of M_2) and positive (greatest length of frontals, foramen magnum height, and length of mandibular foramen to condyle) loadings in the shape-related axes II and IV of the PCA of all southern African species (Table 4.5). Greatest length of skull, a highly negative size-related character on PC Axis I was also included. There is no overlap in mean $\pm$ 1 *SD* (Sneath and Sokal 1973) of the ratios greatest length of frontals to greatest length of skull between *A. silindensis* and *A. ineptus*; foramen magnum height to greatest length of skull between *A. silindensis* and *A. chrysophilus*, *A. ineptus*, *A. namaquensis*, and *A. granti*; length of mandibular foramen to condyle to greatest length of skull between *A. granti*, *A. chrysophilus*, *A. ineptus*, *A. silindensis*, and *A. namaquensis*. Differential ratios of external characters include length of tail to length of head and body between *A. namaquensis* and *A. silindensis* and *A. granti*. In the case of a pairwise comparison in the ratio length of tail to

length of head and body, the mean ± 1 *SD* ranges overlap only slightly between *A. namaquensis*, *A. chrysophilus* and *A. ineptus*.

4.3.4 Nomenclature

In the PCA, MST and UPGMA cluster analyses undertaken to resolve the nomenclature of southern African *Aethomys* (not illustrated), the holotypes of *A. chrysophilus* and the taxa *acticola* and *imago* consistently grouped with the 2n = 50 cytotype. In a diagnostic CVA they had classificatory probabilities of 1.00, 0.58 and 0.55, respectively, of belonging to this cytotype. *Aethomys chrysophilus* De Winton, 1897, is consequently considered the senior synonym for the 2n = 50 cytotype, with *acticola* Thomas and Wroughton, 1908, and *imago* Thomas, 1927, as junior synonyms. The holotypes of the remaining eight taxa, *ineptus* Thomas and Wroughton, 1908, *tzaneenensis* Jameson, 1909, *pretoriae* Roberts, 1913, *magalakuini* Roberts, 1926, *capricornis* Roberts, 1926, *tongensis* Roberts, 1931, *fouriei* Roberts, 1946, and *harei* Roberts, 1946, grouped within the 2n = 44 subcluster (all with probabilities of 1.00). The oldest available name, *ineptus* Thomas and Wroughton, 1908, is applied to the 2n = 44 cytotype and the remaining seven taxa considered junior synonyms.

In the remaining species, the respective species' and subspecies' type specimens, including the damaged holotype of *A. namaquensis* (based on a seven-variable analysis), and the *A. nyikae* OTUs were placed within their nominate groups (not illustrated). Importantly, however, there was no phenetic association of *A. nyikae* specimens with any of the 194 OTUs of

southern African *Aethomys* analysed.

Of the non-analysed taxa, *albiventer* Jentink, 1909, is allocated as a junior synonym of *A. namaquensis* because its type locality (Mossel Bay, South Africa) falls within the distributional range of *A. namaquensis*. The type localities of *alborarius* Peters, 1852 (Tete, Mozambique), and *namibensis* Roberts, 1946 (Karub, Namibia), however, fall within the distributional ranges of both *A. chrysophilus* and *A. ineptus* and are provisionally referred to *A. namaquensis* based on previous allocations (Peters 1852; Roberts 1946).

4.4 DISCUSSION

4.4.1 Delineation of Southern African Species of *Aethomys*

Based on multivariate morphometric analyses of cranial variables, *Aethomys* is represented in southern Africa by five species, *A. namaquensis*, *A. granti*, *A. silindensis*, *A. chrysophilus* and the newly recognized species *A. ineptus*. *Aethomys namaquensis*, *A. granti* and *A. silindensis* differ markedly in cranial size and/or shape, while the separation between *A. chrysophilus* and *A. ineptus* is based on subtle cranial shape differences.

The recognition of these species is supported by qualitative cranial morphology and is in agreement with previous studies on chromosome morphology, protein electrophoresis and sperm and cuticular hair morphology (see below). Analyses involving the extralimital *A. nyikae*, including its holotype, support the specific status of this taxon but provide no evidence for its

occurrence in southern Africa.

Aethomys silindensis is a well-delineated species that differs in cranial size and/or shape from the other southern African species. It can also be distinguished by the configuration of the presphenoid and the *canalis nervi pterygoidei*. Previous studies have also drawn attention to the robustness of the skull, extent of development of the supraorbital ridges, number of roots on M^1, position of the anterior cusp on M^3 and the length, groove characteristics and scale patterns of cuticular hair (Meester *et al.* 1964; Keogh 1985).

Aethomys namaquensis differs from *A. silindensis*, *A. chrysophilus* and *A. ineptus* in cranial size and/or shape. It is morphometrically closest to *A. granti*, but the two species differ in the configuration of the posterior mandibular region. The extent of concavity in the posterior ascending ramus and the degree of distortion on M^1 are strong differential characters. Differential characters reported in previous studies include the diploid number (2n = 24), haemoglobin electromorph mobility and banding patterns, sperm head and bacular shaft morphology, the number of cusps in the anterior row of M_1 and the breadth, groove characteristics and scale patterns of cuticular hair (Gordon and Rautenbach 1980; Keogh 1985; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker *et al.* 1988; Breed *et al.* 1988). The length of the tail relative to head and body has also been used to distinguish *A. namaquensis* from other *Aethomys* species (Meester *et al.* 1986; Skinner and Smithers 1990).

Aethomys granti differs from other southern African *Aethomys* species in cranial size and/or shape. The extent of concavity of

the posterior ascending ramus, the degree of distortion on M^1, triangulation of t_8 on M^3, the diploid number (2n = 32) and the breadth, groove characteristics and scale patterns of cuticular hair are unique characters of this species (Keogh 1985; Visser and Robinson 1986). Sperm morphology is essentially similar to that of *A. namaquensis* but proportional differences exist (Visser and Robinson 1987). Tail characteristics (hairiness, scale patterns and its relative length to head and body) and ventral pelage colour have also been used to distinguish *A. granti*, particularly from *A. namaquensis* (Meester *et al.* 1986; Skinner and Smithers 1990).

Morphometric analyses of cytogenetically known specimens showed that *A. chrysophilus* (*sensu lato*) comprises two sympatric, cryptic species, *A. chrysophilus* and *A. ineptus*, which differ in cranial and dental configuration. The distinction between the two species is supported by the configuration of the alisphenoid process of the squamosal. The two species also show notable differences in diploid number (2n = 50 vs 44), haemoglobin electromorph mobility and banding patterns, and sperm head morphology (Gordon and Rautenbach 1980; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker *et al.* 1988; Breed *et al.* 1988). Moreover, marked differences also exist in the relative lengths of the distal cartilaginous element of the baculum and the transition between the shaft and the base of this element (Visser and Robinson 1987).

By contrast, the southern African species of *Aethomys* cannot be distinguished on pelage colour. Although variation in colour is slight in *A. silindensis* and *A. granti*, there is considerable geographic variation in *A. namaquensis*, *A. chrysophilus* and *A.*

ineptus. Previous studies have also drawn attention to the wide variety of colour forms (Smithers 1971; Smithers and Tello 1976; Smithers and Wilson 1979; De Graaff 1981; Musser and Carleton 1993).

4.4.2 Geographical Distributions of Southern African Species of *Aethomys*

The most widely distributed species in southern Africa is *A. namaquensis*. It occurs throughout the subregion except much of central and coastal Mozambique (Figure 4.6*a*) and is sympatric with all other southern African species of *Aethomys*. Both *A. chrysophilus* and *A. ineptus* are also widely distributed in southern Africa north of latitude 23°S and east of longitude 23°E and their geographic ranges overlap extensively (Figure 4.6*b-c*). They occur in sympatry at the type locality of *A. chrysophilus* (Mazoe, Zimbabwe), and also with all other southern African species of *Aethomys* except *A. granti*. By contrast, the endemic *A. silindensis* and *A. granti* have restricted distributions in southern Africa. *Aethomys silindensis* is known only from the type locality, Mount Selinda, and two adjacent localities in eastern Zimbabwe (Figure 4.6*d*), whereas *A. granti* is restricted to the Karoo in south-central South Africa (Figure 4.6*e*).

4.4.3 Subgeneric Classification

The southern African species of *Aethomys* are currently classified into two subgenera on the basis of dental characteristics (Ellerman *et al*. 1953; Meester *et al*. 1986). The

subgenus *Micaelamys* includes *A. namaquensis* and *A. granti*, whereas the subgenus *Aethomys* includes *A. chrysophilus* (*sensu lato*), *A. silindensis*, and *A. nyikae*. The subgeneric division is supported by karyological data, and bacular and sperm morphology (Matthey 1954, 1958, 1964; Visser and Robinson 1986, 1987) although Musser and Carleton (1993) considered that the characters separating *A. namaquensis* and *A. granti* from other species in *Aethomys* are no more significant than other distinguishing traits within the genus. The morphometric analyses in this study provide little support for the recognition of the two subgenera, but a cladistic analysis of qualitative cranial morphological data provided good grounds for the subgeneric separation of *Aethomys* and *Micaelamys* (see Chapter 9).

4.5 KEY TO SPECIES OF SOUTHERN AFRICAN *AETHOMYS*

1. Skull robust (observed range: greatest length of skull 39.0 mm - 41.8 mm; greatest height of skull 12.6 - 13.0 mm; breadth of braincase 15.6 - 16.6 mm), supraorbital ridges well developed, extending posteriorly along frontals and parietals to a point where they meet occipital crest (Figure 4.7*a*). Presphenoid wide (Figure 4.7*b*). *Canalis nervi pterygoidei* wide (Figure 4.7*b*). Posterior incisor to M_3 length, from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus $\geq$ 12.1 mm..... *Aethomys silindensis*

-- Skull less robust (observed range: greatest length of skull 27.1 - 40.6 mm; greatest height of skull 8.9 - 12.7 mm; breadth of braincase 11.9 - 16.6 mm), supraorbital ridges weak or less pronounced with a tendency to fade posteriorly in parietal

region (Figure 4.7*a*). Presphenoid narrow (Figure 4.7*b*). *Canalis nervi pterygoidei* small (Figure 4.7*b*). Posterior incisor to M_3 length $\leq$ 11.9 mm..... 2

2. Tail almost hairless, more coarsely scaled. M_1 with two cusps in anterior row, but often with a small tubercle or cingulum (Figure 4.7*c*). Karyotype 2n = 44 or 50. Baculum with long distal cartilaginous element (ratio of distal to proximal length of cartilaginous baculum 62.3%), well-defined transition between shaft and base..... 3

-- Tail lightly to well haired, more finely and closely scaled. M_1 with three cusps in anterior row (Figure 4.7*c*). Karyotype 2n = 24 or 32. Baculum with short distal cartilaginous element (ratio of distal to proximal length of cartilaginous baculum 71.0%), gradual transition between shaft and base..... 4

3. Alisphenoid process of squamosal wide (Figure 4.7*d*). Ratio of greatest cross-sectional crown width of M^2 to greatest length of frontals 17.4% (mean $\pm$ 1*SD* = 16.9 - 17.9%); ratio of greatest cross-sectional crown width of M_2 to greatest length of frontals 16.3% (mean $\pm$ 1*SD* = 15.8 - 16.7%). Karyotype 2n = 50, "slow" double-banded haemoglobin electromorph, sperm head spatulate..... *Aethomys chrysophilus*

-- Alisphenoid process of squamosal narrow (Figure 4.7*d*). Ratio of greatest cross-sectional crown width of M^2 to greatest length of frontals 16.2% (mean $\pm$ 1*SD* = 15.5 - 16.9%); ratio of greatest cross-sectional crown width of M_2 to greatest length of frontals 15.0% (mean $\pm$ 1*SD* = 14.3 - 15.7%). Karyotype 2n = 44, "fast" double-banded haemoglobin electromorph, sperm head hook-like and ventrally spiked..... *Aethomys ineptus*

4. Concavity in posterior ascending ramus region of mandible pronounced, cutting deeply into ascending ramus: distance between condylar and angular processes narrow, and anterior and posterior edges of ascending ramus parallel to each other (Figure 4.7*e*). M^1 anterolingually distorted: cusps on first and second lamina aligned in a straight line but at oblique angle to longitudinal axis of tooth (Figure 4.7*f*). M^3 with t_8 broadened and distinctly triangular, entire tooth "Ace of Spades"-shaped (more pronounced in worn teeth) (Figure 4.7*g*). Ratio of mandibular foramen - mandibular condyle to greatest skull length 14.9% (mean $\pm$ 1*SD* = 16.6 - 18.4%). Tail well haired with dark bristles becoming denser towards tip, relatively short, on average 104.7% of head and body length (mean $\pm$ 1*SD* = 95.9 - 113.4%). Ventral hairs of body greyish. Karyotype 2n = 32. One or two scales across width of cuticular hair at half-way mark. Scales at half-way mark as deep as broad or cup-shaped. Cuticular hair length variable but always > 9 mm..... *Aethomys granti*

-- Concavity in posterior ascending ramus region of mandible less pronounced: distance between condylar and angular processes wider and anterior and posterior edges of ascending ramus not parallel to each other (Figure 4.7*e*). M^1 anterolingually distorted: cusps on first and second lamina aligned in a straight line but perpendicular to longitudinal axis of tooth (Figure 4.7*f*). M^3 with t_8 not distinctly triangular, and not "Ace of Spades"-shaped (Figure 4.7*g*). Ratio of mandibular foramen - mandibular condyle length to greatest skull length 12.9% (mean $\pm$ 1*SD* = 14.7 - 16.4%). Tail lightly haired and relatively long, on average 136.0% of head and body length (mean $\pm$ 1*SD*: 123.3 - 149.1%). Ventral hairs of body whitish. Karyotype 2n = 24. Never

fewer than two (usually > 2) scales across width of cuticular hair. Scales at mid-point broad and shallow. Cup-shaped scales frequently present on sides of groove. Cuticular hair length > 10 mm..... *Aethomys namaquensis*

4.6 CONCLUSIONS

Five species of African rock rats of the genus *Aethomys*, *A. namaquensis*, *A. granti*, *A. silindensis*, *A. chrysophilus* and *A. ineptus*, are recognized in southern Africa. Morphometric analysis indicate that *A. namaquensis*, *A. granti* and *A. silindensis* differ markedly in cranial size and/or shape. Morphometric analysis of cytogenetically known specimens of *A. chrysophilus* revealed two sympatric, morphologically similar species referred to *A. chrysophilus* and *A. ineptus*. This is concordant with observations on cranial morphology and earlier investigations involving cytogenetics, protein electrophoresis and sperm morphology. In addition, the morphometric data show that, contrary to published reports, the Central African *A. nyikae* does not extend into southern Africa, and the single previous record from eastern Zimbabwe is probably based on a misidentification.

4.7 TAXONOMY

4.7.1 Genus: *Aethomys* Thomas, 1915

Aethomys Thomas, 1915: *Ann. Mag. Nat. Hist* (8)16:477.

Type species.- *Epimys hindei*, Thomas, 1915: *Ann. Mag. Nat.*

Hist (8)16:477.

4.7.2 Subgenus: *Aethomys*

4.7.2.1 *Aethomys chrysophilus* (De Winton, 1897)

Mus chrysophilus De Winton, 1897: *Proc. Zool. Soc. Lond.* for 1896:801.

Mus chrysophilus acticola Thomas and Wroughton, 1908: *Proc. Zool. Soc. Lond.*:547.

Aethomys chrysophilus imago Thomas, 1927: *Proc. Zool. Soc. Lond.*:387.

4.7.2.1.1 Holotype

BM 95.11.3.23 (original No. 54); adult female; Mazoe, Mashonaland, eastern Zimbabwe.

4.7.2.1.2 Distribution

Widely distributed in southern Africa, from northern Namibia, northern and eastern Botswana, Zimbabwe, Mozambique, the Mpumalanga, Gauteng, North-West and Northern Provinces of South Africa to Swaziland and southern KwaZulu-Natal, and the northern sector of the Northern Cape Province around Kuruman, but conspicuously absent from south of latitude 23°S and west of longitude 23°E (Figures 1.1 and 4.6*b*).

4.7.2.1.3 Diagnosis

Medium-sized (observed range: head and body length 120 - 169 mm; greatest skull length 32.1 - 40.6 mm; greatest height of skull 10.4 - 12.7 mm; breadth of braincase 13.6 - 16.6 mm); tail longer than head and body (103.7 - 125.3%). Ratio of greatest cross-sectional crown width of M^2 to greatest length of frontals 17.4% (mean $\pm$ 1*SD* = 16.9 - 17.9%); ratio of greatest cross-sectional crown width of M_2 to greatest length of frontals 16.3% (mean $\pm$ 1*SD* = 15.8 - 16.7%). Dorsal and ventral colour clearly demarcated; upper parts brown (7.5YR 4/3), sprinkled with brownish black (7.5YR 3/1) hairs; cheeks, sides and thighs light grey (7.5YR 8/2); underparts, feet light yellow-orange (7.5YR 8/4); ears naked apart from few scattered yellow-orange (7.5YR 7/8) hairs; tail almost naked and more coarsely scaled apart from a few short adpressed hairs which increase in number and length towards the tip; shiny, mica-like scales present; basal half bicoloured, brown (7.5YR 4/6) above and orange (7.5YR 6/8) below; terminal portion unicoloured yellow-orange (7.5YR 7/8). Alisphenoid process of squamosal wide; M_1 with two cusps in anterior row, often with a small tubercle or cingulum. Karyotype 2n = 50; "slow" double-banded haemoglobin electromorph; sperm head spatulate; bacula with relatively long distal cartilaginous element and well-defined transition between shaft and base.

4.7.2.1.4 Etymology

A combination of two Latin words, *chrysos* = gold and *philos* = having affinity for, to denote the golden dorsal surface.

4.7.2.1.5 Remarks

The proposed name for the 2n = 50 cytotype is in agreement with a suggestion by Gordon and Rautenbach (1980). On the basis of the occurrence of the 2n = 50 cytotype at Mazoe (Zimbabwe), the type locality of *A. chrysophilus*, they suggested that the 2n = 50 cytotype be referred to *A. chrysophilus*.

4.7.2.2 *Aethomys ineptus* (Thomas and Wroughton, 1908)

Mus chrysophilus ineptus Thomas and Wroughton, 1908: *Proc. Zool. Soc. Lond.*:546.

Mus chrysophilus tzaneenensis Jameson, 1909: *Ann. Mag. Nat. Hist.* (8)4:460.

Mus chrysophilus pretoriae Roberts, 1913: *Ann. Tvl. Mus.* 4:85.

Aethomys chrysophilus magalakuini Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Aethomys chrysophilus capricornis Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Aethomys chrysophilus tongensis Roberts, 1931: *Ann. Tvl. Mus.* 14:235.

Aethomys chrysophilus fouriei Roberts, 1946: *Ann. Tvl. Mus.* 20:319.

Aethomys chrysophilus harei Roberts, 1946: *Ann. Tvl. Mus.* 20:320.

4.7.2.2.1 Holotype

BM 8.4.3.73 (original No. 1949); adult male; Tette (= Tete), Zambezi River, Mozambique.

4.7.2.2.2 Distribution

Similar to that of *A. chrysophilus* in being widely distributed in southern Africa, from northern Namibia, northern and eastern Botswana, Zimbabwe, Mozambique, the Mpumalanga, Gauteng, North-West and Northern Provinces of South Africa to Swaziland and southern KwaZulu-Natal, and the northern sector of the Northern Cape Province around Kuruman, but conspicuously absent from south of latitude 23°S and west of longitude 23°E (Figures 1.1 and 4.6*c*).

4.7.2.2.3 Diagnosis

Body (observed range: head and body length 117 - 190 mm) and skull (observed range: greatest skull length: 32.5 - 40.5 mm; greatest height of skull 10.4 - 12.3 mm; breadth of braincase 13.2 - 16.5 mm) size, length of tail to head and body proportions (102.7 - 123.5%), and colour as in *A. chrysophilus*, but paler with brownish black (7.5YR 3/1) bases of hairs markedly paler both on upper and underparts of body; all other external, cranial and dental characteristics as in *A. chrysophilus*, but alisphenoid process of squamosal narrow. Ratio of greatest cross-sectional crown width of M^2 to greatest length of frontals 16.2% (mean $\pm$ 1*SD* = 15.5 - 16.9%); ratio of greatest cross-sectional crown width of M_2 to greatest length of frontals 15.0% (mean $\pm$ 1*SD* = 14.3 - 15.7%). Karyotype 2n = 44, "fast" double-banded haemoglobin electromorph, sperm head hook-like and ventrally spiked.

4.7.2.2.4 Etymology

The species name is probably derived from the Latin word "*ineptus*" meaning "unsuitable, out of place, tasteless, silly" suggesting that Thomas and Wroughton (1908) considered the paler colour not to conform and therefore "unsuitable" for a typical "golden"-coloured *A. chrysophilus*. The common English name "Tete veld rat", after the type locality, is proposed.

4.7.2.2.5 Remarks

Using the unbanded morphology of the submetacentric X chromosome, Gordon and Rautenbach (1980) suggested that the 2n = 44 cytotypes recorded from the Ivory Coast (Matthey 1954) and southern Africa should provisionally be referred to as species A and B. However, *A. chrysophilus* does not occur in the Ivory Coast (Musser and Carleton 1993), and Matthey's material originated from South Africa (M. Tranier *in litt.*[1]). Gordon and Rautenbach (1980) also identified the X chromosome for this species as smaller than the Y chromosome, while Baker *et al.* (1988) concluded the opposite.

4.7.2.3 *Aethomys silindensis* Roberts, 1938

Aethomys silindensis Roberts, 1938: *Ann. Tvl. Mus.* 19:245.

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[1] M. Tranier, Laboratoire Mammifères et Oiseaux, Museum National d'Histoire Naturelle, Paris, France.

4.7.2.3.1 Holotype

TM 8370; adult male; Chirinda Forest, Mount Selinda, eastern Zimbabwe.

4.7.2.3.2 Distribution

Known only from the vicinity of the type locality, Mount Selinda, eastern Zimbabwe (Figures 1.1 and 4.6*e*). Roberts (1951) and Skinner and Smithers (1990) suggest that the species may extend northwards along escarpment in eastern Zimbabwe, and the adjacent, ecologically similar areas in the western Vila Pery District in Mozambique.

4.7.2.3.3 Diagnosis

Large (observed range: head and body length 155 - 200 mm; greatest skull length 39.0 - 41.8 mm; greatest height of skull 12.6 - 13.0 mm; breadth of braincase 15.6 - 16.6 mm); tail subequal in length to head and body (91.9 - 114.0%). Cranium robust, with pronounced supraorbital ridges extending posteriorly along frontals and parietals to a point where they meet the occipital crest; M^1 five-rooted; isolated anterior cusp on M^3 large; presphenoid relatively wide; *canalis nervi pterygoidei* relatively large. Brown (7.5YR 4/6) to dark brown (7.5YR 3/4) upper parts and light grey (10YR 8/2) underparts merge gradually, base of hairs brownish grey (10YR 5/1); feet bright yellowish brown (10YR 6/6); tail brown (7.5YR 4/4), ears brown (7.5YR 4/4) with a thin covering of bright brown (7.5YR 5/8) hairs; tail

naked with distinct scale rings; hairs long, with deep grooves and rippled, crenate scales.

4.7.2.3.4 Etymology

Named after Mount Selinda, the type locality.

4.7.2.3.5 Remarks

The holotype and paratype were the only known specimens of *A. silindensis* until late 1967 when seven other specimens were collected (Skinner and Smithers 1990). Ellerman *et al.* (1953) regarded it as a subspecies of *A. chrysophilus* (*sensu lato*). On the basis of its large size and a five-rooted condition of M^1 (as opposed to small size and a four-rooted M^1 in *A. chrysophilus*), Meester *et al.* (1964) and Davis (1975) considered it a valid species. Keogh (1985) also showed that the two species differ in cuticular hair scale patterns and groove characteristics.

Davis' (1975) record of *A. nyikae* in Zimbabwe is based on a now missing "broad toothed" juvenile specimen from East Ngorima Forest Reserve. Broadened teeth as well as a strong sagittal crest are characteristic of both *A. nyikae* and *A. silindensis*. The specimen may have been a juvenile *A. silindensis*.

4.7.3 Subgenus: *Micaelamys*

4.7.3.1 *Aethomys namaquensis* (A. Smith, 1834)

Gerbillus namaquensis A. Smith, 1834: *S. Afr. Quart. Journ.*

2:160.

Mus lehocla A. Smith, 1836: *App. Rept. Exped. Explor. S. Afr.*:43.

Mus alborarius Peters, 1852: *Reise nach Mossambique. Saugeth*:152.

Mus auricomis De Winton, 1897: *Proc. Zool. Soc. Lond.*: for 1896:802.

Mus auricomis centralis Schwann, 1906: *Proc. Zool. Soc. Lond.*:107.

Mus avarillus Thomas and Wroughton, 1908: *Proc. Zool. Soc. Lond.*:547.

Mus albiventer Jentink, 1909: *Zool. Jahrb. Syst.* 28:246.

Mus namaquensis monticularis Jameson, 1909: *Ann. Mag. Nat. Hist.* (8)4:461.

Mus namaquensis grahami Roberts, 1915: *Ann. Tvl. Mus.* 5:118.

Aethomys namaquensis calarius Thomas, 1926: *Ann. Mag. Nat. Hist.* (9)17:184.

Aethomys namaquensis siccatus Thomas, 1926: *Proc. Zool. Soc. Lond.*:304.

Praomys namaquensis capensis Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Praomys namaquensis klaverensis Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Praomys namaquensis drakensbergi Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Praomys namaquensis lehochloides Roberts, 1926: *Ann. Tvl. Mus.* 11:255.

Aethomys namaquensis waterbergensis Roberts, 1938: *Ann. Tvl. Mus.* 19:239.

Aethomys namaquensis namibensis Roberts, 1946: *Ann. Tvl. Mus.* 20:320.

4.7.3.1.1 Holotype

BM 45.7.3.16; adult female (skull damaged); Little Namaqualand, Cape Province, South Africa (restricted to Witwater by Shortridge 1942).

4.7.3.1.2 Distribution

Widely distributed in southern Africa but absent from central and coastal Mozambique (Figures 1.1 and 4.6*a*).

4.7.3.1.3 Diagnosis

Small (observed range: head and body length 80 - 147 mm; greatest skull length 27.1 - 34.9 mm; greatest height of skull 8.9 - 11.3 mm; breadth of braincase 11.9 - 14.7 mm) with lightly-haired tail longer than head and body length (123.3 - 149.1%). M^1 anterolingually distorted: cusps on first and second lamina in straight line but perpendicular to main axis of tooth; M_1 with three cusps in anterior row; concavity in posterior ascending ramus region of mandible less pronounced: distance between condylar and angular processes wide and anterior and posterior edges of ascending ramus not parallel to each other. Head, neck and body upper parts dull yellowish brown (10YR 5/4) or yellowish brown (10YR 5/6), underparts light grey (10YR 8/4) to light yellow-orange (10YR 8/3). Karyotype 2n = 24; single-banded haemoglobin electromorph; sperm head hook-like with a short apex; bacula with curved shaft in lateral profile; hairs broad, shallowly grooved and lined with flattened, cup-shaped

scales.

4.7.3.1.4 Etymology

Named after Namaqualand, where the species was originally collected.

4.7.3.2 *Aethomys granti* Wroughton, 1908

Mus granti Wroughton, 1908: *Ann. Mag. Nat. Hist.* 1:257.

4.7.3.2.1 Holotype

BM 2.9.1.86 (original No. 114); adult female; Deelfontein, north of Richmond, Cape Province, South Africa.

4.7.3.2.2 Distribution

Restricted to the Karoo in south-central South Africa (Figures 1.1 and 4.6*d*)

4.7.3.2.3 Diagnosis

Small (observed range: head and body length 93.0 - 125.0 mm; greatest skull length 27.9 - 31.9 mm; greatest height of skull 9.0 - 10.3 mm; breadth of braincase 12.4 - 13.8 mm), tail about equal in length to head and body (95.9 - 113.4%). M^1 anterolingually distorted: cusps on first and second lamina in a

straight line but at an oblique angle to main axis of tooth; t_8 on M^3 broadened and distinctly triangular, tooth a characteristically "Ace of Spades"-shaped (more pronounced in worn teeth); concavity in posterior ascending ramus region of mandible pronounced, cutting deeply into ascending ramus: distance between condylar and angular processes narrow and anterior and posterior edges of ascending ramus parallel to each other. Upper parts either dull yellowish brown (10YR 4/3) or dark brown (10YR 3/3), underparts either light grey (10YR 7/1) or greyish yellow (2.5Y 7/2); tail either brownish black (5YR 2/1) or dark reddish brown (5YR 3/4), almost forming brush at tip. Karyotype 2n = 32; hairs slender, shallowly grooved and lined with petal-shaped scales.

4.7.3.2.4 Etymology

Named after Captain C. H. B. Grant, collector of the holotype.

4.7.3.2.5 Remarks

The taxonomic status of *A. granti* has been much debated (De Graaff 1981; Meester *et al.* 1986; Skinner and Smithers 1990). This problem has been exacerbated by its relative rarity which has led to poor representation in study collections and meagre information on its biology (De Graaff 1981). The species has previously been placed in the genus *Myomys*, in *Micaelamys* as a subgenus of *Rattus*, in *Mastomys* and finally in the genus *Aethomys* (Meester *et al.* 1986). Roberts (1951) regarded *A. granti* as a

synonym of *Mastomys natalensis*, while Ellerman *et al.* (1953) considered it of uncertain status. Based on the occurrence of both *M. natalensis* and *A. namaquensis* at Deelfontein (the type locality of *A. granti*), Ellerman *et al.* (1953) suggested that *A. granti* is a hybrid between these two species. Jameson (1909) considered the species to be a variety (or perhaps the young) of *Aethomys namaquensis centralis*, which was also originally described from Deelfontein.

Figure 4.1 Axes I, II and IV from a principal components analysis of *Aethomys chrysophilus* (2n = 50 cytotype [solid square] and 2n = 44 cytotype [open triangle]), *A. silindensis* (solid triangle), *A. namaquensis* (open square), and *A. granti* (open circle) from southern Africa. Polygons enclose OTUs of the same taxon.

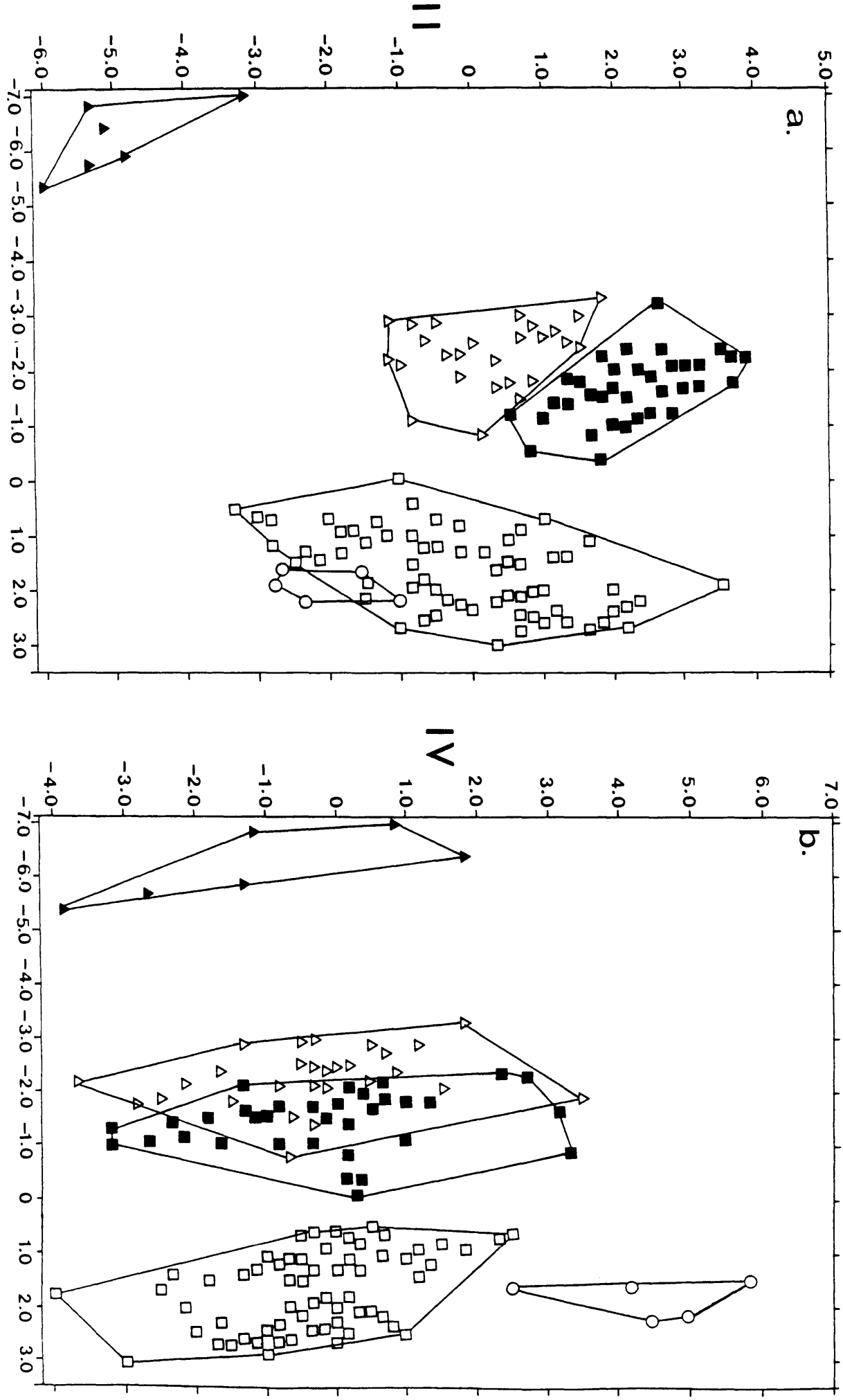


Figure 4.2 Distance phenogram from a cluster analysis of two cytotypes in *Aethomys chrysophilus* (2n = 50, *A. chrysophilus* and 2n = 44, *A. ineptus*), *A. silindensis*, *A. namaquensis* and *A. granti* from southern Africa. Cophenetic correlation coefficient = 0.99.

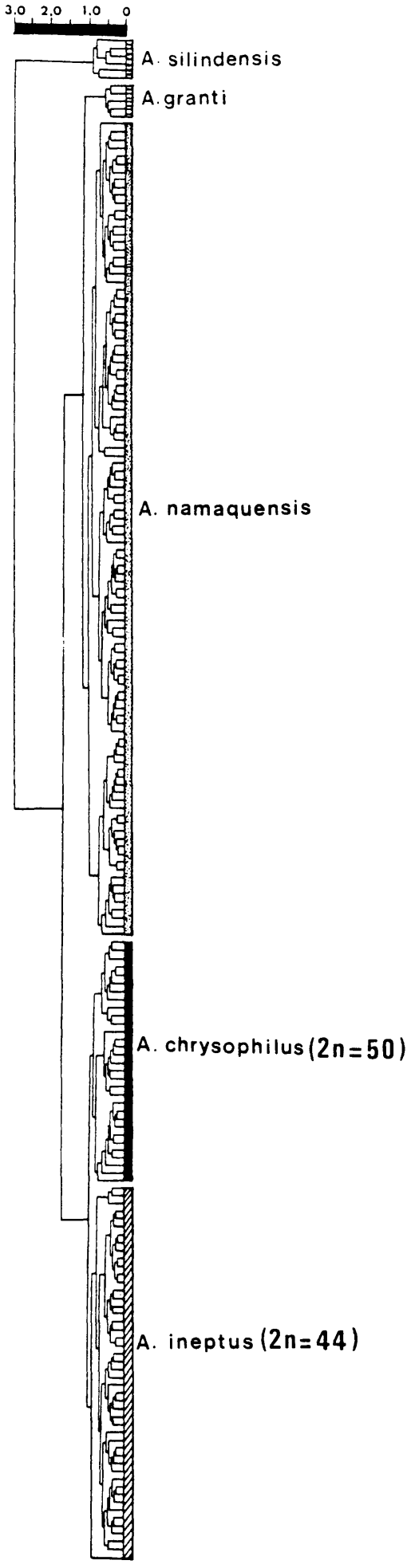


Figure 4.3 Axes I and II from a principal components analysis of cytogenetically known specimens (arrows) of *Aethomys chrysophilus*, 2n = 44 (solid square) and 2n = 50 (open triangle). Also included are specimens of inferred cytogenetic affiliation based on their collection at karyotypically-sampled localities. Polygons enclose specimens of each cytotype.

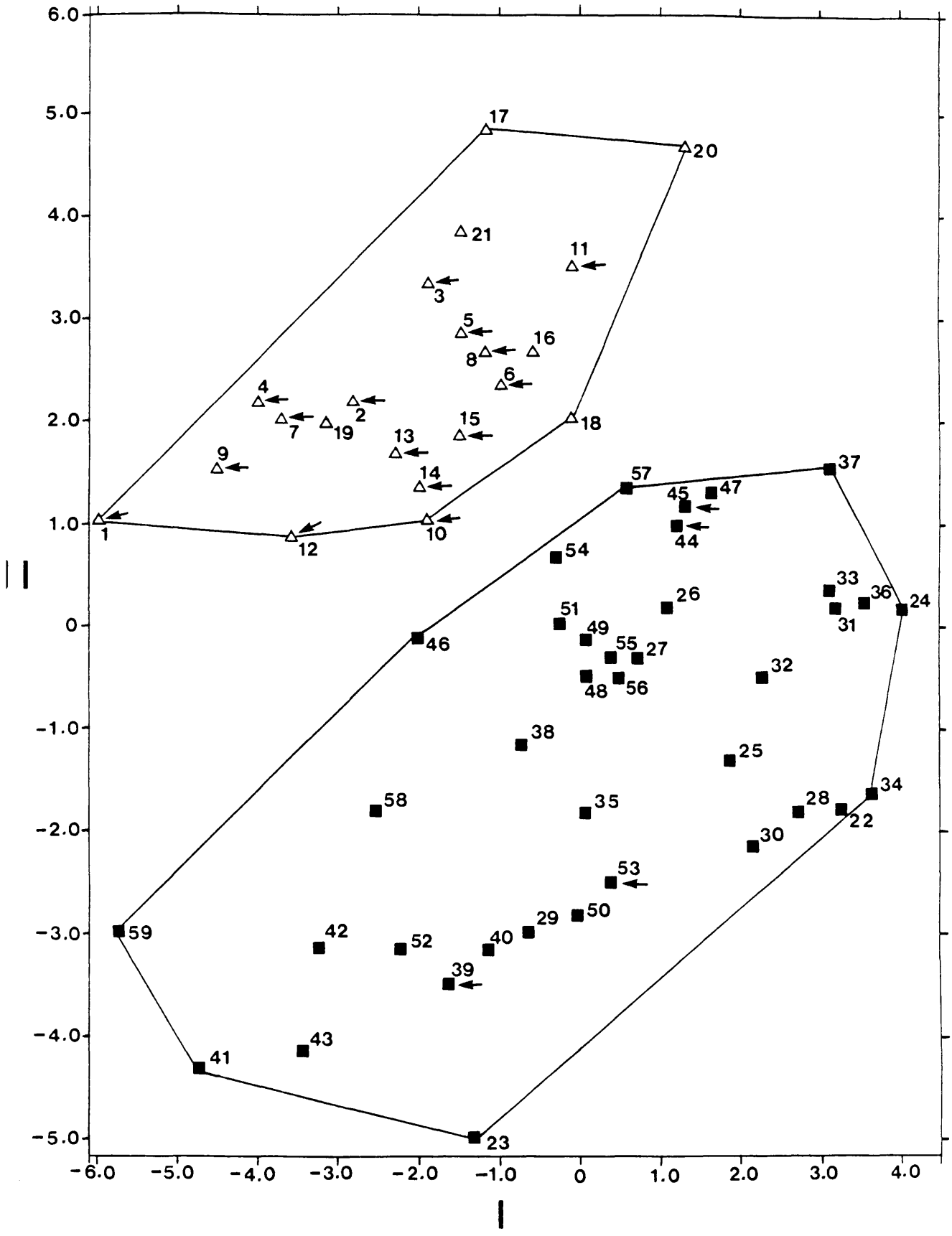


Figure 4.4 Correlation phenogram from a cluster analysis of cytogenetically known specimens (arrows) of *Aethomys chrysophilus*, 2n = 44 and 2n = 50. Also included are specimens of inferred cytogenetic affiliation based on their collection at karyotypically-sampled localities. Cophenetic correlation coefficient = 0.65.

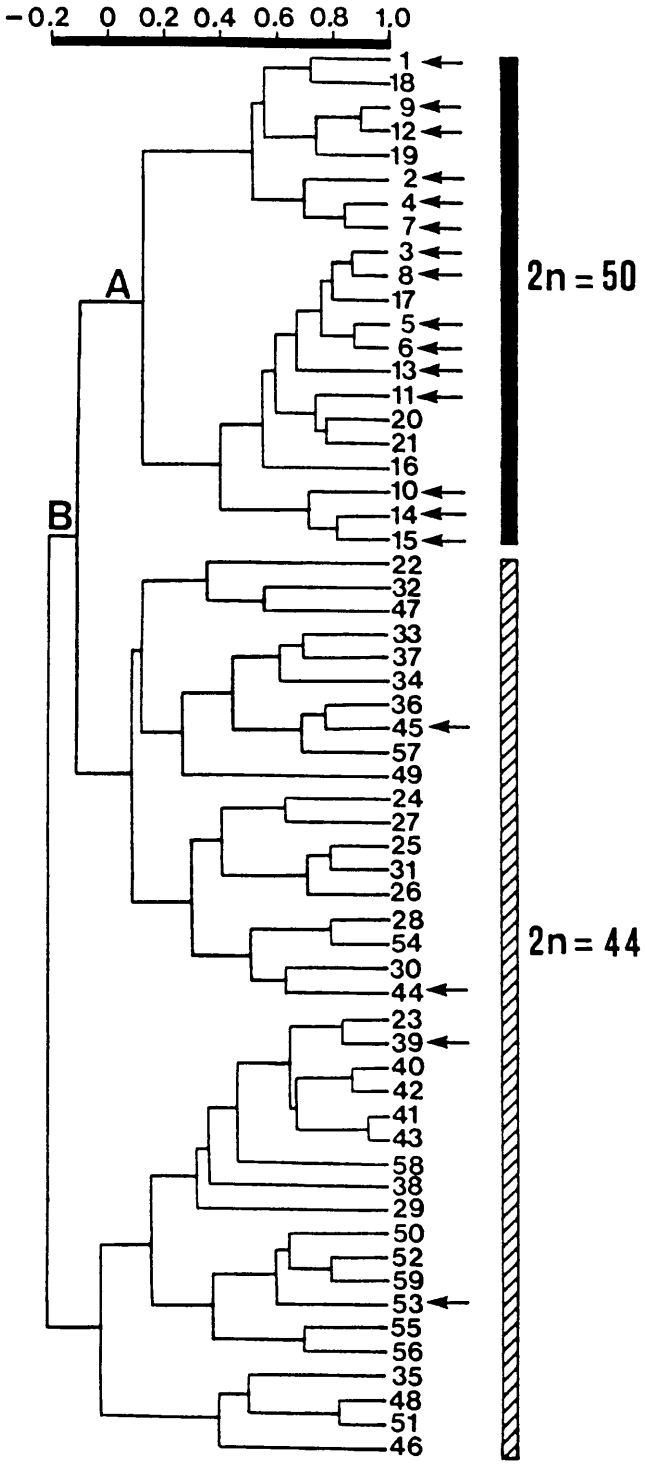


Figure 4.5 Histogram of discriminant scores from a two-group canonical variates analysis of cytogenetically known specimens of *Aethomys chrysophilus*, 2n = 44 (diagonal bars) and 2n = 50 (solid bars), as well as specimens of inferred cytogenetic affiliation based on their collection at karyotypically-sampled localities.

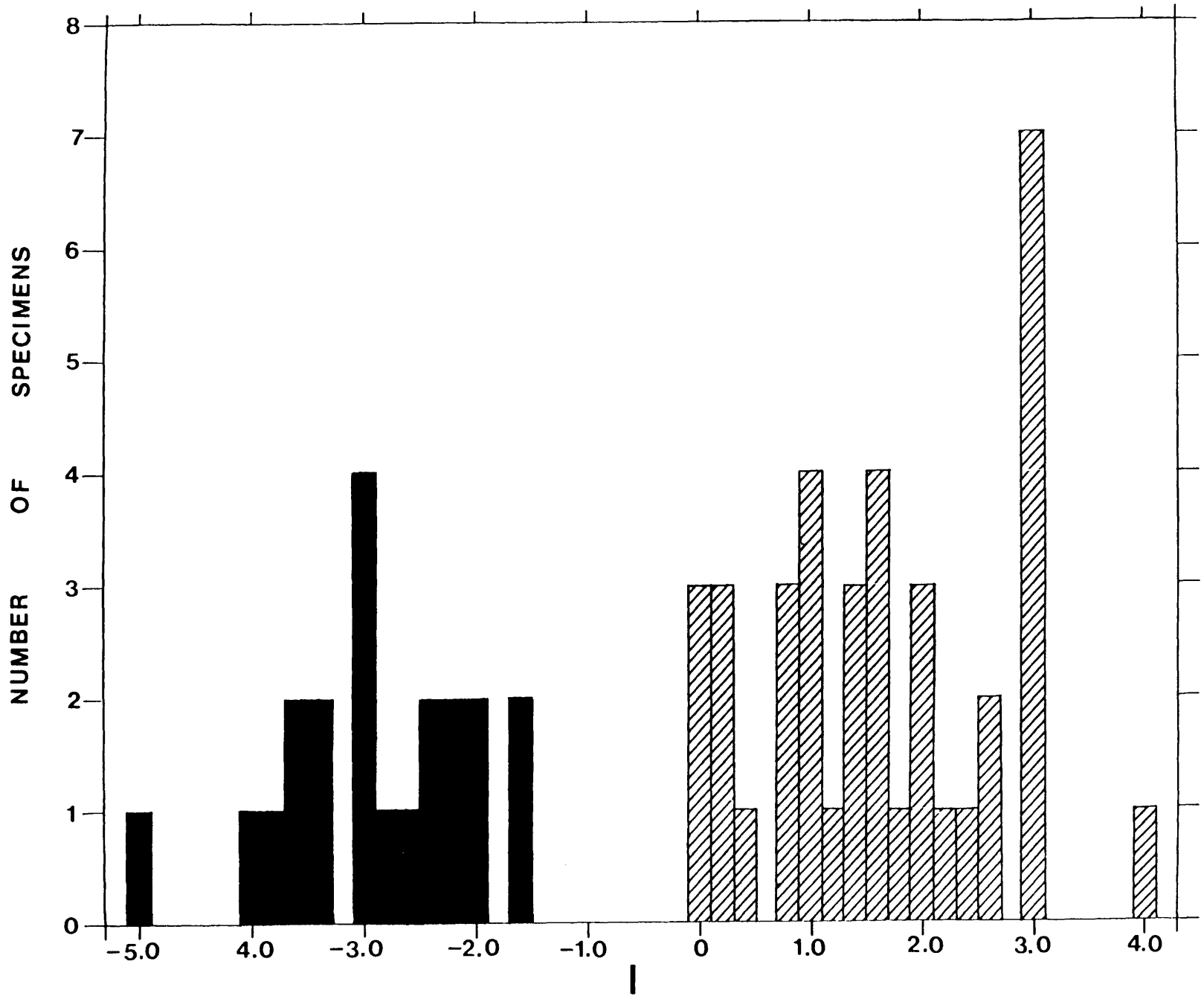
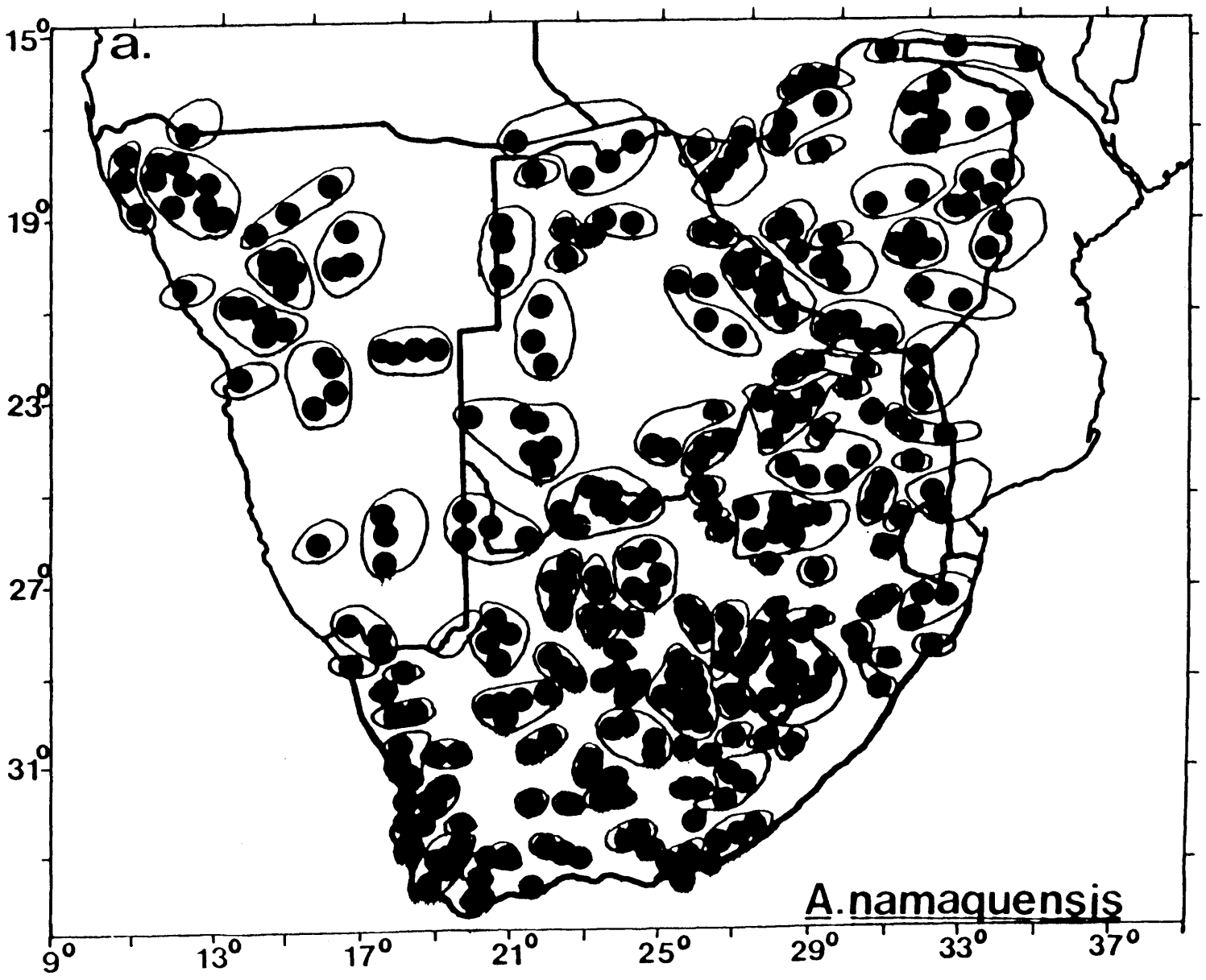
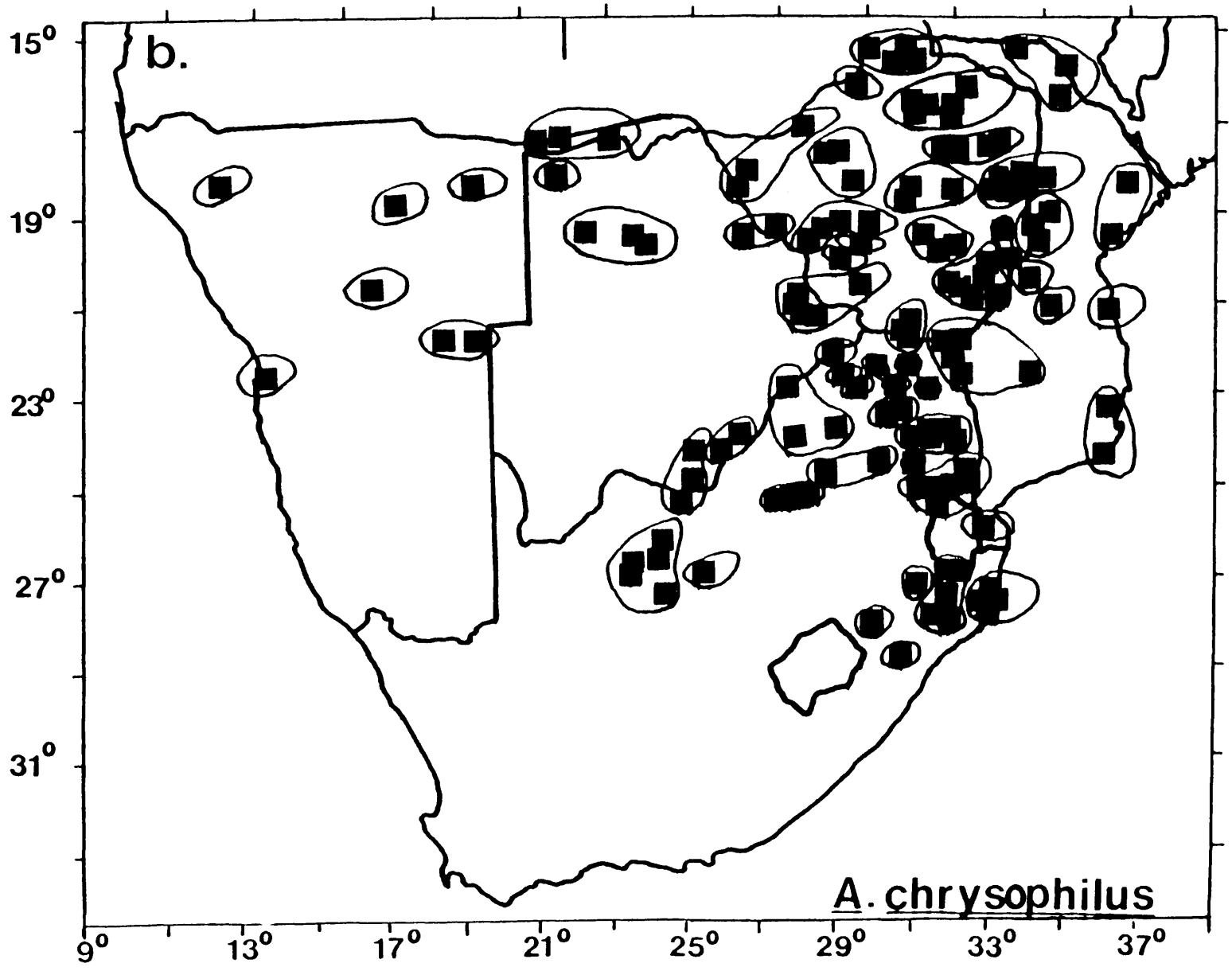
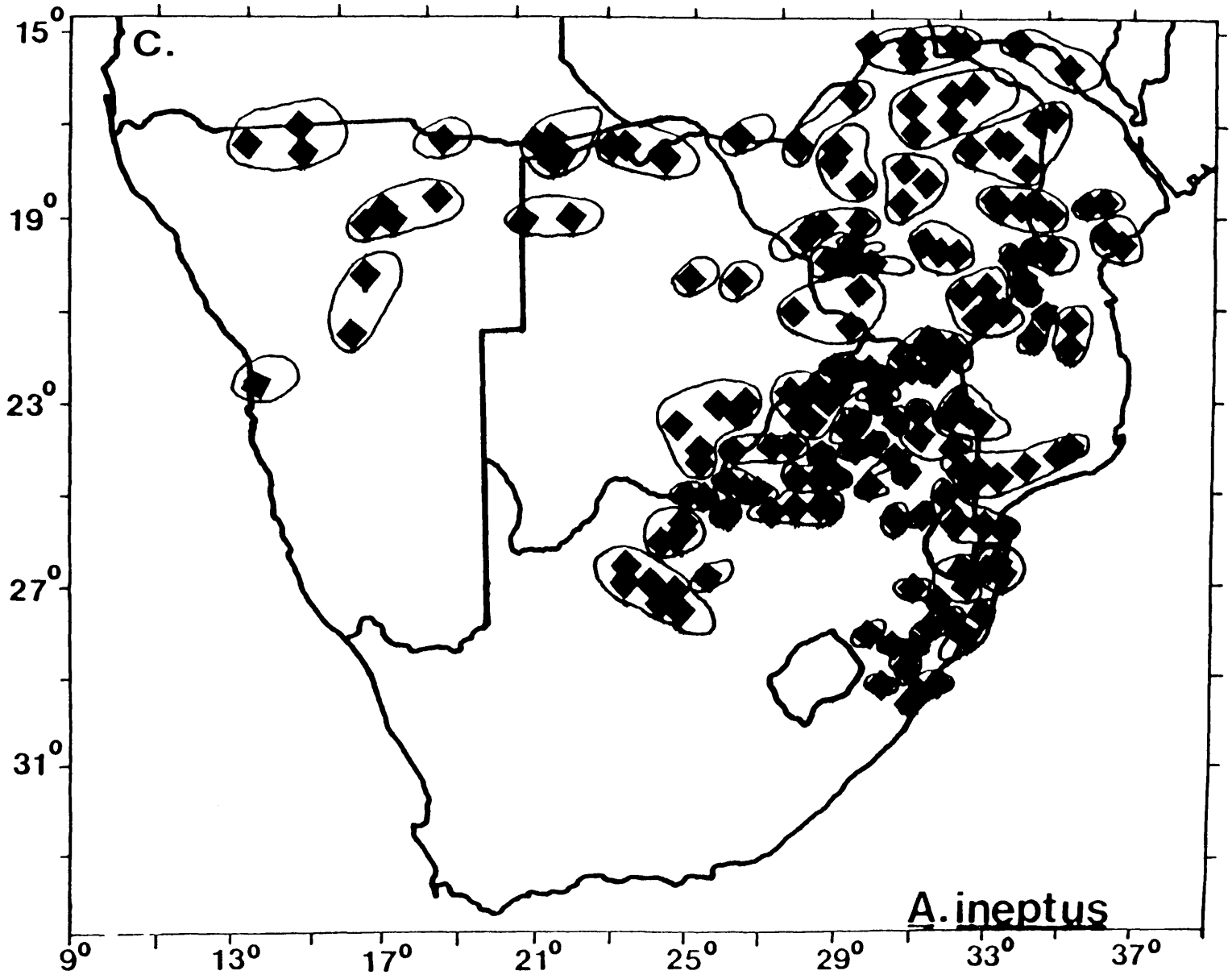


Figure 4.6 Geographical distribution and pooled localities of: **a**) *Aethomys namaquensis*; **b**) *A. chrysophilus*; **c**) *A. ineptus*; **d**) *A. granti*; and **e**) *A. silindensis* in southern Africa. All sampled localities are plotted, regardless of sample size.







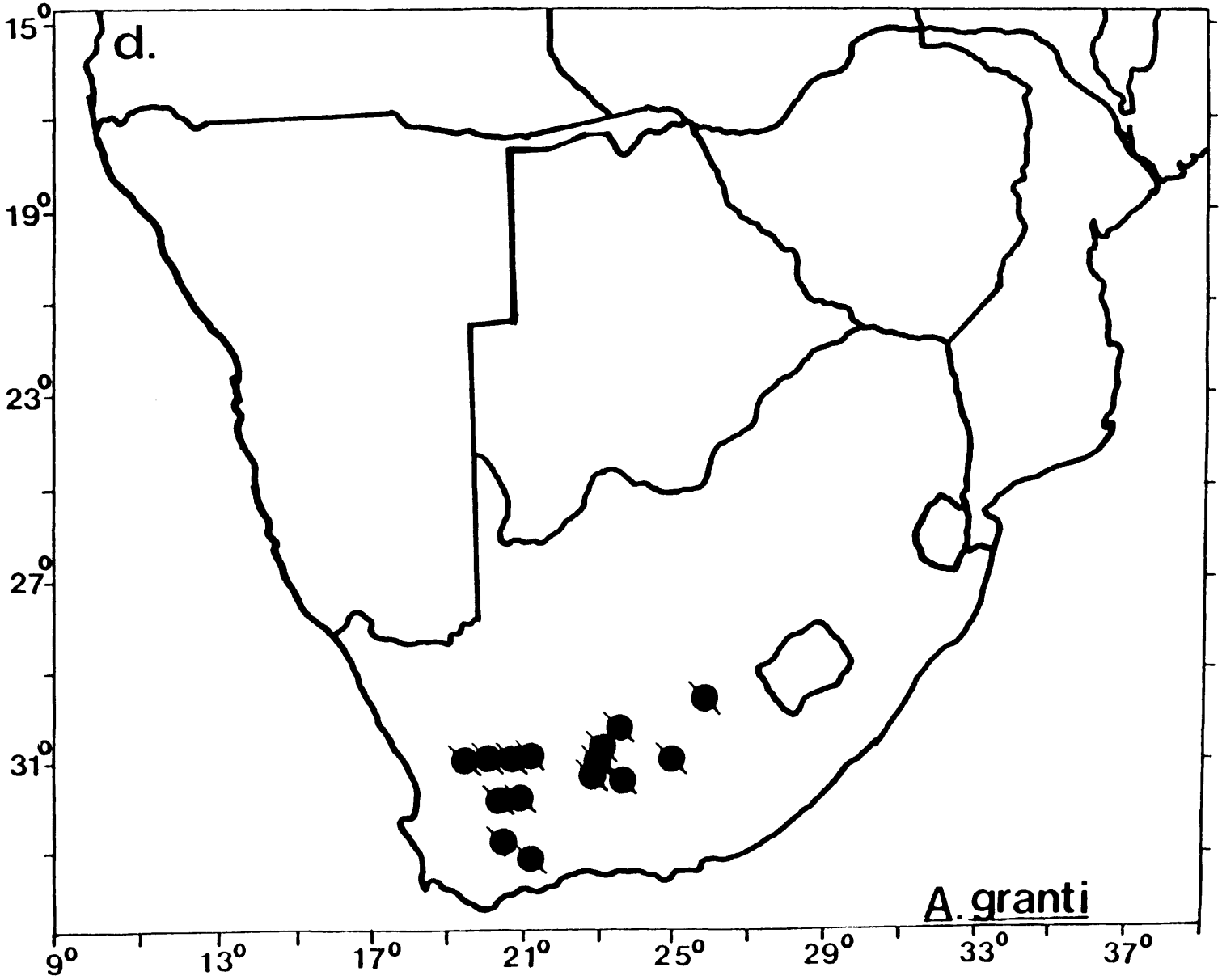


Figure 4.7 Diagnostic qualitative cranial characters of adult *Aethomys chrysophilus* (chr; TM 44240), *A. ineptus* (ine; TM 32311), *A. silindensis* (sil; TM 8371), *A. namaquensis* (nam; TM 34037) and *A. granti* (gra; TM 478) from southern Africa. Dorsal view of cranium (**a**) showing extent of development of supraorbital ridges. Ventral view of cranium (**b**) showing wideness of presphenoid (**pre**) and *canalis nervi pterygoidei* (**cnp**). Occlusal view of left lower toothrow (**c**) showing two or three (or a small extra tubercle or cingulum; **smc**) cusps on M_1 of *A. chrysophilus*, *A. ineptus* and *A. namaquensis*. Posterolateral view of cranium (**d**) showing alisphenoid process of squamosal (**aps**) in *A. chrysophilus* and *A. ineptus*. Lateral view of posterior part of mandible (**e**) in *A. granti* and *A. namaquensis* showing the degree of concavity in the posterior ascending ramus (**as**). Occlusal views of first left maxillary molar in *A. granti* and *A. namaquensis* showing (**f**) cusp alignment on M^1, and (**g**) extent of triangulation of t_8 on M^3. Abbreviations: **ab** = auditory bulla, **aps** = alisphenoid process of squamosal, **as** = ascending ramus, **cnp** = *canalis nervi pterygoidei*, **pre** = presphenoid, **smc** = small extra tubercle or cingulum on M_1, **sq** = squamosal bone.

Table 4.1 Loadings of variables on components I, II and IV from a principal components analysis of *Aethomys* species from southern Africa. The percent variance contributions appear in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components		
	I	II	IV
Greatest length of skull	-0.981 (96.314)	0.119 (1.407)	-0.011 (0.011)
Greatest length of frontals	-0.904 (81.811)	0.340 (11.587)	-0.146 (2.129)
Length of nasals to zygomatic arch	-0.970 (94.080)	0.165 (2.733)	-0.029 (0.081)
Greatest width of bulla	-0.969 (93.887)	0.088 (0.767)	-0.080 (0.643)
Foramen magnum height	-0.697 (48.559)	0.514 (26.389)	0.082 (0.664)
Length of M^1	-0.957 (91.514)	-0.160 (2.572)	-0.067 (0.443)
Width of M^2	-0.782 (61.159)	-0.554 (30.700)	-0.033 (0.110)
Length of angular process to mandibular condyle	-0.978 (95.567)	0.097 (0.936)	0.002 (0.001)
Length of mandibular foramen to condyle	-0.922 (85.044)	-0.089 (0.796)	0.342 (11.667)
Length of I_1 to M_3	-0.983 (96.539)	-0.046 (0.216)	0.002 (0.000)
Width of M_2	-0.847 (71.707)	-0.481 (23.147)	-0.046 (0.211)
% Trace:	Axis I = 83.3%;	Axis II = 9.2%;	Axis IV = 1.5%

Table 4.2 Loadings of variables on the first two components from a principal components analysis of 2n = 44 and 2n = 50 cytotypes in *Aethomys chrysophilus* from South Africa. The percent variance contributions appear in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components	
	I	II
Greatest length of skull	-0.823 (67.67)	-0.359 (12.86)
Greatest length of frontals	-0.310 (9.62)	-0.565 (31.87)
Length of nasals to zygomatic arch	-0.662 (43.78)	-0.499 (24.93)
Greatest width of bulla	-0.422 (17.80)	0.267 (7.10)
Foramen magnum height	0.374 (13.99)	0.535 (28.66)
Length of M^1	-0.577 (33.34)	0.383 (14.63)
Width of M^2	-0.411 (16.92)	0.679 (46.07)
Length of angular process to mandibular condyle	-0.734 (53.89)	-0.189 (3.56)
Length of mandibular foramen to condyle	-0.794 (63.03)	-0.099 (0.97)
Length of I_1 to M_3	-0.736 (54.22)	0.315 (9.94)
Width of M_2	-0.586 (34.33)	0.636 (40.47)
% Trace:	Axis I = 37.1%;	Axis II = 20.1%

Table 4.3 Loadings of variables and standardized canonical vectors from a canonical variates analysis of 2n = 50 and 2n = 44 cytotypes in *Aethomys chrysophilus* from South Africa. Measurements are defined in Figure 2.5. The standardized canonical coefficients generated by the canonical variates analysis may be used to identify individual specimens lacking cytogenetic data or museum specimens of dubious provenance (Chapman *et al.* 1992). A discriminant score for an unknown is calculated by subtracting the overall means from the corresponding measurements of the unknown, multiplying the results with the corresponding standardized coefficients, and summing the resulting values.

Variable	Canonical variate I	Overall means	Standardized coefficients
Greatest length of skull	-0.066	35.39	-0.734
Greatest length of frontals	0.138	11.12	1.131
Length of nasals to zygomatic arch	0.045	24.71	1.273
Greatest width of bulla	-0.169	5.71	-0.388
Foramen magnum height	-0.083	4.89	-1.000
Length of M^1	-0.306	2.78	-3.471
Width of M^2	-0.500	1.87	-12.762
Length of angular process to mandibular condyle	-0.106	7.37	-0.531
Length of mandibular foramen to condyle	-0.140	5.27	-0.424
Length of I_1 to M_3	-0.280	10.21	0.551
Width of M_2	-0.573	1.74	-16.768

Table 4.4 Standard statistics of external and cranial measurements in millimetres of *Aethomys* species from southern Africa. $\bar{X}$ = arithmetic mean; *SD* = standard deviation; *n* = sample size; *CV* = coefficient of variation; *Range* = observed range. External measurements were obtained from specimen labels. Measurements are defined in Figure 2.5.

Variable	Species				
	A. chrysophilus	*A. ineptus*	*A. silindensis*	*A. namaquensis*	*A. granti*
Length of head and body					
$\bar{X}$	143.15	140.86	173.57	113.39	111.81
SD	10.25	10.15	14.77	9.27	7.28
n	128	370	7	2012	55
CV	7.16	7.20	8.51	8.18	6.51
Range	120.0-169.0	117.0-190.0	155.0-200.0	80.0-147.0	93.0-125.0
Length of tail					
$\bar{X}$	163.29	158.87	177.71	153.72	116.82
SD	12.52	13.28	10.01	12.54	9.24
n	128	370	7	2012	55
CV	7.67	8.36	5.63	8.16	7.91
Range	135.0-190.0	110.0-193.0	166.0-194.0	107.0-197.0	96.0-138.0
Length of hind foot					
$\bar{X}$	29.23	28.58	33.63	25.83	24.09
SD	2.30	2.12	1.30	1.94	0.91
n	128	370	8	2012	55
CV	7.85	7.43	3.87	7.51	3.77
Range	20.0-35.0	24.0-38.0	32.0-35.0	16.0-32.0	22.0-26.0
Length of ear					
$\bar{X}$	20.56	20.66	22.63	17.89	17.65
SD	1.83	1.60	1.30	1.80	0.87
n	128	367	8	2007	55
CV	8.92	7.73	5.76	10.07	4.90
Range	15.0-27.0	15.0-30.0	21.0-25.0	11.0-24.0	16.0-20.0
Greatest length of skull					
$\bar{X}$	36.38	35.95	40.39	31.26	30.02
SD	1.40	1.31	1.32	1.19	0.94
n	365	612	6	2730	86
CV	3.86	3.65	2.84	3.79	3.14
Range	32.05-40.59	32.45-40.53	39.00-41.79	27.08-34.91	27.95-31.85
Greatest length of frontals					
$\bar{X}$	11.27	11.39	11.70	9.69	8.80
SD	0.51	0.42	0.10	0.27	0.27
n	365	612	6	2730	86
CV	4.56	3.73	0.86	2.75	3.08
Range	9.64-12.14	9.72-12.43	11.58-11.84	8.20-11.31	8.09-9.69

Table 4.4.--*Continued.*

Variable	Species				
	A. chrysophilus	*A. ineptus*	*A. silindensis*	*A. namaquensis*	*A. granti*
Length of nasals to zygomatic arch					
$\bar{X}$	25.29	25.27	27.64	22.07	20.90
SD	1.08	0.98	0.82	0.85	0.88
n	365	612	6	2730	86
CV	4.27	3.87	2.97	3.84	4.19
Range	21.82-28.67	22.37-28.56	26.91-28.64	19.01-24.81	19.00-22.86
Breadth of braincase					
$\bar{X}$	14.88	14.61	16.20	13.29	13.02
SD	0.51	0.50	0.34	0.41	0.32
n	365	612	6	2730	86
CV	3.45	3.44	2.12	3.12	2.44
Range	13.57-16.62	13.24-16.45	15.62-16.58	11.87-14.66	12.36-13.79
Interorbital breadth					
$\bar{X}$	5.15	5.10	5.93	4.53	4.43
SD	0.26	0.23	0.22	0.20	0.15
n	365	612	6	2730	86
CV	5.01	4.58	3.70	4.50	3.36
Range	4.52-6.00	4.51-5.89	5.57-6.16	3.89-5.17	4.07-4.80
Greatest length of bulla					
$\bar{X}$	7.51	7.51	8.48	6.61	6.38
SD	0.30	0.29	0.12	0.23	0.25
n	365	612	6	2730	86
CV	4.04	3.87	1.44	3.55	3.94
Range	6.67-8.81	6.60-8.27	8.36-8.66	5.67-7.30	5.92-7.22
Greatest width of bulla					
$\bar{X}$	5.55	5.50	6.14	4.79	4.78
SD	0.23	0.25	0.16	0.19	0.21
n	365	612	6	2730	86
CV	4.12	4.56	2.67	4.05	4.43
Range	4.79-6.34	4.88-6.14	5.93-6.35	4.15-5.60	4.28-5.49
Greatest height of skull					
$\bar{X}$	11.53	11.45	12.84	9.96	9.60
SD	0.34	0.33	0.15	0.36	0.27
n	365	612	6	2730	86
CV	2.96	2.87	1.14	3.62	2.77
Range	10.40-12.67	10.44-12.27	12.57-12.98	8.94-11.30	9.04-10.31
Foramen magnum height					
$\bar{X}$	4.84	4.80	4.71	4.56	4.51
SD	0.24	0.25	0.17	0.24	0.21
n	365	612	6	2730	86
CV	4.97	5.31	3.65	5.21	4.58
Range	4.09-5.49	4.02-5.61	4.54-5.00	4.00-5.55	4.01-5.13

Table 4.4.--*Continued.*

Variable	Species				
	A. chrysophilus	*A. ineptus*	*A. silindensis*	*A. namaquensis*	*A. granti*
Length of M^1					
$\bar{X}$	2.86	2.72	3.36	2.47	2.50
SD	0.15	0.15	0.08	0.14	0.13
n	365	612	6	2730	86
CV	5.25	5.63	2.49	5.68	5.27
Range	2.48-3.42	2.18-3.25	3.24-3.49	2.01-3.01	2.22-2.84
Width of M^2					
$\bar{X}$	1.95	1.83	2.18	1.80	1.78
SD	0.07	0.06	0.01	0.09	0.06
n	365	612	6	2730	86
CV	3.34	3.38	0.45	5.50	3.54
Range	1.78-2.19	1.62-2.00	2.17-2.19	1.41-2.01	1.57-1.91
Length of angular process to mandibular condyle					
$\bar{X}$	7.44	7.41	8.43	6.29	6.06
SD	0.42	0.37	0.18	0.36	0.32
n	365	612	6	2730	86
CV	5.64	5.00	2.09	5.66	5.36
Range	5.99-8.68	6.11-8.77	8.25-8.66	5.17-7.39	5.17-6.71
Length of mandibular foramen to condyle					
$\bar{X}$	5.52	5.41	6.18	4.87	5.26
SD	0.37	0.34	0.25	0.30	0.30
n	365	612	6	2730	86
CV	6.70	6.29	4.08	6.23	5.67
Range	4.44-7.00	4.29-6.69	5.84-6.48	3.84-6.16	4.19-5.99
Length of I_1 to M_3					
$\bar{X}$	10.43	10.30	12.52	9.06	9.16
SD	0.38	0.37	0.29	0.39	0.33
n	365	612	6	2730	86
CV	3.65	3.62	2.33	4.29	3.57
Range	9.00-11.92	9.08-11.82	12.08-12.78	7.98-10.30	8.41-10.21
Width of M_2					
$\bar{X}$	1.81	1.70	2.08	1.65	1.68
SD	0.06	0.06	0.02	0.09	0.06
n	365	612	6	2730	86
CV	3.39	3.32	1.03	5.19	3.78
Range	1.65-2.05	1.51-1.87	2.06-2.12	1.31-1.90	1.53-1.84

Table 4.5 Differential external and cranial ratios (%) of *Aethomys* species from southern Africa. $\overline{X}$ = arithmetic mean; *SD* = standard deviation; *n* = sample size; *Range* = observed range. Measurements are defined in Figure 2.5.

Ratio	Species				
	A. chrysophilus	*A. ineptus*	*A. silindensis*	*A. namaquensis*	*A. granti*
Length of tail to length of head and body					
$\overline{X}$	114.52	113.09	103.09	136.19	104.69
SD	10.79	10.38	11.21	12.86	8.74
n	128	370	7	2012	55
Range	93.75-142.30	75.76-141.86	83.00-121.25	83.59-187.64	88.18-146.23
$\overline{X} \pm 1SD$	103.73-125.31	102.71-123.47	91.88-114.30	123.33-149.05	95.95-113.43
Greatest length of frontals to greatest length of skull					
$\overline{X}$	31.00	31.71	29.00	31.05	29.33
SD	1.39	1.34	0.82	1.19	1.11
n	366	612	6	2730	86
Range	25.01-34.74	26.84-35.60	27.71-30.00	26.69-34.82	26.43-31.65
$\overline{X} \pm 1SD$	29.61-32.39	30.37-33.05	28.18-29.81	29.85-32.24	28.22-30.44
Foramen magnum height to greatest length of skull					
$\overline{X}$	13.33	13.37	11.66	14.59	15.05
SD	0.88	0.87	0.47	0.86	0.89
n	366	612	6	2730	86
Range	10.98-15.60	10.98-15.99	10.95-12.33	12.01-17.63	12.85-17.39
$\overline{X} \pm 1SD$	12.45-14.41	12.50-14.24	11.19-12.13	13.72-15.45	14.16-15.94
Length of mandibular foramen to condyle to greatest length of skull					
$\overline{X}$	15.17	15.07	15.30	15.55	17.52
SD	0.82	0.76	0.67	0.81	0.88
n	366	612	6	2730	86
Range	13.05-17.89	12.64-17.77	14.73-16.62	12.93-20.36	14.66-19.51
$\overline{X} \pm 1SD$	14.35-15.98	14.31-15.83	14.64-15.97	14.73-16.36	16.64-18.40

CHAPTER 5

GEOGRAPHIC VARIATION IN *AETHOMYS NAMAQUENSIS* FROM SOUTHERN AFRICA

5.1 INTRODUCTION

The Namaqua rock rat, *Aethomys namaquensis*, is widely distributed in southern Africa (Chapter 4) and shows considerable variation in body size, tail length and pelage colouration among geographical samples (Smithers 1971; De Graaff 1981; Musser and Carleton 1993). This variation led to suggestions that it may reflect either a complex of species (Musser and Carleton 1993) or subspecies (Smithers 1971; De Graaff 1981).

Aethomys namaquensis has, however, been shown to be a valid, widely distributed species in southern Africa (Chapter 4), which confirmed earlier reports by Roberts (1951), Ellerman *et al.* (1953) and Meester *et al.* (1964), who recognized sixteen subspecies: *lehocla* A. Smith, 1836; *alborarius* Peters, 1852; *auricomis* De Winton, 1897; *centralis* Schwann, 1906; *avarillus* Thomas and Wroughton, 1908; *albiventer* Jentink, 1909; *monticularis* Jameson, 1909; *grahami* Roberts, 1915; *calarius* Thomas, 1926; *siccatus* Thomas, 1926; *capensis* Roberts, 1926; *drakensbergi* Roberts, 1926; *klaverensis* Roberts, 1926; *lehochloides* Roberts, 1926; *waterbergensis* Roberts, 1938; and *namibensis* Roberts, 1946.

These infraspecific distinctions were made with little or no assessment of patterns of geographic variation over the entire range of the species. Moreover, they were primarily based on non-statistical comparisons of type material and/or small,

geographically restricted samples (Smithers 1971; Smithers and Tello 1976; Smithers and Wilson 1979). Major reviews of the genus (Davis 1975; De Graaff 1981; Meester *et al.* 1986; Skinner and Smithers 1990; Musser and Carleton 1993) refrained from recognizing subspecies and provisionally regarded all described forms as synonyms of *A. namaquensis*. To date, the nature and extent of geographic variation in this species remain virtually unknown.

This chapter constitutes the first major attempt to evaluate both morphometric and morphological patterns of intraspecific variation in *A. namaquensis* from southern Africa across a more comprehensive geographical range than has hitherto been considered.

5.2 MATERIAL AND METHODS

The analysis of geographic variation in *A. namaquensis* is based on a subset of data that formed part of the revision of the genus in southern Africa (Chapter 4) in which the homogeneity of the sample as representative of a single, widely distributed species was confirmed. This included 2669 specimens from 501 localities, which provided a good geographical coverage of the species in southern Africa (Figure 5.1). Specimens examined and a gazetteer are given in Appendices IV, V and VI.

5.2.1 Multivariate Analyses

Geographic variation among OTUs was examined by multivariate analyses using UPGMA cluster analyses, PCA and MST of 104 OTU

means based on standardized variables (Chapter 4). The UPGMA cluster analyses and MSTs were performed on both average taxonomic distances and product-moment correlation coefficients among OTUs, whereas PCA was computed from product-moment correlation coefficients among characters. Although sample means were used, the observed major patterns were verified by analyses of specimens (including holotypes) from the entire range of *A. namaquensis* in southern Africa.

The phenetic groupings obtained were further examined by pairwise CVAs. In some of these comparisons, however, the data matrices were too large for simultaneous specimen-level analyses. Consequently, the CVAs were based on three groupings of data: 1) all specimens if computationally manageable; 2) randomly selected specimens within the delineated phena; and 3) specimens from a zone of parapatry of the delineated phena. Diagnostic CVAs were, however, used to classify specimens excluded from the above analyses. The statistical integrity of the observed patterns was further evaluated by MANOVA. All multivariate procedures were based on eleven basic cranial measurements (Chapter 2; Chimimba and Dippenaar 1995).

5.2.2 Univariate Analyses

Geographic variation among the 104 OTUs was assessed by Model I ANOVA. To comply with the maximum number of groups of n = 100 that could be analysed by UNIVAR (Power 1970), however, it became necessary to further combine the following geographically contiguous OTUs from similar phytogeographical zones: 36 and 38 (= A; see Figure 5.1); 44 and 45 (B); 64 and 66 (C); and 77 and

78 (D). Where significant differences were detected, maximally non-significant subsets were derived by the *a posteriori* sum of squares simultaneous test procedure (SS-STP; Gabriel and Sokal 1969; Sokal and Rohlf 1981) using ranked means (Power 1970). All univariate analyses were based on eleven basic and four descriptive cranial characters (Chapter 2; Chimimba and Dippenaar 1995).

5.2.3 Qualitative Morphological Variation

After having delineated phena morphometrically, representative specimens (n = 1503) of each phenon (including holotypes) were re-examined for qualitative morphological differences. This included the comparison of pelage colouration in natural light using the colour standards of Oyama *et al.* (1967).

5.2.4 Infraspecific Nomenclature

The infraspecific nomenclature of delineated phena was resolved by multivariate analyses that included the holotypes of *A. namaquensis* and 13 of its 16 described subspecies: *lehocla*, *auricomis*, *centralis*, *avarillus*, *monticularis*, *grahami*, *calarius*, *siccatus*, *capensis*, *drakensbergi*, *klaverensis*, *lehochloides* and *waterbergensis*. The taxonomic affiliation of these holotypes to *A. namaquensis* were previously confirmed by multivariate analyses (Chapter 4).

The holotypes of *alborarius*, *albiventer* and *namibensis* were not available for examination. However, *albiventer* was allocated

to *A. namaquensis* (Chapter 4) because its type locality (Mossel Bay, South Africa; Jentink 1909) falls within the distributional range of *A. namaquensis* only. The two remaining forms, *alborarius* and *namibensis*, were provisionally referred to *A. namaquensis* (Chapter 4) based on previous taxonomic allocations (Peters 1852; Roberts 1946). To accommodate the damaged holotype of *A. namaquensis*, some analyses were based on a subset of seven variables. The type material examined is given in Appendix IV.

5.3 RESULTS

5.3.1 Multivariate Assessment

A distance phenogram showed two discrete clusters, designated A and B (Figure 5.2*a*). Relationships within these clusters broadly coincide with major biomes of southern Africa (Rutherford and Westfall 1986; Figure 5.3). Within cluster A, subcluster C comprises OTUs from the Savanna biome. (OTUs of uncertain placement in cluster analyses with regard to biomes of southern Africa as delineated by Rutherford and Westfall (1986) are indicated by arrows). Most OTUs in subcluster D are from the Nama-Karoo but also includes OTUs from its border with the Savanna in the North-West as well as OTUs 46 and 49 from southwestern Northern Provinces of South Africa, suggesting a northeastern extension of biome-related assemblage of OTUs (see below). Within cluster B, subcluster E represents OTUs from a combination of Fynbos and Savanna OTUs from the southern coastal region of the Eastern Cape Province of South Africa. OTUs in subcluster F are predominantly from the Grassland while

subcluster G mainly represents Succulent Karoo OTUs.

A correlation phenogram also showed two discrete clusters, designated A and B (Figure 5.2*b*). Within cluster A, subcluster C comprises OTUs from the Succulent Karoo while subcluster D mostly consists of Savanna OTUs, which also includes Savanna OTUs from the southern coastal region of the Eastern Cape delineated in the distance phenogram. Within cluster B, subcluster E consists of OTUs from the Nama-Karoo and its border with the Savanna in the North-West Province of South Africa while OTUs in subcluster F are mainly from the Grassland. Fynbos OTUs were associated with three of the four delineated subclusters: two OTUs (66 and 67) fell within the Succulent Karoo, one (70) within the Savanna, and three (69, 71 and 72) within the Grassland biomes.

The correlation and distance phenograms either broadly correspond, particularly with regard to OTUs from the Savanna, Nama-Karoo (and its border with the Savanna in the North-West Province of South Africa) and Grassland, or are complementary. Generally, most of the uncertain OTUs in both distance and correlation phenograms were from close to borders between biomes. Some of the uncertain OTUs in the correlation phenogram, however, were correctly clustered to their appropriate biome-related assemblages of OTUs in the distance phenogram and vice versa. This suggests that the interpretation of relationships in both distance and correlation phenograms need to be considered together. This was extended to include the biome-related phena collated from the cluster analyses as references to demarcate morphometric boundaries in PCA scatterplots. Such a treatment allowed the resolution of the status of ambiguously placed OTUs and the refinement of morphometric boundaries of biome-related

assemblages of OTUs.

By so doing, the PCA scattergram indicates the presence of four size- and shape-related phena, A, B, C and D (Figure 5.4). Subcluster A broadly corresponds with the Savanna. While OTUs 1 and 2 are from the border between the Desert, Nama-Karoo and Savanna, and OTU 6 is from the Desert biome (Figure 5.3), they closely associate with the Savanna in the PCA. OTU 1 associated with the Savanna in the distance phenogram while OTUs 2 and 6 grouped with the Savanna in all cluster analyses, suggesting a statistical robustness of this assemblage of OTUs. Subcluster B consists of Nama-Karoo OTUs and confirms its phenetic association with northeastern OTUs from the border with the Savanna in the North-West as well as OTUs 46 and 49 from southwestern Northern Provinces of South Africa (hereafter referred to as Nama-Karoo) delineated by the distance phenogram. This assemblage of OTUs overlapped with the Savanna by two OTUs (5 and 7) only. These two OTUs, however, consistently clustered with the Nama-Karoo in all cluster analyses (Figure 5.2).

Subcluster C clarifies the status of Succulent Karoo, Fynbos and Savanna OTUs from the southern coastal region of the Eastern Cape Province of South Africa. While the Succulent Karoo tended to form a distinct cluster of its own in all cluster analyses, it also included Fynbos and the southern coastal OTUs from the Eastern Cape. More importantly, the distance phenogram also included OTUs 44 (Savanna/Grassland border: eastern Mpumalanga) and 96 and 97 (Savanna/Grassland border: coastal KwaZulu-Natal). Similarly, the subcluster of a combination of Fynbos and Savanna OTUs from the southern coastal region of the Eastern Cape included OTU 45. The PCA, however, shows no geographically

discernible pattern among these OTUs in multivariate space, suggesting a continuous coastal assemblage of OTUs that extends from the Succulent Karoo, Fynbos to the southern coastal Savanna/Grassland region of the Eastern Cape, Kwazulu-Natal and the eastern Mpumalanga Provinces of South Africa (hereafter referred to as coastal). This grouping of OTUs, however, includes two uncertain OTUs (10 and 30) from the Savanna. Subcluster D is predominantly Grassland. While OTU 48 clustered with the Nama-Karoo in the distance phenogram and the Grassland in the correlation phenogram, the PCA suggests an allocation to the latter, with a similar treatment also applying to OTUs 47 and 74.

Although the degree of overlap was much greater, the delineation of the four phena was also evident in independent exploratory correlation-based cluster analyses within subclusters A and B derived from the distance and correlation phenograms, and their corresponding PCA scatterplots (not illustrated). Given the dominance of size between Savanna and coastal OTUs, and between Nama-Karoo and Grassland OTUs (Figure 5.4), additional exploratory correlation-based UPGMA cluster analyses were undertaken to evaluate the extent of shape-related variation between these size-related phena. The results (not illustrated) suggest that apart from size, there are also shape-related differences between these pairs of OTU assemblages as reflected by the correlation phenogram.

The importance of size in the separation of OTU assemblages (Figure 5.4) was shown by principal component I (59.2% of variance) which had both relatively high negative loadings and percent variances on most measurements (Table 5.1). The importance of shape (Figure 5.6) was shown by the second PCA axis

(14.9% variance) which had both positive and negative loadings and percent variances of different magnitudes (Table 5.1). Measurements that featured prominently on axis II related to greatest length of frontals, foramen magnum height, and greatest cross-sectional crown widths of M^2 and M_2 (Table 5.1). This suggests that cranial shape configuration in the frontal and foramen magnum region and dental characteristics on both the upper jaw and the mandible differ between geographic samples of *A. namaquensis* in southern Africa.

Similar discrete assemblages as in cluster analyses and PCA were prominent when MSTs, based on both distance and correlation coefficients, were superimposed on the PCA scattergram (not illustrated). Similarly, the phenetic allocation of specimens excluded from multivariate analyses because of small sample sizes were verified by additional distance- and correlation-based UPGMA cluster analyses, PCA and MST.

To assess the integrity of the designated groups, pairwise CVAs were performed. Analyses based on three groupings of data were broadly similar. Results presented are those derived from specimens collected in zones of parapatry of the delineated phena. Despite overlaps in discriminant score ranges, correct *a posteriori* classifications ranged from 73% to 88% (Table 5.2). All MANOVAs showed *F*-values ranging from 4.77 to 17.43, all of which indicate significant differences between group centroids ($P < 0.001$) (Table 5.2).

Generally, the multivariate analyses support the integrity of Savanna, Nama-Karoo, coastal and Grassland OTUs. A summary (Figure 5.5), however, indicates that the morphometric placement of 2 of the 104 OTUs (10 and 30) does not conform with the

biome-related pattern of variation. Of particular importance is that these two OTUs closely associate with ecologically unique habitats. OTU 10 closely associates with the ecologically unique Okavango Swamp region, while OTU 30 is from the vicinity of relicts of evergreen forests of eastern Zimbabwe. This may independently or in combination suggest: 1) different subspecies; and/or 2) a reflection of biome demarcations that may represent generalizations, and warrant further clarification involving other systematic techniques.

5.3.2 Univariate Assessment

In a Model I ANOVA of the 100 OTUs, statistically significant differences ($P < 0.05$) were detected in all 15 measurements examined (11 basic and four descriptive cranial). The pattern of variation revealed by the order of ranked means indicate three contrasting trends as illustrated by selected measurements (Table 5.3).

The first pattern involved the greatest cross-sectional crown width of M^2 and the greatest cross-sectional crown width of M_2, two measurements with the largest *F*-values (28.10 and 27.22, respectively). As evident in the greatest cross-sectional crown width of M_2 (Table 5.3*a*), there is a trend in the order of ranked means for larger values to be associated with Grassland OTUs (*c.* 1.69 - 1.76 mm), intermediate values with Nama-Karoo and coastal OTUs (*c.* 1.60 - 1.68 mm), and the lowest values with Savanna OTUs (*c.* 1.52 - 1.59 mm). There was a tendency for the three assemblages to be grouped within the same non-significant subset, but there are no discernible geographical patterns within them.

The uniqueness of Grassland and Savanna OTUs was also evident from the multivariate analyses (Section 5.3.1).

The second pattern evidenced from the data involved 12 measurements with relatively intermediate *F*-values (range = 9.81 - 21.48), best exemplified by antero-nasal edge - antero-posterior zygomatic arch length (Table 5.3*b*) and posterior incisor - M_3 length (Table 5.3*c*). Both measurements revealed a trend for larger values to be associated with Grassland and coastal OTUs (*c.* 22.08 - 23.08 mm; 9.10 - 9.58 mm, respectively), while relatively smaller values were associated with Nama-Karoo and Savanna OTUs (*c.* 20.70 - 22.05 mm; 8.52 - 9.09 mm). There was a tendency for the two assemblages, consistent with the two major clusters shown by distance phenogram (Figure 5.2*a*), to appear in the same non-significant subset.

In antero-nasal edge - antero-posterior zygomatic arch length (and three other measurements), however, there was a tendency within the Nama-Karoo and Savanna assemblage for lower ranked means to be broadly associated with Nama-Karoo OTUs. There were no geographically discernible patterns within subsets for the posterior incisor - M_3 length (and five other measurements). The uniqueness of Nama-Karoo and Savanna OTUs were also evident in multivariate analyses (Section 5.3.1).

The third order of ranked means involved greatest length of frontals, greatest bulla length and foramen magnum height, three measurements with relatively low *F*-values (3.46, 3.73 and 5.05, respectively). All three measurements failed to show geographically discernible patterns, a trend best exemplified by foramen magnum height (Table 5.3*d*).

5.3.3 Taxonomic Status of Delineated Phena

The phenetic differences shown by the four delineated phena and their broad association with major biomes of southern Africa, provide support for their recognition as distinct subspecies (see Discussion). To further resolve the infraspecific nomenclature, however, the phenetic affiliations of holotypes of *A. namaquensis* and 13 of its 16 described forms to the four largely biome-related assemblages were verified by UPGMA cluster analysis, PCA, MST and CVA.

All holotypes phenetically associated with groups that also geographically coincided with their type localities (Figure 5.5), regardless of whether analyses were based on 11 or seven variables. As is convention, the earliest described forms within OTU assemblages were considered senior synonyms of the four delineated phena. Consequently, the nominate subspecies, *A. n. namaquensis* A. Smith, 1834, is assigned to the combination of Succulent Karoo, Fynbos and southern coastal Savanna/Grassland region of the Eastern Cape, Kwazulu-Natal and the eastern Mpumalanga Provinces of South Africa, with *albiventer* Jentink, 1909, *grahami* Roberts, 1915, *capensis* Roberts, 1926, *klaverensis* Roberts, 1926, and *drakensbergi* Roberts, 1926, as junior synonyms. *Aethomys namaquensis* was described from Little Namaqualand (restricted to Witwater by Shortridge 1942), Northern Cape Province, South Africa, which falls within this assemblage of OTUs. Nama-Karoo OTUs are allocated to *A. n. lehocla* A. Smith, 1836, with *centralis* Schwann, 1906, and *namibensis* Roberts, 1946, as junior synonyms. Savanna OTUs are assigned to *A. n. alborarius* Peters, 1852, with *auricomis* De Winton, 1897,

avarillus Thomas and Wroughton, 1908, *calarius* Thomas, 1926, *siccatus* Thomas, 1926, *lehochloides* Roberts, 1926, and *waterbergensis* Roberts, 1938, as junior synonyms. Grassland OTUs are allocated to *monticularis* Jameson, 1909.

5.3.4 Diagnostic Morphological and Morphometric Characters

There were neither geographically discernible qualitative morphological nor pelage colour patterns to distinguish the four subspecies. Both within and among the four delineated phena, head, neck and body upper parts ranged from dull yellowish brown (10YR 5/4) to dark brown (10YR 3/4), and underparts from light grey (10YR 8/4) to pale yellow (2.5Y 8/3). This suggests that infraspecific variation in qualitative morphology and pelage colour within *A. namaquensis* from southern Africa is either subtle or does not form part the delineated patterns of variation.

Standard statistics of the 11 basic cranial, four descriptive cranial and four external measurements of the four subspecies are presented in Table 5.4. Differential cranial ratios (Table 5.5), using all specimens from the subregion, were computed for characters with high negative (greatest cross-sectional crown width of M^2 and greatest cross-sectional crown width of M_2) and positive (greatest length of frontals and foramen magnum height) loadings in the shape-related axes II of PCA (Table 5.1). Greatest length of skull, a highly negative size-related character on PC Axis I, was also included.

There was no overlap in mean $\pm$ 1*SD* of the ratio: greatest cross-sectional crown width of M^2 to greatest length of frontals

between *alborarius* and *monticularis*. Pairwise comparisons for greatest cross-sectional crown widths of M^2 to greatest length of skull and greatest cross-sectional crown widths of M_2 to greatest length of skull showed slight to negligible overlap between *alborarius* and *lehocla*, and between *alborarius* and both *lehocla* and *monticularis*. Differential external ratios were not informative.

5.4 DISCUSSION

The aim of this chapter was to evaluate patterns of intraspecific variation in *A. namaquensis* from southern Africa across a more comprehensive geographical range than has hitherto been considered. As in previous systematic accounts (Smithers 1971; De Graaff 1981; Musser and Carleton 1993), the wide range of morphological procedures used herein showed the presence of remarkable variation among geographical samples. The observed major patterns of variation revealed the presence of four major clusters of OTUs within *A. namaquensis* from southern Africa.

A taxonomic interpretation of this variation suggests that *A. namaquensis* in southern Africa is polytypic and can be separated into four subspecies: *A. n. namaquensis* A. Smith, 1834; *A. n. lehocla* A. Smith 1836; *A. n. alborarius* Peters, 1852; and *A. n. monticularis* Jameson, 1909. This reduces the number of recognized subspecies in *A. namaquensis* from southern Africa from 16 (Roberts 1951; Ellerman *et al.* 1953; Meester *et al.* 1964) to four. As in *A. chrysophilus* from southern Africa (Chapter 6), these taxonomic conclusions exemplify a classical infraspecific taxonomic problem of having to decide whether the four delineated

phena were sufficiently different to justify the recognition of subspecies (see volumes 3 to 5 of *Systematic Zoology* 1954-1956; summaries in Pimentel 1959, and Sokal and Rinkel 1963).

The problem in deciding whether to recognize subspecies was exacerbated by uncertain OTUs which generally associated with ecologically unique habitats, which may be indicative of the presence of more subspecies than recognized in this study. The constituent localities of OTU 30 for example, are from the vicinity of ecologically unique relicts of evergreen forests of eastern Zimbabwe. They also represent the only area where the rare and geographically restricted *A. silindensis* occurs, and is in close proximity to the area from where *Petrodromus tetradactylus swynnertoni* Thomas, 1918; *Nasilio brachyrhynchus selindensis* Roberts, 1937; *Cercopithecus mitis stevensoni* Roberts, 1948; *Graphiurus murinus selindensis* Roberts, 1931; *Thamnomys dolichurus silindensis* Roberts, 1938; and *Cricetomys gambianus selindensis* Roberts, 1946, have previously been described from.

In this study, however, one of the prerequisites considered for recognizing the four subspecies within *A. namaquensis* from southern Africa was the delineated pattern of variation which is both size- and shape-related, and clearly not related to a sampling artefact. More importantly, these phenetic discontinuities coincided largely with the major biomes in southern Africa (Rutherford and Westfall 1986). The subspecies *alborarius* is largely associated with Savanna, *lehocla* with Nama-Karoo, *monticularis* with Grassland and *namaquensis* with a combination of the Succulent Karoo, Fynbos, and southern coastal Savanna/Grassland region of the Eastern Cape, Kwazulu-Natal and

eastern Mpumalanga Provinces of South Africa.

It is possible that the phytogeographical zones may act as a potential barrier to gene flow. Subspecies as units of evolution are expected to be represented by transitional zones that coincide with partial or complete, present or past, geographical or ecological barriers (Endler 1977; Thorpe 1984; Barton and Hewitt 1985). In this study, however, the association between phenetic boundaries and phytogeographical limits as delineated by Rutherford and Westfall (1986) was, in some instances, equivocal. While some of the OTUs may merely be aberrant, others are closely associated with borders between biomes. Independently or in combination, this could suggest different subspecies and/or zones of hybridization. On the other hand, it may reflect phytogeographical demarcations that presumably represent generalizations of biomes in southern Africa.

The results in this study, for example, indicated a tight cluster of Nama-Karoo OTUs that included a northeastern assemblage of Savanna OTUs from the North-West and southwestern Northern Provinces of South Africa. Recent satellite-monitored habitat changes in southern Africa confirms climate-related fluctuations (Jury *et al.* 1997), which may result in an instability of borders between biomes. While the subspecies designations in this study are probably valid in terms of their constitution, their boundaries, however, require further refinement involving other systematic techniques.

Despite some ambiguity in phenetic and phytogeographical limits, the recognition of subspecies in the present study was supported by a variety of both size- and shape-related morphometric characters. Of particular relevance is that these

characters did not show evidence of clinal variation that would render the recognition of subspecies untenable. All these criteria, especially the complex differences in cranial configuration, suggest that the four biome-related assemblages of OTUs in southern Africa are independently evolving entities deserving recognition as distinct subspecies (Johnston and Selander 1971).

In addition, there was no discordant variation observed among characters, regardless of whether variation was examined by univariate or multivariate procedures. The only exception, as noted in previous systematic accounts (Smithers 1971; Smithers and Tello 1976; Smithers and Wilson 1979), was the considerably discordant variation in pelage colouration, both within and among localities. This chequerboard-type variation in pelage colouration, also observed in *A. chrysophilus* (Chapter 6) and *A. ineptus* (Chapter 7) from southern Africa, may reflect the existence of microgeographical races within formally recognized subspecies (Mayr and Ashlock 1991). The broad uniformity in patterns shown by the majority of characters, however, suggests that pelage colouration in these species may be an adaptation to local climatic conditions (Mayr and Ashlock 1991).

Roberts (1951), Ellerman *et. al.* (1953), and Meester *et al.* (1964) allocated specimens with grey bases of ventral hair to *A. n. namaquensis*, with pure white hair to *A. n. alborarius*, with greyish (tinged with red) dorsal hair to *A. n. calarius*, with darker hair to *A. n. lehocla*, and with brighter and redder hair to *A. n. lehochloides*. These pelage colour forms, however, were not discernible in the present study. Major reviews of the genus, however, refrained from recognizing subspecies (Davis 1975; De

Graaff 1981; Meester *et al.* 1986; Skinner and Smithers 1990; Musser and Carleton 1993).

5.5 KEY TO SUBSPECIES OF *AETHOMYS NAMAQUENSIS* FROM SOUTHERN AFRICA

1. Restricted to the Succulent Karoo, Fynbos and the southern coastal Savanna/Grassland region of the Eastern Cape, KwaZulu-Natal and eastern Mpumalanga Provinces of South Africa (Figures 5.3 and 5.5)..... *namaquensis*

-- Occurring outside the above region..... 2

2. Restricted to the Nama-Karoo biome of southern Africa (includes the North-West and southwestern Northern Provinces of South Africa)..... *lehocla*

-- Occurring outside the Nama-Karoo biome of southern Africa..... 3

3. Restricted to the Savanna biome of southern Africa (except southern Savanna/Grassland region of the Eastern Cape, KwaZulu-Natal and eastern Mpumalanga), ratio of greatest cross-sectional crown width of M^2 to greatest length of frontals (Figure 2.5) 17.6% (mean $\pm$ 1*SD* = 16.7 - 18.4%)..... *alborarius*

-- Restricted to the Grassland biome of southern Africa, ratio of greatest cross-sectional crown width of M^2 to greatest length of frontals 19.5% (mean $\pm$ 1*SD* = 18.6 - 20.4%)..... ..... *monticularis*

5.6 CONCLUSIONS

Patterns of intraspecific variation in the southern African *A. namaquensis* suggest the recognition of four subspecies: *A. n. namaquensis* A. Smith, 1834; *A. n. lehocla* A. Smith, 1836; *A. n. alborarius* Peters, 1852; and *A. n. monticularis* Jameson, 1909, which differ both in cranial size and shape. The geographical limits of the proposed subspecies broadly coincide with major phytogeographical zones of southern Africa. This infraspecific treatment of southern African *A. namaquensis* reduces the number of previously recognized subspecies from 16 to four. While the subspecies designations in this study are probably valid in terms of their constitution, their boundaries, however, require further refinement involving other systematic techniques.

5.7 TAXONOMY

5.7.1 *Aethomys namaquensis namaquensis* (A. Smith, 1834)

Gerbillus namaquensis A. Smith, 1834: *S. Afr. Quart. Journ.* 2:160.

Mus albiventer Jentink, 1909: *Zool. Jahrb. Syst.* 28:246.

Mus namaquensis grahami Roberts, 1915: *Ann. Tvl. Mus.* 5:118.

Praomys namaquensis capensis Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Praomys namaquensis klaverensis Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Praomys namaquensis drakensbergi Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

5.7.1.1 Holotype

BM 45.7.3.16; adult female (skull damaged); Little Namaqualand, Cape Province, South Africa (restricted to Witwater by Shortridge 1942)

5.7.1.2 Distribution

Confined to the Succulent Karoo, Fynbos and southern coastal Savanna/Grassland regions of the Eastern Cape, KwaZulu-Natal and eastern Mpumalanga Provinces of South Africa (Figures 1.1, 5.3 and 5.5).

5.7.1.3 Diagnosis

Small (observed range: head and body length 95 - 146 mm; greatest skull length 28.9 - 34.9 mm). Head, neck and body upper parts dull yellowish brown (10YR 5/4) or yellowish brown (10YR 5/6), underparts light grey (10YR 8/4) to light yellow-orange (10YR 8/3).

5.7.1.4 Etymology

Named after Namaqualand, where the nominate species was originally collected.

5.7.1.5 Remarks

Allen (1939) listed *albiventer* as a subspecies of *A.*

chrysophilus, which Meester *et al.* (1986) pointed out to be incorrect, since *A. chrysophilus* does not occur so far south as Mossel Bay, the type locality.

5.7.2 *Aethomys namaquensis lehocla* A. Smith, 1836

Mus lehocla A. Smith, 1836: *App. Rept. Exped. Explor. S. Afr.*:43.

Mus auricomis centralis Schwann, 1906: *Proc. Zool. Soc. Lond.*:107.

Aethomys namaquensis namibensis Roberts, 1946: *Ann. Tvl. Mus.* 20:320.

5.7.2.1 Holotype

BM 45.7.3.18; adult male; Letakun, Kuruman, Cape Province (= Northern Cape), South Africa.

5.7.2.2 Distribution

Confined to the Nama-Karoo biome of southern Africa that includes inland central and southern Namibia, southwestern Botswana, and the North-West and southwestern Northern Provinces of South Africa (Figures 1.1, 5.3 and 5.5).

5.7.2.3 Diagnosis

Small (observed range: head and body length 80 - 144 mm; greatest skull length 27.1 - 33.8 mm). Dorsal pelage dull yellow-orange (10YR 6/4) to dark brown (10YR 3/4); thighs light

grey (10YR 8/2); ventral pelage light grey (2.5Y 8/2); apart from few scattered bright yellowish brown (2.5Y 6/6) hairs, ears naked.

5.7.2.4 Etymology

Could not be established.

5.7.3 *Aethomys namaquensis alborarius* Peters, 1852

Mus alborarius Peters, 1852: *Reise nach Mossambique. Saugeth*:152.

Mus auricomis De Winton, 1897: *Proc. Zool. Soc. Lond.*: for 1896:802.

Mus avarillus Thomas and Wroughton, 1908: *Proc. Zool. Soc. Lond.*:547.

Aethomys namaquensis calarius Thomas, 1926: *Ann. Mag. Nat. Hist.* (9)17:184.

Aethomys namaquensis siccatus Thomas, 1926: *Proc. Zool. Soc. Lond.*:304.

Praomys namaquensis lehochloides Roberts, 1926: *Ann. Tvl. Mus.* 11:255.

Aethomys namaquensis waterbergensis Roberts, 1938: *Ann. Tvl. Mus.* 19:239.

5.7.3.1 Holotype

Not available for examination; sex unknown; Tette (= Tete), Zambezi River, Mozambique (Peters 1852).

5.7.3.2 Distribution

Confined to the Savanna biome of southern Africa (except Savanna regions of the coastal KwaZulu-Natal, Eastern Cape and eastern Mpumalanga Provinces of South Africa) that includes northern Namibia, Botswana (except southwestern part), Zimbabwe, Mozambique, northern Mpumalanga and the Northern Provinces of South Africa (Figures 1.1, 5.3 and 5.5).

5.7.3.3 Diagnosis

Small (observed range: head and body length 80 - 136 mm; greatest skull length 28.2 - 33.9 mm). Dark brown (10YR 3/4) upper parts and pale yellow (2.5Y 8/3) underparts; ears brownish black (10YR 2/3) with a thin covering of bright yellowish brown (10YR 6/8) hairs.

5.7.3.4 Etymology

The subspecies name is probably derived from a Latin root, *alba*, meaning "turning towards white or becoming white", perhaps reflecting its pale yellow dorsal pelage colouration.

5.7.3.5 Remarks

Since the holotype was not examined, all diagnostic references to this taxon were based on topotypical material and the holotype of the junior synonym *lehochloides*. The year of description of *alborarius* is generally regarded to be 1852 (De

Graaff 1981; Meester *et al.* 1986) but Musser and Carleton (1993) consider it to be 1892.

5.7.4 *Aethomys namaquensis monticularis* Jameson, 1909

Mus namaquensis monticularis Jameson, 1909: *Ann. Mag. Nat. Hist.* (8)4:461.

5.7.4.1 Holotype

BM 9.7.2.10; adult female; Johannesburg, Transvaal (= Gauteng) Province, South Africa.

5.7.4.2 Distribution

Confined to the Grassland biome of southern Africa that includes Lesotho, and the northeastern Western Cape, eastern Northern Cape, inland Eastern Cape and Free State Provinces of South Africa (Figures 1.1, 5.3 and 5.5).

5.7.4.3 Diagnosis

Small (observed range: head and body length 82 - 147 mm; greatest skull length 28.3 - 34.6 mm). Upper parts dark brown (7YR 3/3); underparts brownish grey (7YR 4/1) speckled with bright yellowish brown (10YR 7/6).

5.7.4.4 Etymology

The subspecies name is probably derived from the Latin word, *monticola* meaning "a dweller among mountains or highlander", perhaps reflecting the highveld habitat of Johannesburg, the type locality.

Figure 5.1 Collecting localities and pooled samples (OTUs) of *Aethomys namaquensis* from southern Africa. The symbols A, B, C and D represent additionally pooled geographically contiguous localities from similar phytogeographical zones to comply with the sample size requirements of UNIVAR. Insert shows the distribution of the species in southern Africa as determined in chapter 4.

Figure 5.2 Distance (**a**) and correlation (**b**) phenograms from UPGMA cluster analyses of pooled samples (OTUs) of *Aethomys namaquensis* from southern Africa. Operational taxonomic units correspond to those in Figure 5.1. Arrows indicate OTUs of uncertain placement. Cophenetic correlation coefficients = 0.76 and 0.68 respectively.

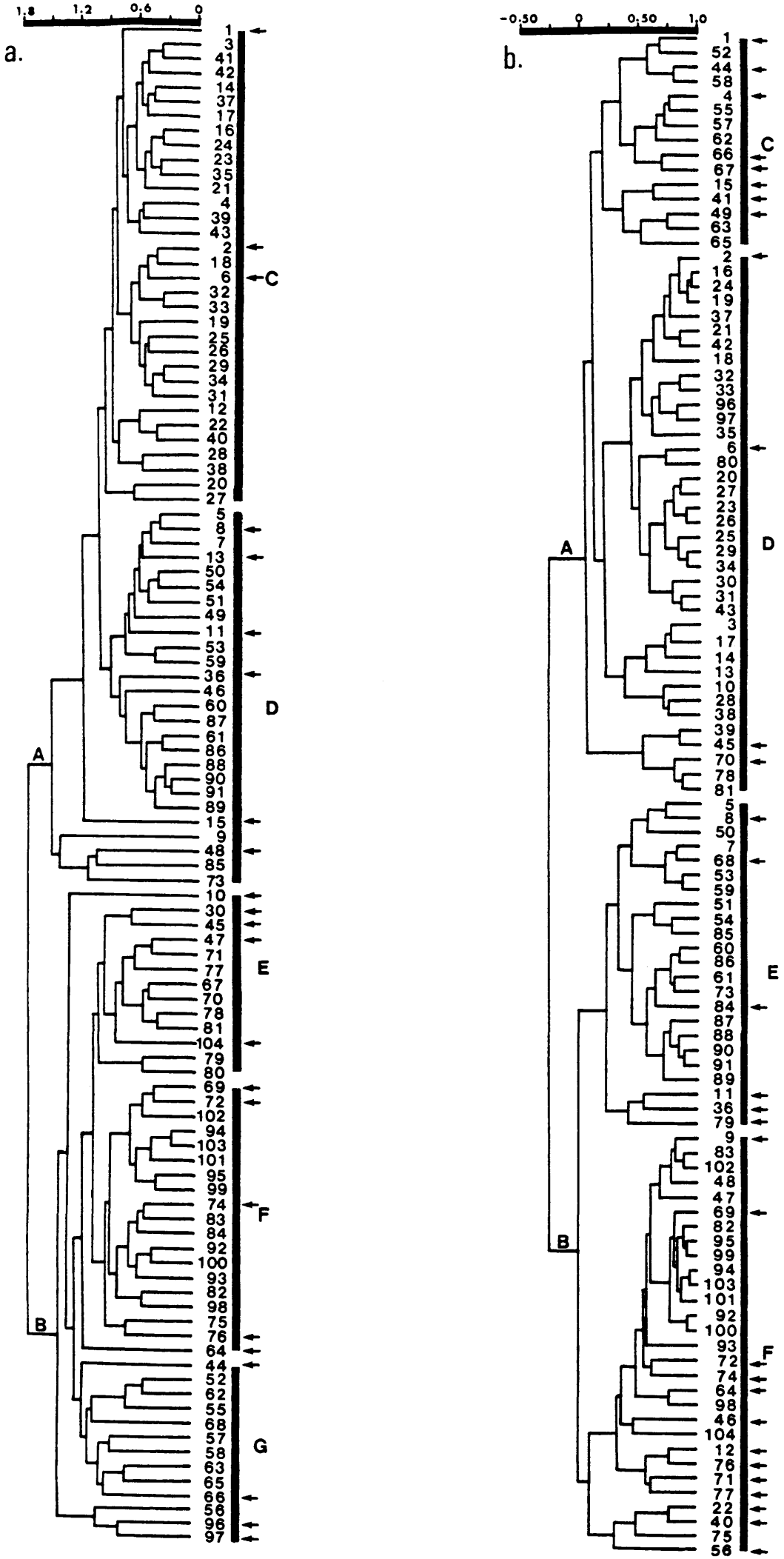


Figure 5.3 Major biomes of southern Africa (after Rutherford and Westfall 1986).

Figure 5.4 Axes I and II from a principal components analysis of pooled samples (OTUs) of *Aethomys namaquensis* from southern Africa. Polygons indicate biome-related phena collated from cluster analyses: Savanna (cf. Figure 5.3) (open circles); Nama-Karoo (solid circles); a combination of Succulent Karoo, Fynbos and southern coastal Savanna OTUs from the Eastern Cape, Kwazulu-Natal and the eastern Mpumalanga (solid squares); and Grassland OTUs (open squares) respectively.

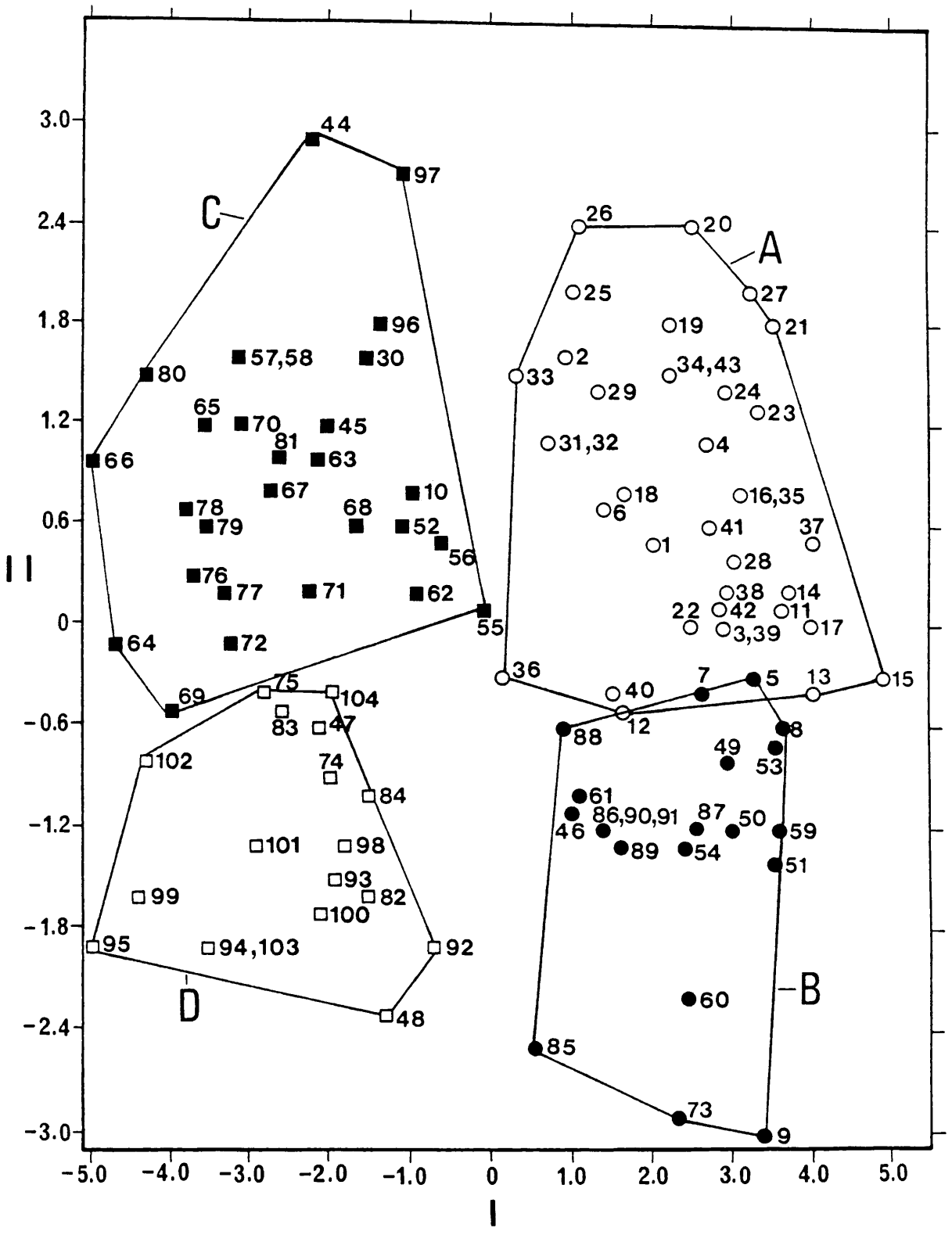


Figure 5.5 A geographical representation of delineated phena in *Aethomys namaquensis* from southern Africa based on collation of UPGMA clustering and principal components analysis results. Samples were largely demarcated into Savanna (cf. Figure 5.3) (horizontal lines); Nama-Karoo (wavy lines); a combination of Succulent Karoo, Fynbos and southern coastal Savanna/Grassland OTUs from the Eastern Cape, Kwazulu-Natal and eastern Mpumalanga (shaded); and Grassland OTUs (diagonal lines). Provisional subspecies boundaries are indicated by dashed lines. Collecting localities and pooled samples (OTUs) correspond to those in Figure 5.1. Abbreviations represent type localities of *A. namaquensis* (nam) and all its described subspecies in southern Africa: albi = *albiventer*, alb = *alborarius*, aur = *auricomis*, ava = *avarillus*, cal = *calarius*, cap = *capensis*, cen = *centralis*, dra = *drakensbergi*, gra = *grahami*, kla = *klaverensis*, leho = *lehochloides*, leh = *lehocla*, mon = *monticularis*, nami = *namibensis*, sic = *siccatus*, wat = *waterbergensis*. Insert represents the distribution of the species in southern Africa as determined in chapter 4.

Table 5.1 Loadings of variables on components I and II from a principal components analysis for pooled samples (OTUs) of *Aethomys namaquensis* from southern Africa. The percent variance contributions appear in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components	
	I	II
Greatest length of skull	-0.344 (77.25)	0.256 (10.70)
Greatest length of frontals	-0.117 (8.80)	0.570 (53.22)
Length of nasals to zygomatic arch	-0.336 (73.44)	0.259 (10.95)
Greatest width of bulla	-0.329 (70.59)	0.043 (0.31)
Foramen magnum height	-0.115 (8.55)	0.400 (26.27)
Length of M^1	-0.297 (57.28)	-0.229 (8.61)
Width of M^2	-0.310 (62.71)	-0.368 (22.20)
Length of angular process to mandibular condyle	-0.347 (78.49)	0.110 (1.98)
Length of mandibular foramen to condyle	-0.326 (69.28)	-0.102 (1.71)
Length of I_1 to M_3	-0.370 (89.17)	-0.010 (0.02)
Width of M_2	-0.292 (55.71)	-0.412 (27.86)
% Trace:	Axis I = 59.2%;	Axis II = 14.9%

Table 5.2 Group centroids, discriminant score ranges and percent correct *a posteriori* classifications in pairwise canonical variates analyses of specimens from zones of parapatry of the delineated biome-related phena in *Aethomys namaquensis* from southern Africa: *n* = sample size; *** = statistical significance at $P < 0.001$.

Biome-related phena[+]	Group Centroid	Discriminant Score Range	*F*-value	*n*	% Correctly Classified
Savanna/Nama-Karoo	0.80/-0.55	0.43-1.21/-1.76-0.82	5.55***	292	74.7
Savanna/Grassland	-0.89/0.91	-1.73-0.35/-0.57-2.15	9.26***	67	79.3
Savanna/Coastal	-1.45/1.02	-2.32-0.66/-0.91-2.42	4.77***	46	87.0
Nama-Karoo/Grassland	-0.49/0.35	-1.61-0.71/-0.75-1.53	5.13***	338	73.0
Nama-Karoo/Coastal	0.59/-0.63	0.17-1.43/-1.51-0.31	17.43***	217	88.0
Grassland/Coastal	-0.37/0.93	-1.36-0.51/-0.17-1.82	8.81***	294	78.0

[+] Coastal phena includes a combination of OTUs from Succulent Karoo, Fynbos and southern coastal Savanna/Grassland OTUs from the Eastern Cape, Kwazulu-Natal and eastern Mpumalanga Provinces of South Africa.

Table 5.3 Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of *Aethomys namaquensis* OTUs from southern Africa. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. Operational taxonomic units correspond to those in Figure 5.1. Measurements are defined in Figure 2.5.

Table 5.3 Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of *Aethomys namaquensis* OTUs from southern Africa. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. Operational taxonomic units correspond to those in Figure 5.1. Measurements are defined in Figure 2.5.

(a)

GREATEST CROSS-SECTIONAL CROWN WIDTH OF M_3 (WMS)

$F = 27.22$; $P < 0.001$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{x}$)	Non-significant subsets
95	13	0.07	1.76	
94	26	0.06	1.76	
99	82	0.05	1.76	
75	10	0.06	1.74	
102	19	0.07	1.74	
85	43	0.06	1.73	
103	28	0.07	1.73	
100	21	0.06	1.72	
69	48	0.07	1.72	
72	61	0.06	1.71	
93	13	0.05	1.71	
84	26	0.06	1.71	
56	7	0.04	1.71	
73	7	0.05	1.70	
64/66	8	0.02	1.70	
101	84	0.07	1.70	
82	6	0.03	1.70	
92	136	0.07	1.70	
48	8	0.04	1.70	
74	11	0.06	1.70	
98	10	0.05	1.69	
57	13	0.04	1.69	
68	5	0.04	1.69	
80	9	0.04	1.69	
65	70	0.05	1.69	
83	52	0.08	1.69	
76	16	0.05	1.68	
47	93	0.05	1.68	
79	7	0.02	1.68	
61	14	0.05	1.68	
91	24	0.06	1.68	
58	60	0.07	1.68	
52	33	0.06	1.67	
55	18	0.07	1.67	
59	25	0.05	1.67	
63	17	0.04	1.67	
89	17	0.06	1.66	
62	48	0.04	1.66	
86	54	0.06	1.66	
60	124	0.06	1.66	
71	7	0.04	1.66	
67	33	0.07	1.66	
77/78	48	0.06	1.66	
90	47	0.06	1.66	
46	54	0.06	1.66	
44/45	9	0.08	1.65	
54	56	0.05	1.65	
96	18	0.05	1.65	
53	19	0.06	1.64	
97	4	0.03	1.64	
88	51	0.07	1.64	
51	8	0.07	1.64	
1	4	0.06	1.63	
9	7	0.08	1.63	
49	9	0.04	1.63	
40	7	0.06	1.63	
104	12	0.05	1.63	
81	105	0.06	1.63	
50	19	0.06	1.62	
70	7	0.07	1.61	
87	60	0.06	1.61	
7	23	0.08	1.61	
10	6	0.06	1.60	
8	20	0.06	1.60	
30	9	0.07	1.59	
3	33	0.07	1.59	
12	7	0.09	1.59	
36/38	14	0.10	1.59	
41	33	0.07	1.59	
32	10	0.05	1.58	
2	17	0.06	1.58	
31	17	0.06	1.58	
33	28	0.07	1.58	
5	20	0.05	1.58	
39	14	0.07	1.58	
42	9	0.05	1.58	
22	15	0.05	1.58	
18	7	0.06	1.58	
29	20	0.06	1.57	
15	4	0.03	1.57	
11	7	0.08	1.57	
6	10	0.06	1.57	
13	14	0.06	1.56	
25	7	0.07	1.56	
14	9	0.06	1.56	
34	63	0.06	1.55	
35	60	0.06	1.55	
4	22	0.05	1.55	
20	16	0.07	1.55	
28	6	0.07	1.55	
16	55	0.06	1.55	
17	4	0.03	1.55	
43	10	0.07	1.54	
26	7	0.04	1.54	
21	8	0.07	1.54	
19	36	0.05	1.54	
27	6	0.06	1.53	
24	28	0.06	1.52	
37	31	0.06	1.52	
23	14	0.05	1.52	

(b)

ANTERO-NASAL EDGE - ANTERO-POSTERIOR ZYGOMATIC ARCH LENGTH (NPP)

$F = 13.01$; $P < 0.001$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{x}$)	Non-significant subsets
64/66	8	0.39	23.08	
44/45	9	0.48	22.96	
80	9	0.56	22.84	
70	7	0.43	22.84	
95	13	0.91	22.81	
30	9	0.65	22.80	
77/78	48	0.82	22.79	
57	13	0.72	22.79	
99	82	0.61	22.75	
65	70	0.61	22.72	
76	16	0.63	22.71	
96	18	0.67	22.71	
47	93	0.85	22.63	
102	19	0.79	22.63	
67	33	0.70	22.62	
81	105	0.71	22.59	
63	17	0.63	22.59	
71	7	0.61	22.58	
97	4	0.84	22.57	
103	28	0.87	22.56	
69	48	0.70	22.54	
32	10	0.73	22.52	
72	61	0.74	22.51	
101	84	0.72	22.50	
58	60	0.58	22.48	
79	7	0.58	22.48	
33	28	0.63	22.48	
94	26	0.58	22.45	
55	18	0.40	22.42	
104	12	0.45	22.36	
82	6	0.65	22.34	
83	52	0.99	22.31	
74	11	0.66	22.31	
93	13	0.59	22.26	
98	10	0.80	22.24	
11	17	1.02	22.20	
75	10	0.64	22.20	
100	21	0.72	22.20	
52	33	0.56	22.19	
2	17	0.70	22.17	
62	48	0.88	22.15	
43	10	0.60	22.14	
29	20	0.71	22.11	
48	8	0.57	22.08	
85	43	0.80	22.05	
25	7	0.73	22.05	
6	10	0.37	22.04	
18	7	0.52	22.04	
92	136	0.79	21.99	
40	7	0.19	21.98	
46	54	0.73	21.97	
39	14	0.56	21.97	
19	16	0.61	21.95	
26	7	0.78	21.94	
34	63	0.66	21.92	
10	6	0.42	21.92	
84	26	0.59	21.89	
56	7	0.71	21.86	
41	33	0.80	21.85	
28	6	0.74	21.85	
12	7	0.63	21.83	
42	9	0.67	21.80	
24	28	0.55	21.79	
22	15	0.75	21.79	
36/38	14	0.62	21.78	
27	6	0.89	21.76	
35	60	0.72	21.75	
89	17	0.77	21.75	
21	8	1.10	21.74	
68	5	0.26	21.74	
11	7	0.27	21.74	
54	56	0.60	21.73	
1	4	0.59	21.69	
4	22	0.53	21.67	
16	55	0.55	21.65	
88	51	0.78	21.63	
20	16	0.62	21.62	
50	19	0.54	21.60	
15	4	0.25	21.58	
91	24	0.34	21.57	
86	54	0.69	21.55	
37	31	0.54	21.55	
23	14	0.71	21.55	
87	60	0.71	21.53	
90	47	0.64	21.51	
51	8	0.86	21.50	
3	33	0.61	21.48	
7	23	0.57	21.48	
49	9	0.65	21.47	
5	20	0.64	21.46	
61	14	0.62	21.42	
14	9	0.75	21.36	
17	4	0.92	21.30	
60	124	0.77	21.29	
9	7	0.92	21.27	
8	20	0.80	21.22	
53	19	0.78	21.18	
13	14	0.53	21.15	
59	25	0.80	21.03	
73	7	0.84	20.70	

Table 5.3.--*Continued*.

(c)

POSTERIOR INCISOR - M_1 LENGTH (IML)

$F = 21.03$; $P < 0.001$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{y}$)	Non-significant subsets
64/66	8	0.14	9.58	
69	48	0.32	9.54	
65	70	0.25	9.48	
70	7	0.12	9.44	
95	13	0.33	9.44	
76	16	0.25	9.42	
63	17	0.24	9.42	
72	61	0.24	9.40	
102	19	0.30	9.39	
103	28	0.31	9.39	
67	33	0.29	9.39	
77/78	48	0.31	9.38	
97	4	0.12	9.38	
79	7	0.23	9.37	
94	26	0.33	9.37	
99	82	0.27	9.36	
30	9	0.17	9.34	
47	93	0.30	9.34	
58	60	0.25	9.31	
71	7	0.21	9.29	
81	105	0.35	9.29	
100	21	0.29	9.28	
75	10	0.22	9.25	
83	52	0.29	9.25	
82	6	0.23	9.25	
93	13	0.21	9.24	
62	48	0.36	9.24	
80	9	0.15	9.23	
101	84	0.26	9.23	
98	10	0.34	9.23	
57	13	0.23	9.23	
85	43	0.24	9.21	
[illegible]	12	0.10	9.20	
[illegible]	6	0.17	9.18	
52	33	0.26	9.14	
74	11	0.24	9.14	
68	5	0.08	9.14	
44/45	9	0.22	9.14	
92	136	0.35	9.13	
84	26	0.26	9.12	
96	18	0.24	9.10	
33	28	0.26	9.10	
31	17	0.47	9.09	
32	10	0.16	9.08	
48	8	0.12	9.06	
55	18	0.34	9.04	
26	7	0.24	9.02	
29	20	0.29	9.01	
49	9	0.28	8.98	
12	7	0.44	8.96	
61	14	0.32	8.94	
91	24	0.25	8.94	
90	47	0.32	8.94	
88	51	0.40	8.93	
86	54	0.31	8.91	
89	17	0.31	8.91	
40	7	0.44	8.91	
56	7	0.36	8.91	
46	54	0.29	8.90	
22	15	0.19	8.88	
73	7	0.18	8.87	
60	124	0.32	8.85	
43	10	0.18	8.85	
42	9	0.26	8.85	
19	36	0.22	8.83	
36/46	14	0.30	8.82	
41	33	0.29	8.82	
34	63	0.27	8.82	
18	7	0.34	8.81	
15	4	0.05	8.81	
1	4	0.23	8.80	
87	60	0.31	8.80	
25	7	0.63	8.80	
59	25	0.23	8.79	
2	17	0.32	8.78	
39	14	0.29	8.78	
7	23	0.26	8.77	
6	10	0.24	8.77	
9	7	0.32	8.76	
13	14	0.24	8.76	
54	56	0.36	8.76	
27	6	0.16	8.76	
23	14	0.31	8.75	
16	55	0.27	8.75	
3	33	0.24	8.75	
20	16	0.25	8.74	
24	28	0.27	8.74	
53	19	0.27	8.73	
5	20	0.34	8.73	
37	31	0.33	8.72	
6	22	0.22	8.69	
21	8	0.20	8.69	
28	6	0.40	8.69	
14	9	0.25	8.68	
8	20	0.29	8.68	
50	19	0.28	8.67	
11	7	0.21	8.66	
35	60	0.32	8.66	
51	8	0.25	8.57	
17	4	0.44	8.52	

(d)

FORAMEN MAGNUM HEIGHT (FMH)

$F = 5.05$; $P < 0.001$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{y}$)	Non-significant subsets
58	60	0.21	4.87	
68	5	0.17	4.81	
63	17	0.25	4.78	
44/45	9	0.36	4.78	
57	13	0.23	4.75	
79	7	0.22	4.74	
62	48	0.26	4.70	
65	70	0.23	4.70	
80	9	0.15	4.69	
30	9	0.12	4.69	
52	33	0.25	4.68	
25	7	0.20	4.68	
67	33	0.20	4.66	
7	23	0.17	4.65	
70	7	0.26	4.65	
29	20	0.18	4.65	
55	18	0.26	4.65	
4	22	0.25	4.64	
10	6	0.11	4.64	
27	6	0.12	4.64	
81	105	0.24	4.63	
73	7	0.35	4.63	
49	9	0.13	4.63	
26	7	0.28	4.62	
102	19	0.16	4.62	
61	14	0.22	4.62	
34	63	0.16	4.61	
83	52	0.20	4.61	
43	10	0.24	4.61	
2	17	0.26	4.61	
64/66	8	0.18	4.61	
77/78	48	0.23	4.61	
19	36	0.18	4.60	
1	4	0.17	4.60	
84	26	0.19	4.60	
8	20	0.23	4.60	
72	61	0.19	4.60	
31	17	0.25	4.59	
47	93	0.25	4.59	
5	20	0.18	4.59	
86	54	0.25	4.58	
50	19	0.19	4.58	
104	12	0.14	4.57	
48	8	0.17	4.57	
41	33	0.24	4.57	
59	25	0.16	4.57	
69	48	0.21	4.57	
3	33	0.23	4.56	
42	9	0.20	4.56	
39	14	0.19	4.56	
74	11	0.20	4.56	
17	4	0.19	4.56	
23	14	0.25	4.55	
71	7	0.11	4.55	
53	19	0.19	4.54	
6	10	0.19	4.54	
24	28	0.20	4.53	
75	10	0.28	4.53	
93	13	0.29	4.53	
20	16	0.20	4.53	
88	51	0.29	4.52	
16	55	0.19	4.52	
94	26	0.23	4.52	
21	8	0.21	4.52	
96	18	0.22	4.51	
32	10	0.28	4.51	
56	7	0.21	4.51	
91	24	0.23	4.51	
33	28	0.22	4.51	
46	54	0.19	4.51	
101	84	0.23	4.51	
54	56	0.23	4.51	
13	14	0.25	4.51	
15	4	0.06	4.50	
97	4	0.17	4.50	
37	31	0.23	4.50	
14	9	0.20	4.50	
90	47	0.25	4.50	
103	28	0.18	4.49	
18	7	0.19	4.49	
11	7	0.20	4.49	
99	82	0.19	4.48	
76	16	0.20	4.47	
35	60	0.19	4.47	
36/38	14	0.21	4.47	
60	124	0.20	4.46	
28	6	0.24	4.46	
87	60	0.25	4.46	
22	15	0.20	4.46	
100	21	0.17	4.45	
85	43	0.23	4.45	
51	8	0.28	4.44	
89	17	0.25	4.44	
95	13	0.20	4.44	
92	136	0.24	4.42	
98	10	0.19	4.42	
40	7	0.18	4.41	
12	7	0.19	4.38	
82	6	0.24	4.37	
9	7	0.27	4.37	

Table 5.4 Standard statistics of external and cranial measurements in millimetres of *Aethomys namaquensis* subspecies from southern Africa: *A. n. alborarius*, *A. n. lehocla*, *A. n. monticularis* and *A. n. namaquensis*. $\bar{X}$ = arithmetic mean; *SD* = standard deviation; *n* = sample size; *CV* = coefficient of variation; *Range* = observed range. External measurements were obtained from specimen labels. Measurements are defined in Figure 2.5.

Variable	Subspecies			
	alborarius	*lehocla*	*monticularis*	*namaquensis*
Length of head and body				
$\bar{X}$	112.46	110.55	111.35	118.96
SD	8.74	7.78	9.98	8.13
n	474	486	526	521
CV	7.53	7.04	8.96	6.83
Range	80.0-136.0	80.0-144.0	82.0-147.0	95.0-146.0
Length of tail				
$\bar{X}$	152.56	148.11	153.05	160.79
SD	12.09	10.30	12.27	11.86
n	474	486	526	521
CV	7.93	6.95	8.02	7.37
Range	107.0-190.0	112.0-177.0	119.0-197.0	117.0-196.0
Length of hind foot				
$\bar{X}$	25.39	24.33	26.56	26.88
SD	1.44	1.59	2.07	1.42
n	474	486	526	521
CV	5.58	6.52	7.79	5.29
Range	20.0-30.0	19.0-32.0	21.0-32.0	16.0-31.0
Length of ear				
$\bar{X}$	17.49	16.86	17.97	19.13
SD	1.40	1.34	2.03	1.48
n	474	486	526	521
CV	8.02	7.95	11.30	7.74
Range	11.0-23.0	11.0-21.0	11.0-24.0	13.0-23.0
Greatest length of skull				
$\bar{X}$	30.97	30.30	31.74	32.04
SD	0.92	0.97	1.05	0.94
n	652	701	638	678
CV	2.98	3.19	3.32	2.92
Range	28.20-33.91	27.08-33.77	28.25-34.58	28.93-34.91
Greatest length of frontals				
$\bar{X}$	9.72	9.62	9.66	9.76
SD	0.20	0.30	0.24	0.25
n	652	701	638	678
CV	2.06	3.15	2.47	2.55
Range	9.06-10.35	8.20-10.94	9.01-10.43	8.91-10.92

Table 5.4.--*Continued.*

Variable	Subspecies			
	alborarius	*lehocla*	*monticularis*	*namaquensis*
Length of M^1				
$\bar{X}$	2.40	2.43	2.55	2.49
SD	0.12	0.13	0.13	0.13
n	652	701	638	678
CV	5.08	5.25	5.09	5.21
Range	2.07-2.78	2.11-3.01	2.13-2.98	2.10-2.98
Width of M^2				
$\bar{X}$	1.71	1.80	1.88	1.84
SD	0.07	0.08	0.07	0.08
n	652	701	638	678
CV	4.29	4.32	3.79	4.56
Range	1.50-1.93	1.56-2.01	1.60-2.00	1.41-1.99
Length of angular process to mandibular condyle				
$\bar{X}$	6.13	6.09	6.43	6.50
SD	0.29	0.31	0.33	0.28
n	652	701	638	678
CV	4.78	5.10	5.16	4.35
Range	5.17-7.03	5.28-6.98	5.44-7.39	5.65-7.33
Length of mandibular foramen to condyle				
$\bar{X}$	4.71	4.80	5.02	4.97
SD	0.26	0.29	0.28	0.28
n	652	701	638	678
CV	5.47	5.95	5.66	5.62
Range	4.06-6.00	3.92-5.93	4.04-6.16	4.30-5.93
Length of I_1 to M_3				
$\bar{X}$	8.80	8.86	9.26	9.33
SD	0.30	0.33	0.31	0.31
n	652	701	638	678
CV	3.45	3.71	3.35	3.30
Range	8.01-10.10	7.98-9.88	8.24-10.18	8.28-10.30
Width of M_2				
$\bar{X}$	1.56	1.65	1.71	1.67
SD	0.06	0.07	0.07	0.06
n	652	701	638	678
CV	4.12	4.11	3.91	3.86
Range	1.39-1.77	1.43-1.86	1.45-1.90	1.31-1.89

Table 5.5 Differential cranial ratios (%) of four subspecies of *Aethomys namaquensis*, *A. n. alborarius*, *A. n. lehocla*, *A. n. monticularis* and *A. n. namaquensis*, from southern Africa. $\bar{X}$ = arithmetic mean; *SD* = standard deviation; *n* = sample size; *Range* = observed range. Measurements are defined in Figure 2.5.

Ratio	Subspecies			
	alborarius	*lehocla*	*monticularis*	*namaquensis*
Width of M^2 to greatest length of skull				
$\bar{X}$	5.52	5.95	5.93	5.73
SD	0.26	0.30	0.27	0.29
n	652	701	638	678
Range	4.78-6.36	5.10-6.83	4.73-6.75	4.56-6.50
$\bar{X} \pm 1SD$	5.26-5.78	5.65-6.25	5.66-6.20	5.44-6.02
Width of M_2 to greatest length of skull				
$\bar{X}$	5.04	5.46	5.39	5.21
SD	0.23	0.26	0.24	0.24
n	652	701	638	678
Range	4.39-5.77	4.71-6.28	4.32-6.16	4.24-5.93
$\bar{X} \pm 1SD$	4.81-5.27	5.20-5.72	5.15-5.63	4.97-5.45
Foramen magnum height to greatest length of frontals				
$\bar{X}$	46.79	46.96	46.73	47.76
SD	2.44	2.72	2.61	2.73
n	652	701	638	678
Range	40.53-55.63	40.04-58.29	40.22-55.08	40.40-57.33
$\bar{X} \pm 1SD$	44.35-49.23	44.24-49.68	44.12-49.34	45.03-50.49
Width of M^2 to greatest length of frontals				
$\bar{X}$	17.58	18.74	19.47	18.80
SD	0.84	0.98	0.89	0.95
n	652	701	638	678
Range	15.31-20.13	15.85-22.28	16.75-21.77	14.84-20.93
$\bar{X} \pm 1SD$	16.74-18.42	17.76-19.72	18.58-20.36	17.85-19.75

CHAPTER 6

GEOGRAPHIC VARIATION IN *AETHOMYS CHRYSOPHILUS* FROM SOUTHERN AFRICA

6.1 INTRODUCTION

The Red Veld rat, *Aethomys chrysophilus* (*sensu lato*), comprises two cryptic species, *A. chrysophilus* and *A. ineptus* in southern Africa (Chapter 4). After the analysis of type material, two taxa, *acticola* Thomas and Wroughton, 1908, and *imago* Thomas, 1927, were assigned to *A. chrysophilus* as junior synonyms (Chapter 4).

This chapter represents the first major attempt to evaluate both morphometric and morphological patterns of intraspecific variation in *A. chrysophilus* from southern Africa over a more extensive geographical range than has previously been considered.

6.2 MATERIAL AND METHODS

The analysis of geographic variation in *A. chrysophilus* is based on a subset of data that formed part of the revision of the genus in southern Africa (Chapter 4) in which the homogeneity of the sample as representative of a single, widely distributed species was confirmed. This included 365 specimens from 161 localities, which provided an adequate geographical coverage of the species in southern Africa (Figure 6.1). Specimens examined and a gazetteer are given in Appendices III, IV, V and VI.

6.2.1 Multivariate Analyses

Geographic variation among OTUs was examined by multivariate analyses using UPGMA cluster analyses, PCA and MST of 31 OTU means (Chapter 4) based on standardized variables. The UPGMA cluster analyses and MST were performed on both average taxonomic distances and product-moment correlation coefficients among OTUs, whereas PCA was computed from product-moment correlation coefficients among characters. Although sample means were used for analyses, the observed major patterns were verified by analyses of individual specimens (including holotypes) from the entire range of *A. chrysophilus* in southern Africa.

The phenetic groupings obtained were further examined by pairwise CVAs based on two groupings of data: 1) all specimens within delineated phena; and 2) specimens from a zone of parapatry of the delineated phena. Diagnostic CVAs, however, were used to classify specimens excluded from the analyses. The statistical integrity of the observed patterns was further evaluated by MANOVA. All multivariate analyses were based on eleven basic cranial measurements (Chapter 2; Chimimba and Dippenaar 1995).

6.2.2 Univariate Analyses

Geographic variation among the 31 OTUs was assessed by Model I ANOVA. Where significant differences were detected, maximally non-significant subsets were derived by the *a posteriori* sum of squares simultaneous test procedure (SS-STP; Gabriel and Sokal 1969; Sokal and Rohlf 1981) using ranked means (Power 1970). All

univariate analyses were based on 11 basic and four descriptive cranial characters (Chapter 2; Chimimba and Dippenaar 1995).

6.2.3 Qualitative Morphological Variation

After having delineated phena morphometrically, representative specimens (*n* = 204) of each phenon (including holotypes) were re-examined for qualitative morphological differences. This included the comparison of pelage colouration in natural light using the colour standards of Oyama *et al.* (1967).

6.2.4 Infraspecific Nomenclature

The infraspecific nomenclature of delineated phena was resolved by multivariate analyses that included the holotypes of *A. chrysophilus* and its two junior synonyms, *acticola* and *imago* (Chapter 4). The type material examined is given in Appendix IV.

6.3 RESULTS

6.3.1 Multivariate Assessment

A distance phenogram showed two discrete geographical clusters, designated A and B (Figure 6.2*a*) which broadly coincide with an altitudinal limit in the eastern part of southern Africa (Clark 1967; Figure 6.3). With the exception of OTUs 12, 17, and 26 (indicated by arrows), cluster A comprises OTUs from above 500 m above sea level, whereas cluster B consists of OTUs from below

500 m above sea level.

A correlation phenogram showed similar discrete geographical clusters (A and B; Figure 6.2*b*), although phenetic relationships were more evident than those shown by the distance phenogram. Except for OTU 12, the other two OTUs (17 and 26) that were "misplaced" in the distance phenogram fell within the appropriate grouping of OTUs in the correlation phenogram.

The cluster analysis-derived phena were subsequently used as reference groupings to demarcate clusters in PCA scatterplots. This included the superimposition of MSTs based on both distance and correlation coefficients. There was evidence of two size- and shape-related groups, A and B within both the distance phenogram- (Figure 6.4*a*) and correlation-based (Figure 6.4*b*) PCA scatterplots, which are consistent with the corresponding cluster analyses (Figures 6.2*a* and 6.2*b*).

Apart from OTU 12, both distance- and correlation-based MSTs connected OTUs 17 and 26, "misplaced" in cluster analyses, to their appropriate geographical clusters of OTUs in multivariate space. The first component, a general size component with the majority of eigenvector loadings of similar sign (negative) and relative magnitude, accounted for 46.4% of the variation (Table 6.1). The second component, a shape vector dominated by greatest width of bulla and foramen magnum height (positive eigenvector loadings), and width of M^2 (negative loading) accounted for 14.9% of the variation. These results indicate that geographic variation in *A. chrysophilus* is dominated by cranial shape configuration of the bulla and foramen magnum region, and by dental characteristics of the upper jaw. The phenetic affiliation of specimens excluded from all multivariate analyses because of

small sample sizes were verified by additional distance- and correlation-based UPGMA cluster analyses, PCA and MST.

A geographical summary of these results (Figure 6.5) suggest two cranially distinct, size- and shape-related phena which broadly coincide with localities from either below or above 500 m above sea level in the eastern part of southern Africa. OTU 12 is tentatively referred to the OTU assemblages from below 500 m above sea level since most of the OTUs broadly clustered with their geographical groupings of OTUs.

Pairwise CVAs based on two groupings of data were broadly similar. Results presented are those based on specimens from zones of parapatry of the two delineated phena. Despite overlaps in discriminant score ranges, pairwise discriminant analyses of the two delineated phena produced a 74% correct *a posteriori* classification (n = 365). A MANOVA indicated significant differences between group centroids (F = 6.90; P < 0.001: group centroid of OTUs from above 500 m above sea level = -0.80; score range: -3.01 - 1.42; OTUs from below 500 m above sea level: centroid = 0.52; range = -1.96 - 2.63).

6.3.2 Univariate Assessment

Model I ANOVA of 31 OTUs revealed statistically significant differences (P < 0.05) in 14 of the 15 measurements examined (11 basic and four descriptive cranial). Patterns of variation revealed by the order of ranked means indicate three contrasting trends as illustrated by selected measurements (Table 6.2).

The first pattern involved four measurements with F-values ranging from 3.22 to 5.44. As is evident in greatest bulla width

(Table 6.2*a*), there is a trend in the order of ranked means for larger values (*c*. 5.61 - 5.77 mm) to be associated with low-altitude OTUs and lower values (*c*. 5.27 - 5.60 mm) with high-altitude OTUs. The uniqueness of high- and low-altitude OTUs was supported by all multivariate analyses (Figures 6.2 and 6.4).

The second pattern evident from the data involved greatest cross-sectional crown width of M^2 (*F*-value = 2.04; Table 6.2*b*), in which a trend opposite to that in greatest bulla width (Table 6.2*a*) was revealed. There was a tendency for lower values (*c*. 1.89 - 1.94 mm) to be associated with low-altitude OTUs and larger values (*c*. 1.94 - 1.99 mm) with high-altitude OTUs. These two assemblages are also consistent with the two major patterns revealed by all multivariate analyses (Figures 6.2 and 6.4).

The third order of ranked means involved nine measurements with broadly overlapping non-significant subsets (*F*-value range: 1.68 - 5.62). All these measurements failed to show geographically discernible patterns, as exemplified by breadth of brain-case and greatest height of skull (Tables 6.2*c* and 6.2*d*). A similar pattern was also evident in foramen magnum height, the measurement with the lowest, and the only statistically non-significant *F*-value (*F*-value = 1.45; $P > 0.05$) among the 15 measurements examined.

6.3.3 Taxonomic Status of Delineated Phena

The morphological differences between the two delineated phena and their association with altitudinal limits of either below or above 500 m above sea level in the eastern part of southern Africa, provide support for their recognition as

distinct subspecies (see Discussion). To further resolve the infraspecific nomenclature, however, the phenetic affiliations of holotypes of *A. chrysophilus* and the two described forms, *acticola* and *imago* (Chapter 4), were verified by UPGMA cluster analyses, PCA, MST and CVA.

All holotypes associated phenetically with groups that also geographically coincided with their type localities (Figures 6.5). As is convention, the earliest described taxa within OTU assemblages were considered senior synonyms of the two delineated phena. Consequently, the nominate subspecies, *chrysophilus* De Winton, 1897, is assigned to low-altitude OTUs from the eastern part of southern Africa, with *acticola* Thomas and Wroughton, 1908, as a junior synonym. *Aethomys chrysophilus* was described from Mazoe in eastern Zimbabwe, which falls within the low-altitude assemblage of OTUs. High-altitude OTUs are allocated to *A. c. imago* Thomas, 1927.

6.3.4 Diagnostic Morphological and Morphometric Characters

There were neither geographically discernible qualitative morphological nor pelage colour patterns to distinguish the two subspecies. Both within and among the two delineated phena, upper parts ranged from brown (7.5YR 4/3) to dark brown (7.5YR 3/4), sprinkled with brownish black (7.5YR 3/1) to very dark brown (7.5YR 2/3) hairs; cheeks, sides and thighs from light grey (7.5YR 8/2) to light brown-grey (7.5YR 7/2); underparts and feet from light yellow-orange (7.5YR 8/4) to orange (7.5YR 6/8); the few scattered hairs on ears from yellow-orange (7.5YR 7/8) to orange (7.5YR 6/8); the bicoloured basal half of tail from brown

(7.5YR 4/6) to dark brown (7.5YR 3/4) above and orange (7.5YR 6/8) to bright brown (7.5YR 5/8) below, and the unicoloured terminal portion from yellow-orange (7.5YR 7/8) to orange (7.5YR 6/8). This suggests that intraspecific variation in qualitative morphology and pelage colour within *A. chrysophilus* from southern Africa is either subtle or does not form part the delineated patterns of cranial and dental morphological variation.

As an additional aid to subspecies identification, a search was made for simple ratios from standard statistics of 11 basic cranial, four descriptive cranial and four external measurements (Table 6.3). Cranial ratios, using all specimens from the subregion, were computed for characters with high negative (greatest cross-sectional crown width of M^2) and positive (greatest width of bulla and foramen magnum height) loadings in the shape-related axes II of PCA (Table 6.1). Greatest length of skull, one of the two highly negative size-related character on PC Axis I was also included, but all combinations, including external ratios were not informative.

6.4 DISCUSSION

The aim of this chapter was to evaluate patterns of intraspecific variation in *A. chrysophilus* from southern Africa over a more extensive geographical range than has previously been considered. Both distance- and correlation-based phenograms revealed the presence of two major clusters of OTUs within *A. chrysophilus* from southern Africa.

A taxonomic interpretation of the detected variation suggests that *A. chrysophilus* in southern Africa is polytypic and

can be separated into two subspecies: *A. c. chrysophilus* De Winton, 1897 and *A. c. imago* Thomas, 1927. As in *A. namaquensis* from southern Africa (Chapter 5), these results presented the classical infraspecific taxonomic problem of having to decide whether the two delineated phena were sufficiently different to justify the recognition of subspecies (see debates in volumes 3 to 5 of *Systematic Zoology* 1954-1956; summaries in Pimentel 1959, and Sokal and Rinkel 1963).

In this study, however, one of the prerequisites considered for recognizing the two subspecies within *A. chrysophilus* from southern Africa was the pattern of variation which was both size- and shape-related. More importantly, the phenetic discontinuity broadly corresponds with altitudinal limits of either below or above 500 m above sea level in the eastern part of southern Africa (Clark 1967). The subspecies *A. c. chrysophilus* occurs below 500 m above sea level in the eastern part of southern Africa, whereas *A. c. imago* occurs outside this region. Subspecies as units of evolution are expected to be represented by transitional zones that coincide with partial or complete, present or past, geographical or ecological barriers (Endler 1977; Thorpe 1984; Barton and Hewitt 1985).

Of additional importance is that the recognition of subspecies was supported by a variety of both size- and shape-related morphometric characters, which also showed no evidence of clinal variation. The identification key below, however, is based only on geographical distributions because the characters were so subtle to be useful for practical diagnostic

purposes.

An examination of pelage colouration in *A. chrysophilus* showed considerable and geographically discordant variation. This was also evident in *A. namaquensis* (Chapter 5) and *A. ineptus* (Chapter 7) from southern Africa, and may be interpreted as an adaptive response to local climatic conditions. In Botswana, Smithers (1971) considered specimens of *A. chrysophilus* (*sensu lato*) with pure white or nearly pure white under parts to occur on the fringes of the Kalahari but refrained from recognizing subspecies. These pelage colour forms were not discernible in the present study.

6.5 KEY TO SUBSPECIES OF *AETHOMYS CHRYSOPHILUS* FROM SOUTHERN AFRICA

1. Restricted to eastern part of southern Africa, below 500 m above sea level (Figures 6.3 and 6.5)..... *chrysophilus*

2. Occurring outside the above region..... *imago*

6.6 CONCLUSIONS

Patterns of infraspecific variation in the southern African *A. chrysophilus* suggest the recognition of two subspecies: *A. c. chrysophilus* De Winton, 1897 and *A. c. imago* Thomas, 1927, which differ both in cranial size and shape. The morphological discontinuity of the proposed subspecies broadly coincides with altitudinal limits of either below or above 500 m above sea level in the eastern part of southern Africa.

6.7 TAXONOMY

6.7.1 *Aethomys chrysophilus chrysophilus* (De Winton, 1897)

Mus chrysophilus De Winton, 1897: *Proc. Zool. Soc. Lond.* for 1896:801.

Mus chrysophilus acticola Thomas and Wroughton, 1908: *Proc. Zool. Soc. Lond.*:547.

6.7.1.1 Holotype

BM 95.11.3.23 (original No. 54); adult female; Mazoe, Mashonaland, eastern Zimbabwe.

6.7.1.2 Distribution

Occurring in the eastern part of southern Africa, below 500 m above sea level, including Mozambique, eastern Zimbabwe, eastern Northern Province, eastern Mpumalanga and eastern KwaZulu-Natal (Figures 1.1, 6.3 and 6.5).

6.7.1.3 Diagnosis

Medium-sized (observed range: head and body length: 125 - 169 mm; greatest skull length: 33.7 - 39.8 mm); Dorsal and ventral colour clearly demarcated; upper parts brown (7.5YR 4/3), sprinkled with brownish black (7.5YR 3/1) hairs; cheeks, sides and thighs light grey (7.5YR 8/2); underparts and feet light yellow-orange (7.5YR 8/4); ears naked apart from few scattered

yellow-orange (7.5YR 7/8) hairs; apart from a few short adpressed hairs that increase in number and length towards the tip, tail almost naked and more coarsely scaled; shiny, mica-like scales present; basal half bicoloured, brown (7.5YR 4/6) above and orange (7.5YR 6/8) below; terminal portion unicoloured yellow orange (7.5YR 7/8).

6.7.1.4 Etymology

A combination of two Latin words, *chrysos* = gold and *philos* = having affinity for, to denote the golden dorsal surface.

6.7.2 *Aethomys chrysophilus imago* Thomas, 1927

Aethomys chrysophilus imago Thomas, 1927: *Proc. Zool. Soc. Lond.*:387.

6.7.2.1 Holotype

BM 26.12.7.220 (original No. 1832); adult male; Stampriet, eastern Gobabis, east-central Namibia.

6.7.2.2 Distribution

Occurring widely in southern Africa above 500 m above sea level, from northern and central Namibia, northern and eastern Botswana to western Zimbabwe, western Northern Province and the northern sector of the Northern Cape Province around Kuruman (Figures 1.1, 6.3 and 6.5).

6.7.2.3 Diagnosis

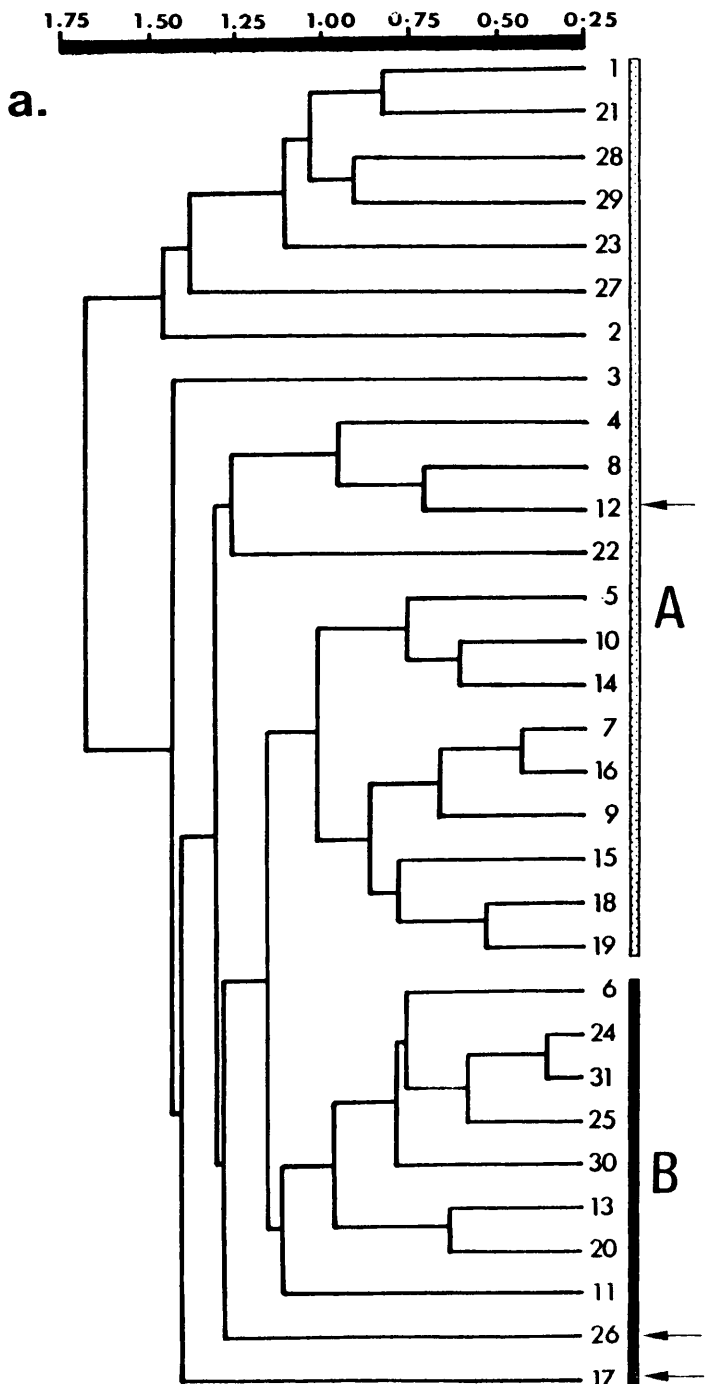
Medium-sized (observed range: head and body length: 120 - 165 mm; greatest skull length: 32.1 - 40.6 mm); Dorsal and ventral colour clearly demarcated; upper parts yellowish brown (10YR 5/6), sprinkled with dark brown (10YR 3/4); underparts, thighs light grey (10YR 8/1); ears naked apart from few scattered bright yellowish brown (10YR 6/8) hairs; basal half of tail bicoloured, brown (10YR 4/4) above and bright yellowish brown (10YR 7/6) below; terminal portion unicoloured dark brown (10YR 3/3).

6.7.2.4 Etymology

The subspecies name is probably derived from the Latin word, *imago* meaning "image, copy, likeness, similarity", perhaps reflecting its resemblance to the nominate subspecies.

Figure 6.1 Collecting localities and pooled samples (OTUs) of *Aethomys chrysophilus* from southern Africa. Insert shows the distribution of the species in southern Africa as determined in Chapter 4.

Figure 6.2 Distance (**a**) and correlation (**b**) phenograms from UPGMA cluster analyses of pooled samples (OTUs) of *Aethomys chrysophilus* from southern Africa. Operational taxonomic units correspond to those in Figure 6.1. Arrows indicate incorrectly clustered OTUs. Cophenetic correlation coefficients = 0.66 and 0.69 respectively.



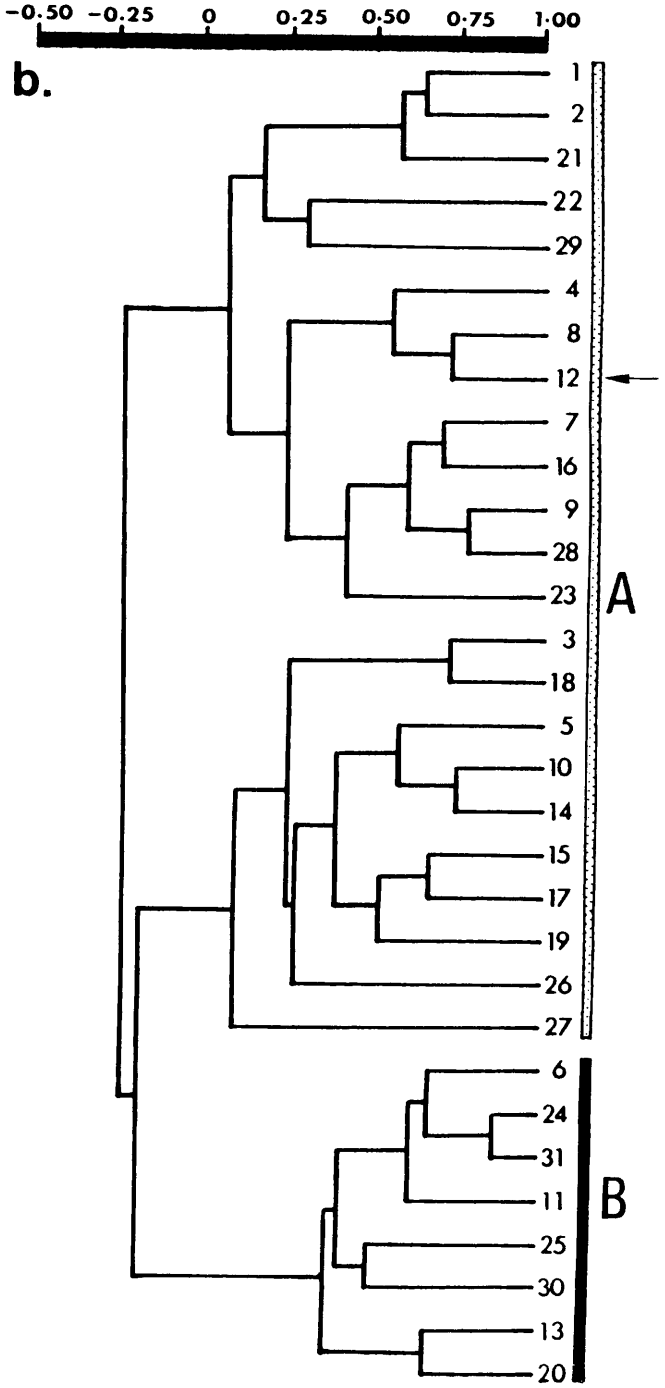


Figure 6.3 Topographic map of southern Africa (after Clark 1967).

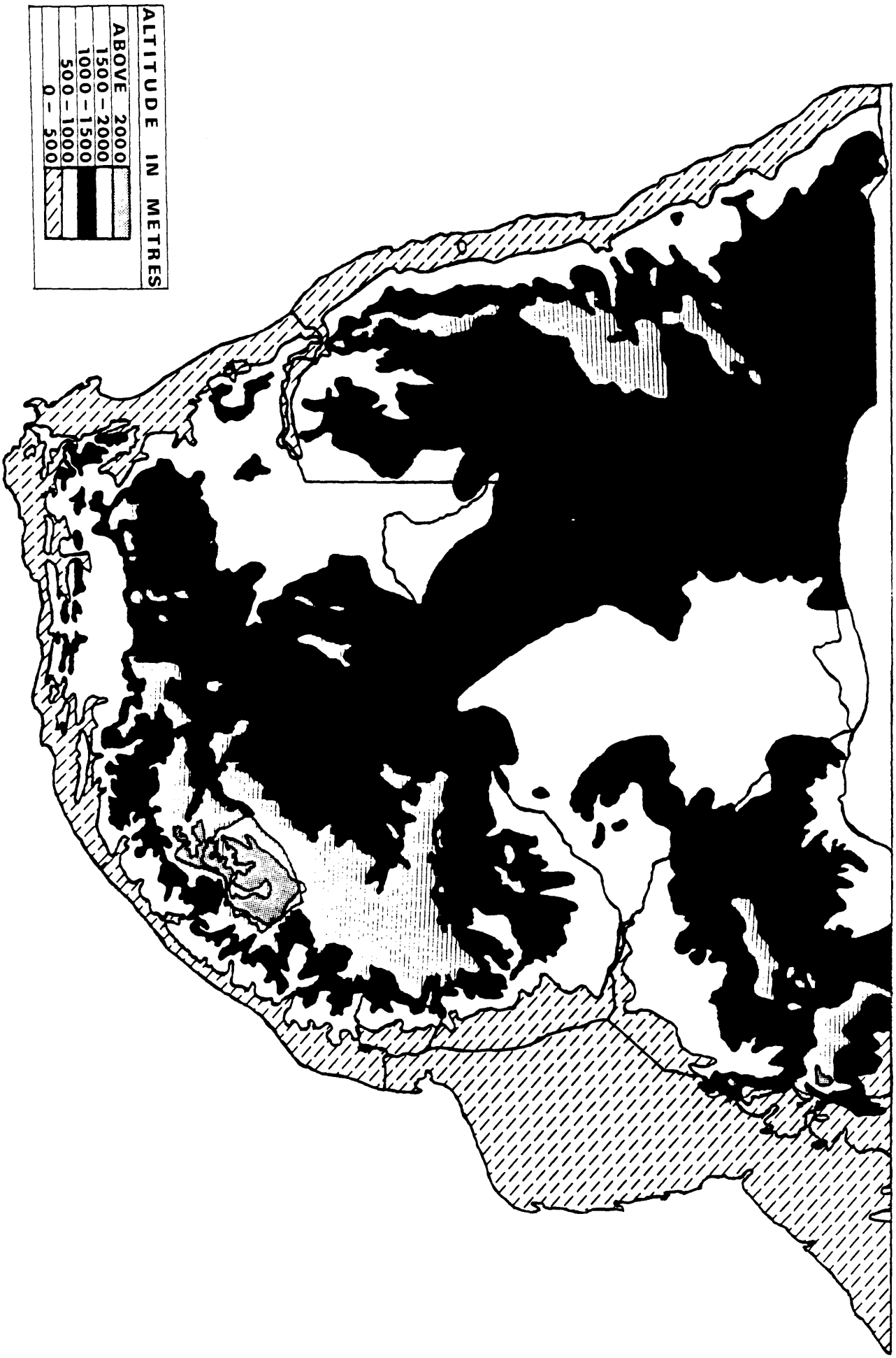


Figure 6.4 Axes I and II from a principal components analysis of *Aethomys chrysophilus* from southern Africa. A minimum spanning tree is superimposed. Symbols indicate OTUs from major clusters A (solid diamonds) and B (open triangles) delineated by (**a**) distance (Figure 6.2*a*) and (**b**) correlation (Figure 6.2*b*) phenograms. Arrows indicate incorrectly clustered OTUs. Operational taxonomic units correspond to those in Figure 6.1.

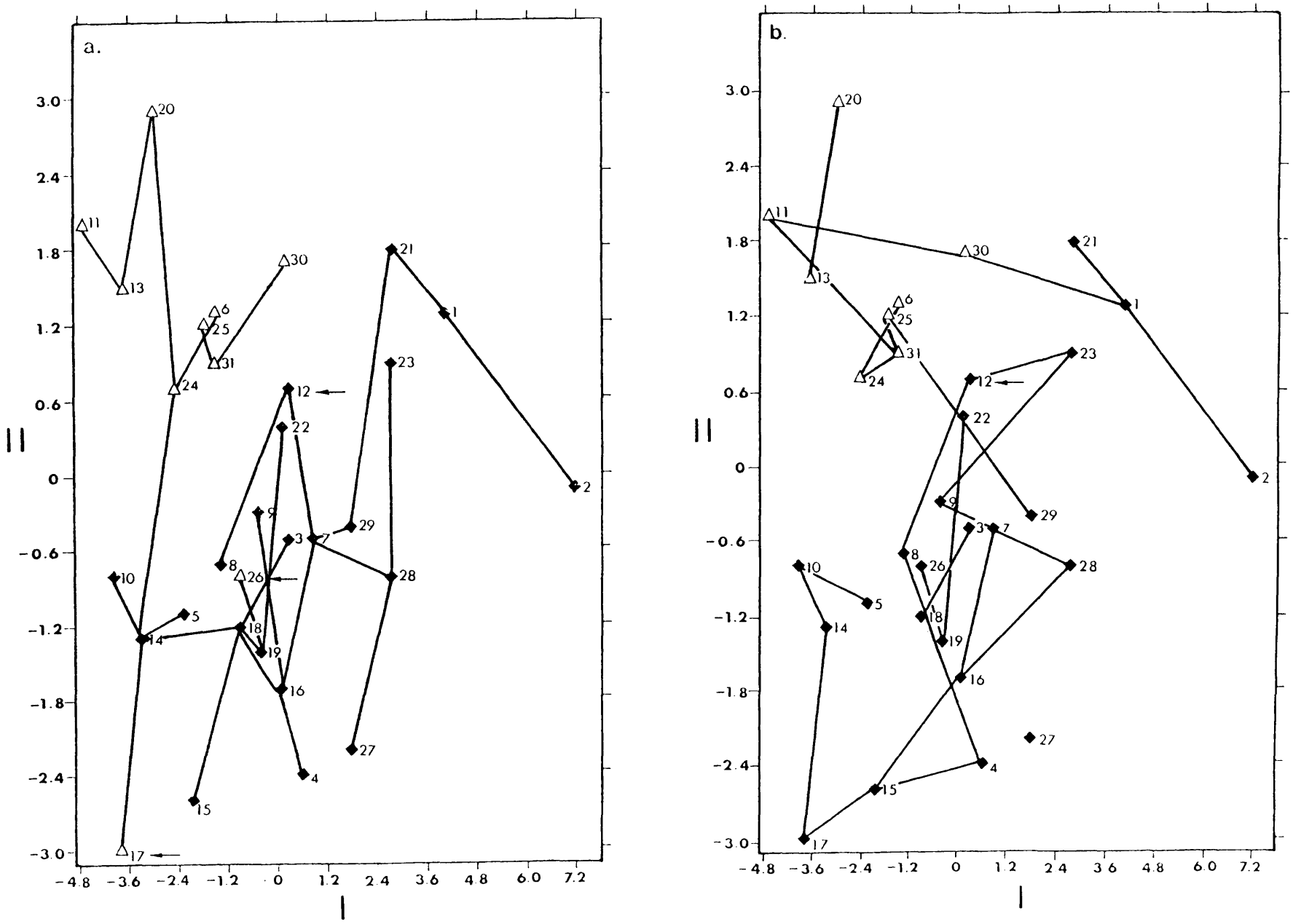


Figure 6.5 A geographical representation of delineated phena in *Aethomys chrysophilus* from southern Africa based on collation of UPGMA clustering, minimum spanning trees and principal components analysis results, and the correct placement of OTU 12. Samples were largely demarcated into OTU assemblages that correspond to the eastern (shaded) part of southern Africa, 500 metres below sea level, and western (horizontal lines) part of this region (cf. Clark 1967; Figure 6.3). Collecting localities and pooled samples correspond to those in Figure 6.1. Abbreviations represent type localities of *A. chrysophilus* (chr) and its two described subspecies in southern Africa, *acticola* (act) and *imago* (ima). Insert represents the distribution of the species in southern Africa as determined in Chapter 4.

Table 6.1 Loadings of variables on components I and II from a principal components analysis for samples of *Aethomys chrysophilus* from southern Africa. The percent variance contributions appear in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components	
	I	II
Greatest length of skull	-0.423 (91.11)	-0.032 (0.16)
Greatest length of frontals	-0.314 (50.16)	-0.063 (0.65)
Length of nasals to zygomatic arch	-0.426 (92.44)	-0.013 (0.03)
Greatest width of bulla	0.158 (12.79)	0.548 (49.34)
Foramen magnum height	0.040 (0.83)	0.421 (29.13)
Length of M^1	-0.269 (37.01)	0.025 (0.11)
Width of M^2	-0.108 (6.00)	-0.606 (60.45)
Length of angular process to mandibular condyle	-0.394 (79.18)	0.124 (2.53)
Length of mandibular foramen to condyle	-0.294 (44.23)	-0.186 (5.67)
Length of I_1 to M_3	-0.369 (69.34)	0.227 (8.48)
Width of M_2	-0.230 (27.06)	-0.218 (7.79)
% Trace:	Axis I = 46.4%;	Axis II = 14.9%

Table 6.2 Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of *Aethomys chrysophilus* OTUs from southern Africa. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. Operational taxonomic units correspond to those in Figure 6.1. Measurements are defined in Figure 2.5.

(a)

GREATEST BULLA WIDTH (BUW)

(F= 4.28; P < 0.05)

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{Y}$)	Non-significant subsets
20	22	0.11	5.77	
25	11	0.27	5.74	
12	7	0.09	5.72	
6	4	0.25	5.69	
21	6	0.27	5.68	
22	10	0.14	5.68	
13	6	0.19	5.67	
11	15	0.16	5.64	
31	8	0.12	5.63	
24	11	0.19	5.62	
26	4	0.20	5.62	
30	7	0.18	5.61	
3	4	0.32	5.60	
9	9	0.17	5.58	
29	6	0.32	5.57	
10	10	0.24	5.57	
19	11	0.16	5.52	
18	13	0.20	5.51	
14	46	0.22	5.50	
23	5	0.21	5.50	
7	29	0.23	5.48	
16	12	0.16	5.45	
5	6	0.35	5.44	
15	23	0.18	5.43	
17	9	0.17	5.42	
28	5	0.07	5.38	
1	5	0.11	5.37	
2	8	0.20	5.31	
27	6	0.14	5.29	
8	4	0.30	5.28	
4	4	0.08	5.27	

(b)

GREATEST CROSS-SECTIONAL CROWN WIDTH OF M^2 (WSM)

(F = 2.04; P < 0.05)

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{Y}$)	Non-significant subsets
15	23	0.08	1.99	
16	12	0.07	1.99	
17	9	0.08	1.99	
9	9	0.08	1.98	
4	4	0.13	1.98	
5	6	0.05	1.97	
11	15	0.06	1.96	
18	13	0.06	1.96	
7	29	0.07	1.96	
14	46	0.07	1.96	
3	4	0.06	1.95	
8	4	0.06	1.95	
19	11	0.07	1.95	
28	5	0.02	1.95	
10	10	0.05	1.95	
29	6	0.07	1.94	
27	6	0.05	1.94	
25	11	0.06	1.94	
6	4	0.04	1.94	
22	10	0.06	1.93	
23	5	0.05	1.93	
13	6	0.05	1.92	
31	8	0.03	1.92	
20	22	0.03	1.92	
24	11	0.05	1.92	
21	6	0.06	1.91	
30	7	0.03	1.91	
1	5	0.05	1.90	
12	7	0.06	1.90	
26	4	0.02	1.90	
2	8	0.05	1.89	

(c)

BREADTH OF BRAIN-CASE (BBC)

(F = 4.93; P < 0.05)

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{Y}$)	Non-significant subsets
11	15	0.61	15.46	
13	6	0.37	15.28	
14	46	0.44	15.19	
6	4	0.33	15.10	
15	23	0.40	15.06	
8	4	0.60	15.05	
24	11	0.62	15.03	
4	4	0.38	15.02	
17	9	0.41	15.01	
10	10	0.49	15.00	
18	13	0.55	14.99	
9	9	0.39	14.98	
5	6	0.76	14.88	
7	29	0.39	14.85	
12	7	0.35	14.85	
3	4	0.56	14.84	
22	10	0.42	14.84	
20	22	0.34	14.83	
16	12	0.54	14.77	
30	7	0.38	14.76	
26	4	0.53	14.75	
25	11	0.46	14.73	
19	11	0.43	14.71	
21	6	0.37	14.59	
28	5	0.20	14.56	
31	8	0.25	14.49	
27	6	0.34	14.37	
1	5	0.38	14.26	
29	6	0.29	14.21	
2	8	0.40	14.15	
23	5	0.29	14.09	

(d)

GREATEST HEIGHT OF SKULL (GHS)

(F = 1.68; P < 0.05)

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean ($\bar{Y}$)	Non-significant subsets
8	4	0.29	11.85	
11	15	0.25	11.82	
3	4	0.40	11.77	
10	10	0.42	11.71	
5	6	0.61	11.69	
6	4	0.17	11.69	
4	4	0.27	11.69	
15	23	0.27	11.68	
16	12	0.37	11.61	
9	9	0.43	11.57	
31	8	0.26	11.57	
7	29	0.31	11.56	
13	6	0.25	11.54	
24	11	0.33	11.53	
25	11	0.41	11.51	
17	9	0.27	11.50	
28	5	0.25	11.50	
20	22	0.30	11.46	
14	46	0.32	11.46	
29	6	0.48	11.44	
23	5	0.22	11.43	
18	13	0.30	11.42	
27	6	0.27	11.41	
12	7	0.38	11.41	
30	7	0.36	11.38	
2	8	0.39	11.36	
19	11	0.39	11.36	
21	6	0.35	11.36	
26	4	0.11	11.36	
22	10	0.25	11.35	
1	5	0.30	11.33	

Table 6.3 Standard statistics of external and cranial measurements in millimetres of *Aethomys chrysophilus* subspecies from southern Africa: *A. c. chrysophilus* and *A. c. imago*. $\bar{X}$ = arithmetic mean; *SD* = standard deviation; *n* = sample size; *CV* = coefficient of variation; *Range* = observed range of variation. External measurements were obtained from specimen labels. Measurements are defined in Figure 2.5.

Variable	*chrysophilus*					*imago*				
	$\bar{X}$	*SD*	*n*	*CV*	*Range*	$\bar{X}$	*SD*	*n*	*CV*	*Range*
Length of head and body	143.47	10.85	47	7.57	125.0-169.0	143.13	10.01	79	7.00	120.0-165.0
Length of tail	167.70	10.64	47	6.34	144.0-185.0	160.47	12.93	79	8.06	135.0-190.0
Length of hind foot	29.68	2.47	47	8.32	21.0-35.0	28.99	2.19	79	7.54	20.0-33.0
Length of ear	20.85	1.65	47	7.94	16.0-25.0	20.39	1.94	79	9.53	15.0-27.0
Greatest length of skull	36.58	1.36	91	3.71	33.68-39.81	36.33	1.40	235	3.87	32.05-40.59
Greatest length of frontals	11.35	0.39	91	3.42	9.96-12.13	11.24	0.53	235	4.72	9.64-12.11
Length of nasals to zygomatic arch	25.55	1.02	91	3.98	23.54-28.13	25.18	1.09	235	4.32	21.82-27.66
Breadth of braincase	14.96	0.52	91	3.46	14.00-16.52	14.86	0.52	235	3.48	13.57-16.10
Interorbital breadth	5.22	0.24	91	4.66	4.71-6.00	5.12	0.25	235	4.94	4.52-5.92
Greatest length of bulla	7.68	0.23	91	3.02	6.95-8.48	7.45	0.31	235	4.13	6.67-8.61
Greatest width of bulla	5.69	0.18	91	3.09	5.22-6.34	5.48	0.22	235	4.04	4.79-6.22
Greatest height of skull	11.55	0.33	91	2.86	10.65-12.24	11.51	0.35	235	3.01	10.40-12.67
Foramen magnum height	4.89	0.22	91	4.46	4.37-5.35	4.82	0.25	235	5.15	4.09-5.49
Length of M^1	2.87	0.11	91	3.96	2.61-3.42	2.86	0.16	235	5.65	2.49-3.38
Length of M^2	1.93	0.05	91	2.57	1.78-2.07	1.95	0.07	235	3.53	1.79-2.19
Length of angular process to mandibular condyle	7.60	0.33	91	4.38	6.42-8.68	7.39	0.44	235	5.97	6.99-8.43
Length of mandibular foramen to condyle	5.56	0.30	91	5.34	4.95-6.41	5.51	0.38	235	6.88	4.44-6.57
Length of I_1 to M_3	10.56	0.37	91	3.50	9.71-11.86	10.38	0.36	235	3.52	9.00-11.30
Width of M_2	1.80	0.05	91	2.97	1.65-1.97	1.81	0.07	235	3.63	1.65-2.05

CHAPTER 7

GEOGRAPHIC VARIATION IN *AETHOMYS INEPTUS* FROM SOUTHERN AFRICA

7.1 INTRODUCTION

The recognition of the Tete Veld rat, *Aethomys ineptus* is based on the taxonomic elevation of one of the ten previously recognized subspecies of *A. chrysophilus* (*sensu lato*) from southern Africa (Thomas and Wroughton 1908; Chapter 4). After the analysis of type material, seven of the nine previously recognized subspecies within *A. chrysophilus* (*sensu lato*), namely *tzaneenensis* Jameson, 1909; *pretoriae* Roberts, 1913; *magalakuini* Roberts, 1926; *capricornis* Roberts, 1926; *tongensis* Roberts, 1931; *fouriei* Roberts, 1946; and *harei* Roberts, 1946, were re-allocated to *A. ineptus* as junior synonyms (Chapter 4).

This chapter represents the first attempt to evaluate both morphometric and morphological patterns of intraspecific variation in *A. ineptus* from southern Africa across a more comprehensive geographical range than has previously been considered.

7.2 MATERIAL AND METHODS

The analysis of geographic variation in *A. ineptus* is based on a subset of data that formed part of the revision of the genus in southern Africa (Chapter 4) in which the homogeneity of the sample as representative of a single, widely distributed species was confirmed. This included 612 specimens from 249 localities,

which provided adequate geographical coverage of the species in southern Africa (Figure 7.1). Specimens examined and a gazetteer are given in Appendices III, V and VI.

7.2.1 Multivariate Analyses

Infraspecific variation among OTUs was examined by multivariate analyses using UPGMA cluster analyses, PCA and MST of 48 OTU means (Chapter 4) based on standardized variables. The UPGMA cluster analyses and MST were performed on both average taxonomic distances and product-moment correlation coefficients among OTUs, whereas PCA was computed from product-moment correlation coefficients among characters. Although sample means were used for analyses, the observed major patterns were verified by analyses of individual specimens (including holotypes) from the entire range of *A. ineptus* in southern Africa. All multivariate analyses were based on 11 basic cranial measurements (Chimimba and Dippenaar 1995; Chapter 2).

7.2.2 Univariate Analyses

Infraspecific variation among the 48 OTUs was assessed by Model I ANOVA. Where significant differences were detected, maximally non-significant subsets were delineated by the *a posteriori* sum of squares simultaneous test procedure (SS-STP; Gabriel and Sokal 1969; Sokal and Rohlf 1981) using ranked means (Power 1970).

Patterns of variation were also evaluated by whole model regression analyses. Analyses were performed on the PCA scores

of OTUs and 11 basic and four descriptive cranial characters (Chapter 2; Chimimba and Dippenaar 1995), with longitude and latitude as covariates. All univariate analyses were based on 11 basic and four descriptive cranial characters (Chapter 2; Chimimba and Dippenaar 1995).

7.2.3 Qualitative Morphological Variation

After having identified trends of intraspecific variation morphometrically, representative specimens (*n* = 388) (including holotypes) from the entire range of *A. ineptus* in southern Africa were re-examined for qualitative morphological patterns. This included the comparison of pelage colouration in natural light using the colour standards of Oyama *et al.* (1967).

7.2.4 Infraspecific Nomenclature

The relationship between delineated patterns of variation and infraspecific nomenclature were resolved by morphometric analyses that included holotypes of *A. ineptus* and its seven junior synonyms: *tzaneenensis*, *pretoriae*, *magalakuini*, *capricornis*, *tongensis*, *fouriei*, and *harei* (Chapter 4). The type material examined is given in Appendix IV.

7.3 RESULTS

7.3.1 Multivariate Assessment

Neither distance (Figure 7.2*a*) nor correlation (Figure 7.2*b*)

phenograms of the 48 OTUs show geographically discernible patterns. Lack of geographically discernible patterns was also evident when distance- and correlation-based MSTs were superimposed on a PCA scattergram (not illustrated). In the PCA scatterplot of the first two components, however, there is a tendency for OTU scores along the first PCA axis to increase with increasing longitude (Figure 7.3).

The first component, which contributes 48.3% of the variance, and also has most measurements with both relatively high negative scores and percent variances (Table 7.1), shows that overall size accounts for the greatest portion of the variation. The second component, which accounts for 13.5% of the variance (Table 7.1), indicates that dental configuration is also intraspecifically important in *A. ineptus* from southern Africa. It has both positive and negative loadings and percent variances of different magnitudes, and is dominated by two measurements, greatest cross-sectional crown widths of M^2 and M_2 (Table 7.1).

In order to ascertain the geographic directionality in patterns of variation, whole model regression analyses were performed on OTU scores of all 11 PCA axes, 11 basic and four descriptive cranial characters, with longitude and latitude as covariates. Regressions of PCA axis I scores revealed a positive and significant longitudinal effect (Table 7.2*a*), with scores generally showing a gradual increase with increasing longitude (Figure 7.4). These results suggest a clinal continuum of a morphometric character complex, with western OTUs being on average smaller than eastern OTUs.

There were no geographically discernible patterns when latitude was entered as a covariate, and when OTU scores of PCA

axis II were regressed against longitude and latitude (Table 7.2*a*). Similarly, a consideration of component scores III to XI did not reveal geographically discernible patterns. Positive and significant longitudinal clinal trends of variation were, however, evident in regressions of 12 of the 15 single variables considered (Table 7.2*b*). These longitudinal patterns of variation are best illustrated by three measurements with the highest correlation coefficients (Table 7.2*b*): greatest length of skull (Figure 7.5*a*), length of nasals to zygomatic arch (Figure 7.5*b*) and breadth of braincase (Figure 7.5*c*). Greatest length of skull and length of nasals to zygomatic arch also represent the two measurements with the highest loadings on the first PCA axis (Table 7.1), while breadth of braincase represents one of the four characters initially incorporated in the data set for descriptive purposes (Chapter 2).

Although four of the 15 measurements, breadth of braincase, interorbital breadth, greatest length of bulla and length of M^1 showed statistically significant latitudinal effect (Table 7.2*b*), their plots showed no geographical patterns. Similarly, the interaction between longitude and latitude showed no statistically significant effect on all dependent variables examined.

The delineated longitudinal trends of variation were also evident at the specimen level which incorporated those excluded from analyses because of small sample sizes. This trend is best illustrated when measurements of holotypes of *A. ineptus* and its seven junior synonyms are superimposed on regressions of single variables as exemplified in Figure 7.5. There is a tendency for measurements of the holotypes to increase gradually with

increasing longitude. Generally, however, patterns of variation as revealed by regression analyses suggest that evidence of clinal variation in *A. ineptus* from southern Africa is best expressed by a complex rather than single variables. The highest correlation coefficient (0.64; Table 7.2) in all regression analyses was revealed by the analysis of scores of the first principal component.

7.3.2 Univariate Assessment

In a Model I ANOVA of the 48 OTUs, statistically significant differences ($P < 0.05$) were detected in 14 of 15 measurements examined (11 basic and four descriptive cranial). Patterns of variation revealed by the order of ranked means indicate two contrasting trends as illustrated by selected measurements (Table 7.3).

The first and major pattern involved 13 measurements with F-values ranging from 1.97 to 5.15. As was evident in regression analyses (Figures 7.4 and 7.5), all these measurements show a general trend for the order of ranked means to increase from west to east. Despite broad similarities in all 13 measurements, the longitudinal patterns of variation are best illustrated by three characters with the highest F-values: greatest length of skull (Table 7.3*a*), length of nasals to zygomatic arch (Table 7.3*b*) and breadth of braincase (Table 7.3*c*). All three measurements also showed the highest correlation coefficients in the regression analyses (Table 7.2). Greatest length of skull and length of nasals to zygomatic arch also represent the two measurements with the highest loadings on the first PCA axis (Table 7.1). Breadth

of braincase represents one of the four cranial characters initially incorporated in the data set for descriptive purposes (Chapter 2).

The second order of ranked means, which involved a single measurement, foramen magnum height (F-value = 1.72), was not meaningful geographically (Tables 7.3*d*). Lack of geographical pattern was also evident in greatest cross-sectional crown width of M^2, the measurement with the lowest, and the only statistically non-significant F-value (F-value = 1.11; $P > 0.05$) among the 15 measurements examined. These two measurements also had the lowest loadings on the first PCA axis (Table 7.1) and also represent two of the three measurements that showed statistically non-significant longitudinal relationships in the regression analyses (Table 7.2*b*).

7.3.3 Infraspecific Nomenclature

Regressions of PCA axis I scores of OTUs as well as single variables revealed evidence of a longitudinal morphometric clinal continuum, suggesting no justification in recognizing subspecies within *A. ineptus* from southern Africa (see Discussion). To resolve the infraspecific nomenclature, however, the holotypes of *A. ineptus* and its seven junior synonyms, *tzaneenensis*, *pretoriae*, *magalakuini*, *capricornis*, *tongensis*, *fouriei*, and *harei* (Chapter 4), were re-examined with reference to the delineated longitudinal morphometric continuum. As exemplified in regressions in Figure 7.5, all holotypes plotted close to topotypical OTUs, and *A. ineptus* is consequently considered a monotypic species.

7.3.4 Qualitative Morphological Variation

In contrast to the general morphometric delineation of clinal patterns of variation, there were neither geographically discernible qualitative morphological nor general pelage colour patterns associated with a geographical gradient in character change. Both within and among the 48 localities, upper parts ranged from brown (7.5YR 4/3) to dark brown (7.5YR 3/4), sprinkled with brownish black (7.5YR 3/1) to very dark brown (7.5YR 2/3) hairs; cheeks, sides and thighs from light grey (7.5YR 8/2) to light brown-grey (7.5YR 7/2); underparts and feet from light yellow-orange (7.5YR 8/4) to orange (7.5YR 6/8); the few scattered hairs on ears from yellow-orange (7.5YR 7/8) to orange (7.5YR 6/8); the bicoloured basal half of tail from brown (7.5YR 4/6) to dark brown (7.5YR 3/4) above and orange (7.5YR 6/8) to bright brown (7.5YR 5/8) below, and the unicoloured terminal portion from yellow-orange (7.5YR 7/8) to orange (7.5YR 6/8).

7.4 DISCUSSION

The aim of this chapter was to evaluate patterns of intraspecific variation within *A. ineptus* from southern Africa across a broader geographical range than has previously been considered. Regression analyses and multiple-range tests revealed evidence of clinal variation, where overall cranial size was positively and significantly correlated with longitude, leading to a decision not to recognize subspecies within *A. ineptus* in southern Africa.

The decision not to recognize subspecies is based on evidence of a clinal continuum in which multiple-range tests showed no evidence of pronounced steps. These patterns of variation were apparent even at the specimen level. Despite widely divergent views on the subspecies concept, there is consensus against splitting a cline into subspecies (James 1970; Mayr and Ashlock 1991).

Instances of clinal variation have also been recorded in numerous other animal groups in general (summaries in Brennan and Fairbairn 1995) and small mammals in particular (Smithers 1971; Smith 1979; Robinson 1981; Searle 1984; Quin *et al.* 1996). In homeotherms, size clines have often been interpreted in terms of Bergmann's (1847) rule, which predicts positive correlations between overall size and latitude. In *A. ineptus* from southern Africa, however, the relationship involved longitude, while in *A. granti* (Chapter 8) there are indications that this may involve a southwesterly-northeasterly clinal pattern of variation. Other studies suggest that size clines may not be a function of temperature alone, but due to a complex combination of clinally interdependent climatic factors (Sokal and Rinkel 1963; Rising 1970; Gould and Johnston 1972; Elder 1977). In the case of *A. ineptus* and *A. granti*, however, causal analysis of size clines may require further elucidation using Geographic Information Systems (GIS; McLaren and Braun 1993) technology.

It has also been demonstrated that size clines may not be due to adaptation of a few characters, but involve a multidimensional coadaptation of many characters (Sokal and Rinkel 1963; Gould and Johnston 1972). Other studies also suggest that the delineation of clinal variation based on regressions of

single characters can be due to stochastic processes (Brennan and Fairbairn 1995). Despite evidence of clinal variation in single variables in *A. ineptus* from southern Africa, the correlation coefficient was significantly higher when multidimensional principal component scores rather than single characters were examined.

An examination of pelage colouration in *A. ineptus* showed considerable and geographically discordant variation. This was also evident in *A. namaquensis* (Chapter 5) and *A. chrysophilus* (Chapter 6) from southern Africa, and may be interpreted as an adaptive response to local climatic conditions. In Botswana, Smithers (1971) considered specimens of *A. chrysophilus* (*sensu lato*) with pure white or nearly pure white under parts to occur on the fringes of the Kalahari, but refrained from recognizing subspecies. These pelage colour forms were not discernible in the present study.

7.5 CONCLUSIONS

Geographical trends among samples of *A. ineptus* from southern Africa revealed clinal patterns of variation in which overall cranial size was positively and significantly correlated with longitude. Consequently, the seven described subspecies assigned to *A. ineptus* Thomas and Wroughton, 1908, in southern Africa: *A. c. tzaneenensis* Jameson, 1909; *A. c. pretoriae* Roberts, 1913; *A. c. magalakuini* Roberts, 1926; *A. c. capricornis* Roberts, 1926; *A. c. tongensis* Roberts, 1931; *A. c. fouriei* Roberts, 1946; and *A. c. harei* Roberts, 1946, are synonymized.

7.6 TAXONOMY

7.6.1 *Aethomys ineptus* (Thomas and Wroughton, 1908)

Mus chrysophilus ineptus Thomas and Wroughton, 1908: *Proc. Zool. Soc. Lond.*:546.

Mus chrysophilus tzaneenensis Jameson, 1909: *Ann. Mag. Nat. Hist.* (8)4:460.

Mus chrysophilus pretoriae Roberts, 1913: *Ann. Tvl. Mus.* 4:85.

Aethomys chrysophilus magalakuini Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Aethomys chrysophilus capricornis Roberts, 1926: *Ann. Tvl. Mus.* 11:254.

Aethomys chrysophilus tongensis Roberts, 1931: *Ann. Tvl. Mus.* 14:235.

Aethomys chrysophilus fouriei Roberts, 1946: *Ann. Tvl. Mus.* 20:319.

Aethomys chrysophilus harei Roberts, 1946: *Ann. Tvl. Mus.* 20:320.

Figure 7.1 Collecting localities and pooled samples (OTUs) of *Aethomys ineptus* from southern Africa. Abbreviations indicate type localities of *A. ineptus* (ine) and its seven junior synonyms (Chapter 4): tza = *tzaneenensis*, pre = *pretoriae*, mag = *magalakuini*, cap = *capricornis*, ton = *tongensis*, fou = *fouriei*, har = *harei*. Insert shows the distribution of the species in southern Africa as determined in Chapter 4.

Figure 7.2 Distance (**a**) and correlation (**b**) phenograms from UPGMA cluster analyses of pooled samples (OTUs) of *Aethomys ineptus* from southern Africa. Operational taxonomic units correspond to those in Figure 7.1. Cophenetic correlation coefficients = 0.81 and 0.60 respectively.

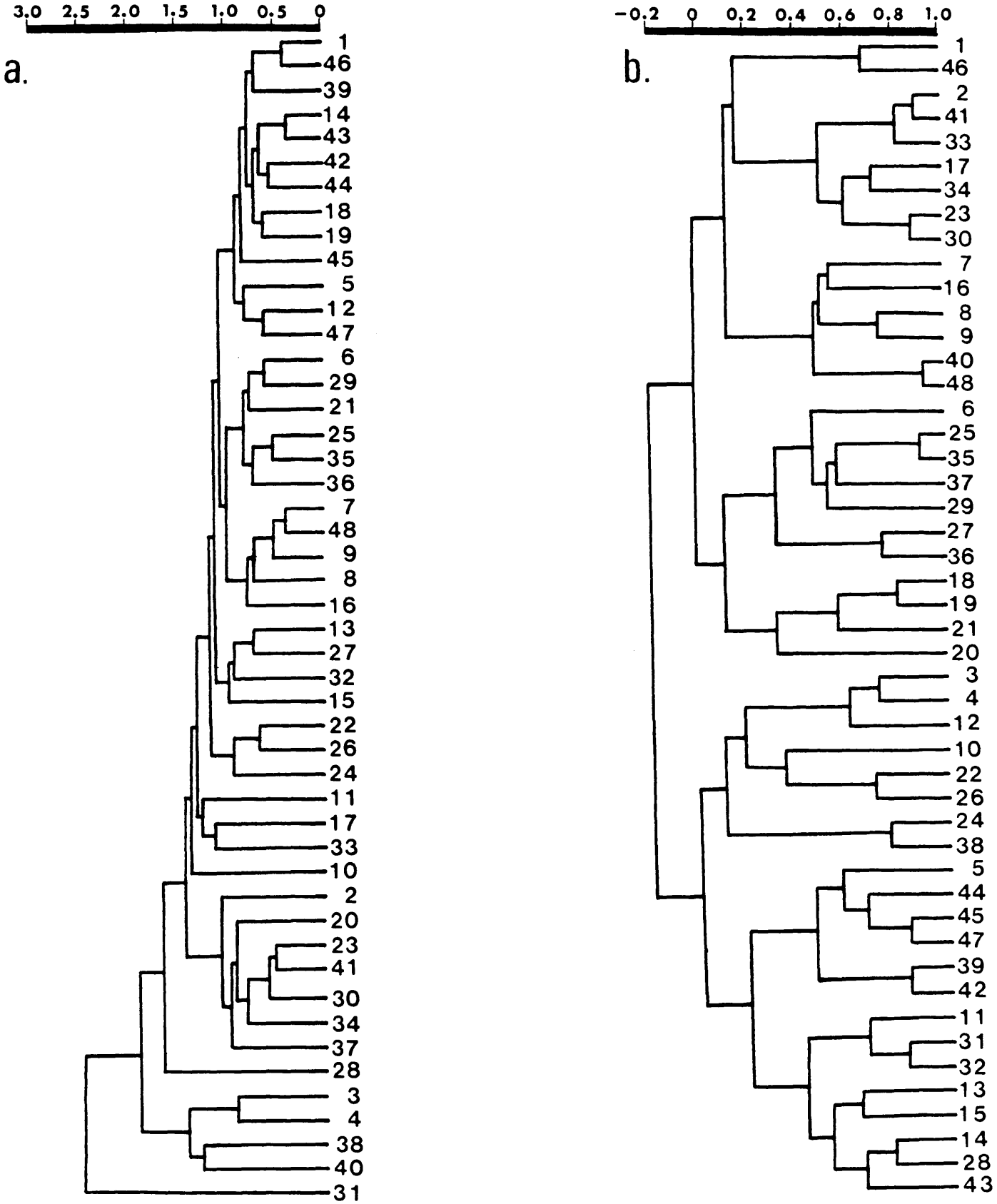


Figure 7.3 Axes I and II from a principal components analysis of pooled samples (OTUs) of *Aethomys ineptus* from southern Africa. Operational taxonomic units correspond to those in Figure 7.1.

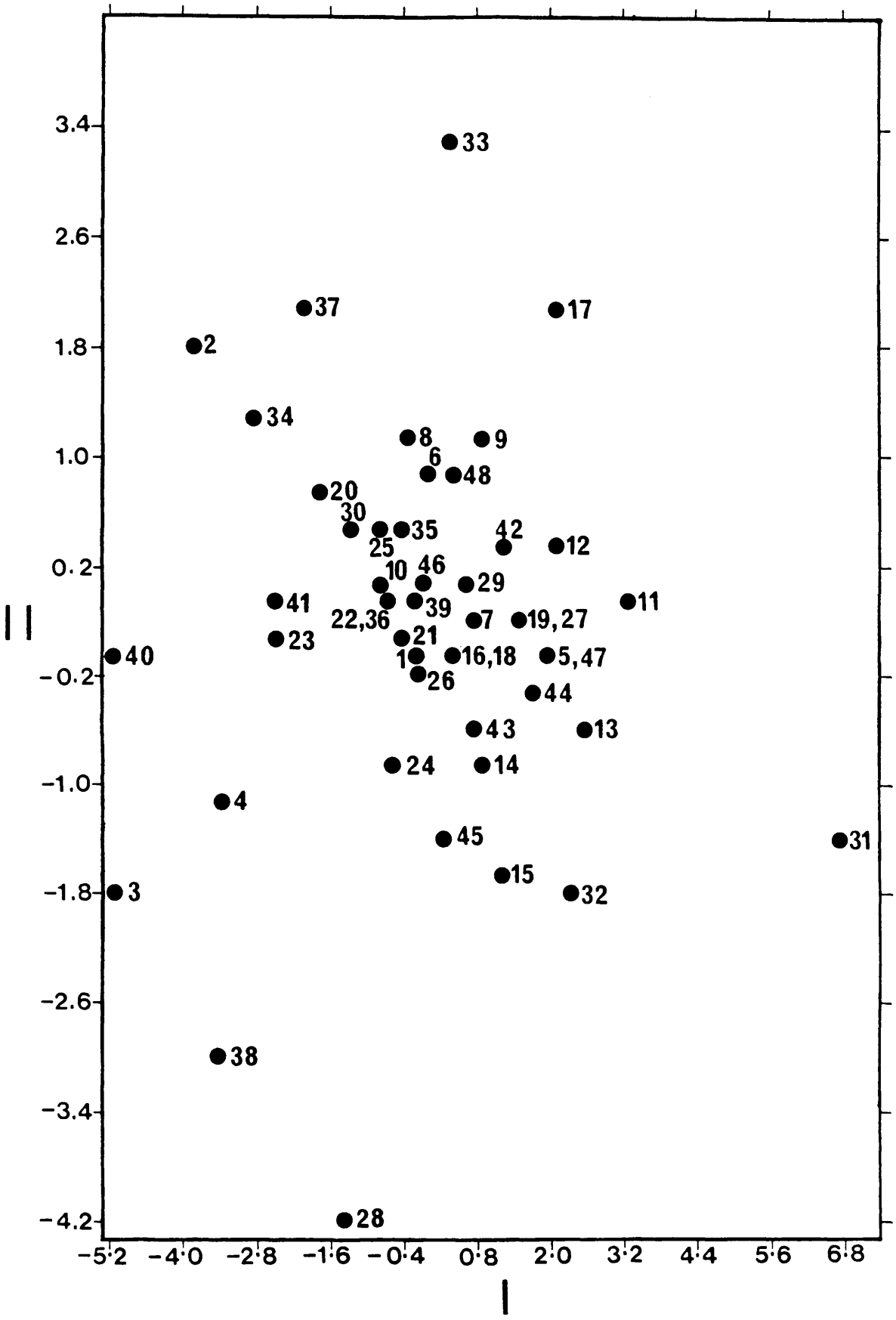


Figure 7.4 Regression analysis of principal component I scores of pooled samples (OTUs) of *Aethomys ineptus* from southern Africa with longitude. Operational taxonomic units correspond to those in Figure 7.1.

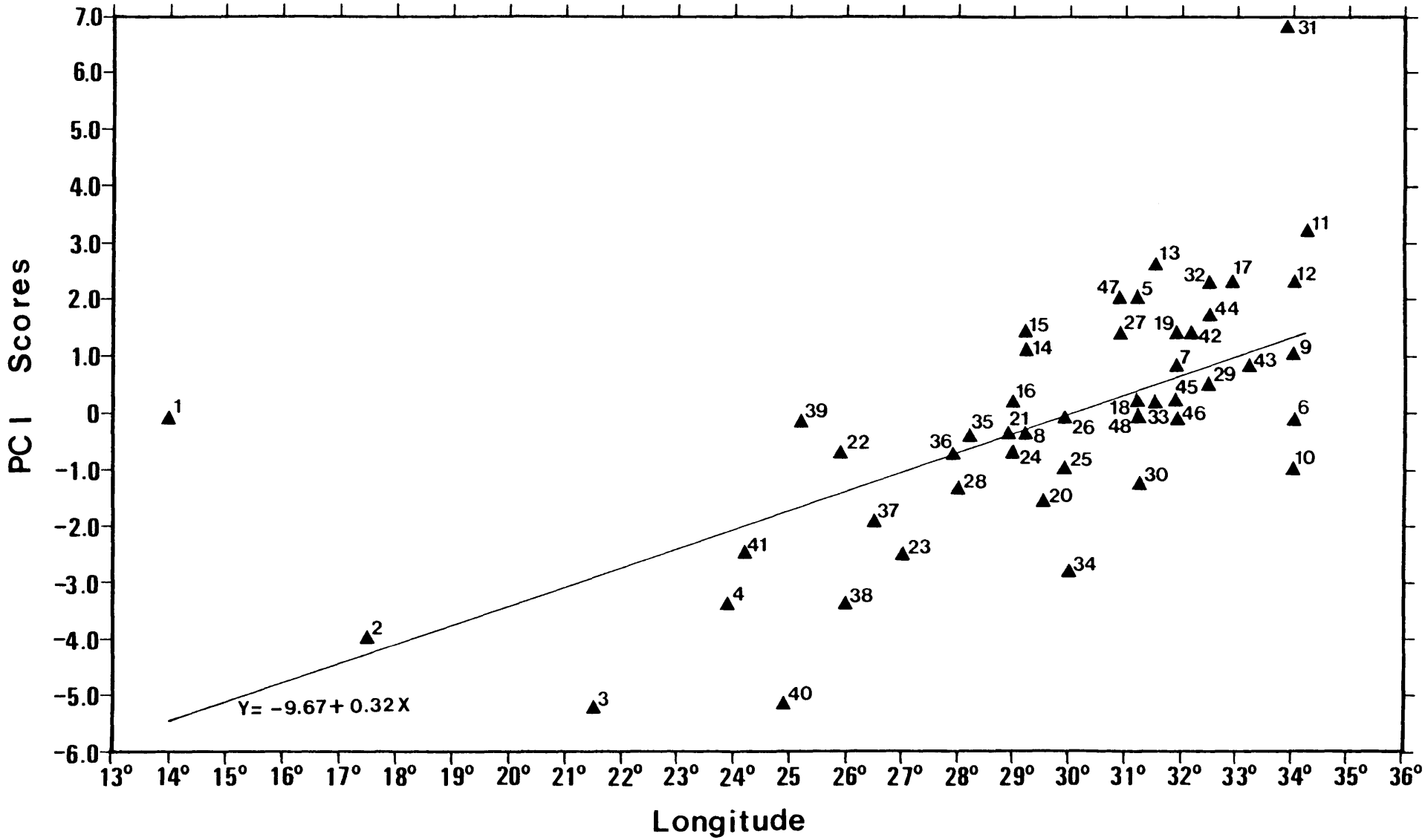


Figure 7.5 Regression analysis of selected cranial measurements of samples (OTUs) of *Aethomys ineptus* from southern Africa with longitude: (**a**) greatest length of skull; (**b**) length of nasals to zygomatic arch; and (**c**) breadth of braincase. Operational taxonomic units correspond to those in Figure 7.1. Abbreviations indicate holotypes of *A. ineptus* (ine) and its seven junior synonyms: tza = *tzaneenensis*, pre = *pretoriae*, mag = *magalakuini*, cap = *capricornis*, ton = *tongensis*, fou = *fouriei*, har = *harei*. Measurements are defined in Figure 2.5.

Figure 7.5 Regression analysis of selected cranial measurements of samples (OTUs) of *Aethomys ineptus* from southern Africa with longitude: (**a**) greatest length of skull; (**b**) length of nasals to zygomatic arch; and (**c**) breadth of braincase. Operational taxonomic units correspond to those in Figure 7.1. Abbreviations indicate holotypes of *A. ineptus* (ine) and its seven junior synonyms: tza = *tzaneenensis*, pre = *pretoriae*, mag = *magalakuini*, cap = *capricornis*, ton = *tongensis*, fou = *fouriei*, har = *harei*. Measurements are defined in Figure 2.5.

Table 7.1 Loadings of variables on components I and II from a principal components analysis for samples of *Aethomys ineptus* from southern Africa. The percent variance contributions appear in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components	
	I	II
Greatest length of skull	-0.400 (86.33)	-0.138 (3.13)
Greatest length of frontals	-0.314 (53.27)	0.060 (0.59)
Length of nasals to zygomatic arch	-0.406 (89.05)	-0.179 (5.24)
Greatest width of bulla	-0.224 (27.16)	0.280 (12.80)
Foramen magnum height	-0.117 (7.43)	0.165 (4.45)
Length of M^1	-0.340 (62.47)	0.088 (1.26)
Width of M^2	-0.069 (2.59)	0.595 (57.83)
Length of angular process to mandibular condyle	-0.352 (66.72)	-0.257 (10.82)
Length of mandibular foramen to condyle	-0.306 (50.57)	-0.179 (5.21)
Length of I_1 to M_3	-0.385 (79.98)	0.006 (0.01)
Width of M_2	-0.160 (13.81)	0.616 (62.11)
% Trace:	Axis I = 48.3%;	Axis II = 13.5%

Table 7.2 Results of whole model regressions of the first and second principal component scores (**a**) and single variables (**b**) for samples of *Aethomys ineptus* from southern Africa. * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; ns = not statistically significant. Measurements are defined in Figure 2.5.

Dependent variable	Correlation coefficients (r)	
	Longitude	Latitude
(**a**)		
Principal component I scores	0.64***	0.01 ns
Principal component II scores	0.10 ns	-0.02 ns
(**b**)		
Greatest length of skull	0.58***	-0.06 ns
Greatest length of frontals	0.56***	0.13 ns
Length of nasals to zygomatic arch	0.58***	0.08 ns
Breadth of braincase	0.58***	-0.24**
Interorbital breadth	0.40**	0.45**
Greatest length of bulla	0.38*	0.36*
Greatest width of bulla	0.35*	0.28 ns
Greatest height of skull	0.19 ns	0.09 ns
Foramen magnum height	0.15 ns	0.03 ns
Length of M^1	0.52***	-0.21*
Width of M^2	-0.01 ns	-0.02 ns
Length of angular process to mandibular condyle	0.51***	0.19 ns
Length of mandibular foramen to condyle	0.43**	0.01 ns
Length of I_1 to M_3	0.51***	-0.20 ns
Width of M_2	0.31*	-0.16 ns

Table 7.3 Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of *Aethomys ineptus* from southern Africa. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. Operational taxonomic units correspond to those in Figure 7.1. Measurements are defined in Figure 2.5.

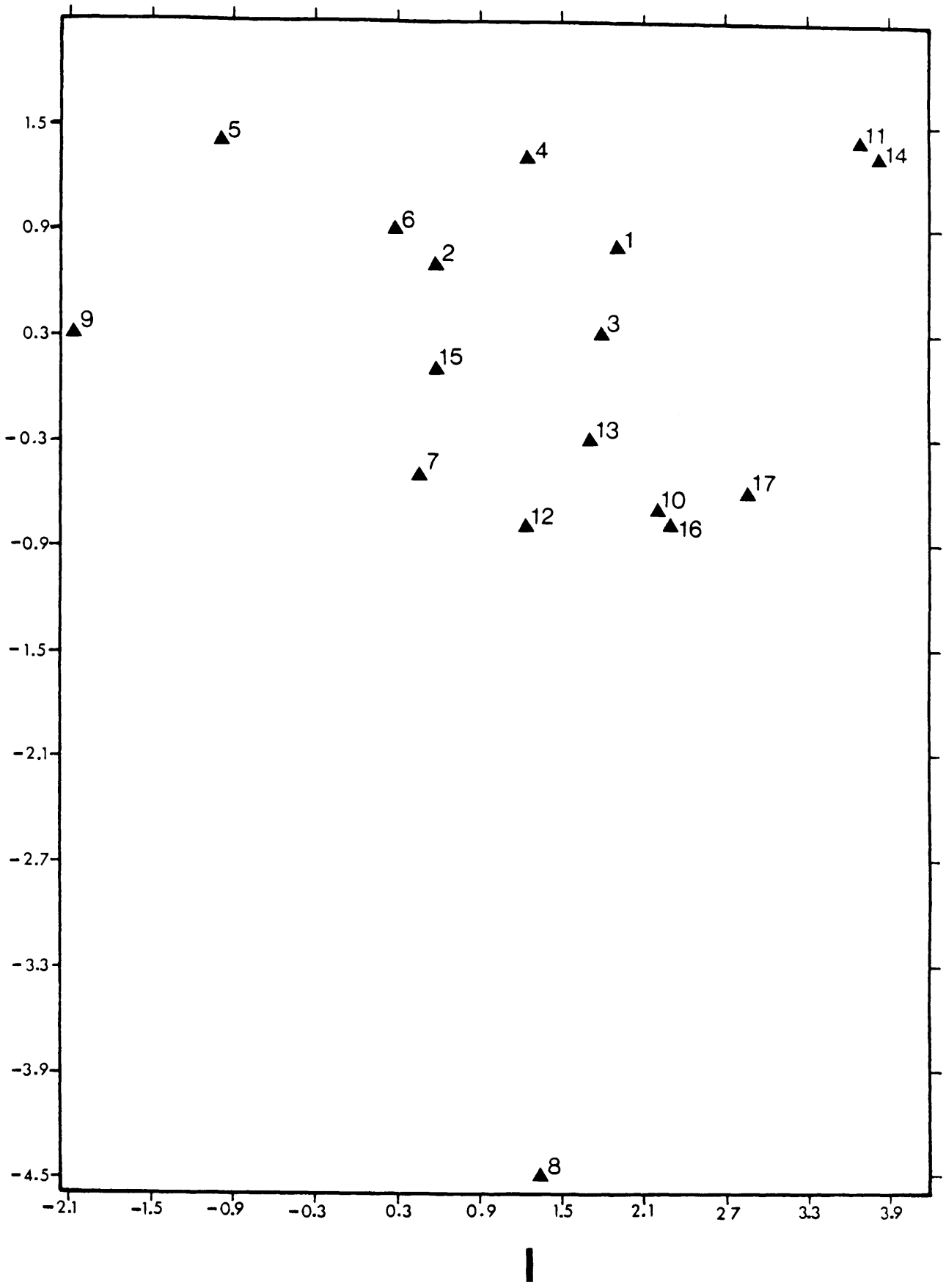


Figure 8.4 Regression analyses of: (**a**) breadth of braincase; (**b**) greatest width of bulla; and (**c**) length of angular process to mandibular condyle with longitude for *Aethomys granti* based on samples from 17 localities (OTUs). Operational taxonomic units correspond to those in Figure 8.1. Measurements are defined in Figure 2.5.

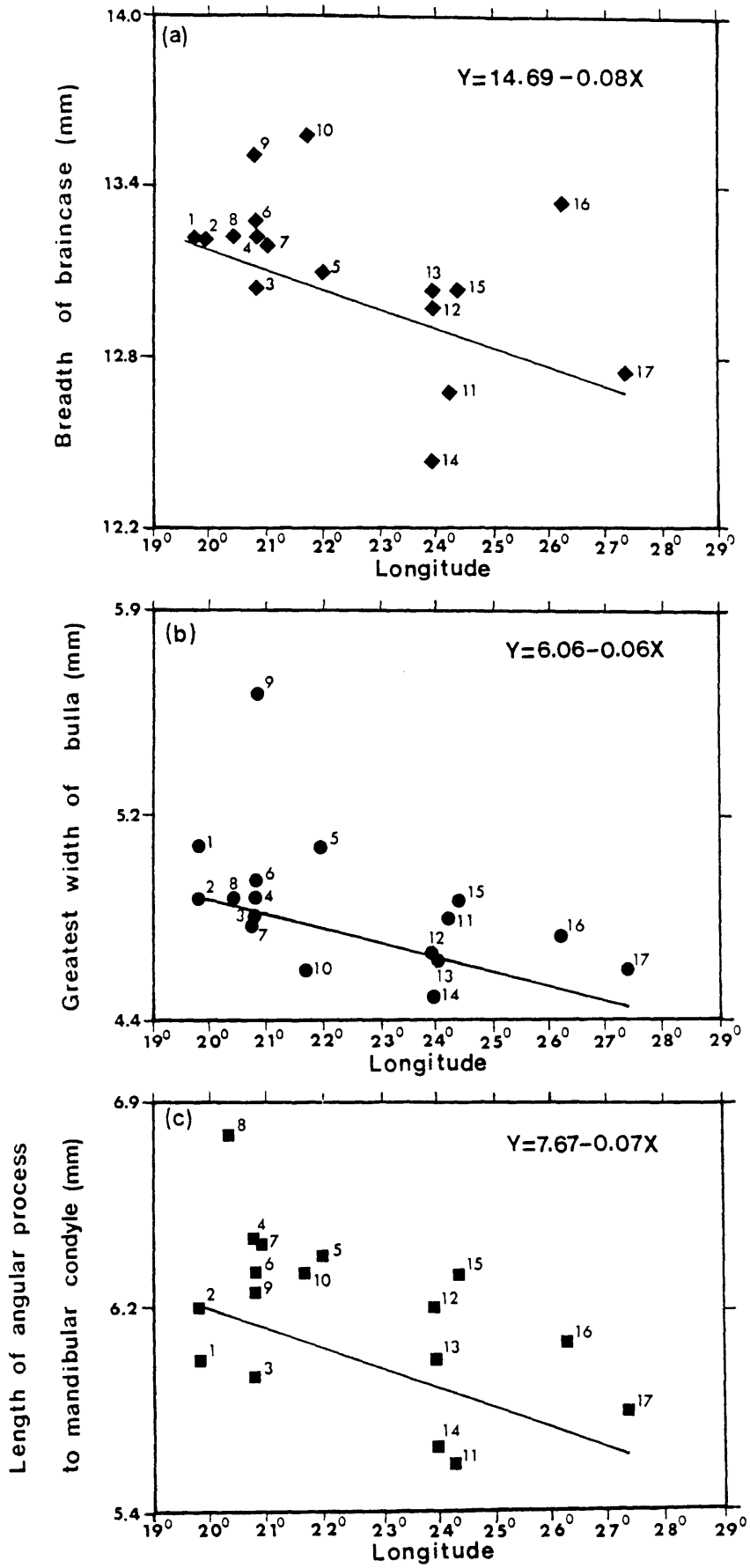


Figure 8.5 Regression analyses of: (**a**) breadth of braincase; (**b**) length of angular process to mandibular condyle; (**c**) length of mandibular foramen to condyle with latitude for *Aethomys granti* based on samples from 17 localities (OTUs). Operational taxonomic units correspond to those in Figure 8.1. Measurements are defined in Figure 2.5.

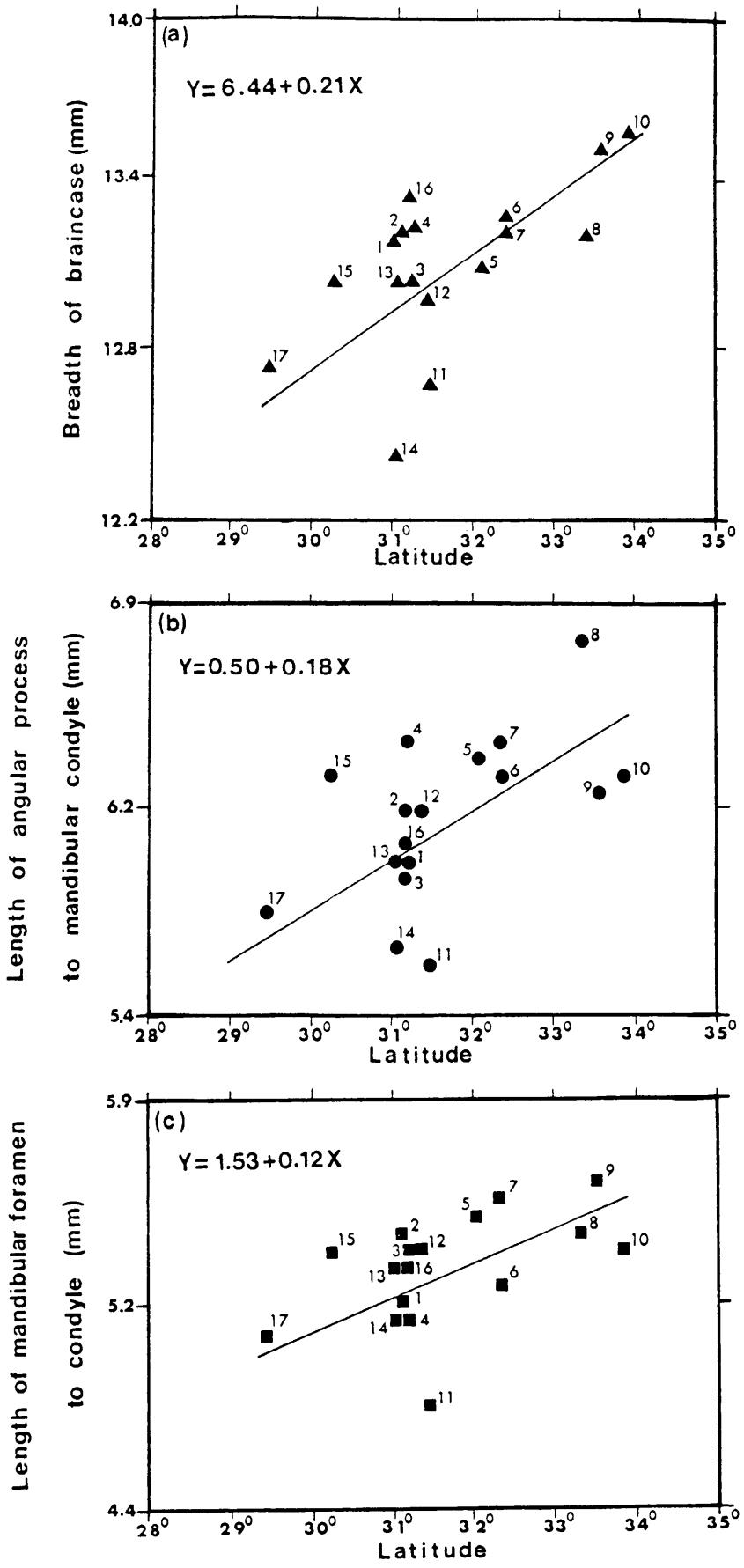


Table 8.1 Loadings of variables on components I and II from a principal components analysis of *Aethomys granti* based on (**a**) 17 localities as OTUs and (**b**) 86 specimens. The percent variance contributions appear in brackets. Measurements are defined in Figure 2.5.

Variable	Principal components	
	I	II
(**a**)		
Greatest length of skull	-0.955 (91.25)	0.062 (0.39)
Greatest length of frontals	-0.676 (45.70)	0.481 (23.17)
Length of nasals to zygomatic arch	-0.956 (91.47)	-0.009 (0.01)
Greatest width of bulla	-0.820 (67.28)	0.096 (0.92)
Foramen magnum height	-0.207 (4.27)	-0.442 (19.54)
Length of M^1	-0.861 (74.21)	-0.011 (0.01)
Width of M^2	0.040 (0.16)	0.882 (77.85)
Length of angular process to mandibular condyle	-0.622 (38.67)	-0.518 (26.84)
Length of mandibular foramen to condyle	-0.794 (63.07)	-0.352 (12.38)
Length of I_1 to M_3	-0.850 (72.29)	0.017 (0.03)
Width of M_2	-0.325 (10.58)	0.825 (67.99)
% Trace:	Axis I = 50.8%;	Axis II = 20.8%
(**b**)		
Greatest length of skull	0.918 (84.27)	-0.036 (0.13)
Greatest length of frontals	0.313 (9.77)	0.309 (9.54)
Length of nasals to zygomatic arch	0.896 (80.31)	-0.060 (0.36)
Greatest width of bulla	0.760 (57.75)	0.129 (1.67)
Foramen magnum height	-0.103 (1.07)	-0.276 (7.63)
Length of M^1	0.681 (46.44)	-0.145 (2.10)
Width of M^2	-0.087 (0.76)	0.845 (71.36)
Length of angular process to mandibular condyle	0.673 (45.23)	-0.248 (6.14)
Length of mandibular foramen to condyle	0.579 (33.48)	-0.006 (0.01)
Length of I_1 to M_3	0.775 (60.06)	0.094 (0.89)
Width of M_2	0.174 (3.03)	0.758 (57.46)
% Trace:	Axis I = 38.4%;	Axis II = 14.3%

Table 8.2 Results of whole model regressions of (**a**) the first and second principal component scores and (**b**) single variables for *Aethomys granti* based on samples from 17 localities (OTUs). * = $P < 0.05$; ** = $P < 0.01$; ns = not statistically significant. Measurements are defined in Figure 2.5.

Dependent variable	Correlation coefficients (r)	
	Longitude	Latitude
(**a**)		
Principal component I scores	0.47 ns	-0.42 ns
Principal component II scores	-0.02 ns	-0.33 ns
(**b**)		
Greatest length of skull	-0.39 ns	0.30 ns
Greatest length of frontals	-0.33 ns	0.26 ns
Length of nasals to zygomatic arch	-0.46 ns	0.41 ns
Breadth of braincase	-0.51*	0.64**
Interorbital breadth	-0.11 ns	0.16 ns
Greatest length of bulla	-0.35 ns	0.46 ns
Greatest width of bulla	-0.49*	0.40 ns
Greatest height of skull	-0.40 ns	0.38 ns
Foramen magnum height	0.08 ns	0.20 ns
Length of M^1	-0.33 ns	0.35 ns
Width of M^2	0.05 ns	-0.22 ns
Length of angular process to mandibular condyle	-0.51*	0.55*
Length of mandibular foramen to condyle	-0.44 ns	0.51*
Length of I_1 to M_3	-0.24 ns	0.19 ns
Width of M_2	-0.28 ns	-0.23 ns

Table 8.3 Results of sum of squares simultaneous test procedure (SS-STP) of selected cranial measurements of *Aethomys granti* based on five OTUs with $n \geq 4$. Non-significant subsets ($P > 0.05$) are indicated by vertical lines to the right of each array of means. Operational taxonomic units correspond to those in Figure 8.1. Measurements are defined in Figure 2.5.

a)

GREATEST LENGTH OF BULLA (BUL)

$F = 3.71$; $P < 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
6	19	0.23	6.54	
2	6	0.17	6.37	
3	22	0.24	6.36	
12	5	0.17	6.20	
15	4	0.10	6.15	

b)

GREATEST WIDTH OF BULLA (BLW)

$F = 5.19$; $P < 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
6	19	0.20	4.95	
2	6	0.18	4.81	
3	22	0.15	4.74	
15	4	0.07	4.71	
12	5	0.17	4.62	

c)

BREADTH OF BRAINCASE (BBC)

$F = 1.21$; $P > 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
2	6	0.23	13.19	
3	22	0.31	12.98	
6	19	0.32	12.98	
12	5	0.33	12.92	
15	4	0.13	12.91	

d)

GREATEST HEIGHT OF SKULL (GHS)

$F = 3.63$; $P < 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
6	19	0.28	9.79	
12	5	0.30	9.68	
2	6	0.21	9.64	
3	22	0.20	9.53	
15	4	0.11	9.45	

e)

FORAMEN MAGNUM HEIGHT (FMH)

$F = 3.11$; $P < 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
15	4	0.10	4.68	
12	5	0.18	4.55	
3	22	0.22	4.52	
2	6	0.22	4.48	
6	19	0.17	4.37	

f)

GREATEST LENGTH OF SKULL (GLS)

$F = 7.60$; $P < 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
6	19	0.65	30.79	
2	6	0.62	30.58	
15	4	0.13	30.31	
12	5	0.45	30.19	
3	22	0.67	29.60	

g)

LENGTH OF NASALS TO ZYGOMATIC ARCH (NPP)

$F = 16.25$; $P < 0.05$

Locality code	Sample size (n)	Standard deviation (SD)	Arithmetic mean (Y)	Non-significant subsets
6	19	0.48	21.82	
2	6	0.60	21.20	
12	5	0.70	21.16	
15	4	0.33	20.62	
3	22	0.46	20.27	

CHAPTER 9

PHYLOGENETIC RELATIONSHIPS IN THE GENUS *AETHOMYS*

9.1 INTRODUCTION

Phylogenetic relationships between *Aethomys* and other African murines are uncertain (Musser and Carleton 1993). Ellerman (1941) considered characteristics of the genus to overlap to some extent with *Rattus* and *Arvicanthis*. The genus has also been considered to be closely related to *Mus* (De Winton 1897), *Rattus* (Thomas and Wroughton 1908), *Praomys* (= *Mastomys*), *Thallomys*, *Zelotomys* (Roberts 1926, 1946, 1951; Misonne 1969; De Graaff 1981), *Stochomys*, *Dephomys*, *Dasymys* and *Pelomys* (Davis 1965; 1968; 1975; Misonne 1969; Bonhomme *et al*. 1985; Denys 1990*a*; 1990*b*).

Little is also known about evolutionary relationships among the 11 currently recognized species of *Aethomys*, namely *A. bocagei*, *A. chrysophilus*, *A. granti*, *A. hindei*, *A. ineptus*, *A. kaiseri*, *A. namaquensis*, *A. nyikae*, *A. silindensis*, *A. stannarius* and *A. thomasi* (Musser and Carleton 1993; Chapter 4). No evolutionary study has considered all currently recognized species in the genus simultaneously. Previous studies have largely been limited to biogeographically restricted comparisons involving a few species. Musser and Carleton (1993), for example, considered the Angolan *A. bocagei* and *A. thomasi* to be closely related to *A. silindensis* and *A. kaiseri*, respectively. The two cryptic species, *A. chrysophilus* and the newly recognized *A. ineptus* (Chapter 4) may also be considered to be phylogenetically

closely related.

Other relationships can be postulated from previous taxonomic treatments of some members of the genus. For example, the currently recognized *A. nyikae* and *A. hindei* have variably been considered to be closely related to *A. kaiseri*; the former as a synonym of *A. kaiseri* (Delany 1975; Davis 1975; Ansell 1978), and the latter as a subspecies of *A. kaiseri* (Hollister 1919; Swynnerton and Hayman 1951). The currently recognized West African endemic, *A. stannarius*, has similarly been treated as a subspecies of *A. hindei* (Ellerman 1941; Rosevear 1969; Davis 1975; Hutterer and Joger 1982), suggesting a close relationship between all of these taxa.

Davis (1975), in contrast, attempted an inclusive interpretation of species' relationships within the genus. He supported the widely held view of a close affinity between *A. namaquensis* and *A. granti*, and their inclusion in the subgenus *Micaelamys* (Ellerman *et al.* 1953). Following traditional treatments of the genus, he allocated the remaining species to the nominate subgenus *Aethomys*, but subdivided it further into "*kaiseri*" and "*hindei*" groups. The former included *A. kaiseri*, while the latter included *A. hindei*, *A. bocagei*, *A. chrysophilus* (*sensu lato*), *A. nyikae*, *A. silindensis*, and *A. thomasi*. This treatment, however, excluded *A. stannarius* that was then considered a subspecies of *A. hindei* (Ellerman 1941; Rosevear 1969; Davis 1975; Hutterer and Joger 1982), and obviously *A. ineptus* (Chapter 4).

Fossils representing *A. namaquensis* and *A. chrysophilus* (*sensu lato*) have been reported from South Africa (De Graaff 1960, 1961; Avery 1981, 1982, 1995; Hendey 1981; Pocock 1987; C.

Denys *pers. comm.*[1]; J.F. Thackeray *pers. comm.*[2]). Recently, two sympatric Pliocene fossil species, the oldest known representatives of the genus in Africa, have been described from Langebaanweg, Western Cape Province, South Africa: a small-sized *A. modernis* and a large-sized *A. adamanticola* (Denys 1990*a*, 1990*b*).

Aethomys modernis is very similar to extant southern African *Aethomys*, particularly *A. chrysophilus* (*sensu lato*) (Denys 1990*a*, 1990*b*). *Aethomys adamanticola* is different from any other known *Aethomys*, but shows characteristics reminiscent of *A. namaquensis* and *A. hindei* that have been interpreted as plesiomorphic for the genus. Denys (1990*a*, 1990*b*) also suggested that this species may represent an advanced stage of an early Miocene lineage that is closely related, but not ancestral to *Dasymys*.

Other palaeontological records include two East African Plio-Pleistocene fossil species, *A. lavocati* (Jaeger 1976, 1979) from Lake Natron and *A. deheinzelini* (Wesselman 1984) from Lake Turkana (Black and Krishtalka 1986; Denys 1987). There is no indication of a close relationship between these fossil species and those from South Africa to allow speculation on the origin and time of divergence of the genus (Denys 1990*a*, 1990*b*).

Most phylogenetic inferences outlined above were not tested rigorously, were often based on different data sets, or not subjected to cladistic analyses. Previous classifications of the genus have, similarly, never been critically examined with

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reference to current principles of classification. The present investigation represents the first attempt to develop a hypothesis of phylogenetic relationships in the genus, and to derive a classification of currently recognized species also with reference to palaeontological data.

To this end, cladistic analyses of integrated qualitative cranial, mandibular and dental traits are used to: a) elucidate phylogenetic relationships within the genus using all recognized species; b) derive a classification; c) assess supraspecific taxonomic implications, particularly with regard to the subgenera *Micaelamys* and *Aethomys* in southern Africa; and d) to develop a biogeographical hypothesis in an attempt to explain the group's evolutionary relationships.

9.2 MATERIAL AND METHODS

9.2.1 Ingroup Taxa

While specific and infraspecific systematic problems in southern African *Aethomys* have been considered in Chapters 4 - 8, the status of some extant extralimital taxa is still uncertain. There is, for example, considerable variation in morphological traits among geographical samples in *A. hindei* and *A. kaiseri* (Carleton and Musser 1993). This variation suggests that these taxa may represent a complex of species (Denys and Tranier 1992; Denys 1995; C. Denys *pers. comm.*[1]).

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Similarly, the nature and extent of morphological variation in *A. chrysophilus* and *A. namaquensis* outside southern Africa is largely unknown (Ansell and Dowsett 1988; Musser and Carleton 1993). Moreover, *A. ineptus* (which has a wide geographical distribution similar to *A. chrysophilus* in southern Africa; Chapter 4) probably extends beyond southern Africa. Its status and pattern of intraspecific variation outside the southern African subregion have yet to be investigated.

In an attempt to develop a phylogenetic hypothesis for the genus, the 11 currently recognized species were provisionally accepted and analysed as members of the ingroup. Nevertheless, it was not assumed that any of the currently recognized extant extralimital taxa (Musser and Carleton 1993) are valid. Attempts were made to confirm the integrity of the extralimital taxa by coding characters using type specimens as references. Holotypes of southern African species were also included to accommodate species that may also occur to the north of the Zambezi and Kunene Rivers, and for a broader systematic perspective. Ten of the 11 holotypes of the currently recognized species were examined (Appendix IV). The holotype of *A. kaiseri* was not available for examination; instead the type of *A. k. verneyi* (Ellerman 1941) was used as a reference for this species.

While relationships incorporating fossil taxa are considered unstable (Gingerich 1980; Cracraft 1981; Patterson 1981; Huelsenbeck 1991), others regard it as important in elucidating phylogenetic relationships (Gauthier *et al.* 1988). In this investigation, however, a large number of missing characters precluded the incorporation of fossil taxa.

Processes other than phylogeny, such as developmental and

ecological constraints, may influence the distribution of character-states in organisms (Seutin *et al.* 1995). Consequently, attempts were made to minimize the possible impact of intra-OTU morphological variation in character-state assignments by: 1) coding morphological traits from adult specimens, irrespective of sex (Chapter 3; Chimimba and Dippenaar 1994); and 2) examining character-state distribution from a minimum of 20 specimens drawn from geographically and ecologically disparate localities. Exceptions to the minimum sample size requirement included *A. bocagei* (n = 5), *A. nyikae* (9), *A. silindensis* (6), and *A. stannarius* (9) (Appendices IV and V).

There were clear indications of the integrity of ingroup taxa considered above. Similarly, there were no discernible intraspecific differences in character-states among specimens, regardless of their origin. The 11 species, rather than local populations, were therefore treated as OTUs in all analyses.

9.2.2 Outgroup Taxa

Since phylogenetic analysis using a single outgroup may not always give the most parsimonious solution (Maddison *et al.* 1984), the present study used more than one outgroup. The selection of possible outgroups for *Aethomys* was difficult, however, because of its previous systematic links to numerous taxa (Section 9.1). Outgroup choice was particularly constrained by the need to sample informative combinations of apomorphic and plesiomorphic character-states with minimum ambiguity (see Section 9.2.4 below). It has been demonstrated that character polarity decisions are more robust the closer and more

comprehensive the outgroups are to the ingroup (Maddison *et al.* 1984). Consequently, outgroups that show some relationships among themselves, and also to the target lineage, were sought.

Representatives of all possible outgroups (except *Stochomys* and *Dephomys*; Section 9.1) were available for examination. Preliminary screening of character-state distribution among all possible outgroups, relative to ingroup taxa, showed numerous instances of character polarities except for *Dasymys incomtus* and *Rattus rattus*. Consequently, these two species were considered as outgroups in the elucidation of phylogenetic relationships in the genus *Aethomys*. Their suitability as potential outgroups is supported by molecular data (Verheyen *et al.* 1995) and morphological traits based on both extant material (Ellerman 1941) and palaeontological data (Denys 1990*a*, 1990*b*).

9.2.3 Definition of Characters

The elucidation of phylogenetic relationships is dependent on hypotheses of homology. Apart from a few dental characteristics (e.g. Denys 1990*a*, 1990*b*; Denys and Tranier 1992), neither explicit nor *a priori* proposals of homology have been investigated for *Aethomys*. Following Mayr and Ashlock (1991), homologous characters were defined as features in two or more taxa that could be postulated to be derived from the same (or equivalent) features of their nearest common ancestor. Given the 11 provisionally accepted species of *Aethomys* and the two outgroups, homologous characters were hypothesized from the comparability (i.e. similarity by positional correspondence) of morphological traits (transformational homology; Rieppel 1980;

Patterson 1982; Smith 1990). This step was considered necessary to establish that each character was truly homologous with the other characters with which it was compared (Bock 1981).

Characters were selected from cranial, dental and mandibular morphology. These included previously used characters, particularly from original descriptions and additional characters identified in Chapter 4. Some dental cusp patterns reported by Denys (1990*a*, 1990*b*) and Denys and Tranier (1992) from extant and fossil taxa were also incorporated. While other potentially useful data on karyology, protein electrophoresis, sperm and bacular morphology, and their staining properties and cuticular hair morphology are available from the literature (Chapter 4; and references therein), these are limited to a few taxa. Since their incorporation would have resulted in a large number of missing characters, they were not considered for analysis.

Twenty-two encodable discrete and meristic characters presumed to be free from the influence of size were identified (Appendix VII). Character-states were either assigned values ranging from 0 to 4, or coded as present or absent. Since there were no *a priori* reasons to assume intermediacy or evolutionary directionality, all characters were treated as unordered transformation series.

The derived data matrix of character-state values coded for each ingroup and outgroup taxon is given in Appendix VIII. In some taxa, the number of roots on M^1 (character 12; Appendix VII) could not be determined without causing damage to the specimen. This character-state was denoted by a "9" (Appendix VIII) and treated as either "inapplicable" or "missing" in subsequent analyses.

9.2.4 Character Analysis

Outgroup comparison (Waltrous and Wheeler 1981; Maddison *et al.* 1984) was used to designate apomorphic and plesiomorphic character-states (taxic homology; Rieppel 1980; Patterson 1982; Smith 1990). A character with two or more states within the ingroup, the state occurring in the outgroups was assumed to be the plesiomorphic state (Maddison *et al.* 1984; Wiley *et al.* 1991). This approach was considered necessary to document patterns of outgroup variation to reach an unambiguous conclusion of plesiomorphy (Maddison *et al.* 1984). In so doing, plesiomorphy was decisively designated in 18 characters (characters 1-3, 6-9, 11-12, 14-22; Appendices VII and VIII) since they did not vary between *D. incomtus* and *R. rattus*. Character polarity decisions of these characters are summarized in Appendix VII, where character-states presumed to be plesiomorphic are denoted by a "P". All other character-states among the 18 characters were presumed to fall within an unordered transformation series of apomorphic characters.

The remaining four of the 22 characters (development of interorbital constriction - character 4; zygomatic arch development - 5; lower molar cusp development - 10; the extent of cusp development on M^3 - 13) varied among the outgroups, leading to equivocal polarity decisions. Since unpolarized characters are considered valuable data with no basis for their exclusion (J. McGuire *in litt.*[1]), phylogenetic analyses were based on all 22 characters.

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9.2.5 Analytical Procedure

9.2.5.1 Phylogenetic Reconstruction Using Parsimony

The equally most-parsimonious tree(s) were initially sought through heuristic or exhaustive search algorithms using "MULPARS" and "SWAP = GLOBAL" options in PAUP (Swofford 1993) in combination with MacClade (Maddison and Maddison 1992), and "xsteps" commands in Hennig86 (Farris 1988; Fitzhugh 1989). These analyses were followed by searches for exact solutions using "branch-and-bound" and the "ie*" exhaustive search algorithms in PAUP in combination with MacClade and Hennig86, respectively.

In cases of multiple, equally parsimonious trees, the conservative strict consensus trees (Page 1989; Barrett *et al.* 1991) were constructed using the "CONTREE" option in PAUP and the "NELSEN" command in Hennig86.

9.2.5.2 Character Weighting

There were no *a priori* hypotheses of phylogenetic transformation. All characters were therefore weighted equally in the reconstruction of phylogeny.

9.2.5.3 Measures of Homoplasy

Levels of homoplasy for individual traits and all characters combined, expressed as deviations of the cladogram from a perfect fit to the data (Klassen *et al.* 1991) were assessed using the consistency index (CI; Kluge and Farris 1969) and, for

comparison, the retention index (RI; Farris 1989). The values of these indices were compared to values that would be expected from random data (Klassen *et al.* 1991). Some analyses were performed excluding uninformative characters. To correct for possible inadequacies of the CI, additional analyses were based on a rescaled CI (Archie 1989; Meier *et al.* 1991) and on an expected CI when compared to 60 data sets (Sanderson and Donoghue 1989), measures less prone to the influence of the number of taxa or characters.

9.2.5.4 Assessment of Phylogenetic Structure

The distinction between random noise and phylogenetic structure in the data set was evaluated by calculating the skewness (g_1 statistic) of tree-length distribution for 1000 randomly generated trees (Hillis and Huelsenbeck 1992) using the "randtrees" option in PAUP. A strongly left-skewed distribution is indicative of phylogenetic signal (Hillis and Huelsenbeck 1992). To test for the significance of the phylogenetic signal in the data set, the g_1 statistic was compared to tables of critical probability values for tree-length distribution in Hillis and Huelsenbeck (1992).

9.2.5.5 Assessment of Confidence Limits in Internal Branches

The reliability of individual nodes on the most-parsimonious tree(s) was estimated by bootstrap resampling (i.e. with replacement) (Felsenstein 1985; Hillis and Bull 1993) with 200 iterations using the "BOOTSTRAP" option in PAUP. Bootstrap

proportions of ≥ 70% usually correspond to a probability of ≥ 95% that the corresponding clade is meaningful (Hillis and Bull 1993).

9.2.5.6 Character Analysis

Character-state assignments at internal basal nodes were obtained via the "describe trees: possible state assignments" command in PAUP. Ambiguity in character-state assignment was evaluated by extracting the most-parsimonious hypotheses of character evolution using two character-optimization procedures: delayed transformation (DELTRAN; Swofford and Maddison 1987) and accelerated transformation (ACCTRAN; Farris 1970). In DELTRAN, transformations are delayed so that parallelisms are preferred over reversals, while ACCTRAN does the opposite (Swofford and Maddison 1987; Wiley *et al.* 1991). The utilization of two character-optimization procedures assisted in avoiding making errors in incorrectly assuming that a character-state unambiguously supports a node.

9.2.5.7 Conversion of Inferred Phylogeny into a Classification

The inferred phylogeny was converted into a Linnaean hierarchy based on principles of cladistic and evolutionary classifications. In the cladistic classification, ranking was based on two basic criteria (Wiley *et al.* 1991). The first was to consistently place sister groups in the classification at the same rank or equivalent rank. The second was to reflect the branching sequence exactly but not requiring that every

monophyletic group be ranked.

In the evolutionary classification, ranking was based on the combination of the inferred phylogeny and the degree of phenetic difference (Mayr and Ashlock 1991). This was achieved by the identification of phylogenetic gaps evident from the amount of total change in weighted character-states. While there was no *a priori* basis for weighting character-states in the reconstruction of phylogeny, it was considered imperative in this case because of the need to reflect their taxonomic importance (Mayr and Ashlock 1991).

Following the evolutionary classification procedures of Brothers (1975), Mayr and Ashlock (1991) and D. J. Brothers (*pers. comm.*[1]), the total distribution of character-states on the completed cladogram was used to assess character weighting based on specified principles. Parallel character-states that appear more than once on the cladogram were each given a value equal to the reciprocal of the number of times it appears on the cladogram. Reversals, or derived character-states, that resemble primitive character-states (at the outgroup node) were treated similarly. Unique character-states that appeared nowhere else on the cladogram were given unit weight. Cases with no inferred character changes were given zero weight. The individual character-state values were subsequently summed to provide an anagenetic gap value (AGV) for each internode.

The more taxa that have a given derived character-state, the greater the survival potential that character-state may be

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[1] D. J. Brothers, Department of Zoology and Entomology, University of Natal, Pietermaritzburg, South Africa.

presumed to have, and thus the more weight that character-state should be given. Each internode on a cladogram extends into a number of taxa, and these numbers were used to allocate a subtended taxa value (STV) for each internode. However, the use of absolute number of taxa per internode has been shown to place unnecessary weight on STV (Mayr and Ashlock 1991). In studies that involve small to a moderate number of taxa, the square root of the absolute number of taxa per internode is recommended (Mayr and Ashlock 1991). The new values give an adjusted subtended taxa value (ASTV).

The AGVs were multiplied by ASTVs to obtain a taxonomic gap value (TGV). To assess the amount of total change on the cladogram, TGVs were expressed as a percentage of their sum. Following Mayr and Ashlock (1991), a phylogram was constructed by calculating the ratio between the first and last taxon, and the sum of % TGV values for the outside internodes of the phylogram. Each % TGV was multiplied by the ratio between the first and last taxon to provide the phylogram's proportional length values (Mayr and Ashlock 1991).

A phenetic classification (Sneath and Sokal 1973) was not considered in the present investigation because of its reliance on overall similarity, without regard for phylogeny (Wiley 1981). Phenetic information was, however, incorporated in the resulting classification. Similarly, the recently suggested phylogenetic taxonomy (de Queiroz and Gauthier 1990, 1992, 1994; Cannatella and Hillis 1993; Bryant 1996; Wyss and Meng 1996), which makes the controversial suggestion of abandoning the entire Linnaean classification system, was not considered. While there may be merit in the new approach, the present investigation nevertheless

adhered to the typological Linnaean hierarchical system for comparison with the majority of previous studies.

9.3 RESULTS

9.3.1 Phylogenetic Relationships

Both heuristic search and branch-and-bound parsimony analyses of 22 characters using PAUP generated a single tree, 40 steps in length, with consistency (CI) and retention (RI) indices of 0.73 (Figure 9.1). The CI was 0.69 if uninformative characters were excluded, and 0.53 if rescaling was invoked. All CIs were greater than or approximated that expected for an analysis of 13 taxa (expected CI = 0.58; Sanderson and Donoghue 1989), indicating that there is less homoplasy in this data set than expected when compared with the 60 data sets re-examined by Sanderson and Donoghue (1989).

The 11 currently recognized species of *Aethomys* separated into three clades that included: 1) *A. bocagei*, *A. thomasi*, *A. silindensis*, *A. kaiseri* and *A. nyikae*; 2) *A. chrysophilus*, *A. ineptus* and *A. hindei*; and 3) *A. granti*, *A. namaquensis* and *A. stannarius*. An independent corroboration of the tree topology generally showed that the first clade included broad-faced skull forms, the second represented intermediately broad-faced skull forms, while the third corresponded with slender-faced skull forms.

Within the first clade, the Angolan *A. bocagei* and *A. thomasi* are shown to be sister species, both of which are sister species of *A. silindensis*. The two cryptic species, *A.*

chrysophilus and *A. ineptus*, appear as sister taxa in the second clade, closely related to *A. hindei*. In the third clade, *A. namaquensis* and *A. granti* are shown as sister species, closely related to the geographically restricted West African endemic *A. stannarius*.

Both exhaustive and branch-and-bound searches of the 22 characters using Hennig86 produced four equally parsimonious trees of 42 steps in length, and a CI and RI of 0.71 and 0.73, respectively. A strict consensus tree of the four alternative trees is illustrated in Figure 9.2. The cladogram is topologically identical to that generated by PAUP (Figure 9.1), except that *A. kaiseri* and *A. nyikae* are shown as sister species. Reanalysis of the cladogram produced by PAUP using MacClade produced a similar tree of 40 steps in length. A similar treatment of the consensus cladogram produced by Hennig86, on the other hand, produced a tree of 41 steps in length indicating that Hennig86 produced a two-step longer tree than PAUP. This suggests that the two algorithms may not necessarily give the same solution.

9.3.2 Reliability of the Inferred Phylogeny

Analyses by both PAUP and Hennig86 revealed that the majority of characters had CIs and RIs well above values expected from random data (Table 1). This suggests that the characters selected for analysis are potentially useful for estimating the phylogeny of *Aethomys*.

The distribution of tree lengths for 1000 randomly selected trees generated by PAUP was significantly and strongly skewed to

the left. The g_1 statistic was -1.07 ($P < 0.01$), suggesting that the data contain a significant phylogenetic signal. However, only three internal branches from a 50% majority-rule consensus output based on 200 bootstrap iterations were well supported (≥ 70%; Figure 9.3). The strongest support (97%) was obtained for the node uniting *A. granti* and *A. namaquensis*, the two species currently placed in the subgenus *Micaelamys* in southern Africa. Good support (78%) was also obtained for the node uniting *A. chrysophilus* and *A. ineptus*, two of the species currently placed in the subgenus *Aethomys* in southern Africa.

Similarly, the node uniting all ingroup taxa showed relatively strong bootstrap support (68%). The majority of internodes collapsed, except for weak support for two internal branches: one linking *A. bocagei* and *A. thomasi* (53%), and the other leading to *A. granti*, *A. namaquensis* and *A. stannarius* (54%).

9.3.3 Character Analysis

The placement of the 22 characters used for phylogenetic analysis on branches of the most parsimonious tree showed the majority of branches were supported by unambiguous synapomorphies (Figure 9.4). This was particularly evident in the two internal branches that were strongly supported by bootstrap analysis. The branch uniting *A. granti* and *A. namaquensis* was supported by six unambiguous synapomorphies: skull robustness/ossification (character 1, derived character-state 1; Appendix VII; Table 9.2), development of interorbital constriction (4,1), zygomatic arch development (5,0), extent of bulla inflation (8,2), lower

molar cusp development (10,2), and mandibular development (22,1). The branch leading to *A. chrysophilus* and *A. ineptus* was supported by three unambiguous synapomorphies: cranial ridge development (Character 2, derived character-state 2; Appendix VII; Table 9.2), central upper molar row cusp development (14,2), and development of t_3 and t_5 on M^2 (20,1).

The number of character changes for each branch inferred using ACCTRAN and DELTRAN character-optimizations are given in Table 9.2. The number of all possible character assignments were the same under both character-optimization procedures. There was only one exception: while ACCTRAN inferred six character changes on the branch leading from node 17 to 16, DELTRAN inferred seven character changes (Table 9.2).

The minimum and maximum number of changes over the most parsimonious reconstruction were identical for the two character-optimizations (Table 9.2). Similarly, as in number of character changes above, any changes inferred for characters were identical, except for node 17 to 16. Because of the similarity, results presented are those for character changes inferred from DELTRAN. The additional character change inferred for node 17 to 16 under DELTRAN relates to cranial ridge development (character 2). This character, presumed to change from the plesiomorphic state (pronounced or well developed; character-state 3) to apomorphic state (slight or weak; character-state 0); Table 9.2) was the only character shown to be phylogenetically uninformative (Figure 9.4). It also appeared more than once, suggesting a parallelism. There were no inferred character changes on terminal branches leading to *A. chrysophilus*, *A. hindei* and *A. kaiseri* in the two character-optimization procedures (Table 9.2).

9.3.4 Cladistic Classification

Conversion of the inferred phylogeny (Figures 9.1 and 9.2) into a Linnaean hierarchical classification based on the cladistic criterion of placing sister groups at the same rank, or equivalent rank, led to biogeographically and ecologically heterogenous categories. This is particularly evident in the grouping of the geographically and ecologically disparate *A. stannarius* with *A. namaquensis* and *A. granti*. Heterogenous categories were also obtained when an exact reflection of the branching sequence but not requiring that every monophyletic group be ranked (Wiley *et al.* 1991) was adopted.

9.3.5 Evolutionary Classification

Results of anagenetic computations are summarized in Table 9.3. The sum of % taxonomic gap values (% TGVs) between pairs of species used to derive a ratio between outside internodes are shown in Table 9.4. The largest distance between outside internodes was 68.07, and was between *A. granti*, and *A. bocagei* and *A. thomasi*, while the smallest (2.90) was between *A. chrysophilus* and *A. ineptus*. The largest distance gave a rounded off ratio of 3.0 if a width of 200 millimeters between outside internodes was considered (i.e. 200/68.07). The ratio was used to derive the phylogram's proportional length values given in the last column of Table 9.3.

The resultant alteration of the inferred phylogeny into a phylogram is shown in Figure 9.5. It shows a biogeographically and ecologically homogeneous division separated by the largest

patristic distance (24.5%) on internode 17-16 (arrowed; Figure 9.5). This internode coincided with the subgeneric separation of *Micaelamys* and *Aethomys*. The internode also represented one of the three well supported internodes in bootstrap analysis (thick lines; Figure 9.5). All other relationships indicated by the most-parsimonious topology were broadly congruent with those of the phylogram. The only exception was the biogeographical and ecological clarification of the position of *A. stannarius* which is closer to *A. namaquensis* and *A. granti* on the cladogram, but closer to the clade comprising *A. hindei*, *A. chrysophilus* and *A. ineptus* on the phylogram. However, the discrepancy between the cladogram and the phylogram only involves a single informative character (lower anterior zygomatic arch development; Character 6 - Appendix VII; Figure 9.4).

9.4 DISCUSSION

9.4.1 Phylogenetic Relationships Within the Genus *Aethomys*

Cladistic analyses accomplished by different algorithms (Farris 1988; Maddison and Maddison 1992; Swofford 1993) were largely congruent. These results, based on analyses of all currently recognized species of *Aethomys* (Musser and Carleton 1993; Chapter 4), suggest the presence of three clades that include: 1) *A. bocagei*, *A. thomasi*, *A. silindensis*, *A. kaiseri*, and *A. nyikae*; 2) *A. chrysophilus*, *A. ineptus*, and *A. hindei*; 3) *A. granti*, *A. namaquensis*, and *A. stannarius*. Despite general lack of bootstrap support, the three clades are, nevertheless, supported by unambiguous synapomorphies.

More importantly, an independent corroboration of the tree topology indicates a general contrast in overall cranial configuration characterizing each clade. There is a broad reflection of: 1) broad-faced skull forms; 2) intermediately broad-faced skull forms; and 3) slender-faced skull forms. Evolutionary trends towards either an increase in overall broadness of the facial region, or its reduction, is illustrated by similar changes in morphology of fossil specimens attributed to species within the genus *Aethomys* (Jaeger 1976, 1979; Wesselman 1984; Denys 1990*a*, 1990*b*).

Of particular relevance within each of the three clades is that relationships between various combinations of species are broadly consistent with previously postulated relationships. Although not reflecting the suggested sister-group relationships, all species in the first clade have, variably, been considered to be closely related to each other. Musser and Carleton (1993) for example, suggested a sister-taxon relationship between *A. bocagei* and *A. silindensis*, and also between *A. thomasi* and *A. kaiseri*. Similarly, before their validity was established, *A. kaiseri* was considered a synonym of *A. nyikae* (Delany 1975; Davis 1975; Ansell 1978).

Most prominent on the second clade is the sister-taxon relationship between the two cryptic species, *A. chrysophilus* and *A. ineptus* which, until recently, were considered a single species. Support for this affinity was also apparent in phenetic analyses (Chapter 4), and their separation by the smallest taxonomic gap among all currently recognized species of *Aethomys*. Based on a marked change in sperm morphology, Visser and Robinson (1987) considered that the two species may be distantly related.

Breed *et al.* (1988), however, considered it a possibility, even in closely related species, for divergent sperm forms to evolve, and act as a prezygotic reproductive isolating mechanism (Phillips *et al.*, 1985).

More importantly, the third clade draws attention to the well-documented close evolutionary relationship between *A. namaquensis* and *A. granti*. This affinity has also been observed in other studies based on dental morphology (Ellerman *et al.* 1953), karyology (Matthey 1954, 1958, 1964; Visser and Robinson 1986), sperm and bacular morphology together with their staining properties (Visser and Robinson 1987) and phenetic analyses (Chapter 4).

By contrast, the suggested association between the West African endemic, *A. stannarius* and *A. hindei* (Ellerman 1941; Rosevear 1969; Davis 1975; Hutterer and Joger 1982), and *A. hindei* and *A. kaiseri* (Hollister 1919; Swynnerton and Hayman 1951) was not substantiated by the analysis of the present data (but see discussion on biogeographical implications).

9.4.2 Taxonomic Implications

The criterion of cladistic classification in placing sister groups at the same rank or equivalent rank indicated biogeographically and ecologically heterogeneous categories. This was also evident when an exact reflection of the branching sequence but not requiring that every monophyletic group be ranked was adopted (Mayr and Ashlock 1991). Although attempts to incorporate phenetic distinctiveness into taxonomies may be

considered inappropriate (Wiley *et al.* 1991), an evolutionary classification, on the other hand, produced biogeographically and ecologically homogeneous categories and is adopted in the present investigation. It allowed a balanced Linnaean hierarchical ranking that considered monophyly through the presence of synapomorphies and the explanation of homoplasies. Also considered was the totality of characters, phenetic divergence, and both branching (cladogenesis) and divergent (anagenesis) evolution (Michener 1970; Mayr and Ashlock 1991).

The phylogram substantiated the close evolutionary relationship between *A. namaquensis* and *A. granti*. Both species are separated from all other species of *Aethomys* by a large anagenetic gap, with evidential support provided by a high bootstrap value (97%) and six unambiguous synapomorphies.

The data based on an evolutionary classification therefore provide good grounds for the subgeneric separation of *Aethomys* and *Micaelamys*, and is consistent with a traditionally held view based on dental morphology (Ellerman *et al.* 1953). Of additional importance is the marked contrast, in representatives of each subgenus, in modes of karyotypic change, and gross sperm and bacular morphology, and their staining properties (Matthey 1954, 1958, 1964; Visser and Robinson 1986; 1987).

If the recognition of the subgenera were to be interpreted in terms of a cladistic classification, the subgenus *Aethomys* would be paraphyletic. However, the only exception between the cladogram and the phylogram was the placement of *A. stannarius*, and this discrepancy only involved a single informative character (lower zygomatic arch development). This weak synapomorphic support together with a low bootstrap value (54%) indicates that

the clade may not be meaningful, suggesting a high degree of correspondence between the cladogram and the phylogram. It is possible that the character involved may be under the influence of either developmental or ecological constraints, rather than phylogeny (Seutin *et al.* 1995).

Musser and Carleton (1993) considered the characters separating *A. namaquensis* and *A. granti* from other species of *Aethomys* to be no more significant than those distinguishing the other species. Similarly, morphometric analyses (Chapter 4) provided little support for the recognition of the two subgenera. The subdivision of the subgenus *Aethomys* into "*kaiseri*" and "*hindei*" groups (Davis 1975) was also not substantiated by the analyses of the present data.

9.4.3 Biogeographical Implications

The absence of an explicit hypothesis of phylogeny has precluded interpretation of biogeography in the genus *Aethomys*. This problem has been exacerbated by the apparent lack of any close relationships between fossil species of *Aethomys* found in East and South Africa, which precluded speculation on their origin and time of divergence (Denys 1990*a*, 1990*b*). Despite the need for additional palaeontological and molecular data, collation of generalized distributional information with the proposed evolutionary classification (Table 9.5) allows a biogeographical hypothesis to be developed.

The two species in *Micaelamys* are in large part confined to southern Africa, while six of the nine species in the subgenus *Aethomys* are endemic to the north of the subregion. Two species,

A. chrysophilus and *A. ineptus* represent the only widely distributed species common to southern as well as East and Central Africa. Of particular relevance is the similarity between *A. chrysophilus* and one of the two oldest known fossil species of *Aethomys*, *A. modernis* (Denys 1990*a*, 1990*b*). If an evolutionary classification is considered, it is tempting to postulate that a form ancestral to *A. chrysophilus* and *A. ineptus* may have given rise to all extant species in the genus *Aethomys*. Baker *et al.* (1988) proposed that the acrocentric morphology of chromosome 5, 14, 15, and 20, identical to those found in *A. ineptus*, are primitive for the ancestor of the Muridae and Sigmodontidae rodent lineages.

It is possible that there may have been a split in the ancestral form, with one lineage giving rise to extant East, Central and West African taxa in the subgenus *Aethomys*, and the other to southern African taxa in the subgenus *Micaelamys*. This suggestion may be supported by *A. hindei* which has been shown to be phylogenetically close to *A. chrysophilus* and *A. ineptus*. *Aethomys adamanticola*, one of the two oldest known species of *Aethomys*, shows characteristics reminiscent of representatives of the two subgenera, *A. hindei* and *A. namaquensis*, that have been interpreted as plesiomorphic for the genus (Denys 1990*a*, 1990*b*). This interpretation, however, is not consistent with a cladistic classification.

Of particular interest is the contrast in modes of karyotypic change in representatives of each subgenus (Matthey 1954, 1958, 1964; Visser and Robinson 1986). Visser and Robinson (1986) suggested a rapid and extensive genomic reorganization since divergence from a common ancestor. Both species in

Micaelamys inhabit rocky and mountainous habitats, while species of the subgenus *Aethomys* occur in open savanna. Visser and Robinson (1986) proposed that the disjunct distribution shown by the former may have facilitated the fixation of structural rearrangements through fragmentation of the species into isolated demes, while the latter may be less prone to isolation.

Within the subgenus *Micaelamys*, *A. namaquensis* is widely distributed and extends from southern Africa, southern Angola, southern Malawi to southeastern Zambia (Musser and Carleton 1993), while *A. granti* is restricted to south-central South Africa. Despite the presence of palaeontological sites within or near the present geographic range of *A. granti*, the species (or extinct forms allied to it) are not represented in the fossil record (De Graaff 1981). Its teeth are, however, characteristic and sufficiently robust to facilitate preservation (De Graaff 1981), suggesting that lack of preservation or misidentification is unlikely. This suggests that *A. granti* is of more recent origin, perhaps emanating from an *A. namaquensis*-like form.

Within the subgenus *Aethomys*, the geographically restricted *A. bocagei*, *A. thomasi*, and *A. silindensis* are also phylogenetically close. This may be indicative of recent speciation, perhaps descending from an *A. kaiseri*- or *A. nyikae*-like form, whose extant forms have a wide distribution in East and Central Africa.

The only difference between the cladogram and the phylogram was the position of the West African endemic, *A. stannarius*. It was closer to the allopatric *A. namaquensis* and *A. granti* on the cladogram, but showed greater affinity to the clade comprising the geographically proximate *A. hindei*, *A. chrysophilus* and *A.*

ineptus on the phylogram. Of particular relevance is that *A. stannarius* has previously been treated as a subspecies of *A. hindei* (Ellerman 1941; Rosevear 1969; Davis 1975; Hutterer and Joger 1982), suggesting a close relationship between them. This may suggest that *A. stannarius* may have evolved from an ancestor to the geographically proximate grouping, probably an *A. hindei*-like form, the extant form of which is also the geographically closest.

9.5 CONCLUSIONS

Cladistic analyses of all currently recognized species within *Aethomys*, based on qualitative morphological data suggest the presence of three clades that include: 1) *A. bocagei*, *A. thomasi*, *A. silindensis*, *A. kaiseri* and *A. nyikae*; 2) *A. chrysophilus*, *A. ineptus* and *A. hindei*; 3) *A. granti*, *A. namaquensis* and *A. stannarius*. Despite the general lack of bootstrap support, the three clades are, nevertheless, supported by unambiguous synapomorphies. An independent corroboration of the tree topology showed that the three clades generally correspond with facial characteristics that also conform to evolutionary trends illustrated by palaeontological data.

An evolutionary classification provided homogeneous categories and is adopted in the present investigation. It provides good grounds for the subgeneric separation of *Aethomys* and *Micaelamys*, and is consistent with a traditionally held view. Similarly, an evolutionary classification allowed the development of a biogeographical hypothesis in an attempt to explain the group's evolutionary relationships.

Figure 9.1 Maximum parsimony tree, 40 steps in length, derived by Phylogenetic Analysis Using Parsimony (PAUP) for *Aethomys* and outgroups, based on 22 qualitative cranial characters.

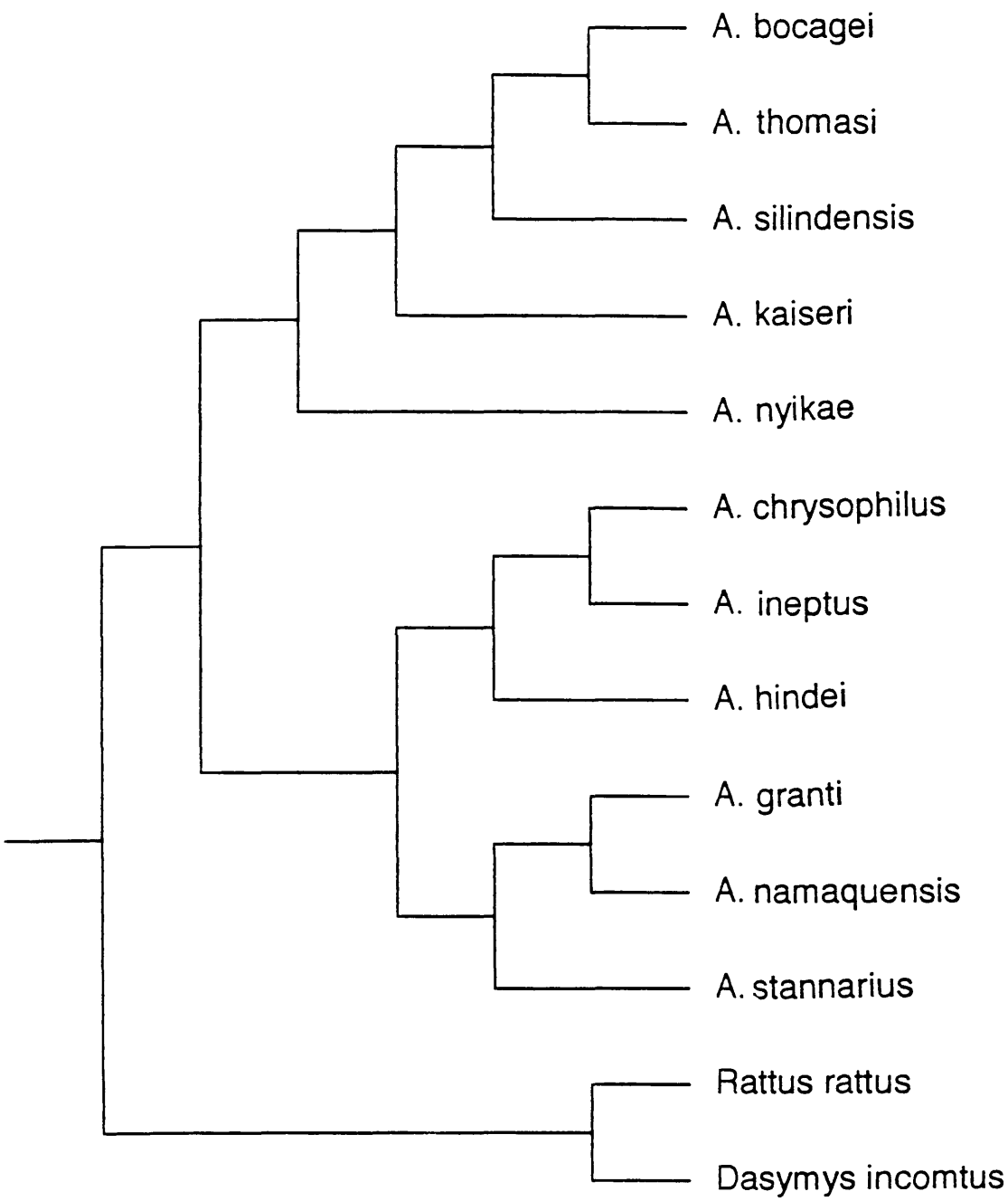

Figure 9.2 Strict consensus cladogram from four equally parsimonious cladograms, 42 steps in length, derived by Hennig86 for *Aethomys* and outgroups, based on 22 qualitative cranial characters.

Figure 9.3 A 50% majority-rule branch-and-bound bootstrap consensus cladogram derived by Phylogenetic Analysis Using Parsimony (PAUP) for *Aethomys* and outgroups based on 22 qualitative cranial characters. Numbers represent bootstrap support values for internal branches based on 200 iterations.

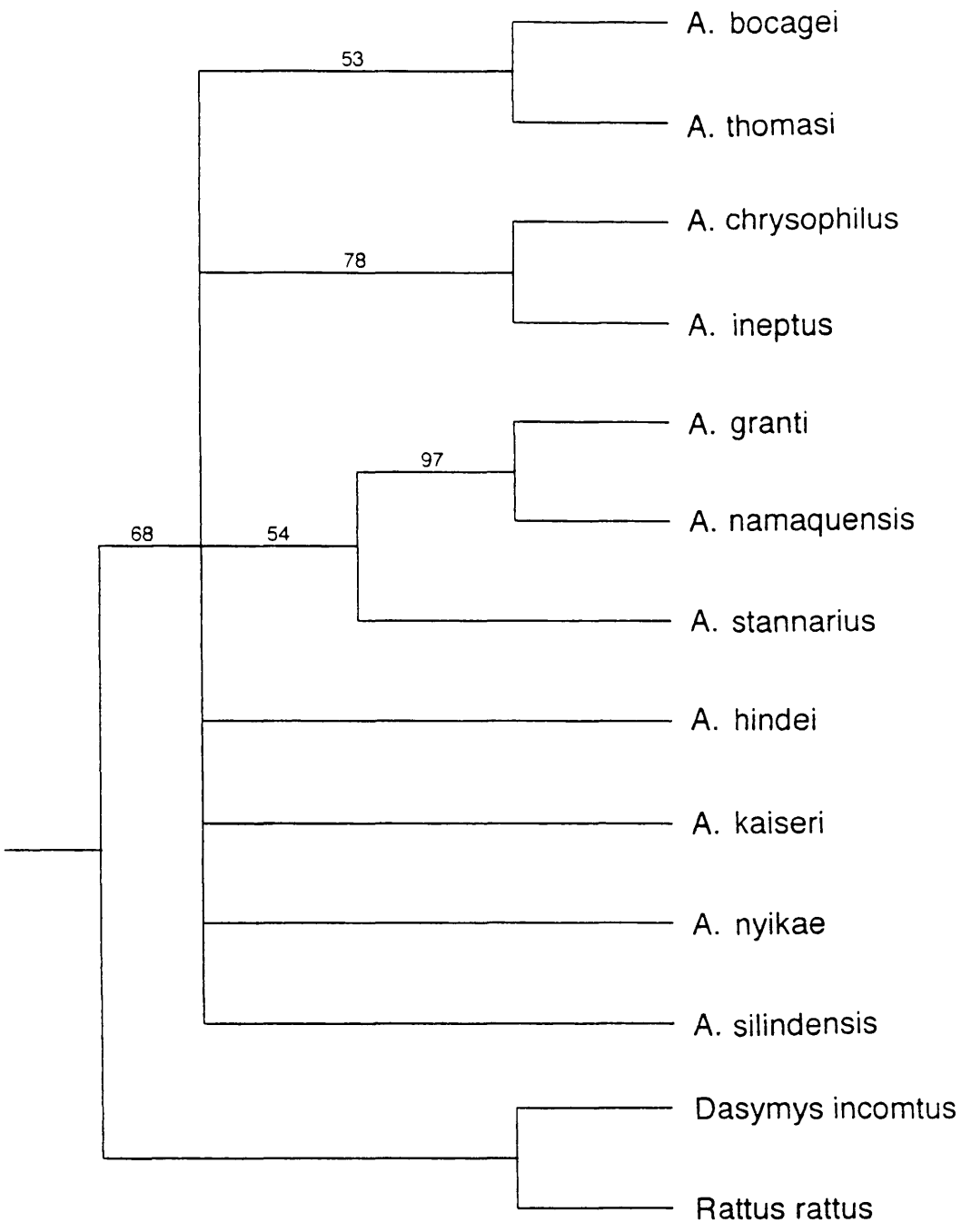

Figure 9.4 Patterns of character evolution defining lineages for *Aethomys* and outgroups based on DELTRAN optimized interpretation of the most-parsimonious topology. Phylogenetically informative characters are indicated by thick bars and normal numbers, while uninformative characters are indicated by thin bars and italicized numbers. Character-state changes are indicated as superscripts. Absence of character numbers on terminal branches indicate no inferred characters. Branch numbers for internal nodes are encircled. Character numbering corresponds to that in Appendix VII.

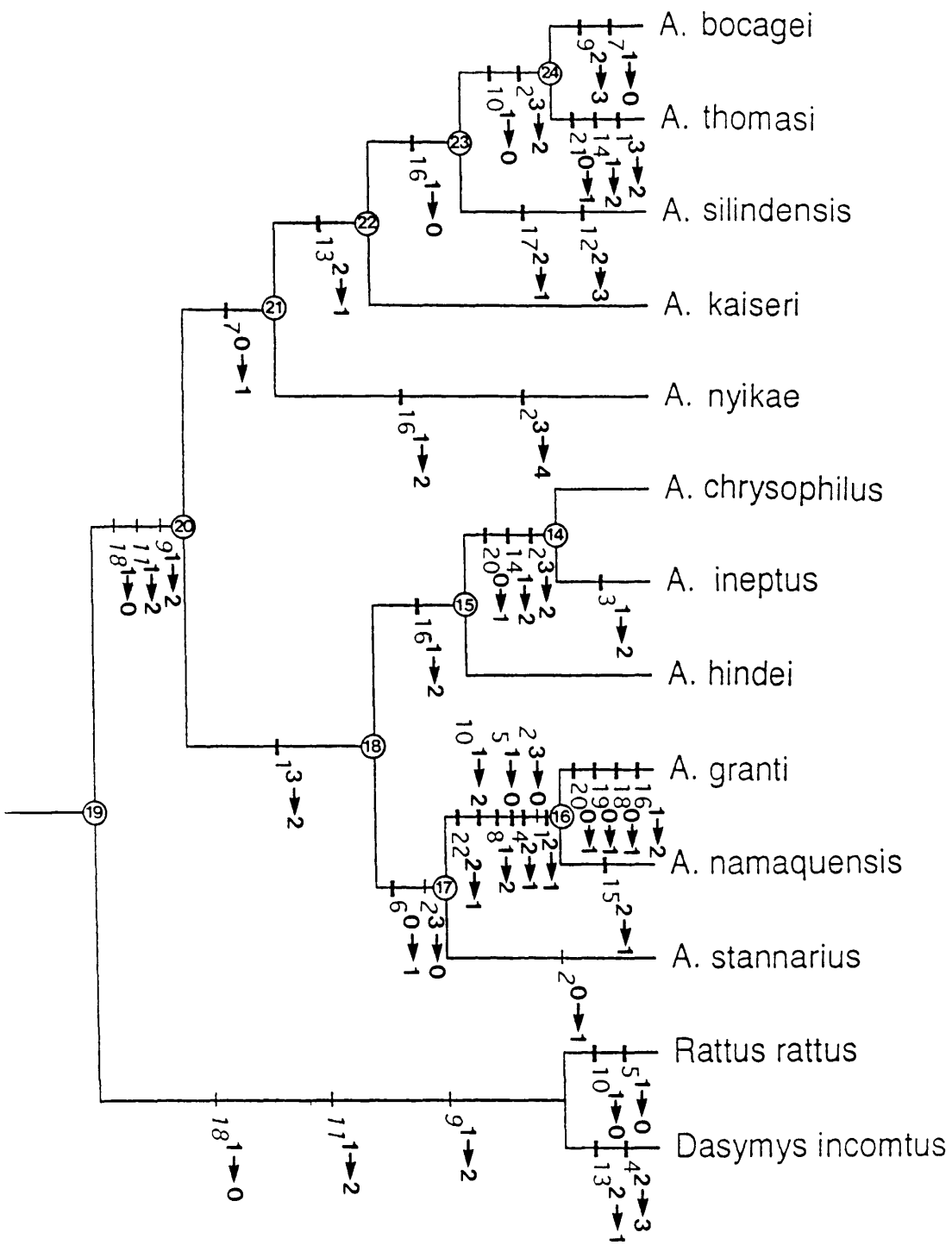

Figure 9.5 A phylogram for *Aethomys* derived from the cladogram in Figure 9.4 and character-optimizations in Table 9.2. Patristic distances along horizontal axis are proportional to the percent taxonomic gap values (% TGVs) adjacent to each internode. Internodes leading to *A. kaiseri* and *A. stannarius* were slightly offset to avoid overlaps. Internodes well supported by bootstrap analysis are indicated by bold lines. The midpoint of maximum anagenetic divergence is indicated by an arrow. Branch numbers for internal nodes are encircled.

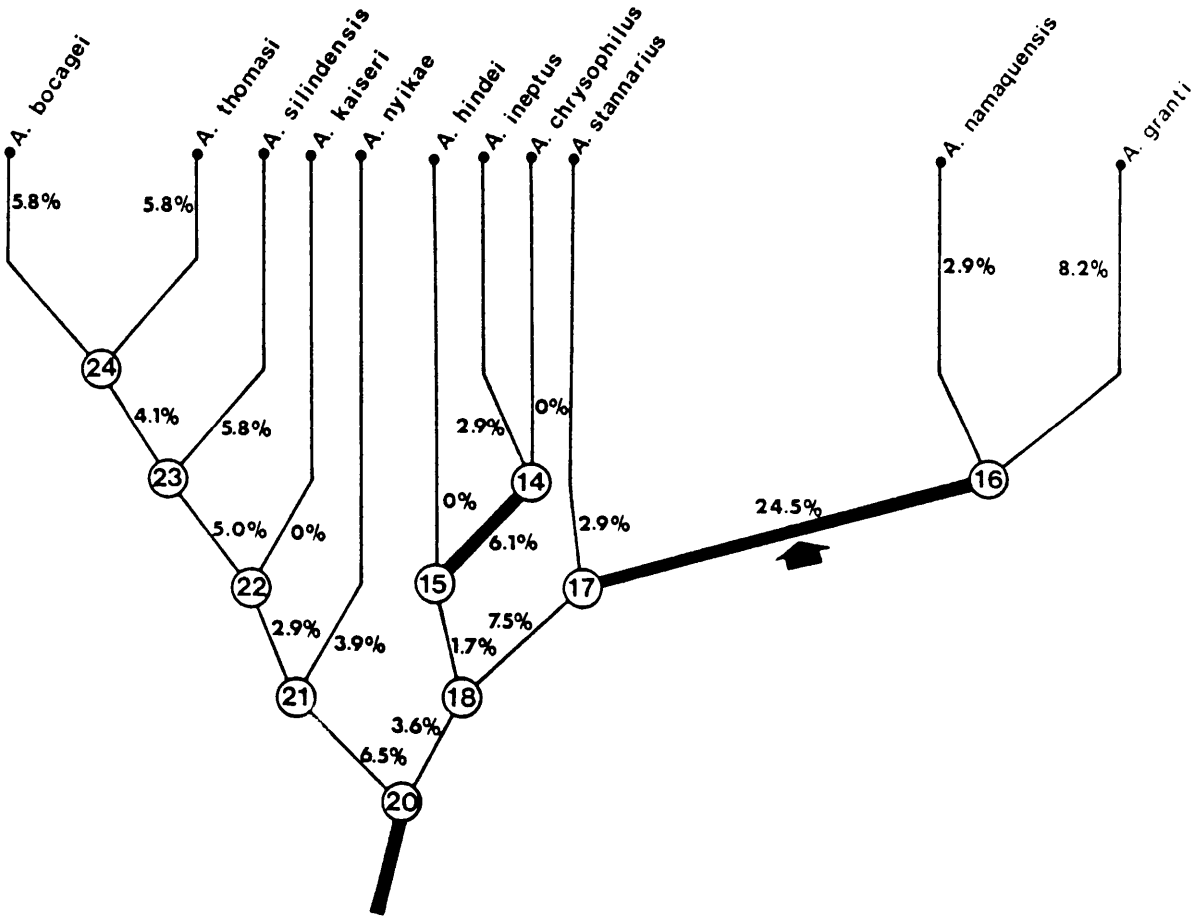

Table 9.1 Consistency (CI) and retention (RI) indices for each character generated by Phylogenetic Analysis Using Parsimony (PAUP) and Henning86 from analyses based on cranial characters of all currently recognized species of *Aethomys*.

Character	PAUP		Hennig86*	
	CI	RI	CI	RI
1. Skull robustness/ossification	0.67	0.80	0.66	0.83
2. Cranial ridge development	0.80	0.75	0.80	0.87
3. Development of the alisphenoid process of the squamosal	1.00	0.00	1.00	1.00
4. Development of interorbital constriction	1.00	1.00	1.00	1.00
5. Zygomatic arch development	0.50	0.50	0.50	0.50
6. Lower anterior zygomatic plate development	1.00	1.00	1.00	1.00
7. Presence/absence of foramina posterior to anteorbital foramina	0.50	0.67	0.33	0.33
8. Extent of bulla inflation	1.00	1.00	1.00	1.00
9. Upper molar toothrow development	1.00	1.00	1.00	1.00
10. Lower molar cusp development	0.67	0.67	0.66	0.66
11. General molar cusp development	1.00	1.00	1.00	1.00
12. Number of roots on M^1	1.00	0.00	1.00	1.00
13. Extent of cusp development on M^3	0.50	0.75	0.50	0.75
14. Central upper molar row cusp development	0.50	0.50	0.50	0.50
15. Development of t_8 on third lamina of upper molars	1.00	0.00	1.00	1.00
16. Development of t_9 on third lamina of upper molars	0.50	0.67	0.50	0.66
17. t_3 development on M^1	1.00	0.00	1.00	1.00
18. t_4, t_5 and t_6 development on second lamina of M^2	0.50	0.50	0.50	0.50
19. t_4, t_5 and t_6 development on second lamina of M^3	1.00	0.00	1.00	1.00
20. Development of t_3 and t_5 on M^2	0.50	0.50	0.50	0.50
21. General cusp development of M^3	1.00	0.00	1.00	1.00
22. Mandibular development	1.00	1.00	1.00	1.00

* The CI and RI values of all characters for all four trees generated by Hennig86 were similar except for characters 2 (tree 4: CI = 0.66; RI = 0.75), 7 (trees 3 and 4: CI = 0.50; RI = 0.66), and 16 (tree 3: CI = 0.40; RI = 0.50).

Table 9.2 Character changes for each branch of *Aethomys* and outgroups from the cladogram in Figure 9.1, including the number of character changes inferred using ACCTRAN and DELTRAN character-state optimizations, the minimum and maximum numbers of changes, and any changes inferred for characters using DELTRAN. An asterisk denotes terminal branches with no inferred character changes. Characters and character-states are numbered as in Appendix VII.

Branch node	ACCTRAN	DELTRAN	Min-max	Character changes
19-->20	3	3	2-3	9 (1-->2), 11 (1-->2), 18 (1-->0)
20-->21	1	1	1-1	7 (0-->1)
21-->22	1	1	1-1	13 (2-->1)
22-->23	1	1	0-1	16 (1-->0)
23-->24	2	2	0-2	2 (3-->2), 10 (1-->0)
24--> *Aethomys bocagei*	2	2	1-2	7 (1-->0), 9 (2-->3)
24--> *A. thomasi*	3	3	2-3	1 (3-->2), 14 (1-->2), 21 (0-->1)
23--> *A. silindensis*	2	2	2-2	12 (2-->3), 17 (2-->1)
22--> *A. kaiseri**				
21--> *A. nyikae*	2	2	0-2	2 (3-->4), 16 (1-->2)
20-->18	1	1	0-1	1 (3-->2)
18-->17	2	2	1-2	2 (3-->0), 6 (0-->1)
17-->16	6	7	3-7	1 (2-->1), 2 (3-->0), 4 (2-->1), 5 (1-->0), 8 (1-->2), 10 (1-->2), 22 (2-->1)
16--> *A. granti*	4	4	3-4	16 (1-->2), 18 (0-->1), 19 (0-->1), 20 (0-->1)
16--> *A. namaquensis*	1	1	1-1	15 (2-->1)
17--> *A. stannarius*	1	1	0-1	2 (0-->1)
18-->15	1	1	0-1	16 (1-->2)
15-->14	3	3	2-3	2 (3-->2), 14 (1-->2), 20 (0-->1)
14--> *A. chrysophilus**				
14--> *A. ineptus*	1	1	1-1	3 (1-->2)
15--> *A. hindei**				
19--> *Rattus rattus*	2	2	1-2	5 (1-->0), 10 (1-->0)
19--> *Dasymys incomtus*	2	2	1-2	4 (2-->3), 13 (2-->1)

Table 9.3 Anagenetic gap calculation and proportional length values used for phylogram construction as adopted from Brothers (1975), Mayr and Ashlock (1991), and D. J. Brothers (*pers. comm.*[1]) where AGV = anagenetic gap value; STV = subtended taxa value; ASTV = adjusted subtended taxa value, a root of STV; TGV = taxonomic gap value, AGV x ASTV; %TGV = percent taxonomic gap value, TGV/sum of TGV/100. Computation of proportional length values is outlined in Section 9.3.5.

Branch node	AGV	STV	ASTV	TGV	%TGV	Proportional Length
20-->21	1.00	5	2.24	2.24	6.49	19.47
21-->22	0.50	4	2.00	1.00	2.90	8.70
22-->23	1.00	3	1.73	1.73	5.01	15.03
23-->24	1.00	2	1.41	1.41	4.08	12.24
24--> *Aethomys bocagei*	2.00	1	1.00	2.00	5.79	17.37
24--> *A. thomasi*	2.00	1	1.00	2.00	5.79	17.37
23--> *A. silindensis*	2.00	1	1.00	2.00	5.79	17.37
22--> *A. kaiseri*	0.00	1	1.00	0.00	0.00	0.00
21--> *A. nyikae*	1.33	1	1.00	1.33	3.85	11.55
20-->18	0.50	6	2.45	1.23	3.56	10.68
18-->17	1.50	3	1.73	2.60	7.53	22.59
17-->16	6.00	2	1.41	8.46	24.51	73.53
16--> *A. granti*	2.83	1	1.00	2.83	8.20	24.60
16--> *A. namaquensis*	1.00	1	1.00	1.00	2.90	8.70
17--> *A. stannarius*	1.00	1	1.00	1.00	2.90	8.70
18-->15	0.33	3	1.73	0.57	1.65	4.95
15-->14	1.50	2	1.41	2.12	6.14	18.42
14--> *A. chrysophilus*	0.00	1	1.00	0.00	0.00	0.00
14--> *A. ineptus*	1.00	1	1.00	1.00	2.90	8.70
15--> *A. hindei*	0.00	1	1.00	0.00	0.00	0.00
				Σ TGV = 34.52		

[1] D. J. Brothers, Department of Zoology and Entomology, University of Natal, Pietermaritzburg, South Africa.

Table 9.4 Sum of % taxonomic gap values between pairs of species of *Aethomys* used to derive a ratio between outside internodes for the calculation of proportional length values used for phylogram construction. Computational procedure is outlined in Section 9.2.5.7. A.b = *A. bocagei*; A.t = *A. thomasi*; A.s = *A. silindensis*; A.k = *A. kaiseri*; A.ny = *A. nyikae*; A.c = *A. chrysophilus*; A.i = *A. ineptus*; A.h = *A. hindei*; A.g = *A. granti*; A.n = *A. namaquensis*; A.st = *A. stannarius*.

Taxa Code	A.b	A.t	A.s	A.k	A.ny	A.c	A.i	A.h	A.g	A.n	A.st
A.b	-										
A.t	11.58	-									
A.s	15.66	15.66	-								
A.k	14.88	14.88	10.80	-							
A.ny	21.63	21.63	17.55	6.75	-						
A.c	35.62	35.62	31.54	20.74	21.69	-					
A.i	38.52	38.52	34.44	23.64	24.59	2.90	-				
A.h	29.48	29.48	25.40	14.60	15.55	6.14	9.04	-			
A.g	68.07	68.07	63.99	53.19	54.14	48.03	50.93	41.89	-		
A.n	62.77	62.77	58.69	47.89	48.84	42.73	45.63	36.59	11.10	-	
A.st	38.26	38.26	34.18	23.38	24.33	18.22	21.12	12.08	35.61	30.31	-

Table 9.5 Taxonomic and generalized biogeographical correlates for *Aethomys*. Arrangement of taxa corresponds to their placement on the phylogram in Figure 9.5. Biogeographical information was largely obtained from Musser and Carleton (1993) and Chapter 4. The geographical distribution of *A. ineptus* extralimital to southern African subregion is extrapolated from the distribution of *A. chrysophilus* with which it broadly overlaps in southern Africa (Chapter 4).

Taxononic group	Biogeographical Area
Subgenus *Aethomys*:	
A. bocagei	C and W Angola
A. thomasi	C and W Angola
A. silindensis	E Zimbabwe
A. kaiseri	SW Uganda, S Kenya, Rwanda, S and E Zaire, Tanzania, Malawi, Zambia, E Angola
A. nyikae	N Zambia, Malawi, N Angola, S Zaire
A. hindei	N Cameroon, N and NE Zaire, S Sudan, SW Ethiopia, Uganda, Kenya, S Tanzania
A. ineptus	SE Kenya, Tanzania, Malawi, Zambia, Mozambique, Zimbabwe, N and E Botswana, N and E South Africa, N and C Namibia
A. chrysophilus	SE Kenya, Tanzania, Malawi, Zambia, Mozambique, Zimbabwe, N and E Botswana, N and E South Africa, N and C Namibia
A. stannarius	N Nigeria, W Cameroon
Subgenus *Micaelamys*:	
A. namaquensis	Southern Africa, S Angola, S Malawi, SE Zambia
A. granti	SC South Africa

CHAPTER 10

GENERAL DISCUSSION

The objective of this study was to clarify the systematic status of the genus *Aethomys* in southern Africa using a wider range of morphological techniques than has hitherto been applied to the group. The study has resulted in proposed changes to the systematics of *Aethomys* in southern Africa. This chapter provides a synthesis and general discussion of the principal findings of the entire study and includes a revised classification for the genus.

10.1 Morphometrics and the Resolution of Species Relationships

Morphometric analyses played a major role in the resolution of systematic problems in this study and allowed a more fundamental understanding of species identities based on morphology. The validity of *A. granti*, *A. namaquensis* and *A. silindensis* in southern Africa was confirmed, while *A. chrysophilus* (*sensu lato*) was shown to comprise two cryptic species recognized as *A. chrysophilus* and *A. ineptus*.

The analytical procedures utilized will allow the identification of material that has accumulated over a period of close to 100 years in study collections throughout the world. Similarly, the simple and practical identification schemes devised could assist health and agricultural authorities in the identification of these problem rodents in southern Africa.

The use of statistical techniques, however, is based on

probability statements in which the data may not conform to hypothetical models on which the techniques are based (Thorpe 1976; Lele and Richtsmeier 1990). These include the assumptions of random sampling, normality, and homoscedasticity (Sokal and Rohlf 1981; Pimentel and Smith 1986*a*, 1986*b*).

Although biological data are generally considered to conform to most statistical assumptions (Pimentel and Smith 1986*a*, 1986*b*), in this study some of the assumptions were tested for (Chapter 2). Additional steps were also taken to check for outliers on a locality by locality basis. Where detected, the outliers were often re-measured, and specimens not considered representative of the population excluded from subsequent analyses (Chapters 2, 3, and 4).

10.2 Support for Morphometric-based Systematic Conclusions

The morphometric-based recognition of the southern African species of *Aethomys* is supported by independent data sets based on qualitative morphology (Chapter 4) as well as previous studies on karyology, protein electrophoresis, and sperm and cuticular hair morphology (Gordon and Rautenbach 1980; Keogh 1985; Gordon and Watson 1986; Visser and Robinson 1986, 1987; Baker *et al.* 1988; Breed *et al.* 1988).

The systematic conclusions are also strengthened by the inclusion of some cytogenetically known specimens as well as holotypes. This also involved the examination of extralimital material which allowed a broad summary of relationships and the retention of a nomenclatural perspective. The validity of the Central African *A. nyikae*, for example, was confirmed but there

was no evidence that it occurs in southern Africa.

Further support emanates from an extensive sampling of the genus over its entire range in southern Africa. The resultant data matrix, however, was too large for simultaneous multivariate analyses. This necessitated the pooling of specimens from geographically contiguous localities with the underlying assumption that geographic variation among the pooled localities is practically negligible. Although pooling of data is a debatable procedure (Thorpe 1976; Dippenaar and Rautenbach 1986), in this study it was considered a practical necessity, and an attempt was made to be as conservative as possible. More importantly, the observed major patterns of variation based on sample means were always verified by analyses of individual specimens drawn from the entire range of *Aethomys* in southern Africa.

Equally relevant was the preliminary evaluation of non-geographic variation to establish whether sexes should be treated separately or together, and to identify adult specimens which would be eligible for subsequent measurement recording and analyses. Although the ageing criterion was, for practical reasons, based on arbitrary tooth-wear classes (Verheyen and Bracke 1966; Morris 1972; Perrin 1982; Dippenaar and Rautenbach 1986), its robustness was subsequently confirmed by a wide range of statistical procedures.

Of additional importance was the use of selected samples (two samples each of two species) to extrapolate on patterns of postnatal growth and sexual dimorphism (Thorpe 1976; Dippenaar and Rautenbach 1986) for the genus over its entire range in southern Africa. The results, however, showed that such a

treatment had little effect on the main taxonomic conclusions, and also conform to patterns found in other southern African murid rodents such as *Acomys* (Dippenaar and Rautenbach 1986). Other potential sources of variation such as seasonal variation at either the individual or the population level, were not tested for. Small samples precluded subdivision of data into single or pooled months to allow a meaningful statistical treatment.

10.3 Geographical Distributions of Southern African Species of *Aethomys*

The taxonomic clarification of southern African species of *Aethomys* allowed a re-examination of their patterns of geographical distribution. Previously determined distributions of *A. namaquensis*, *A. granti* and *A. silindensis* were confirmed.

The two cryptic species, *A. chrysophilus* and *A. ineptus*, on the other hand, were shown to be widely distributed and broadly sympatric in southern Africa (Chapter 4). This pattern is, however, contrary to parapatric distributions suggested by cytogenetic data (Gordon and Watson 1986; Gordon and Rautenbach 1987). It is tempting to suggest from the broadly sympatric distributions determined by the morphometric data that the two species may be utilizing different microhabitats such that sampling efforts may be biased towards the numerically dominant species within the sampled vicinity. In areas of sympatry, Gordon and Watson (1986) found the numerical dominance of two sibling species of *Mastomys*, *M. natalensis* and *M. coucha*, depended on a particular *Acacia* species. Similarly, ecological differences were found in *A. chrysophilus* (*sensu lato*) in Zimbabwe where the two

cryptic species are sympatric (Linzey and Kesner 1995; A. V. Linzey *pers. comm.*[1]).

10.4 Geographic Variation Within Southern African Species of *Aethomys*

The re-examination of geographical distributions in turn allowed the assessment of patterns of geographic variation in four of the five species recognized (*A. namaquensis*, *A. chrysophilus*, *A. ineptus* and *A. granti*). Too little material precluded the analysis of geographic variation in *A. silindensis*.

These analyses provided a sound basis for making taxonomic decisions. This was particularly evident in the two cryptic species, *A. chrysophilus* and *A. ineptus* which, despite the distributional discrepancies between morphometric and previous cytogenetic data, showed different but geographically explicable patterns of variation. The delineated patterns of intraspecific variation in some cases also led to the recognition of subspecies. The infraspecific and species relationships together with patterns of geographical distribution may provide a baseline for subsequent studies of the genus.

10.5 Taxonomic Characters

Of particular relevance is that relationships at the species as well as infraspecific levels were supported by both size- and

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[1] A. V. Linzey, Department of Biology, Indiana University of Pennsylvania, Indiana, Pennsylvania, U. S. A.

shape-related morphometric cranial variables. Characters in this revision were based on a preliminary selection of meaningful taxonomic characters that took into account an adequate coverage of the phenotype, a summary of their relationships, and the removal of redundant variables. This approach, which is consistent with the morphological integration concept of Olson and Miller (1958), could find wider application in morphometric studies of other taxa.

Among the 11 basic measurements selected, almost the same characters were delineated as important in shape-related aspects of the revision (Table 10.1). Analyses based on the selected characters and exploratory analyses based on these shape-related variables suggest that the 11 characters could be reduced even further without compromising the degree of systematic resolution. More importantly, univariate ratio combinations involving these shape-related parameters were in some cases diagnostic and even incorporated in identification keys, and could form a baseline for future systematic studies of the genus. With the recent developments in landmark-/outline-based methods (Mousseau 1991; Rohlf and Marcus 1993), it could be possible to focus on parts associated with these characters to capture three-dimensional profiles of the cranium.

On the other hand, an additional focus could also be directed at characters that were incorporated in the data set because of their descriptive properties and/or traditional use. Their utility allowed an insight into patterns of intraspecific variation, and in relating morphometric results to the nomenclature through diagnostic ratios and identification keys.

10.6 Phylogenetic Relationships Within the Genus *Aethomys*

Apart from the shape-related morphometric measurements, other diagnostic qualitative cranial characters were also identified within *Aethomys* from southern Africa. These were expanded upon to include morphological traits of all currently recognized species of *Aethomys* to provide a synapomorphic character suite for the elucidation of phylogenetic relationships within the genus. Although the delineation of synapomorphies is difficult (Barghoorn 1977), the identified traits inferred a phylogeny that is broadly consistent with previous postulations of relationships (Chapter 9) and provided a basis for making supraspecific taxonomic decisions. While the morphometric analyses provided little support for the recognition of the subgenera *Aethomys* and *Micaelamys* in southern Africa, conversion of the inferred phylogeny into an evolutionary classification (Chapter 9), suggested the retention of the two subgenera. This taxonomic conclusion is consistent with a traditionally held view based on dental morphology, karyology and sperm and bacular morphology (Ellerman *et al.* 1953; Matthey 1954, 1958, 1964; Visser and Robinson 1986, 1987).

The inferred phylogeny also allowed the development of a biogeographical hypothesis in which a split in the ancestral form is postulated to have given rise to a lineage that led to the present-day members of the subgenus *Aethomys*, and the other to the subgenus *Micaelamys*. Although tentative, this biogeographical scenario is supported by modes of karyotypic change in representatives of each subgenus (Matthey 1954, 1958, 1964; Visser and Robinson 1986) as well as palaeontological data (Denys

1990*a*, 1990*b*).

Given this hypothesis, it may be possible to develop a possible model of speciation for the two sibling species, *A. chrysophilus* and *A. ineptus*, particularly with regard to their origin and time of divergence. Breed *et al.* (1988) suggested a recent time of divergence based on an instant prezygotic isolation mechanism (Phillips *et al.* 1985) due to a radical change in sperm morphology. However, the present-day wide distribution, the level of subspeciation in *A. chrysophilus* and extensively overlapping ranges of the two species may suggest a considerable time of divergence from a common ancestor.

From a combination of cytogenetic and sperm morphological data, it is tempting to suggest an allopatric model of speciation (Endler 1977). It could be possible that chromosomal re-arrangements followed by reinforcement (Robinson and Roux 1985; Moritz 1986) may have given rise to post-zygotic isolation without overt phenotypic change (Meester 1988). Although a similar scenario has recently been mooted for other southern African murid rodents, such as *Otomys* and *Parotomys* (Meester *et al.* 1992), in the case of *Aethomys*, it may require further elucidation using molecular data.

10.7 A Proposed Classification for the Genus *Aethomys*

The inferred phylogeny provided a basis for the derivation of a classification for the genus. Consequently, this study is concluded by the provision of a proposed classification for the genus (Table 10.2) as derived from phylogenetic analyses of qualitative cranial data (Chapter 9).

The general suprageneric classification of extant rodents is adopted from the systematic treatment of Simpson (1945). The systematic treatment of the remaining taxa is based on Davis (1975), De Graaff (1981), Meester *et al.* (1986) and Musser and Carleton (1993). The exceptions are the present study's formal recognition of *A. ineptus* Thomas and Wroughton, 1908 (Chapter 4), the recognition of four subspecies within *A. namaquensis* (*A. n. namaquensis* A. Smith, 1834; *A. n. lehocla* A. Smith, 1836; *A. n. alborarius* Peters, 1852; and *A. n. monticularis* Jameson, 1909) (Chapter 5), and two subspecies within *A. chrysophilus* De Winton, 1897 (*A. c. chrysophilus* De Winton, 1897; *A. c. imago* Thomas, 1927) (Chapter 6).

Table 10.1 Characters shown to be important in the second, shape-related principal component axis (+) from principal components analyses of geographic and non-geographic variation, and species relationships of *Aethomys* from southern Africa. Abbreviations represent: *Aethomys chrysophilus* (chr), *A. granti* (gra), *A. ineptus* (ine) and *A. namaquensis* (nam). Measurements are defined in Figure 2.5.

Variable	Analysis					
	Non-geographic variation*	Species Relationships+	Geographic variation[x]			
			chr	ine	nam	gra
Greatest length of skull						
Greatest length of frontals	+	+			+	+
Length of nasals to zygomatic arch		+				
Greatest width of bulla			+			
Foramen magnum height	+	+	+			+
Length of M^1						
Width of M^2	+	+	+	+	+	+
Length of angular process to mandibular condyle						+
Length of mandibular foramen to condyle						
Length of I_1 to M_3						
Width of M_2	+	+		+	+	+

* Although the analysis of non-geographic variation was based on two samples each of *A. chrysophilus* and *A. namaquensis*, character loadings in all samples were broadly similar.

\+ Species relationships include all southern African species, and the exclusive treatment of the *A. chrysophilus* species complex; the character loadings of which were broadly similar.

x Sample size limitations precluded the analysis of geographic variation in *A. silindensis*.

Table 10.2 A proposed classification for the genus *Aethomys* as derived from phylogenetic analyses of qualitative cranial data. The suprageneric classification follows Simpson (1945). The systematic treatment of the remaining taxa is based on Davis (1975), De Graaff (1981), Meester *et al.* (1986), Musser and Carleton (1993) and the present study.

Order: Rodentia Bowdich, 1821
Suborder: Myomorpha Brandt, 1855
Superfamily: Muroidea Miller and Gidley, 1918
Family: Muridae Gray, 1821
Subfamily: Murinae Murray, 1866
Genus: *Aethomys* Thomas, 1915
Subgenus: *Aethomys* Thomas, 1915
Species: *A* (*A*) *kaiseri* Noack, 1887
A (*A*) *chrysophilus* De Winton, 1897
Subspecies: *A. c. chrysophilus* De Winton, 1897
A. c. imago Thomas, 1927
A (*A*) *nyikae* Thomas, 1897
A (*A*) *thomasi* De Winton, 1897
A (*A*) *hindei* Thomas, 1902
A (*A*) *bocagei* Thomas, 1904
A (*A*) *ineptus* Thomas and Wroughton, 1908
A (*A*) *stannarius* Thomas 1913
A (*A*) *silindensis* Roberts, 1938

Subgenus: *Micaelamys* Ellerman, 1941
Species: *A* (*M*) *namaquensis* A. Smith, 1834
Subspecies: *A. n. namaquensis* A. Smith, 1834
A. n. lehocla A. Smith, 1836
A. n. alborarius Peters, 1852
A. n. monticularis Jameson, 1909
A (*M*) *granti* Wroughton, 1908

SUMMARY

Five species of African rock rats of the genus *Aethomys*, *A. namaquensis*, *A. granti*, *A. silindensis*, *A. chrysophilus* and *A. ineptus* are recognized in southern Africa. Morphometric analyses indicated that *A. namaquensis*, *A. granti* and *A. silindensis* differ markedly in cranial size and/or shape. Morphometric analyses involving cytogenetically known specimens of *A. chrysophilus* revealed that it comprises two sympatric, morphologically similar species, *A. chrysophilus* and *A. ineptus*. This is concordant with observations on cranial morphology and earlier investigations involving cytogenetics, protein electrophoresis and sperm morphology. Contrary to published reports, the morphometric data showed that the Central African *A. nyikae* does not extend into southern Africa, and the single previous record from eastern Zimbabwe is probably based on a misidentification.

Patterns of intraspecific variation in *A. namaquensis* support the recognition of four subspecies, *A. n. namaquensis*, *A. n. lehocla*, *A. n. alborarius* and *A. n. monticularis*. There are strong indications that the morphological discontinuities of the subspecies broadly coincide with the major biomes of southern Africa. Similarly, within *A. chrysophilus*, there is support for the recognition of two subspecies, *A. c. chrysophilus* and *A. c. imago*. The morphological discontinuity of the subspecies coincided with an altitudinal limit of the eastern part of southern Africa. All subspecies recognized herein differ in both cranial size and shape, and their treatment considerably reduces the number of previously recognized races within species of

Aethomys in southern Africa.

Geographic variation among populations of *A. ineptus* is clinal, and size was positively and significantly correlated with longitude. Intraspecific variation in the geographically restricted *A. granti*, on the other hand, was highly suggestive of a southwesterly-northeasterly cline.

A cladistic appraisal of phylogenetic relationships among the 11 recognized species of *Aethomys* in Africa, based on qualitative cranial morphological characters, suggested the retention of *Micaelamys* and *Aethomys* as subgenera.

OPSOMMING

Vyf klipmuis-spesies van die genus *Aethomys*, nl. *A. namaquensis*, *A. granti*, *A. silindensis*, *A. chrysophilus* en *A. ineptus*, word in suider-Afrika aangetref. Morfometriese analises het aangedui aan dat *A. namaquensis*, *A. granti* en *A. silindensis* opvallend in kraniale grootte en/of vorm verskil. Morfometriese analises, wat sitogeneties bekende eksemplare van *A. chrysophilus* insluit, het aangedui aan dat die takson twee spesies, wat simpatries is en morfologiese ooreenkomste toon, insluit nl. *A. chrysophilus* en *A. ineptus*. Dit stem ooreen met waarnemings van kraniale morfologie en voorlopige ondersoeke wat sitogenetika, proteïn-elektroforese en sperm-morfologie aanraak. In teenstelling met gepubliseerde beskrywings toon morfometriese data dat die sentraal-Afrikaanse *A. nyikae* nie in suider-Afrika voorkom nie en dat die enkele rekord, wat voorheen in oos-Zimbabwe aangemeld is, heelwaarskynlik op 'n foutiewe identifikasie gebaseer was.

Intraspesifieke variasie in *A. namaquensis* onderskryf die bestaan van vier subspesies, nl. *A. n. namaquensis*, *A. n. lehocla*, *A. n. alborarius* en *A. n. monticularis*. Daar is sterk aanduidings dat morfometriese oorgangsones van die subspesies breedweg met die belangrikste biome in suider-Afrika ooreenstem. Binne *A. chrysophilus* is daar soortgelyke steun vir die erkenning van twee subspesies, *A. c. chrysophilus* en *A. c. imago*. Die morfometriese oorgangsones van die subspesies stem ooreen met lengtegraadgrense van die oostelike Platorand. Alle subspesies wat hier erken word verskil beide in kraniale grootte en vorm en hierdie oorsig verminder die aantal rasse wat in *Aethomys* spesies

in suider-Afrika erken word.

Geografiese variasie binne berolkings van *A. ineptus* is klinaal, en grootte kon positief en betekenisvol met lengtegraad gekorreleer word. Intraspesifieke variasie van die geografies beperkte *A. granti* het 'n sterk aanduiding van 'n suidwestelik-noordoostelike klinus getoon.

'n Kladistiese ondersoek van filogenetiese verwantskappe onder die elf erkende spesies van *Aethomys* in Afrika, gebaseer op kwalitatiewe karakters, dui aan dat *Micaelamys* en *Aethomys* as subgenera behou moet word.

REFERENCES

ACOCKS, J. P. H. 1988. Veld types of South Africa. The Government Printer, Pretoria.

ADAMS, E. N. 1972. Consensus techniques and the comparison of taxonomic trees. *Syst. Zool.* 21:390-397.

ALBRECHT, F. O., AND BLACKITH, R. E. 1957. Phase and molting polymorphism in locusts. *Evolution* 11:166-177.

ALLEN, G. M. 1939. A checklist of African mammals. *Bull. Mus. comp. Zool., Harvard* 83:1-763.

ANSELL, W. F. H. 1978. The mammals of Zambia. The National Parks and Wildlife Service, Chilanga, Zambia.

ANSELL, W. F. H., DOWSETT, R. J. 1988. Mammals of Malawi: An annotated check list and atlas. The Trendrine Press, Zennor, St. Ives, Cornwall.

ARCHIE, J. W. 1989. Homoplasy excess ratios: New indices for measuring levels of homoplasy in phylogenetic systematics and a critique of the consistency index. *Syst. Zool.* 38:253-269.

ASHLOCK, P. D. 1971. Monophyly and associated terms. *Syst. Zool.* 20:63-69.

ASHTON AND TATE SOFTWARE INC. rBase. Ashton-Tate, Berkeley, California.

AVERY, D. M. 1981. Holocene micromammalian faunas from the northern Cape Province, South Africa. *S. Afr. J. Sci.* 77:265-273.

AVERY, D. M. 1982. Micromammals as palaeoenvironmental indicators and an interpretation of the late Quarternary in the southern Cape Province, South Africa. *Ann. S. Afr. Mus.*

85:183-374.

AVERY, D. M. 1995. A preliminary assessment of the micromammalian remains from Gladysvale Cave, South Africa. *Palaeont. Afr.* 32:1-10.

BAILEY, R. C., AND BYRNES, J. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. *Syst. Zool.* 39:124-130.

BAKER, R. J., QUMSIYEH, M. B., AND RAUTENBACH, I. L.. 1988. Evidence for eight tandem and five centric fusions in the evolution of the karyotype of *Aethomys namaquensis* A. Smith (Rodentia:Muridae). *Genetica* 76:161-169.

BARRETT, M., DONOGHUE, M. J., AND SOBER, E. 1991. Against consensus. *Syst. Zool.* 40:486-493.

BARTON, N. H., AND HEWITT, G. M. 1985. Analysis of hybrid zones. *Annu. Rev. Ecol. Syst.* 16:113-148.

BELBIN, L. 1989. PATN pattern analysis package. Technical reference manual. CSIRO Division of Wildlife and Ecology, Canberra.

BENZECRI, J. P. 1977. Histoire et prehistoire de l'analyse des donnees. 5-L'analyse des correspondances. *Cahiers de l'Analyse des Donnees*, 2:9-40.

BERGMANN, C. 1847. Ueber die Verhaltnisse der Warmeokonomie der Thiere zu ihrer Grosse. *Gottinger studien* 3:595-708.

BEST, T. L. 1978. Variation in Kangaroo rats (Genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. *J. Mamm.* 59:160-175.

BLACK, C. G., AND KRISHTALKA, L. 1986. Rodents, bats, and insectivores from Plio-Pleistocene sediments to the east of Lake Turkana, Kenya. *Contr. Sci.* 372:1-15.

BLACKITH, R. E., AND REYMENT, R. A. 1971. Multivariate Morphometrics. Academic Press, London.

BOCK, W. J. 1981. Functional-adaptive analysis in evolutionary classification. *Amer. Zool.* 27:5-20.

BONHOMME, F., ISKANDER, D., THALER, L., AND PETTER, F. 1985. Electromorphs and phylogeny muroid rodents. Pp. 671-683, *in* Evolutionary relationships among rodents, a multidisciplinary analysis (P. W. Luckett and J. L. Hartenberger, eds.). NATO ASI Series, S. A. Life Sciences 92.

BOOKSTEIN, F. L. 1994. Can biometrical shape be a homologous character. Pp 197-226, *in* Homology: The hierarchical basis of comparative biology (B. K. Hall, ed.). Academic Press, New York.

BOOKSTEIN, F. L., CHERNOFF, B. C., ELDER, L. R., HUMPHRIES, J. M., SMITH, G. R., AND STRAUSS, R. E. 1985. Morphometrics in Evolutionary Biology. Special Publication No. 15, Academy of Natural Sciences of Philadelphia, Philadelphia.

BORGIA, G. 1994. The scandals of San Marco. *Quart. Rev. Biol.* 69:373-375.

BORLAND INTERNATIONAL INC. (1987). Quattro. Scotts Valley, California.

BREED, W. G., COX, G. A., LEIGH, C. M., AND HAWKINS, P. 1988. Sperm head structure of a murid rodent from southern Africa: The red veld rat *Aethomys chrysophilus*. *Gamete Res.* 19:191-202.

BRENNAN, J. M., AND FAIRBAIRN, D. J. 1995. Clinal variation in morphology among eastern populations of the waterstrider, *Aquarius remigis* Say (Hemiptera: Gerridae). *Biol. J. Linn.*

Soc. 54:151-171.

BROADLEY, D. G. 1966. Localities in South-East Africa from which herpetological material has been collected, with quarter-degree grid references. Unpublished. National Museum of Zimbabwe, Bulawayo.

BROOKS, D. R., AND WILEY, E. O. 1985. Theories and methods in different approaches to phylogenetic systematics. *Cladistics* 1:1-11.

BROTHERS, D. J. 1975. Phylogeny and classification of the aculeata Hymenoptera, with special reference to Mutillidae. *Univ. Kansas Sci. Bull*. 50:483-648.

BRYANT, H. N. 1996. Explicitness, stability, and universality in the phylogenetic definition and usage of taxon names: A case study of the phylogenetic taxonomy of the Carnivora (Mammalia). *Syst. Biol*. 45:174-189.

CAMPBELL, N. A, AND ATCHLEY, W. R. 1981. The geometry of canonical variates analysis. *Syst. Zool*. 30:268-280.

CANE, W. P. 1993. The ontogeny of postcranial integration in the common tern, *Sterna hirundo*. *Evolution* 47:1138-1151.

CANNATELLA, D. C., AND HILLIS, D. M. 1993. Amphibian relationships: Phylogenetic analysis of morphology and molecules. *Herpetol. Monogr*. 7:1-7.

CAVALLI-SFORZA, L. L., AND EDWARDS, A. W. F. 1967. Phylogenetic analysis: Models and estimation procedures. *Evolution* 32:550-570.

CHAPMAN, J. A., KRAMER, K. L., DIPPENAAR, N. J., AND ROBINSON, T. J. 1992. Systematics and biogeography of the New England cottontail, *Sylvilagus transitionalis* (Bangs, 1895), with description of a new species from the Appalachian Mountains.

Proc. Biol. Soc. Washington 105:841-866.

CHEVERUD, J. M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36:499-516.

CHEVERUD, J. M., WAGNER, G. P., AND DOW, M. M. 1989. Methods for the comparative analysis of variation patterns. *Syst. Zool.* 38:201-213.

CHIMIMBA, C. T., AND DIPPENAAR, N. J. 1994. Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa. *S. Afr. J. Zool.* 29:107-117.

CHIMIMBA C. T., AND DIPPENAAR, N. J. 1995. The selection of taxonomic characters for morphometric analysis: A case study based on southern African *Aethomys* (Mammalia: Rodentia: Muridae). *Ann. Carnegie Mus.* 64:197-217.

CHIMIMBA, C. T., AND KITCHENER, D. J. 1991. A systematic revision of Australian Emballonuridae (Mammalia: Chiroptera). *Rec. West. Aust. Mus.* 15:203-265.

CLARK, J. D. 1967. Atlas of African prehistory (+ maps and overlays). The University of Chicago Press, Chicago and London.

CRACRAFT, J. 1981. Pattern and process in paleobiology: the role of cladistic analysis in systematic paleontology. *Paleobiol.* 7:456-468.

CRANSTON, P. S., AND HUMPHRIES, C. J. 1988. Cladistics and computers: A chironomid conundrum? *Cladistics* 4:72-92.

CREEL, N. 1986. Size and phylogeny in hominid primates. *Syst. Zool.* 35:81-99.

CRISP, M. D., AND WESTON, P. H. 1993. Geographic and ontogenetic

variation in morphology of Australian waratahs (*Teleopea*: Proteaceae). *Syst. Biol.* 42:49-76.

DAVIS, D. H. S. 1965. Classification problems of African Muridae. *Zool. Afr.* 1:121-145.

DAVIS, D. H. S. 1968. A preliminary identification manual for African mammals. 20. Rodentia, Murinae: Genus *Aethomys*. Smithsonian institution, Washington D. C.

DAVIS, D. H. S. 1975. Genus *Aethomys*. Part 6.6, *in* The Mammals of Africa: An Identification Manual (J. Meester and H. W. Setzer, eds.). Smithsonian Institution Press, Washington, D. C.

DAVIS, D. H. S., AND MISONNE, X. 1964. Gazetteer of collecting localities of African rodents. *Mus. r Afr. cent., Tervuren. Zool.* 7:100.

DE BLASE, A. F., AND MARTIN, R. E. 1981. A Manual of Mammalogy, with Key to Families of the World. Wm. C. Brown Company Publishers, Dubuque, Iowa.

DE GRAAFF, G. 1960. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal system. *Palaeont. Afr.* 7:79-118.

DE GRAAFF, G. 1961. On the fossil mammalian microfauna collected at Kromdraai by Draper in 1895. *S. Afr. J. Sci.* 56:259-260.

DE GRAAFF, G. 1981. The Rodents of Southern Africa. Butterworths, Pretoria.

DELANY, M. J. 1975. The Rodents of Uganda. Trustees of the British Museum (Natural History), London.

DENYS, C. 1987. Micromammals from the west Natron Pleistocene deposits (Tanzania): Biostratigraphy and paleoecology. *Sci. Geol. Bull.* 40: 185-201.

DENYS, C. 1990*a*. Implications paleoecologiques et paleobiogeographiques de l'etude de rongeurs plio-pleistocenes d'Afrique orientale et australe. Ph.D. thesis, Universite Paris, Paris.

DENYS, C. 1990*b*. Deux nouvelles especes d'*Aethomys* (Rodentia: Muridae) a Langebaanweg (Pliocene, Afrique du Sud): Implications phylogenetiques et paleoecologiques. *Ann. Paleontol.* (*Vert.-Invert.*) 76:41-69.

DENYS, C. 1995. The *A. hindei* (Rodentia, Muridae) complex revisited through morphological and biometrical analysis and its phylogenetic position within the genus *Aethomys*. Abstract of Papers and Posters. Small Mammal Symposium, Itala Game Reserve, KwaZulu-Natal, South Africa.

DENYS, C., AND TRANIER, M. 1992. Presence d'*Aethomys* (Mammalia, Rodentia, Muridae) au Tchad et analyse morphometrique preliminaire du complex *A. hindei*. *Mammalia* 56:625-656.

DE QUEIROZ, K., AND GAUTHIER, J. A. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. Syst. Zool. 39:307-322.

DE QUEIROZ, K., AND GAUTHIER, J. A. 1992. Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* 23:449-480.

DE QUEIROZ, K., AND GAUTHIER, J. A. 1994. Toward a phylogenetic system of biological nomenclature. *Trends Ecol. Evol.* 9:27-31.

DE WINTON, W. E. 1897. On Collections of Rodents made by Mr. J. ffolliot Darling in Mashunaland, and Mr. F. C. Selous in Matabeleland, with short Field-notes by the Collectors. *Proc. Zool. Soc. Lond.* for 1896:798-808.

DIPPENAAR, N. J., AND RAUTENBACH., I. L. 1986. Morphometrics and

karyology of the southern African species of the genus *Acomys* I. Geoffroy Saint-Hilaire, 1838 (Rodentia:Muridae). *Ann. Tvl. Mus.* 34:129-183.

DIXON, W. J. (ed.). 1985. BMDP statistical software. Univ. California Press, Berkeley.

DOWLING, T. E., SMITH, G. R., AND BROWN, W. M. 1989. Reproductive isolation and introgression between *Notropis cornutus* and *Notropis chysocephalus* (Family Ciprinidae): Comparison of morphology, allozymes, and mitochondrial DNA. *Evolution* 43:620-634.

DUELLMAN, W. E., AND HILLIS, D. M. 1987. Marsupial frogs (Anura: Hylidae: *Gastrotheca*) of the Equadorian Andes: Resolution of taxonomic problems and phylogenetic relationships. *Herpetologica* 43:135-167.

ELLERMAN, J. R. 1941. The Families and Genera of Living Rodents. British Museum of Natural History, London.

ELLERMAN, J. R., MORRISON-SCOTT, T. C. S., AND HAYMAN, R. W. 1953. Southern African Mammals 1758 to 1951: A classification. British Museum of Natural History, London.

ENDLER, J. A. 1977. Geographic variation, Speciation, and Clines. Princeton University Press, Princeton, New Jersey.

FAITH, D. P. 1991. Cladistic permutation tests for monophyly and nonmonophyly. *Syst. Zool.* 40:366-375.

FARRIS, J. S. 1970. Methods for computing Wagner trees. *Syst. Zool.* 19:83-92.

FARRIS, J. S. 1982. Outgroups and parsimony. *Syst. Zool.* 31:328-334.

FARRIS, J. S. 1983. The logical basis of phylogenetic analysis. Pp 7-36, *in* Advances in Cladistics, Proceedings of the Willi

Hennig Society Vol. 2 (N. I. Platnick and V. A. Funk, eds.). Columbia University Press, New York.

FARRIS, J. S. 1985. Distance data revisited. *Cladistics* 1:67-85.

FARRIS, J. S. 1988. Hennig86, version 1.5. Distributed by the author, Port Jefferson Station, New York.

FELSENSTEIN, J. 1982. Numerical methods for inferring evolutionary trees. *Quart. Rev. Biol.* 57:379-404.

FELSENSTEIN, J. 1985. Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39:783-791.

FELSENSTEIN, J. 1986. Distance methods: A reply to Farris. *Cladistics* 2:130-143.

FINK, W. L., AND ZELDITCH, M. L. 1995. Phylogenetic analysis of ontogenetic shape transformations: A reassessment of the Piranha genus *Pygocentrus* (Teleostei). *Syst. Biol.* 44:343-360.

FITZHUGH, K. 1989. Cladistics in the fast lane. *J. New York Entomol. Soc.* 97:234-241.

GABRIEL, K. R., AND SOKAL, R. R. 1969. A new statistical approach to geographic variation analysis. *Syst. Zool.* 18:259-278.

GANS, C, AND NORTHCUTT, R. G. 1983. Neural crest and the origin of vertebrates: A new head. *Science* 220:268-273.

GAUTHIER, J., ESTES, R., AND DE QUEIROZ, 1988. A phylogenetic analysis of Lepidosauromorpha. Pp. 15-98, *in* Phylogenetic relationships of the lizard families: Essays commemorating Charles L. Camp (R. Estes and G. K. Pregill, eds.). Stanford University Press, Stanford, California.

GEAR, J. H. S., DAVIS, D. H. S., AND PITCHFORD, R. J. 1966. The susceptibility of rodents to schistom infection, with special reference to *Schistosoma haematobium*. *Bull. World*

Health Org. 35:213-221.

GENOWAYS, H. H., AND CHOATE, J. R. 1972. A multivariate analysis of systematic relationships among populations of the short-tailed shrew (Genus *Blarina*) in Nebraska. *Syst. Zool.* 21:106-116.

GENOWAYS, H. H., AND JONES,Jr., J. K. 1972. Variation and ecology in a local population of the vesper mouse (*Nyctomys sumichrasti*). *Occas. Papers Mus., Texas Tech Univ.* 3: 1-22.

GENOWAYS, H. H., AND SCHLITTER, D. A. 1981. Collections of recent mammals of the world, exclusive of Canada and the United States. *Ann. Carnegie Mus.* 50:47-80.

GEORGE, S. B., CHOATE, J. R., GENOWAYS, H. H. 1981. Distribution and taxonomic status of *Blarina hylophaga* Elliot (Insectivora: Soricidae). *Ann. Carnegie Mus.* 50:493-513.

GINGERICH, P. D. 1980. Paleontology, phylogeny, and classification: an example from the mammalian fossil record. *Syst. Zool.* 28:41-464.

GORDON, D. H., AND RAUTENBACH, I. L. 1980. Species complexes in medically important rodents: Chromosome studies of *Aethomys*, *Tatera* and *Saccostomus* (Rodentia: Muridae, Cricetidae). *S. Afr. J. Sci.* 76:559-561.

GORDON, D. H., AND WATSON, C. R. B. 1986. Identification of cryptic species of rodents (*Mastomys*, *Aethomys*, *Saccostomus*) in the Kruger National Park. *S. Afr. J. Zool.* 21:95-99.

GOULD, S. J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: A way of studying non- adaptation. *Syst. Zool.* 33:217-237.

GOULD, S. J., AND JOHNSTON, R. F. 1972. Geographic variation. *Annu. Rev. Ecol. Syst.* 3:457-498.

GOULD, S. J., AND LEWONTIN, R. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptionist program. *Proc. Roy. Soc. Lond.* B205:581-598.

GOULD, S. J., WOODRUFF, D. F., AND MARTIN, J. P. 1974. Genetics and morphometrics of *Cerion* at Pongo Carpet: A new systematic approach to this enigmatic land snail. *Syst. Zool.* 23:518-535.

GREENACRE, M. J. 1984. Theory and Applications of Correspondence Analysis. Academic Press, London.

GREENACRE, M. J. 1986. SimCA: A program to perform simple correspondence analysis. *Amer. Statist.* 40:230-231.

GREENACRE, M. J. 1990. SimCA, User's Manual. Department of Statistics, University of South Africa (UNISA), Pretoria.

GREENACRE, M. J., AND VRBA, E. S. 1984. Graphical display and interpretation of antelope census data in African wildlife areas, using correspondence analysis. *Ecology* 65:984-997.

HALDANE, J. B. S. 1955. The measurement of variation. *Evolution* 9:484.

HALL, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley and Los Angeles.

HALLET, A. F., McNEILL, D., AND MEYER, K. F. 1970. A serological survey of small mammals for plague in southern Africa. *S. Afr. Med. J.* 44:831-837.

HANDY, M. D., AND PENNY, D. 1982. Branch and bound algorithms to determine minimal evolutionary trees. *Math. Biosc.* 59:277-290.

HARTLEY, H. O. 1950. The maximum *F*-ratio as a short cut test for heterogeneity of variances. *Biometrika* 37:308-312.

HEBEL, R., AND STROMBERG, M. W. 1976. Anatomy of the Laboratory

Rat. Williams and Wilkens, Baltimore.

HENDEY, Q. B. 1981. Paleoecology of the late tertiary fossil occurrences in "E" Quarry, Langebaanweg, South Africa and a re-introduction of their geological context. *Ann. S. Afr. Mus.* 84:1-104.

HENNIG, W. 1966. Phylogenetic Systematics (transl. D. D. Davis and R. Zangerl). University of Illinois Press, Urbana.

HILL, J. E. 1935. Cranial foramina in rodents. *J. Mamm.* 16:121-129.

HILL, M. O. 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61:237-251.

HILL, M. O. 1974. Correspondence analysis: a neglected multivariate method. *Appl. Statist.* 23:340-354.

HILLIS, D. M. 1985. Evolutionary genetics of the Andean lizard genus *Pholidobolus* (Sauria: Gymnophtalmidae): Phylogeny, biogeography, and a comparison of tree construction techniques. *Syst. Zool.* 34:109-126.

HILLIS, D. M. 1987. Molecular versus morphological approaches to systematics. *Annu. Rev. Ecol. Syst.* 18:23-42.

HILLIS, D. M. 1995. Approaches for assessing phylogenetic accuracy. *Syst. Biol.* 44:3-16.

HILLIS, D. M., AND BULL, J. J. 1993. An empirical test of bootstrapping as a method for assessing confidence in phylogenetic analysis. *Syst. Biol.* 42:182-192.

HILLIS, D. M., AND HUELSENBECK, J. P. 1992. Signal, noise, and reliability in molecular phylogenetic analysis. *J. Hered.* 83:189-195.

HILLIS, D. M., BULL, J. J., WHITE, M. E., BADGETT, M. R., AND MOLINEUX, I. J. 1993. Experimental approaches to

phylogenetic analysis. *Syst. Biol.* 42:90-92.

HOLLISTER, N. 1919. East African mammals in the United States National Museum. Part II. Rodentia, Lagomorpha and Tubulidentata. *Smithsonian Institution United States Nat. Mus. Bull.* 99:1-181.

HOOD, C. S., AND SMITH, J. D. 1982. Cladistic analysis of female reproductive histomorphology in phyllostomatoid bats. *Syst. Zool.* 31:241-251.

HUELSENBECK, J. P. 1991. Tree-length distribution skewness: An indicator of phylogenetic information. *Syst. Zool.* 49:257-270.

HULL, D. L. 1970. Contemporary systematic philosophies. *Annu. Rev. Ecol. Syst.* 1:19-54.

HUMPHRIES, J. M., BOOKSTEIN, F. L., CHERNOFF, B., SMITH, G. R., ELDER, R. L., AND POSS, S. G. 1981. Multivariate discrimination by shape in relation to size. *Syst. Zool.* 30:291-308.

HUTTERER, R., AND JOGER, U. 1982. Klensauger aus dem hochland von Adamaoua, Kamerun. *Bonn. Zool. Beitr.* 33:119-132.

JAEGER, J. J. 1976. Les rongeurs (Mammalia, Rodentia) du Pleistocene inferieur d'Olduvai Bed I (Tanzanie). 1e parti: les Murides. Pp. 58-120, *in* Fossil vertebrates of Africa (R. J. G. Savage and S. C. Coryndon, eds.). Academic Press, New York and London.

JAEGER, J J. 1979. Les faunes de rongeurs et de lagomorphes du Pliocene et du Pleistocene d'Afrique orientale. *Bull. Soc. Geol. France* 7:301-308.

JAMES, F. C. 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51:365-390.

JAMES, F. C., AND McCULLOCH, C. E. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's Box? *Annu. Rev. Ecol. Syst.* 21:129-166.

JAMESON, H. L. 1909. On a collection of mammals from South Africa. *Ann. Mag. Nat. Hist.* 4 ser. 8:455-474.

JENTINK, F. A. 1909. Beitrage zur Kenntnis der Fauna von Sud-Afrika. *Zool. Jahrb. Syst.* 28:239-262.

JOHNSTON, R. E. 1973. Evolution in the house sparrow. IV. Replicate studies in phenetic covariation. *Syst. Zool.* 22:219-226.

JOHNSTON, R. F., AND SELANDER, R. K. 1971. Evolution in the house sparrow. II. Adaptive differentiation in North American populations. *Evolution* 25:1-28.

JOLLIFFE, I. T. 1986. Principal component analysis. Springer Verlag, New York.

JURY, M. R., WEEKS, S., AND GONDWE, M. P. 1997. Satellite-observed vegetation as an indicator of climate variability over southern Africa. *S. Afr. J. Sci.* 93:34-38.

KEAY, R. W. J. 1959. Explanatory notes on vegetation map of Africa south of the Tropic of Cancer (and map). Oxford University Press, London.

KEOGH, H. J. 1985. A photographic reference system based on the cuticular scale patterns and groove of the hair of 44 species of southern African Cricetidae and Muridae. *S. Afr. J. Wildl. Res.* 15:109-159.

KIM, J. O. 1975. Factor analysis. Pp. 468-514, *in* Statistical Package for the Social Sciences (N. H. Nie, C. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds.). McGraw-Hill Book Company, New York.

KLASSEN G. J., MOOI, R. D., AND LOCKE, A. 1991. Consistency indices and random data. *Syst. Zool.* 40:446-457.

KLECKA, W. R. 1975. Discriminant analysis. Pp. 434-467, *in* Statistical Package for the Social Sciences (N. H. Nie, C. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds.). McGraw-Hill Book Company, New York.

KLUGE, A. G., AND FARRIS, J. S. 1969. Quantitative phyletics and the evolution of Anurans. *Syst. Zool.* 18:1-32.

LEAMY, L. 1983. Variance partitioning and effects of sex and age on morphometric traits in randombred house mice. *J. Mamm.* 64: 55-61.

LEAMY, L. H., AND BADER, R. S. 1968. Components of variance of odontometric traits in a wild derived population of *Peromyscus leucopus*. *Evolution* 22: 826-834.

LEAMY, L., AND BRADLEY, D. 1982. Static and growth allometry of morphometric traits in randombred house mice. *Evolution* 36:1200-1212.

LEAMY, L., AND THORPE, R. S. 1984. Morphometric studies in inbred and hybrid house mice. Heterosis, homeostasis and heritability of size and shape. *Biol. J. Linn. Soc.* 22:233-241.

LELE, S., AND RICHTSMEIER, J. T. 1990. Statistical models in morphometrics: Are they realistic? *Syst. Biol.* 39:60-69.

LEWONTIN, R. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York.

LINZEY, A. V., AND KESNER, M. H. 1995. Small mammal community structure in a savanna woodland ecosystem. Abstract of Papers and Posters. Small Mammal Symposium, Itala Game Reserve, KwaZulu-Natal, South Africa.

LIVEZEY, B. C. 1989. Morphometric patterns in recent and fossil penguins (Aves, Sphenisciformes). *J. Zool. Lond.* 219:269-307.

LIVEZEY, B. C. 1990. Evolutionary morphology of flightlessness in the Auckland Islands teal. *Condor* 92:639-673.

LIVEZEY, B. C., AND STORER, R. W. 1992. Morphometric comparison of skeletons on the western grebe complex *Aechmophorus* of the United States and Canada. *Condor* 94:668-679.

LOUGHEED, S. C., ARNOLD, T. W., AND BAILEY, R. C. 1991. Measurement error of external and skeletal variables in birds and its effect on principal components. *Auk* 108:432-436.

LUNDBERG, J. G. 1973. More on primitiveness, higher level phylogenies and ontogenetic transformations. *Syst. Zool.* 22:327-329.

LUNDHOLM, B. G. 1955. Descriptions of new mammals. *Ann. Tvl. Mus.* 22:279-303.

MADDISON, W. P., DONOGHUE, M. J., AND MADDISON, D. R. 1984. Outgroup analysis and parsimony. *Syst. Zool.* 33:83-103.

MADDISON, W. P., AND MADDISON, D. R. 1992. MacClade: Analysis of phylogenetic and character evolution, version 3.01. Sinauer, Sunderland, Massachusetts.

MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. *Proc. Nat. Instit. Sci.* (*India*) 2:49-55.

MAHALANOBIS, P. C., MAJUMDAR, D. M., AND RAO, C. R. 1949. Anthropometric survey of the United Provinces, 1941; a statistical study. *Sankhya* 3:35-40.

MARCUS, L. F. 1990. Traditional morphometrics. Pp. 77-122, *in* Proceedings of the Michigan Morphometrics Workshop (F. J.

Rohlf and F. L. Bookstein, eds.). Special Publication No. 2. University of Michigan Museum of Comparative Zoology, Ann Arbor.

MARCUS L. F., Bello, E, AND GARCIA-VALDECASAS, A., eds. 1993. Contributions to morphometrics. Monografias del Museo Nacional de Ciencias Naturales, Madrid.

MARGUSH, T., AND McMORRIS, F. R. 1981. Consensus n-trees. *Bull. Math. Biol.* 43:239-244.

MATTHEY, R. 1954. Nouvelles recherches sur les chromosomes des Muridae. *Caryologia* 6:1-44.

MATTHEY, R. 1958. Les chromosomes et al position systematique de quelques Murinae Africains. *Acta. Trop.* 15:97-117.

MATTHEY, R. 1964. Analyse caryologique de cing especes de Muridae Africains (Mammalia, Rodentia). *Mammalia* 28:403-418.

MAYR, E. 1942. Systematics and the Origin of Species. Columbia University Press, New York.

MAYR, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts.

MAYR, E. 1976. Evolution and the Diversity of Life. Harvard University Press, Cambridge, Massachusetts.

MAYR, E. 1969. Principles of Systematic Zoology. First edition. McGraw-Hill Inc., New York.

MAYR, E. 1981. Biological classification: Toward a synthesis of opposing methodologies. *Science* 214:510-516.

MAYR E., AND ASHLOCK, P. D. 1991. Principles of Systematic Zoology. Second edition. McGraw-Hill, Inc., New York.

McFARLANE, J. E. 1964. Factors affecting growth and wing polymorphism on *Gryllodes sigllatus* (Walk.): Dietary protein level and a possible effect of photoperiod. *Can. J. Zool.*

42:767-771.

McLAREN, S. B. AND BRAUN, J. K., eds. 1993. GIS Applications in Mammalogy. Special Publications of the Oklahoma Museum of Natural History in collaboration with The Carnegie Museum of Natural History, Norman.

MEESTER, J. 1988. Chromosomal speciation in Southern African small mammals. *S. Afr. J. Sci.* 84:721-724.

MEESTER, J., DAVIS, D. H. S., AND COETZEE, C. G. 1964. An interim classification of southern African Mammals. Mimeograph of the Zoological Society of Southern Africa and the Council for Scientific and Industrial Research, South Africa.

MEESTER, J. A. J., RAUTENBACH, I. L., DIPPENAAR, N. J., AND BAKER, C. M. 1986. Classification of southern African mammals. *Tvl. Mus. Monogr.* 5:1-359.

MEESTER, J., TAYLOR, P. J., CONTRAFATTO,G. -C., CAMPBELL, G. K., WILLAN, K. LAMB, J. M., AND PILLAY, N. 1992. Chromosomal speciation in Southern African Otomyinae (Rodentia: Muridae): a review. *Durban Mus. Novit.* 17:58-63.

MEIER, R., KORES, P., AND DARWIN, S. 1991. Homoplasy slope ratio: A better measurement of observed homoplasy in cladistic analyses. *Syst. Zool.* 40:74-88.

MICHENER, C. D. 1970. Diverse approaches to systematics. *Evol. Biol.* 4: 1-38.

MICKEVICH, M. F., AND FARRIS, J. S. 1981. The implications of congruence in *Menidia*. *Syst. Zool.* 30:351-370.

MICKEVICH, M. F., AND JOHNSON, M. S. 1976. Congruence between morphological and allozyme data in evolutionary inference and character evolution. *Syst. Zool.* 25:269-270. (Correction, Vol. 26:252).

MISONNE, X. 1969. African and Indo-Australian Muridae evolutionary trends. *Ann. Mus. Roy. Afr. Centr. Tervuren Sci. Zool.* 172:1-219.

MIYAMOTO, M. M. 1981. Congruence among character sets in phylogenetic studies of the frog genus *Leptodactylus*. *Syst. Zool.* 30:281-290.

MOORE, W. J. 1981. The Mammalian Skull. Cambridge University Press, Cambridge, England.

MORITZ, C. 1986. The population biology of *Gehyra* (Gekkonidae): chromosome change and speciation. *Syst. Zool.* 35:46-67.

MORRIS, P. 1972. A review of mammalian age determination methods. *Mamm. Rev.* 2:69-104.

MORTON, S. R., AND ALEXANDER, F. 1982. Geographic variation in the external morphology of *Sminthopsis crassicaudatus* (Dasyuridae, Marsupialia). Pp 694-698, *in* Carnivorous Marsupials (M. Archer, ed.). *Roy. Zool. Soc. N.S.W.*, Sydney.

MOSS, M. L., AND YOUNG, R. W. 1960. Functional approach to craniology. *Amer. J. Phys. Anthrop.* 18:281-292.

MOUSSEAU, T. A. 1991. Landmarks in morphometrics, or the shape and size of morphometrics to come. *Evolution* 45:1979-1980.

MUSSER, G. G., AND CARLETON, M. D. 1993. Family Muridae. Pp 501-755, *in* Mammal Species of the World. Second edition (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institution Press, in association with the American Society of Mammalogists, London and Washington.

NEFF, N. A., AND MARCUS, L. F. 1980. A Survey of Multivariate Methods for Systematics. Privately published and *Am. Mus. Nat. Hist.*, New York.

NELSON, G. J. 1978. Ontogeny, phylogeny, paleontology, and the

biogenetic law. *Syst. Zool.* 27:324-345.

NELSON, G. 1979. Cladistic analysis and synthesis: Principles and definitions, with a historical note on Adanson's Familles des Plantes (1763-1764). *Syst. Zool.* 28:1-21.

NIE, N. H., HULL, C., JENKINS, J. G., STEINBRENNER, K., and BENT, D. H., eds. 1975. Statistical Package for the Social Sciences. McGraw-Hill Book Company, New York.

NODEN, D. 1978. The control of avian cephalic neural crest cytodifferentiation. I. Skeletal and connective tissues. *Develop. Biol.* 67:296-312.

NODEN, D. 1983. The embryonic origin of avian cephalic and cervical muscles and associated connective tissues. *Amer. J. Anat.* 168:257-276.

OLSON, E. C., AND MILLER, R. L. 1958. Morphological Integration. University of Chicago Press, Chicago.

OSTLE, B., AND MENSING, R. W. 1975. Statistics in Research. Third edition. Iowa State University Press, Ames.

OYAMA, M., TAKEHARA, H., AND OOI, Y. 1967. Revised standard soil colour charts. Ministry of Agriculture and Forestry, Japan, unpaged.

PAGE, R. D. M. 1989. Comments on component-compatibility in historical biogeography. *Cladistics* 5:167-182.

PANKAKOSKI, E., VAISANEN, R. A., AND NURMI, K. 1987. Variability of muskrat skulls: Measurement error, environmental modification and size allometry. *Syst. Zool.* 36:35-51.

PATTERSON, C. 1981. Significance of fossils in determining evolutionary relationships. *Annu. Rev. Ecol. Syst.* 12:195-223.

PATTERSON, C. 1982. Morphological characters and homology. Pp

21-74, *in* Problems of Phylogenetic Reconstruction (K. A. Joysey, ed.). Academic Press, London.

PERRIN, M. R. 1982. Prey specificity of the barn owl, *Tyto alba*, in the Great Fish River Valley of the eastern Cape Province. *S. Afr. J. Wildl. Res.* 12:14-25.

PETERS, W. C. H. 1852. Naturwissenschaftliche Reise nach Mossambique. Zoologie I. Saugetiere. Berlin: Georg Reimer.

PETIT-MARIE, N, AND PONGE, J. F. 1979. Primate cranial morphology through ontogenesis and phylogenesis, factorial analysis of global variation. *J. Hum. Evol.* 8:233-234.

PHILLIPS, D. M., SHARGI, R., AND DEKEL, W. 1985. Mammalian fertilization as seen with the scanning electron microscope. *Amer. J. Anat.* 174:353-372.

PIMENTEL, R. A. 1959. Mendelian infraspecific divergence levels and their analysis. *Syst. Zool.* 8:139-159.

PIMENTEL, R. A. 1979. Morphometrics: The Multivariate Analysis of Biological Data. Kendall/Hunt Publishing Company, Dubuque.

PIMENTEL, R. A., AND RIGGINS, R. 1987. The nature of cladistic data. *Cladistics*. 3:201-209.

PIMENTEL, R. A., AND SMITH, J. D. 1986*a*. BIOΣTAT I. A Tutorial Manual. Sigma Soft, Placentia, California.

PIMENTEL, R. A., AND SMITH, J. D. 1986*b*. BIOΣTAT II. A Tutorial Manual. Second Edition. Sigma Soft, Placentia, California.

POCOCK, T. N. 1987. Plio-Pleistocene mammalian microfauna in southern Africa - a preliminary report including description of two new fossil muroid genera (Mammalia: Rodentia). *Palaeontol. Afr.* 26:69-71.

POWER, D. M. 1970. Geographic variation of red-winged blackbirds in central North America. *Univ. Kansas Publ. Mus. Nat. Hist.*

19:1-83.

POWER, D. M. 1971. Statistical analysis of character correlations in Brewer's blackbirds. *Syst. Zool.* 20:186-203.

QUIN, D. G., SMITH, A. P., AND NORTON, T. W. 1996. Eco-geographic variation in size and sexual dimorphism in sugar gliders and squirrel gliders (Marsupialia: Petauridae). *Aust. J. Zool.* 44:19-45.

RAUTENBACH, I. L. 1978. The mammals of the Transvaal. Ph.D. thesis, University of Natal, Pietermaritzburg.

REIG, S. 1989. Errors and misjudgment of outliers in morphometric studies. Abstract of Papers and Posters. Fifth International Theriological Congress, Rome.

REIST, J. D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Can. J. Zool.* 63: 1429-1439.

RIEDL, R. 1978. Order in Living Organisms. John Wiley and Sons, New York.

RIEPPEL, O. 1980. Homology, a deductive concept. *Z. Zool. Syst. Evolutionsforsch* 18:315-319.

RISING, J. D. 1970. Morphological variation and evolution in some north American orioles. *Syst. Zool.* 19:315-351.

ROBBINS, C. B. 1973. Non-geographic variation in *Taterillus gracilis* (Thomas) (Rodentia: Cricetidae). *J. Mamm.* 54: 222-238.

ROBERTS, A. 1913. The collection of mammals in the Transvaal Museum registered up to 31st March 1913, with descriptions of new species. *Ann. Tvl. Mus.* 4:65-107.

ROBERTS, A. 1915. Additions to the collection of mammals in the Transvaal Museum. *Ann. Tvl. Mus.* 5:116-124.

ROBERTS, A. 1926. Some new South African mammals and some changes in nomenclature. *Ann. Tvl. Mus.* 11:245-263.

ROBERTS, A. 1931. New forms of South African mammals. *Ann. Tvl. Mus.* 14:221-236.

ROBERTS, A. 1938. Descriptions of new forms of mammals. *Ann. Tvl. Mus.* 19:231-245.

ROBERTS, A. 1946. Descriptions of numerous new subspecies of mammals. *Ann. Tvl. Mus.* 20:303-328.

ROBERTS, A. 1951. The Mammals of South Africa. Trustees of "The Mammals of South Africa" Book Fund, Johannesburg.

ROBINSON, T. J. 1981. Systematics of the southern African Leporidae. D.Sc. thesis, University of Pretoria, Pretoria.

ROBINSON, T. J., AND ROUX, C. Z. 1985. Chromosomal rearrangements in speciation. Pp. 71-73, *in* Species and Speciation (E. S. Vrba, ed.). *Tvl. Mus. Monogr.* 4, Transvaal Museum, Pretoria.

ROHLF, F. J. 1970. Adaptive hierarchical clustering schemes. *Syst. Zool.* 19:58-82.

ROHLF, F. J. 1986. NTSYS-pc. Numerical taxonomy System for the IBM PC microcomputers (and compatibles). Applied Biostatistics Inc. New York.

ROHLF, F. J. 1990. Morphometrics. *Annu. Rev. Ecol. Syst.* 21:299-316.

ROHLF, F. J., AND BOOKSTEIN, F. L. eds. 1990. Proceedings of the Michigan Morphometrics Workshop. Special Publication No. 2, University of Michigan Museum of Zoology, Ann Arbor.

ROHLF, F. J., AND MARCUS, L. F. 1993. A Revolution in morphometrics. *Trends Ecol. Evol.* 8:129-132.

ROSEVEAR, D. R. 1969. The Rodents of West Africa. British Museum of Natural History, London.

RUTHERFORD, M. C., AND WESTFALL, R. H. 1986. Biomes of southern Africa - an objective categorization. *Mem. Bot. Surv. S. Afr.* 54:1-98.

SANDERSON M. J., AND DONOGHUE, M. J. 1989. Patterns of variation in levels of homoplasy. *Evolution* 43:1781-1795.

SAS INSTITUTE, 1990. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, North Calorina.

SCHLITTER, D. A. 1978. Problems and priorities of research on the taxonomy and ecology of African small mammals. Pp. 211-214, *in* Ecology and Taxonomy of African Small Mammals (D. A. Schlitter, ed.), *Bull. Carnegie Mus. Nat. Hist.* 6.

SCHULTZ, D. L. DataQ. Aitken, South Carolina.

SCHWANN, H. 1906. A list of the mammals obtained by Messrs R. B. Woosnam and R. E. Dent in Bechuanaland. *Proc. Zool. Soc. Lond.* 1906:101-111.

SEARLE, J. B. 1984. Three new karyotypic races of the common shrew *Sorex araneus* (Mammalia: Insectivora) and phylogeny. *Syst. Zool.* 33:184-194.

SELZER, J., ed. 1993. Understanding Scientific Prose: Rhetoric of the Human Sciences. University of Wisconsin Press, Madison.

SEUTIN, G., RATCLIFFE, L. M., AND BOAG, P. 1995. Mitochondrial DNA homogeneity in the phenotypically diverse Redpole finch complex (Carduelinae: *Carduelis flammea-hornemanni*. *Evolution* 49:962-973.

SHORTRIDGE, G. C. 1942. Field notes on the first and second expeditions to the Cape museum's Mammal survey of the Cape Province; and descriptions of some new subgenera and subspecies. *Ann. S. Afr. Mus.* 36:27-100.

SIMPSON, G. G. 1945. The principles of classification and a

classification of mammals. *Bull. Amer. Mus. Nat. Hist.* 85: 1-350.

SIMPSON, G. G. 1961. Principles of Animal Taxonomy. Columbia University Press, New York.

SKEAD, C. J. 1973. Zoo-historical Gazetteer. *Ann. Cape Prov. Mus.* 10:1-259.

SKINNER, J. D., AND SMITHERS, R. H. N. 1990. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

SMITH, A. 1834. African zoology: Mammalia. *S. Afr. Quart. J.* 2:160.

SMITH, A. 1836. Report of the expedition for exploring Central Africa, from the Cape of Good Hope: 1834, under the superintendence of A. Smith. Government Gazette Office, Cape Town.

SMITH, M. F. 1979. Geographic variation in genic and morphological characters in *Peromyscus californicus*. *J. Mamm.* 60:705-722.

SMITH, G. R. 1990. Homology in morphometrics and phylogenetics. Pp 325-338, *in* Proceedings of the Michigan Morphometrics Workshop. Special Publication No. 2, University of Michigan Museum of Zoology, Ann Arbor.

SMITHERS, R. H. N. 1971. The Mammals of Botswana. *Mem. Nat. Mus. Rhod.* 4:1-340.

SMITHERS, R. H. N. 1983. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria.

SMITHERS, R. H. N., AND TELLO, J. L. P. L. 1976. Checklist and atlas of the mammals of Mozambique. *Mus. Mem. Nat. Mus. Monum. Rhod.* 8:1-184.

SMITHERS, R. H. N., AND WILSON, V. J. 1979. Checklist and atlas of the mammals of Zimbabwe Rhodesia. *Mus. Mem. Nat. Mus. Monum. Zim. Rhod.* 9:1-193.

SNEATH, P. H. A. 1995. Thirty years of numerical taxonomy. *Syst. Biol.* 44:281-298.

SNEATH, P. H. A. AND SOKAL, R. R. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco.

SOKAL, R. R., AND RINKEL, R. C. 1963. Geographic variation of alate *Pemphigus populi-transversus* in eastern North America. *Univ. Kansas Sci. Bull.* 44:467-507.

SOKAL, R. R., AND ROHLF, F. J. 1969. Biometry. First edition. W. H. Freeman and Company, San Francisco.

SOKAL, R. R., AND ROHLF, F. J. 1981. Biometry. Second edition. W. H. Freeman and Company, New York.

SOMERS, K. M. 1986. Multivariate allometry and removal of size with principal components analysis. *Syst. Zool.* 35: 359-368.

STRANEY, D. O. 1978. Variance partitioning and non-geographic variation. *J. Mamm.* 59: 1-11.

STRAUSS, R. E., AND BOOKSTEIN, F. L. 1982. The truss: Body form reconstructions in morphometrics. *Syst. Zool.* 31:113-135.

STSC INC., 1991. STATIGRAPHICS: Reference manual, version 5. Statistical Graphics Cooperation, U. S. A.

SWANEPOEL, R., BLACKBURN, N. K., EFSTRATIOU, S., AND CONDY, J. B. 1978. Studies on Rift Valley fever in some African murids (Rodentia: Muridae). *J. Hyg. Cambridge* 80:183-196.

SWIDERSKI, D. L. 1993. Morphological evolution of the scapula in tree squirrels (Sciuridae): An analysis using thin-plate splines. *Evolution* 47:1854-1873.

SWOFFORD, D. L. 1993. PAUP: Phylogenetic analysis using

parsimony, version 3.1.2d5. Illinois Natural History Survey, Champaign.

SWOFFORD, D. L., AND MADDISON, W. P. 1987. Reconstructing ancestral character states under Wagner parsimony. *Math. Biosci.* 87:199-229.

SWOFFORD, D. L., AND OLSEN, G. J. 1990. Phylogeny reconstruction. Pp 411-501, *in* Molecular Systematics (D. M. Hillis and C. Moritz, eds.). Sinauer, Sunderland, Massachusetts.

SWYNNERTON, G. H., AND HAYMAN, R. W. 1951. A checklist of the land mammals of the Tanganyika Territory and the Zanzibar Protectorate. *J. East Afr. Nat. Hist. Soc.* 20:274-392.

TAYLOR, P. J. 1990. Infraspecific systematics of the yellow mongoose. Ph.D. thesis, University of Natal, Durban.

TAYLOR, P. J., AND MEESTER, J. 1993. Morphometric variation in the yellow mongoose, *Cynictis penicillata* (Cuvier, 1829) (Carnivora: Viverridae) in southern Africa. *Durban Mus. Novit.* 18:37-71.

THOMAS, O. 1905. Suggestions for the nomenclature of the cranial length measurements and of the cheek-teeth of mammals. *Proc. Biol. Soc. Washington* 18:191-196.

THOMAS, O. 1915*a*. New African rodents and insectivores, mostly collected by Dr Christy for the Congo Museum. *Ann. Mag. Nat. Hist.* ser. 8, 16:146-152.

THOMAS, O. 1915*b*. List of mammals (exclusive of Ungulata) collected by Dr Christy for the Congo Museum, Tervuren. *Ann. Mag. Nat. Hist.* ser. 8, 16:465-481.

THOMAS, O. 1926. The generic position of certain African Muridae, hitherto referred to *Aethomys* and *Praomys*. *Ann. Mag. Nat. Hist.* ser. 9, 17:174-179.

THOMAS, O. 1927. On mammals from the Gobabis district, eastern Damaraland, South-West Africa, obtained during Captain Shortridge's fourth Percy Sladen and Kaffrarian Museum Expedition. With field notes by the collector. *Proc. Zool. Soc. Lond.* 1927:371-398.

THOMAS, P. A. 1968. Variation and covariation in characters of the rabbit tick, *Haemaphysalis leporipalustris*. *Kansas Univ. Sci. Bull.* 47:829-862.

THOMAS, O., AND WROUGHTON, R. C. 1908. The Rudd Exploration of South Africa.- X. List of Mammals collected by Mr. Grant near Tette, Zambesia. *Proc. Zool. Soc. Lond.* 1908:535-553.

THOROGOOD, P., AND TICKLE, C. eds. 1988. Cranial Development: Papers Presented at a Meeting of the British Society for Developmental Biology, University of Bath, 1987. The Company of Biologists Ltd, Cambridge.

THORPE, R. S. 1976. Biometric analysis of geographic variation and racial affinities. *Biol. Rev.* 51:407-457.

THORPE, R. S. 1984. Coding morphometric characters for constructing distance Wagner networks. *Evolution* 38:244-245.

UNITED STATES BOARD OF GEOGRAPHIC NAMES, U. S. Army, U. S. A.

VAN DER KLAAUW, C. J. 1948-1952. Size and position of the functional components of the skull. *Archives Neerlandaises de Zoologie* 9:1-559.

VAN DER STRAETEN, E., AND DIETERLEN, F. 1992. Craniometric comparison of four populations of *Praomys jacksoni* captured at different heights in Eastern Zaire (Kivu). *Mammalia* 56:125-131.

VAN VALEN, L. 1974. Multivariate structural statistics in natural history. *J. Theoret. Biol.* 45:235-257. *Erratum* (1974),

48:501.

VERHEYEN, W., AND BRACKE, E. 1966. The influence of aging on the craniometric characters of *Praomys jacksoni* (De Winton, 1897). *Ann. Mus. Roy. Afr. Centr. IN-8°, Zool.* 144: 91-101.

VERHEYEN, E., COLYN, M., AND VERHEYEN, W. 1995. The phylogeny of some African muroids (Rodentia) based upon partial mitochondrial cytochrome *b* sequences. *Belg. J. Zool.* 125:403-407.

VISSER, D. S., AND ROBINSON, T. J. 1986. Cytosystematics of the South African *Aethomys* (Rodentia: Muridae). *S. Afr. J. Zool.* 21:264-268.

VISSER, D. S., AND ROBINSON, T. J. 1987. Systematic implications of spermatozoan and bacular morphology for the South African *Aethomys*. *Mammalia* 51:447-454.

VOORZANGER, B., AND VAN DER STEEN, W. J. 1982. New perspectives on the Biogenetic Law. *Syst. Zool.* 31:202-205.

WADDINGTON, C. 1957. The Strategy of the Genes. Allen and Unwin, London.

WALTROUS, L. E., AND WHEELER, Q. D. 1981. The out-group comparison method of character analysis. *Syst. Zool.* 30:1-11.

WARD, J. 1963. Hierarchical grouping to optimize an objective function. *J. Amer. Statist. Assoc.* 58:236-243.

WATSON, C. B. R. 1987. The comparative ecology of two small mammal communities in the Kruger National Park. M.Sc. thesis, University of Pretoria, Pretoria.

WATSON, J. P., AND DIPPENAAR, N. J. 1987. The species limits of *Galerella sanguinea* (Ruppell, 1836), *G. pulverulenta* (Wagner, 1839) and *G. nigrata* (Thomas, 1928) in southern

Africa (Carnivora: Viverridae). *Navors. nas. Mus. Bloemfontein* 5:356-413.

WEBSTER, W. D., AND JONES,Jr., J. K. 1985. Non-Geographic variation, reproduction, and demography in the Texas kangaroo rat, *Dipodomys elator* (Rodentia: Heteromyidae). *Texas J. Sci.* 37: 51-61.

WESSELMAN, H. 1984. Omo micromammals. Pp. 219, *in* Contributions to vertebrate evolution (M. K. Hecht and F. S. Szalay, eds.). S. Karger, New York.

WHIFFIN, T. 1982. Variation and evolution in the genus *Flindersia* (Rutaceae). II. Review of methods for geographic variation analysis of volatile oil data. *Aust. J. Bot.* 30:645-657.

WILEY, E. O. 1981. Phylogenetics: The Theory and Practice of Phylogenetic Systematics. John Wiley and Sons, New York, Chichester, Brisbane, Toronto, Singapore.

WILEY, E. O., SIEGEL-CAUSEY, D., BROOKS, D. R., AND FUNK, V. A. 1991. The Compleat Cladist: A Primer of Phylogenetic Procedures. Special Publication No. 19, University of Kansas Museum of Natural History, Lawrence.

WILLIAMS, B. K., AND TITUS, K. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. *Ecology* 69:1275-1285.

WILLIG, M. R., AND OWEN, R. D. 1987. Univariate analyses of morphometric variation do not emulate the results of multivariate analyses. *Syst. Zool.* 36:398-400.

WILLIG, M. R., OWEN, R. D., AND COLBERT, R. L. 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. *Syst. Zool.* 35:195-203.

WILSON, V. J. 1970. Notes on the breeding and feeding habits of a pair of barn owls, *Tyto alba* (Scopoli) in Rhodesia. *Arnodia, Rhodesia* 4:1-8.

WILSON, V. J. 1975. Mammals of the Wankie National Park, Rhodesia. *Mem. Nat. Mus. Monum. Rhod.* 5:1-147.

WITHERS, P. C., LOUW, G. N., AND HENSCHEL, J. R. 1980. Energetics and water relationships of Namib desert rodents. *S. Afr. J. Zool.* 15:131-137.

WOODALL, P. F., AND MACKIE, R. I. 1987. Caecal size and function in the rock elephant shrew *Elephantulus myurus* (Insectivora: Microscelidae) and the Namaqua rock mouse *Aethomys namaquensis* (Rodentia: Muridae). *Comp. Biochem. Physiol.* 87A:311-314.

WRIGHT, S. 1978. Evolution and the Genetics of Populations. Volume 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago.

WRIGHT, S. 1980. Genic and organismic selection. *Evolution* 34:825-843.

WROUGHTON, R. C. 1908. Three new African species of *Mus*. *Ann. Mag. Nat. Hist.* ser 8, 1:255-257.

WYSS, A. R., AND MENG, J. 1996. Application of phylogenetic taxonomy to poorly resolved crown clades: A stem-modified node-based definition of Rodentia. *Syst. Biol.* 45:559-568.

ZAR, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey.

ZELDITCH, M. L., DEBRY, R. W., AND STRANEY, D. O. 1989. Triangulation-measurement schemes in the multivariate analysis of size and shape. *J. Mamm.* 70:571-579.

ZELDITCH, M. L., BOOKSTEIN, F. L., AND LUNDRIGAN, B. L. 1993. The ontogenetic complexity of developmental constraints. *J. Evol. Biol.* 6:621-642.

ZELDITCH, M. L., FINK, W. L., AND SWIDERSKI, D. L. 1995. Morphometrics, homology, and phylogenetics: Quantified characters as synapomorphies. *Syst. Biol.* 44:179-189.

APPENDIX I

SPECIMENS EXAMINED IN THE SELECTION OF TAXONOMIC CHARACTERS FOR MORPHOMETRIC ANALYSIS (CHAPTER 2)

Aethomys chrysophilus: Al-te-ver Farm, 1 km SSE Maasstroom, Northern Province, South Africa: six males (TM 26474, 26541, 26557, 26559, 26612, 26684); ten females (TM 26510, 26514, 26540, 26561, 26574, 26575, 26583, 26611, 26668-69).

Aethomys granti: Sutherland, Northern Cape Province, South Africa: seven males (TM 38526-28, 38530, 38532, 38536, 38538); seven females (TM 38529, 38533-34, 38537, 38541-43).

Aethomys namaquensis: Keimoes Island, Orange River, Northern Cape Province, South Africa: 21 males (USNM 451913-14, 451921, 451933-34, 451941, 451948, 451950-51, 451966, 451983, 451990-91, 452000, 452002, 452019, 452028, 452039, 452041, 452045, 452055); 13 females (USNM 451915, 451924, 451956, 451992, 451994, 452003, 452006, 452016, 452020, 452031a-b, 452035, 452053).

APPENDIX II

SPECIMENS EXAMINED IN THE ANALYSIS OF NON-GEOGRAPHIC VARIATION (CHAPTER 3)

Aethomys chrysophilus: Al-te-ver Farm, 1 km SSE Maasstroom, Northern Province, South Africa: nine males (TM 26474, 26486, 26541, 26557, 26559, 26562, 26612, 26667, 26684); 13 females (TM 26492, 26510, 26514, 26540, 26561, 26565, 26574-75, 26583, 26585, 26611, 26668-69). Olifantspoort Farm 328, 19.2 km S Rustenburg, North-West Province, South Africa: 13 males (TM 19614-16, 19618, 19632, 19648-49, 19651, 19656, 19672-75); eight females (TM 19633-34, 19640-42, 19650, 19670-71).

Aethomys namaquensis: Boekenhoutkloof, Gauteng, South Africa: 25 males (TM 30430, 30432-34, 30439-42, 30959-60, 30967, 30969, 30971-73, 30975-77, 30979, 30984, 31259, 31262-64, 31267); 23 females (TM 30428, 30431, 30435-38, 30458, 30961-64, 30966, 30968, 30970, 30974, 30980-83, 31258, 31261, 31265-66). Narap Farm, 28 km SSE Springbok, Northern Cape Province, South Africa: 15 males (TM 27795, 27801, 27811-13, 27836-38, 27841, 27843, 27878, 27906, 27945, 27948, 28006); 17 females (TM 27794, 27798-27800, 27808-09, 27831-34, 27842, 27877, 27907-08, 27946-47, 28007).

APPENDIX III

CYTOGENETICALLY KNOWN SPECIMENS EXAMINED IN SPECIES ANALYSES (CHAPTER 4)

Aethomys chrysophilus (2n = 50): **MALAWI**: Likabula (= Likhubula) Mission, Mount Mulanje, Mulanje District: one female (TM 41783). Liwonde National Park Headquarters: two males (TM 41773-74). **SOUTH AFRICA, NORTHERN PROVINCE**: Klopperfontein, Kruger National Park: one male (TM 37172). Madimbo, Mabilingwe Area, Limpopo River: four males (TM 44241-44); ten females (TM 44229-30, 44236-40; 44245-47).

Aethomys ineptus (2n = 44): **SOUTH AFRICA, GAUTENG**: Zoutpan (= Soutpan), 30 mi N Pretoria: one female (TM 34290). **KWAZULU-NATAL**: Ngome Forest Area, Ngome, 70 km NE Vryheid: two males (TM 39076, 39089). Paradise Valley, Pinetown: one female (TM 35545). **MPUMALANGA**: Hectorspruit: one male (TM 32313). Othawa Farm, 32 km NW Skukuza, Sabie Sands: two males (TM 32311, 32314).

APPENDIX IV

TYPE SPECIMENS EXAMINED

A. bocagei: Pongo (= Pungo) Andongo, Angola: male (BM 4.4.9.62 [original No. 128]).

A. chrysophilus: Mazoe, Mashonaland, eastern Zimbabwe: female (BM 95.11.3.23 [original No. 54]).

A. c. acticola: Beira, Mozambique: male (BM 7.6.2.59).

A. c. imago: Stampriet, E Gobabis, eastcentral Namibia: male (BM 26.12.7.220 [original No. 1832]).

A. granti: Deelfontein, Richmond, Cape Province (= Northern Cape), South Africa: female (BM 2.9.1.86 [original No. 114]).

A. hindei: Machakos, Kenya: male (BM 1.12.9.9 [original No. 901]).

A. ineptus: Tete, Mozambique: male (BM 8.4.3.73 [original No. 1949]).

A. c. capricornis: Newgate Farm, Soutpansberg, northern Transvaal (= Northern Province), South Africa: male (TM 3626).

A. c. fouriei: Oshikanga, Namibia: male (TM 8149).

A. c. harei: Waterberg, Otjiwarongo, northcentral Namibia: male (TM 8148).

A. c. magalakuini: Wilhanshohe, northern Transvaal (= Northern Province), South Africa: male (TM 3707).

A. c. pretoriae: Fountains Valley, Pretoria, Transvaal (= Gauteng), South Africa: female (TM 1239).

A. c. tongensis: Mangusi Forest, northeastern Natal (= Kwazulu-Natal), South Africa: male (TM 6128).

A. c. tzaneenensis: Tzaneen, northern Transvaal (= Northern Province), South Africa: male (BM 9.7.2.15 [original No. 144]).

A. kaiseri verneyi: Chinonque (= Chiengue), 20 km E Danile, Angola: male (AMNH 85735).

A. namaquensis: Witwater, western Cape Province (= Northern Cape), South Africa: female (BM 45.7.3.16).

A. n. auricomis: Mazoe, eastern Zimbabwe: male (BM 95.11.3.21 [original No. 59]).

A. n. avarillus: Tete, Mozambique: female (BM 8.4.3.79).

A. n. calarius: Lahutitung, Kalahari Desert, Botswana: female (BM 10.6.3.45).

A. n. capensis: L'Ormarin's Farm, Franschhoek Valley, southwestern Cape Province (= Western Cape), South Africa: female (TM 2225).

A. n. centralis: Deelfontein, Richmond, Cape Province (= Northern Cape), South Africa: female (BM 3.1.4.51 [original No. 318]).

A. n. drakensbergi: Klipspruit, Utrecht, northern Natal (= Kwazulu-Natal), South Africa: male (TM 2063).

A. n. grahami: Goodwin's Kloof, Eastern Cape Province, South Africa: unknown sex (TM 1412 [type]); male (TM 1413 [cotype]).

A. n. klaverensis: Klawer, Olifant's River, Western Cape Province, South Africa: male (TM 2227).

A. n. lehochloides: Wilhanshohe, northern Transvaal (= Northern Province), South Africa: male (TM 3720).

A. n. lehocla: Letakun, Kuruman, Cape Province (= Northern Cape), South Africa: male (BM 45.7.3.18).

A. n. monticularis: Johannesburg, Transvaal (= Gauteng), South Africa: female (BM 9.7.2.10).
A. n. siccatus: Rua Cana Falls, Cunene (= Kunene) River, Namibia (BM 25.12.4.164).
A. n. waterbergensis: Okosongomingo, Otjiwarongo, Namibia: female (TM 8155).
A. nyikae: Nyika Plateau, northern Malawi: female (BM 97.10.1.189).
A. silindensis: Mount Selinda, eastern Zimbabwe: male (TM 8370 [holotype]); male (TM 8371 [paratype]).
A. stannarius: Kabwir, Bauch (= Bauchi) Province, Nigeria: female (BM 13.2.5.7 [original No. 47]).
A. thomasi: Galanga, Angola: male (BM 97.8.6.14).

APPENDIX V

ALL OTHER SPECIMENS EXAMINED

The former South African Cape Province includes the new Eastern, Northern, North-West, and Western Cape provincial boundaries, while the Transvaal includes Gauteng, Mpumalanga, Northern, and North-West Provinces (see Figure 1.1).

Aethomys bocagei: **ANGOLA**: Hanha: one male (AM 85730); two females (AM 85726, 85729). Lussinja, Bocoio: one female (TM 14720).

Aethomys chrysophilus: **BOTSWANA**: Foley Siding: (NHMZ 70065-66). Gaberones (= Gaberone), 5 mi W: four males (NHMZ 70019, 70034-35, 70040); one female (TM 70036). Kuki, Makalababedi: one female (NHMZ 70060). Mabate (= Mabati, Mabote): two females (NHMZ 70084-85). Madinare: one male (NHMZ 70530); one female (NHMZ 70531). Moshupa: one female (TM 22275). Nata: one male (TM 22427). Ootsi (= Ootse) Siding, W Ootsi (= Ootse): one male (KM 12584). Ramatlabana (= Ramatlhabama), 10 mi W: three males ([NHMZ 70533], [TM 6918-19]). Riverslea, Tuli Block: (TM 14132). Shashi Siding, 10 mi N: one female (NHMZ 70072). Tsanoga: one female (NHMZ 70540). Tsau, 3 mi S: one male (TM 22437); one female (NHMZ 70534). Tsodilo (= Tsodila) Hills: one female (NHMZ 70515). **MALAWI**: Likabula (= Likhubula) Mission, Mount Mulanje, Mulanje District: one female (TM 41783). Liwonde National Park Headquarters: two males (TM 41773-74). **MOZAMBIQUE**: Chicoa, Tete District: one male (TM 14429). Estatuane (= Changalane): one male (NHMZ 70112). Inhaminga, 8 mi: one male (NHMZ 70162). Malanguene: one male (NHMZ 70161). Maringa, North Bank: one female (TM 10860). Revue River: two males (NHMZ 70131-32). Save River: two males (NHMZ 70137, 70141); one female (NHMZ 70139). Tete: two males (TM 14440, 14443); one female (TM 14442). Zavera (= Zavora): one female (NHMZ 70164). **NAMIBIA**: Andara (Okavango), W Caprivi: five females (KM 5149-53). Diwai (Okavango), near Bagane Drift, W Caprivi: two females (KM 5160, 5168). Gobabis: two females (KM 5121-22). Karakuwisa, Grootfontein District: one male (KM 5135); one female (KM 5137). Nossib, near Tsumeb: one female (TM 11874). Ombombo, Kaokoveld: two males (KM 5133, 5138). Popa Falls, Okavango, W Caprivi: (KM 5175). Quickborn, Okahandja: two females (TM 4138-39). Sandfontein: one male (KM 20785); one female (DM 436). Stampriet, E Gobabis: three females (KM 5124, 5126, 5127). **SOUTH AFRICA: CAPE PROVINCE**: Bellsbank Estates Farm, 44 km W Warrenton: one male (MMKM 4752). Elibank Farm, 36 km SW Setlagoli: one female (MMKM 4784). Kansvat Farm, 22 km NW Vryburg: one female (MMKM 4757). Kuruman, 3 km W: two females (TM 33304, 33429). Kuruman, 11.9 mi on Digatlong Road: one female (TM 22327). Zoetvlei (= Soetvlei), Vryburg: one male (TM 6863). **KWAZULU-NATAL**: Albert Falls Nature Reserve: one male (DM 1679). Black Umfolozi Bridge, South Bank, Nangoma-Mahlabatini Road, Nangoma District: one male (TM 22355). Bumbeni, N Zululand: one male (TM 12373). Graigadam Farm (= Craigadam), Itala Nature Reserve, 9 km NE Louwsburg: two males (TM 28809, 28818). Hluhluwe, 100 yards W South African Railways Bridge, Ingweni River: one male (TM 22299). Hluhluwe Game Reserve: one male (TM 35553). Langewacht, Babanango: one female (DM 1865); one unknown sex (DM 1820). Mkusi (= Mkuzi) River, Ubombo: four males (TM 5639-41, 5643); one female (TM 5635). Mkuzi (= Mkusi) Game Reserve, Caravan Park, Zululand: one male (DM 961). Quixotic Farm, 14 km S Mkuzi on farm road to Transvaal: one male (TM 22339). Spiounkop Nature Reserve: one female (TM 41182). Vryheid Nature Reserve: one female (DM 1476). **TRANSVAAL**: Acornhoek: one male (TM 4364). Acre 2KT Farm, near Serala, Haenertzburg: one male (TM 23690). Al-te-ver Farm, 1 km SSE Maasstroom: six males (TM 26474, 26541, 26557, 26559, 26612, 26684); ten females (TM 26510, 26514, 26540, 26561, 26574, 26575, 26583, 26611, 26668-69).

Barberton: two males (TM 29461, 29469). Blijdschap Private Nature Reserve, 5 km N Bandolierskop: one male (TM 24172). Blouberg: two females (TM 14941, 14943). Cyprus Farm 68, 13 km SW Ofcolaco: one male (TM 25320); one female (TM 25298). De Hoop Private Nature Reserve, 40 km N Roossenekal: one male (TM 25329); one female (TM 25330). Grenshoek Forest: one male (TM 22287). Hennops River on Hartebeesportdam Road, Johannesburg: one male (TM 22372). James' Hut, Limpopo: one male (TM 22439). Klopperfontein, Kruger National Park: one male (TM 37172). Komatipoort, Kruger National Park: one female (TM 29992). Krugerkloof Nature Reserve, Lydenburg: one female (TM 17488). Lanjan Nature Reserve, 7 mi N Vivo: two males (TM 17019, 17022). Louis Trichardt: one female (TM 7506). Madimbo, 10 km E, Limpopo River: two males (TM 24622, 24643); two females (TM 24643, 24654). Madimbo, Mabilingwe Area, Limpopo River: four males (TM 44241-44); ten females (TM 44229-30, 44236-40; 44245-47). Malelane Camp: one female (TM 22333). Malensan Singwetsi Game Reserve: one male (TM 2428). Malta Farm: one male (TM 27522). Mariepskop: five males (TM 4509, 4510-11, 4513, 4515); one female (TM 4517). Messina: two females (TM 20291-92). Mmabolela Estates, 14 km NW Maasstroom: three males (TM 19689, 19758, 19709). Mokeetsi Farm 376, Duiwelskloof, Zoutpansberg: one male (TM 4038). Moorddrift Farm 289, Waterberg, Potgietersrus: two males (TM 612, 1446). Narina Farm, 8 km W Duiwelskloof: one male (TM 25281). Nelspruit, E Transvaal: one female (TM 1386). Nwambia, 1 mi E: one male (TM 22258). Olifantspoort Farm 328, 12 mi S Rustenburg: four males (TM 19615, 19651, 19672-73); two females (TM 19670-71). Paramie (= Uitkyk) Private Nature Reserve, 12 km SSE Nelspruit: one female (TM 20121). Rhoda Farm 9, 13 km S Phalaborwa: two males (TM 24244, 24249). Rosslyn, Pretoria: one male (TM 2893). Sand River, near Messina: one male (TM 592). Scrutton Farm 23 MT, 32 km E Messina: one female (TM 20292). Skukuza Camp: two females (TM 22266, 22402). Soetdoorns Farm 173, 15 mi S Vivo on Kalkfontein Road: one male (TM 22397). Ten Bosch Estates, 10 km NE Hectorspruit: one male (TM 24844). Thabazimbi: one male (TM 20619). Tzaneen Estates: one male (TM 468). Watervalonder on Nelspruit Road: one male (TM 22378). Welgedaan Farm, 28 km NNE Christiana: one female (TM 20796). Worcester Mine, Barberton: one male (TM 2493). Zoutpan (= Soutpan), 30 mi N Pretoria: one male (TM 599). Zoutpansberg (= Soutpansberg): one male (TM 3628). **ZIMBABWE**: Ainsby Farm, Richmond: one female (NHMZ 81464). Alsace (= Alsage) Farm, Harare: one male (NHMZ 53553). Benga: one male (NHMZ 18172). Birchenough Bridge: one female (TM 8644). Borrowdale Brook, Harare: one male (NHMZ 69836). Bulawayo: nine males (NHMZ 760-61, 855, 26690, 53269, 53326, 53947, 54616, 82028); three females (NHMZ 204, 2980, 82040). Bumboosie: one female (NHMZ 69938). Calgary, Harare: two males (NHMZ 69814-15); one female (NHMZ 69842). Chibero: two males (NHMZ 69950-51); three females (NHMZ 69948, 69962, 69976). Chinomwe Clinic, Raffingora: one male (NHMZ 7946). Chipinda Pools: one male (NHMZ 70014). Doddieburn Ranch: three males (NHMZ 80107, 80109, 80112); three females (NHMZ 80108, 80110-11). Dorowa Mine: one male (NHMZ 80404); one female (NHMZ 80394). Eirene Marondera: one male (NHMZ 69954). Essexvale (Esigodini) Ranch: one female (NHMZ 53983). Falcon College, Strcom Bed: six males (NHMZ 80498-99, 80500, 80958, 82032, 82095); nine females (NHMZ 80501, 80503, 80505-6, 80506, 80508, 80951, 81054, 82026, 82035). Fishon, Lundi: two males (NHMZ 53431, 53433). Fletchers, Bembesi: two males (NHMZ 53981-82). Harare: one female (NHMZ 53538). Haroni-Lusitu Beacon: one female (NHMZ 53480). Humani (= Humai) Ranch: two females (NHMZ 53450-51). Ingeli Farm, Gweru (= Gwelo): three males (NHMZ 1685, 1843, 27001); two females (NHMZ 1358, 3065). Kariba (southern river), Game Camp: one male (NHMZ 8803). Kyle National Park: one male (NHMZ 53775). Longani Dam, Lone Star Ranch: two males (NHMZ 54046, 54050). Makoholi (= Makaholi) Research Station: one female (NHMZ 53847). Maitengwe Dam, Nata Reserve: one female (NHMZ 7912). Maleme Rest Camp, Matopos (= Motopos): one male (NHMZ 54077). Manda Farm: one male (NHMZ 53911). Matika Farm, Mutare (= Umtali): one female (NHMZ 69930). Matopos (= Motopos) (eastern): two males (NHMZ 53988, 53990); one female (NHMZ 53996).

Matopos (= Motopos) National Park: three males (NHMZ 53604, 53616, 54004); two females (53605, 54003). Mavhuradonha (= Mavuradonha) Wilderness Area: seven males (NHMZ 82459, 82470, 82487, 82519, 82555, 82836, 82867); seven females (NHMZ 82410, 82431, 82448, 82864-65, 82870, 82872). Mazoe, Mashonaland: one male (TM 459). Mount Selinda: two males (TM 7750, 8643); one female (NHMZ 53459). Msingwenyani, Matibi District: one male (TM 1339). Mtilikwe (= Mtilekwe) River Triangle: three females (NHMZ 53857, 53875, 53891). Muneni River, Mutare (= Umtali): two males (NHMZ 53384, 53404). Mushandike National Park: 16 males (NHMZ 53687, 53675, 53690, 53695, 53711, 53716, 53727, 53736, 53747, 53749, 53751, 53755-56, 53759, 53766, 53770); 16 females (NHMZ 53674, 53676, 53678, 53680, 53686, 53688, 53698, 53702, 53704, 53706-7, 53715, 53742, 53750, 53752, 53757). Mutare (= Umtali): three males (NHMZ 6453, 6457, 27010). Ngezi National Park: two males (NHMZ 69900, 69905). Nkai: one female (NHMZ 69984). Nyamunyeche (= Nyamuyeche): two males (NHMZ 56227, 57508); one female (NHMZ 56226). Nyamunyeche (= Nyamyeche) Chikonyora: one female (NHMZ 69832). Queens, Bulawayo Area: one male (NHMZ 2544). Ranelia Farm Cashel: one male (NHMZ 53494); one female (NHMZ 53496). Rekomitjie River: one female (NHMZ 53601). Rusape: five males (NHMZ 424, 7039, 9989-90, 9993). Rusito Forest (on Rusito River): two males (TM 34772, 34784); one female (TM 34771). Sabi/Lundi Rivers confluence: one female (NHMZ 53439). Saffron Walden, near Harare: two males (NHMZ 53545, 53547); three females (NHMZ 53543, 53546, 53549). Sengwa Wildlife Research Station (= Sengwa Camp): one male (NHMZ 53652). Sinoia: one female (NHMZ 6976). St. Paul's Mission: one male (NHMZ 69942); one female (NHMZ 69945). Thornpark, Harare: one female (NHMZ 53560). Tsabalala Sanctuary, Matopos (= Motopos): two males (NHMZ 80680-81); one female (NHMZ 80659). Umhlanyane, Matopos (= Motopos): two males (NHMZ 80668, 81696). Umvukwesi (= Umvukwes): one male (NHMZ 56143); one female (NHMZ 56144). Umzingwane/Limpopo Rivers junction (= Umzingwani): one female (NHMZ 9517). Zana Farm, Umvukwesi (= Umvukwes): one male (NHMZ 53577). Zewa Hill, Inyanga: one female (NHMZ 53467). Zimbabwe National Park: eight males (NHMZ 53785, 53787, 53789, 53801, 53805, 53809, 53813, 70099); three females (NHMZ 53807, 53817, 53835).

Aethomys granti: **SOUTH AFRICA, CAPE PROVINCE:** Biesjespoort, Karoo (= Karroo): 3 males (KM 11132-33, 11137); two females (KM 11134-35). Deelfontein, Richmond, Karoo (= Karroo): two males (KM 11127, 11130); one female (TM 478). DoornbOom, 6.6 km S, 33.0 km W Ladismith, Ladismith District: two females (KM 29533-34). Fraserburg, 12.8 km S, 10.5 km E, Fraserburg District: one male (USNM 468952). Goma Farm, Renoster River, 54 mi E Calvinia: two females ([TM 10041], [USNM 468845]). Gouna Farm, Rhenoster River, 54 mi E Calvinia: 11 males (KM 12855-56, 12858, 12862-63, 12865, 12868, 12870-71, 12875, 29112), 11 females (KM 12836, 12839-40, 12843-44, 12846-47, 12849, 12851, 12867, 12869). Hantam Range (slopes of), 3 mi NE Calvinia: four males (KM 12823, 12825-26, 12832); two females (KM 12820, 12833). Laingsburg, 19 km SSW: one female (USNM 468958). Matjiesfontein: one female (TM 9072). Middlepost (= Middelpost, Middelpos), 11 mi: two females (KM 14794, 14796). Municipal Farm, Middelburg: one male (KM 11125); one female (KM 11124). Murraysburg, 7.1km N, 17.0 km W, Murraysburg District: one female (KM 23056). Sutherland: seven males ([TM 38526-28, 38530, 38532, 38536, 38538], [USNM 468948-49]); ten females ([TM 38529, 38533-34, 38537, 38540-41, 38543], [USNM 468946, 468947, 468950]). Sutherland, 12 mi: six males (KM 14771, 14774, 14777, 14784, 14786, 14789); seven females (KM 14772, 14775, 14781, 14783, 14790-91, 14800). Victoria West, 1.9 mi N, 1.8 mi E Victoria West District: one male (KM 23112); one female (KM 23111). Victoria West, 7 mi N, 1.5 mi E Victoria West District: one female (KM 23113). Voorspoed, 17.8 km S, 36.6 km W Williston, Calvinia District: two females (KM 29113-14).

Aethomys ineptus: **BOTSWANA**: Aha Hills, 10 mi N: one female (NHMZ 70076). Artesia, 14 mi E: two males (KM 12587-88). Debeeti (= Debeti): one female (NHMZ 70535). Foley Siding: one female (NHMZ 70068). Gaberones (= Gaberone), 5 mi W: six males (NHMZ 70023, 70029, 70037, 70045-46, 70514); two females (NHMZ 70020, 70513). Gensond (= Gesond) Limited: one male (TM 14089). Goha Pan: one female (NHMZ 70546). Makoba Gate, 7 mi W: two males (NHMZ 70058-59). Moshaneng: one female (NHMZ 70517). Nokanen (= Nokaneng), 9.3 km SE: one male (KM 12590). Nthane: one female (NHMZ 70542). Ootsi (= Ootse), NE Ootsi (= Ootse): one female (KM 12585). Ramoutsa Village: one male (KM 12586). Riverslea, Tuli Block: one male (TM 14124). Shakawe: one female (NHMZ 70509). Shakawe, 50 mi W, 12 mi S: one male (NHMZ 70079). **MOZAMBIQUE**: Beira: one female (TM 460). Banamana: one female (TM 19409). Chitenga (= Chitengo), Gorongoza National Park: one female (NHMZ 70159). Dondo: one female (NHMZ 64744). Estatuane (= Changalane): one male (NHMZ 70116); two females (NHMZ 70105, 70108). Magudi: one female (TM 2381). Maringa, North Bank: one male (TM 10859). Mazambo: one male (TM 1701). Moamba: one male (DM 950); one female (DM 945). Muamdzame (= Muandzane), Libondos: one male (NHMZ 70109). Pico Mapenduine (= Meponduine): one male (NHMZ 70110). Ponta S.L., Banamana: one male (NHMZ 62259). Save River: two males (NHMZ 70138, 70142). Tete: two males (TM 1196, 14445). Zambesi (= Zambezi), South Bank: one male (TM 10874). Zinave, 1.0 km S: one female (NHMZ 70152). Zinave National Park: two males (TM 24336, 24347). **NAMIBIA**: Andara (Okavango), W Caprivi: one male (KM 5157); two females (KM 5155-56). Bubus Farm 213, 9 mi Grootfontein on road to Otjituno Reserve: one male (TM 22424). Diwai (Okavango), near Bagane Drift, W Caprivi: four males (KM 5162, 5164-65, 5170); one female (KM 5166). Lupala (= Lupela), Okavango: one male (TM 22879); one female (TM 22406). Marula Tree Camp, 24 mi NW Andoni Ortesian Well on Nemutoni-Ondangua Road: one female (TM 22431). Mohango (= Mahango Omuramba) Drift (Okavango), W Caprivi: one male (KM 5159). Namkaub, Grootfontein District: two males (KM 5144, 5147). Nossib, near Tsumeb: one male (TM 11866). Oshikanga (= Oshikango), Ovambo-Angola Border: one female (TM 8150). Otavifontein Farm, 3.5 mi E Otavi on road to Grootfontein: one female (TM 22415). Oudekaremba Siding, along Elephant River Banks: one male (TM 22432). Popa Falls, Okavango, W Caprivi: two males (KM 5173-74); two females (KM 5171-72). Sandfontein: one male (KM 5130). Sijemba, Okavango, W Caprivi: two females (KM 5178, 5180). Tshandi Finnish Mission, Ukualuthi, Ohopoho: one male (TM 22420). **SOUTH AFRICA: CAPE PROVINCE**: Bellsbank Estates Farm, 44 km W Warrenton: one female (MMKM 4751). Donkerhoek Farm, 24 km WSW Setlagoli: four males (MMKM 4582-83, 4775, 4778); two females (MMKM 4773, 4776). Duikerbult, 16 km W Setlagoli: one female (MMKM 4736). Elibank Farm, 36 km SW Setlagoli: two males (MMKM 4780-81); two females (MMKM 4782-83). Grootfontein Farm, 19 km SW Reivilo: one female (MMKM 4731). Kansvat Farm, 22 km NW Vryburg: one male (MMKM 4756); one female (MMKM 4758). Kuruman, 3 km W: one male (TM 33306); one female (TM 33305). Kuruman, 11.9 mi on Digatlong Road: one male (TM 33305); one female (TM 33429). Marthasdale Farm 190, 23 km NNE Danielskuil: one male (MMKM 4766). Northern Cape Nature Conservation Station, 8 km W Hartswater: one male (MMKM 4744); one female (MMKM 4749). Pitsane, 12 mi E, 3 mi S on Mafeking Road: one male (TM 22395); two females (TM 22272, TM 22281). Ramatulabama, Mafeking: one male (TM 6918). Rooidam, 10 km N Windsorton: one male (MMKM 4742). **KWAZULU-NATAL**: Abercorn Port, Site B1, Usutu River Park: three males (TM 22326, 22336, 22376); two females (TM 22314, 22334). Albert Falls Nature Reserve: one female (DM 1642). Ashburton: two males (TM 26185, 26187). Black Umfolozi Bridge, South Bank, Nangoma-Mahlabatini Road, Nangoma District: five males (TM 22304, 22344-45, 22347, 22354); two females (TM 22356, 22375). Candover, 4.7 mi N on road to N Zululand-Swaziland: one female (TM 22306). Dukuduku Forest, 6 km NNE Mtubatuba: one female (TM 40383). Empangeni (= Epangweni), Hluhluwe: one female (TM 22340). Futululu: one male (DM 1013).

Graigadam Farm (= Craigadam), Itala Nature Reserve, 9 km NE Louwsburg: five males (TM 28808, 28817, 28822, 28828, 31656); five females (TM 28824, 28829, 31655, 31695, 31710). Grenshoek Forest: one male (TM 22343). Gumesi Kraal, Usutu River, Line 2: one male (TM 22324); one female (TM 22323). Gwaliweni, 15 mi S Nqwavuma (= Ngwavuma): two males (TM 22363, 22351); one female (TM 22352). Hazelmere Dam, Verulam: one female (TM 39926). Hluhluwe Game Reserve: five males (TM 29514, 35412, 35546, 35549, 35554); four females (TM 35413, 35547-48, 35913). Hluhluwe River, 4 mi E on main road to Mtubatuba: one male (TM 22305). Ingwaruma (= Ingwarum) Bush, Otobokwim (= Otobokim, Otobitini), Zululand: three males (TM 7200, 7202, 7209); four females (TM 7201, 7203, 7205-6). Itala Nature Reserve, Ranger's House, Pongola/Zinave Rivers confluence: one male (TM 25905); four females (TM 25875-76, 25880, 25883). Jameson's Drift, Tugela River, Kranskop-Vryheid River: one female (TM 22371). Krantzkloof Nature Reserve: two males (DM 1275-76); three females (DM 1273, 1259, 1266). Lake St. Lucia (eastern shores), Hlabisa District, Zululand: three males (TM 24383, 25426, 40429); one female (TM 25425). Lake St. Lucia, north-east Shores, Ubombo District, Zululand: one male (KM 25986). Langewacht, Babanango: one male (DM 1833); three unknown sex (DM 1823-25). Manaba, NE Zululand: one male (TM 6129); one female (TM 6130). Mangusi Forest, Site C, E Neck, 2.5 mi on Maputa Store-Mosi Store, NE Zululand: one male (TM 22303). Mapelane: one male (DM 1010). Mfongozi (= Mfongosi), Zululand: one female (DM 217). Mkusi (= Mkuzi) River, Ubombo: two males (TM 5637-38); two females (TM 5633, 5636). Mkuzi (= Mkusi) Game Reserve, Caravan Park, Zululand: one male (DM 1367); two females (TM 35268-69). Mnuzie Bridge: one male (TM 5444). Nagle Dam: one male (DM 1867); two females (DM 1869-70). Ngome Forest Area, Ngome, 70 km NE Vryheid: eight males (TM 39075-76, 39077-78, 39078, 39083, 39085, 39089); five females ([DM 1014], [TM 39079, 39081, 39087-88). Ngoye Forest, Zululand: one female (TM 41908). Paradise Valley, Pinetown: one female (TM 35545). Pomeroy (= Pameroy), 10.5 mi on road to Greytown: one female (TM 22367). Pongola River, Ubombo: one male (TM 5443). Ringwood, Inchanga: two males (TM 24434, 24437). Sand Dune Forest, W Slope, Lake Sibaya (= Sibayi), Zululand: two males (TM 22413, 25701). Shihangwane (= Sihangwane, Sihangwana), Zululand: one male (TM 25812); two females (TM 22325, 25783). Spiounkop Nature Reserve: two males (TM 40714, 40906); one female (TM 40713). Tete Pan, Lake Śimbu, Ubombo, Tongaland: two males (TM 22343, 22350); two females (TM 22341, 22353). Umfolosi (= Umfolozi) Rivers (at junction): one female (DM 240). Umfolozi (= Umfolosi): one female (TM 35550). Umkomaas River, Ixopo-Richmond Road: one male (TM 22313); one female (TM 22413). Vryheid Nature Reserve: one male (DM 1477). **TRANSVAAL**: Acre 2KT Farm, near Serala, Haenertzburg: one female (TM 23691). Arnhem (= Arnhemburg), Carolina: two males (TM 1789, 1791); two females (TM 1788, 1790). Barberton: one male (TM 29468); six females (TM 29459, 29460, 29462-63, 29465-66). Blijdschap Private Nature Reserve, 5 km N Bandolierskop: two males (TM 24188, 24190); one female (TM 24189). Blouberg: three males (TM 14931, 14937-38); one female (TM 14933). Buffelsdraai, Brits: two males (TM 1703, 1705). Buffelspoort Farm 149 JQ, 3 mi NE Assen: three males (TM 20050, 20063-64); one female (TM 20044). Buzzard Mountain Sanctuary, Louis Trichardt District: two females (TM 41653-54). Chromedale South African Railways Station, 5 mi N: one female (TM 22264). Cyprus Farm 68, 13 km SW Ofcolaco: three females (TM 25297, 25302, 25321). De Hoop Private Nature Reserve, 40 km N Roossenekal: one male (TM 25359); one female (TM 25384). Derby Post Office, Skeenshoek Malaria Camp: one male (TM 22282). Dinokana (= Linokane), Zeerust: one male (TM 22285). Donkerpoort and Zandspruit Farm 449, 24 km E Thabazimbi: seven males (TM 20580-81, 20587-89, 20619, 20629); four females (TM 20579, 20618, 20630, 20643). Dordrecht Farm 578, 20 km S Marken: one male (TM 24696); three females (TM 24672, 24683, 24730). Elandsfontein Farm 74, 6.3 mi De Wilt Post Office on Pretoria W-Brits Road: one female (TM 22235). Fontana Military Area, near Petronella: one female (TM 40999). Fort Klipsdam Farm, 27 km N Pietersburg: two males (TM 24127, 24138).

Geelhoutkloof Farm 275, Waterberg: one female (TM 15227). Georges Valley Farm 632, Haenertzburg: one male (TM 23701). Gravellote, Tzaneen: one female (TM 4040). Groothoek Farm 99, 25 km ESE Potgietersrus: three females (TM 23345, 23355, 23374). Groot Marico, Koster: two males (TM 22310, 22865). Hans Merensky Provincial Nature Reserve, 30 km NE Letsitele: one male (TM 41153); nine females (TM 24542-44, 24562-65, 24570-71). Hectorspruit: five males (TM 32308-9, 32312-13, 32316); one female (TM 1706). Hennops River on Hartebeesportdam Road, Johannesburg: three males (TM 22373, 22384-85); one female (TM 22383). Hermanus-Doorns Post Office: one female (TM 22280). Huwi Private Nature Reserve, 7 mi SE Ellisras: three males (TM 19980-81, 20001); one female (TM 20006). Jacksonstuin (= Jacksonstown) Post Office: two females (TM 22389, 22393). James' Hut, Limpopo: three males (TM 22284, 22289, 22292); one female (TM 22255). Jan Amsterdam, Pietersburg: one male (KM 19753); one female (KM 19756). Khandizwe Plateau, 9 km W Malelane, Kruger National Park: one male (TM 30022); one female (TM 30023). Koster: one male (TM 2977); three females (TM 2975, 2978, 2980). Letaba Ranch 8, 40 km N Phalaborwa: one male (TM 25579). Letaba Rest Camp, Kruger National Park: one male (TM 22259). Leydenburg: one male (TM 6792). Leydsdorp: one male (TM 4778); one female (TM 4779). Loskop Dam Nature Reserve: four males (TM 19843, 19845, 19862, 40928); three females (TM 19807, 19817, 19841). Louis Trichardt: one male (TM 7505). Madimbo, 10 km E, Limpopo River: one male (TM 24621); one female (TM 24624). Magalakwin (= Magalakuin, Magalakwena) Farm 666, Potgietersrus: one male (TM 4096); one female (TM 4097). Mal Cont Camp, Mogol River, Vaalwater: one male (TM 22399). Malta Farm: one male (TM 27557); one female (TM 27549). Mamarango (= Mamaranga), Letaba: one male (TM 2118). Mariepskop: three males (TM 4514, 4518, 4519), two females (TM 4512, 4516). Moedwil Post Office, 2.5 mi E on Rustenburg-ZwartrUggens Road: one male (TM 22867). Mokeetsi Farm 376, Duiwelskloof, Zoutpansberg: one male (TM 2116), one female (TM 2934). Molopene River, near Molopene Rest Camp, Kruger National Park: one male (TM 22257). Mooigenoeg Farm 83, 8 km S Derdepoort: one female (TM 23528). Moonlight, Potgietersrus District: one male (TM 22249). Moorddrift Farm 289, Waterberg, Potgietersrus: four males (TM 1442-43, 1445, 4293); four females (TM 1439-41, 1444). Mosdene Private Nature Reserve, 2 mi SE Naboomspruit: one male (TM 19888); one female (TM 19893). Mutale (= Motale) River: one female (TM 7511). Narina Farm, 8 km W Duiwelskloof: two females (TM 25278, 25280). Newington, 7 mi NE: two males (TM 17254, 24944); four females (TM 17256, 24913, 24951, 24956). Njelele River, Zoutpansberg (= Soutpansberg): one male (TM 2024). Nwambia, 1 mi E: two females (TM 22247, 22254). Nwambienepan, 26 km SSE Pafuri, Kruger National Park: one male (TM 29886). Nwanetsi River Ford (= Fold), 10.7 mi N Letaba on Shingwedzi: one male (TM 22248). Nylstroom: four males ([KM 10939], [TM 2947, 3879, 3880]); three females ([KM 10937], [TM 2379, 2451]). Othawa Farm, 32 km NW Skukuza, Sabie Sands: two males (TM 32311, 323143). Paramie (= Uitkyk) Private Nature Reserve, 12 km SSE Nelspruit: one male (TM 20071); three females (TM 20068, 20070, 20132). Pery (= Percy) Fyfe Nature Reserve: one male (TM 18886). Pienaar's river: one female (TM 22377). Platbos Farm, 32 km NW Vaalwater: one male (TM 24757); three females (TM 24745, 24756, 24815). Potgietersrus, 72 km NW: two females (TM 2377-78). Pretoria Noord (= North): one male (TM 1411). Rochdale Farm 700 MS, 5 mi E Waterpoort: one female (TM 19771). Rustenburg Nature Reserve: one male (TM 22379). Rykvoorby Farm, 9 km N Zeerust: two males (TM 20556, 20564); two females (TM 20525, 20555). Schurwerberg, Pretoria: one male (TM 4141); two females (TM 3858-59). Scrutton Farm 23 MT, 32 km E Messina: one female (TM 20291). Sekororo: one male (TM 3430); one female (TM 3431). Shingwedzi/Dzombo Rivers Confluence, 13 mi SE Shingwedzi: one male (TM 22237). Skukuza, Kruger National Park: one male (TM 13485). Skukuza Camp: three males (TM 22319, 22381, 22412); two females (TM 22405, 22411). Soetdoorns Farm 173, 15 mi S Vivo on Kalkfontein Road: one female (TM 22261).

Tamboekieskloof, Mogol River: one male (TM 15229). Ten Bosch Estates, 10 km NE Hectorspruit: two females (TM 24827, 24875). Thabazimbi: five males (TM 20629, 20580-81, 20588-89); four females (TM 20579, 20618, 20630, TM 20643). Theespruit Farm 156, Carolina/Barberton Glens: one female (TM 1382). Tshakuhma Malaria Camp: one female (TM 22263). Tzaneen Estates: three females (TM 463-64, 467). Uitkomst Farm 499, 35 mi W Pretoria: one female (TM 17494). Urk Farm 10, Blouberg Private Nature Reserve, 13 km W Vivo: one male (TM 24090). Vaalkop Dam Nature Reserve: one female (TM 40974). Vendaland on Levuvhu River: one male (TM 25478); one female (TM 25492). Warmbaths (= Warmbad), 4 mi on Nylstroom Road: one female (TM 22404). Waterkloof, Pretoria: two females (TM 1409-10). Welgedaan Farm, 28 km NNE Christiana: one male (TM 20812); two females (TM 20790, 20792). Welgevoden Farm, 16 km W Steilloop: one female (TM 23316). Wilgekuil Farm 181, Rustenburg, Brits: one female (TM 1878). Wilhanshohe, Magalakuin (= Magalakwin, Magalakwena) River: three males (TM 3712-13, 3716); three females (TM 3708, 3710-11). Windhoek, Louis Trichardt: one male (TM 22416). Woodbush Village, Houtbosdorp: one male (TM 1437); one female (TM 1438). Worcester Mine, Barberton: one male (TM 1998); two females (TM 1385, 1997). Zandspruit Farm 449, 63 km NNW Rustenburg: one female (TM 23604). Zebediela Citrus Estates, 32 km SE Potgietersrus: three females (TM 38765-67). Zoutpan (= Soutpan), 30 mi N Pretoria: three males (TM 472, 600, 19386, 34290); one female (TM 1420). Zoutpansberg (= Soutpansberg): one male (TM 3627). **SWAZILAND**: Ranches Limited: two males (TM 8444, 8452); three females (TM 8440, 8446, 8456). **ZIMBABWE**: Atlantica Ecological Research Station, Harare: one female (NHMZ 53533). Bulawayo: 20 males (NHMZ 820, 1378, 2546, 2987, 26691, 52574, 52863, 53264-65, 53270, 53942-43, 54027, 54029, 54327, 55232, 80188, 82024, 82039, 82088); 15 females (NHMZ 759, 907, 2974, 26998, 27907, 52124, 52583, 53914, 53944, 53959, 54028, 54030, 54338, 54463, 55233). Calgary, Harare: one female (NHMZ 69824). Chipinga: one male (NHMZ 2009); one female (NHMZ 1901). Doddieburn Ranch: one female (NHMZ 53599). Essexvale (Esigodini) Ranch: one female (NHMZ 53984). Falcon College, Strcom Bed: two males (NHMZ 80507, 82098); one female (NHMZ 81053). Fishon, Lundi: one male (NHMZ 53428); one female (NHMZ 53424). Haroni-Lusitu Beacon: one male (NHMZ 54041). Ingeli Farm, Gweru (= Gwelo): one female (NHMZ 1841). Kabera: one male (NHMZ 69991). Kadoma (= Gatooma): one male (NHMZ 1743). Kamaziyo (= Kamazeyo) Camp: one male (NHMZ 22461). Kanyemba: one female (NHMZ 69960). Kyle National Park: one female (NHMZ 53774). Lusitu River: two males (NHMZ 53474, 53479). Maleme Rest Camp, Matopos (= Motopos): one male (NHMZ 50718); one female (NHMZ 51258). Malugwe Pan: one female (NHMZ 53518). Manda Farm: one female (NHMZ 53910). Maranke Reserve: one female (NHMZ 6985). Matopos (eastern): one female (NHMZ 54010). Matopos (= Motopos) National Park: two males (NHMZ 50651, 54014); two females (NHMZ 53991, 53994). Matopos (= Motopos) Research Station: two females (NHMZ 81694-95). Matusiadona Tashinga (= Tashinga Matusiadona): one male (NHMZ 53641); one female (NHMZ 53638). Mavhuradonha (= Mavuradonha) Wilderness Area: five males (NHMZ 82371, 82412, 82414, 82532, 82573); two females (NHMZ 82498, 82868). Mtilikwe (= Mtilekwe) River Triangle: one female (NHMZ 53888). Muneni River, Mutare (= Umtali): one male (NHMZ 53396); one female (NHMZ 53393). Mushandike National Park: four males (NHMZ 53683, 53737, 53741, 53773); three females (NHMZ 53673, 53722, 53745). Ngezi National Park: one female (NHMZ 69897). Nkai: two males (NHMZ 2004, 69982). Nyamucheche Umvukwes (= Umvukwesi) (= Nyamuyeche Farm): one male (NHMZ 56847). Nyamunyeche (= Nyamuyeche): three males (NHMZ 56079, 56230, 56561). Nyamunyeche (= Nyamyeche) Chikonyora: one male (NHMZ 69921); one female (NHMZ 69923). Pombadzi/Lundi Rivers confluence: one female (NHMZ 53438). Ranelia Farm Cashel: one female (NHMZ 53493). Rhodes Inyanga National Park: one male (TM 34724). Rhodes Matopos (= Motopos) National Park: one male (TM 35006). Rusito Forest (on Rusito River): two females (TM 34776, 34798). Sabi/Lundi Rivers confluence: one female (TM 10854). Saffron Walden, near Harare: one female (NHMZ 62001).

Sengwa Wildlife Research Station (= Sengwa Camp): two males ([NHMZ 53654], [TM 34963]); two females (NHMZ 53655-56). Shinda Estates: one female (NHMZ 69878). St. Paul's Mission: one female (NHMZ 69943). Tsabalala Sanctuary, Matopos (= Motopos): one female (NHMZ 80660). Wankie (= Hwange) National Park: one male (NHMZ 53665). Zambezi/Chiwore Rivers junction: one male (NHMZ 53583). Zimbabwe National Park: one male (NHMZ 53797); one female (NHMZ 53840).

Aethomys hindei: **KENYA**: Konglei, 3 mi S: one male (USNM 437416). **TANZANIA**: Muheza, Tanga: one male (TM 31487); one female (TM 31489). **UGANDA**: Rhino Camp, Lado, W Nile: four males (USNM 165054, 165071-72, 165085); four females (USNM 165048, 165051, 165065, 165074).

Aethomys kaiseri: **TANZANIA**: Gonja: one male (TM 16118). Iringa: one male (TM 16120); one female (TM 7417). Manyara National Park, N Tanzania: one male (TM 16119). Muheza, Tanga: one male (TM 16123); one female (TM 16122). Tengeru, Arusha District: one female (TM 31365). **ZAMBIA**: Abercorn Londe National Park: one male (TM 31156). Balovale (= Zambezi): nine males (KM 5185-86, 5194-98, 5200, 5203); eight females (KM 5187-88, 5190-93, 5199, 5201). Chibale: one female (NHMZ 6743). Chikungu Stream: two males (KM 12998-99). Chilanga: three males (KM 11021, 11023-24). Lavushi Manda Game Reserve, Lukulu River: one female (NHMZ 7594). Msofu (= Musofu) Mission, Mkushi District: two males (NHMZ 6697, 6713); one female (NHMZ 6712). Ndola: one male (NHMZ 7407). Ndola, 10 mi SSW: five males (NHMZ 6688, 6691, 6709, 6734, 6738); seven females (NHMZ 6689-90, 6708, 6727, 6747, 6749, 6782). Nsange/Kabompo Rivers confluence: one male (NHMZ 3106). Solwezi Boma: one male (NHMZ 2217); three females (NHMZ 2210, 6703, 6742).

Aethomys namaquensis: **BOTSWANA**: Aha Hills, 10 mi N: one female (NHMZ 70375). Ahartts, Batawana Reserve: one female (TM 15261). Bosha Bohola (= Bosho Boholu, Bosobogolo) Pan: two males (NHMZ 70758-58); six females (NHMZ 70751-53, 70755-57). Bushman's Pits, Nata-Maun Road: one female (TM 13593). Chaugule, Magogopate (= Magogophate, Magogaphate): five females (NHMZ 70423, 70428, 70431-32, 70432, 70437); four females (NHMZ 70410, 70420, 70424-25). Chukutsa Pan: one male (NHMZ 70746). Debeeti (= Debeti): two males (NHMZ 70580, 70592). Dikomo di kai (= Dikgomodikae, Kgomodikae): two females (NHMZ 70563-64). Drodsky's Caves: two males (NHMZ 70380, 70406); three females (NHMZ 70366, 70377, 70401). Foley Siding: one male (NHMZ 70691); two females (NHMZ 70379, 70622). Francistown: two males (NHMZ 70784-85); six females (NHMZ 70763-65, 70770, 70782, 70786). Francistown, 40 mi NW: four males (NHMZ 70394-96, 70472); five females (NHMZ 70386-87, 70393, 70398, 70747). Gaberones (= Gaberone), 5 mi W: one male (NHMZ 70730); three females (NHMZ 70645, 70661, 70712). Gensond (= Gesond): one female (TM 14104). Ghansi (= Ghanzi), 35 mi S: one female (NHMZ 70367). Kalamari (= Kalahari): 12 males (NHMZ 70630, 70566, 70598, 70600, 70606, 70613, 70616, 70619, 70621, 70623-24, 70632); 22 females (NHMZ 70567-68, 70595, 70602-4, 70608, 70611-12, 70615, 70618, 70620, 70625, 70628, 70631, 70633-37, 70639, 79597). Kgolo (= Kgale) Hill, Barabong: three males (NHMZ 70715-17); two females (NHMZ 70713-14). Khuis: one female (NHMZ 70675). Lobatse (= Lobatsi): two females (NHMZ 70727, 70729). Mabate (= Mabati, Mabote): three females (NHMZ 70689-90, 70694). Mabuwa Sefubi (= Mabuasehube, Mabua Sefhubi) Pan: one male (NHMZ 70672). Mamono (= Mamuno), 150 mi S: one female (NHMZ 70677). Mangwedi Hill, Serowe: two males (NHMZ 70679-80), one female (NHMZ 70683). Matjemloeji: two females (NHMZ 70587-88). Matopo Quarantine: two males (NHMZ 70338-39); six females (NHMZ 70322, 70329, 70335, 70344-45, 70348). Maun: two males ([KM 12594], [NHMZ 70482]); one female (KM 12595). Moame, 10 mi on Toteng-Maun Road: one male (TM 22180); one female (TM 22195). Moeloutsie Siding: two males (NHMZ 70459, NHMZ 70463); nine females (NHMZ 70454-58, 70460-61, 70465-66). Molopo River, W War Graves: one female (TM 6921). Mosetse, 62 mi on Francistown-Nata Road: one male (TM 22201); two females (TM 22200, 22211). Mosetsi (= Mosetse) River: five males (NHMZ 70475-76, 70478-80); one female (NHMZ 70481).

Moshaneng: one male (NHMZ 70441); three females (NHMZ 70439, 70442, 70449). Nata River: one female (NHMZ 70741). Nthane: two males (NHMZ 70571, 70578); two females (NHMZ 70575, 70579). Okwa: one male (TM 6418). Ootsi (= Ootse): one female (NHMZ 70724). Pilane: one male (TM 7654). Riverslea, Tuli Block: one male (TM 14119); one female (TM 14118). Samadupi: one male (NHMZ 70360); eight females (NHMZ 70354-59, 70362, 70364). Selinda Spillway (= Makwegana): one female (NHMZ 70539). Serowe, 40 mi NW: two males (NHMZ 70681, 70686); one female (NHMZ 70471). Sevuti: two males (NHMZ 70718, 70720); one female (NHMZ 70719). Tamafupi (= Thamafipa): one male (NHMZ 70591). Tierputts (= Tierpits), Ghanzi (= Ghansi): one female (TM 15264). Tsabong: one male (TM 22122; TM 22103). Tsane, 5 mi S: three males (NHMZ 70649, 70668-69); two females (NHMZ 70655, 70667). Tsanga: one female (NHMZ 70353). Tsodilo (= Tsodila) Hills: two males (NHMZ 70373, 70378); five females (NHMZ 70369, 70371, 70400, 70403, 70405). Wolf's Hills, 12 mi S Francistown: two males (NHMZ 70736-37); two females (NHMZ 70536, 70739). **LESOTHO**: Kofa, Qacha's Nek (White Hill): 10 males (NMB 8312, 8318, 8320, 8323, 8327, 8330, 8333-35, 8338); eight females (NMB 8311, 8314-15, 8321, 8325-26, 8328, 8339). Makhoebeng, Thaba-Tseka: one female (NMB 8504). Makhotlong: one male (TM 22230). Malhanapeng, Thaba-Tseka: three males (NMB 8134, 8148-49); one female (NMB 8147). Marakabei (= Marakabeis), Maseru: two females (NMB 7281, 7347). Mateanong, Makhotlong: three males (NMB 6936-37, 6949); two females (NMB 6935, 6948). Moqotoane, Thaba-Tseka (Sehonghong): four males (NMB 8432, 8447, 8459, 8469); four females (NMB 8430, 8431, 8448, 8463). Mount Morosi (= Moorosi), Quthing: 17 males ([NMB 8179-80, 8182, 8187-88, 8192, 8194-95, 8201, 8205-06, 8211-12, 8215, 8220-21], [TM 30377]); 19 females ([NMB 8178, 8181, 8183-86, 8189-91, 8197, 8200, 8202, 8208-9, 8213-14, 8217-18], [TM 30371]). Sekakes: one male (TM 30381); one female (TM 30387). Siles Village, 12.9 mi E Mafeteng (= Mafeleng): one female (TM 22225). Tsoelike Bridge: two females (TM 30369, 30379). **MOZAMBIQUE**: Mague, Tete District: one male (TM 14434), three females (TM 14433, 14435, 14438). Muamdzame (= Muandzane), Libondos: two females (NHMZ 70496, 70498). Pico Mapenduine (= Meponduine): two males (NHMZ 70500, 70503); two females (NHMZ 70115, 70499). Sabi/Lundi Rivers, north of junction: one female (KM 17398). **NAMIBIA**: Andara (Okavango), W Caprivi: one female (KM 5154). Aus, 38 mi on road to Hehuring Hansen: one female (TM 22160). Bellerode Farm, Windhoek: four males (NHMZ 70487-90); four females (NHMZ 70483, 70485-86, 70491). Berseba, Great Namaqualand: one male (KM 5282); three females (KM 5265, 5267, 5289). Canes Okawa, NW Outjo: one male (KM 5308). Ehomba Mountains, N Kaokoveld: two females (KM 5340-41). Gellap-ost Number 3, 16 km N Keetmanshoop: three males (TM 37530-31); one female (TM 37533). Gobabis: three females (KM 5363, 5365-66); two females (KM 5357, 5360). Kamanjab: two females (TM 8126-27). Karachas, Outjo: two males (TM 9537, 10234); six females (TM 9536, 10230-33, 10235). Karibib, S Damaraland: three males (KM 5298-5300); two females ([KM 31852], [TM 9539]). Katijhuru, central Kaokoveld: one male (KM 5316). Kobos: one female (TM 8134). Kovares (= Otjokavare), S Kaokoveld: three males ([DM 423], [KM 5312-13]); one female (TM 11051). Musterland Farm 113, 11.8 km S, 4.0 km W Outjo, Outjo District: two males (KM 28507-08). Ohopoho: one male (TM 11045). Okowekuatjiuci Farm, 13.0 km S, 3.8 km E Kalkfeld, Otjiwarongo District: two females (KM 31876-77). Ombarahewa Farm 22, 0.7 km N, 35.2 km W Otjiwarongo, Otjiwarongo District: six males (KM 28480-82, 28484, 28489-90); six females (KM 28485-88, 28491, 28495). Ombika Gate, Etosha Park, Outjo District: two males (KM 28497, 28500). Ombombo, Kaokoveld: one male (KM 5335, 5337). Ombu, Erongo: one male (TM 9540); one female (TM 9542). Omuramba Ovambo, 2.8 mi E Tsintsibis: one female (TM 22203). Opelo Sud Farm 39, 14.9 km N, 4.6 km E Omaruru, Omaruru District: one male (KM 31870); three females (KM 31859, 31862, 31865). Oropembe (= Orupembe): one male (KM 17630); one female (KM 17626). Otavifontein Farm, 3.5 mi E Otavi on road to Grootfontein: one female (TM 22208). Otjibingwe, Karibib: three males (TM 16263-65); one female (TM 16262). Otjitambi, near Epembe, N Kaokoveld: one male (KM 5339).

Otjitambi Farm 25, 20.0 km S, 35.0 km E Outjo: 17 males (KM 28492-93, 28511, 28513, 28515-17, 28520-21, 28525-30, 28532, 28535); two females (KM 28531, 28533). Otjitundua, central Kaokoveld: two males (KM 5322, 5330); one female (KM 5327). Otjongoro Farm 20, 0.8 km N, 57.8 km E Kalkfeld: two males (KM 31886, 31888); four females (KM 31878-80, 31885). Pederborne, Huab River, Kaokoveld: one female (TM 8131). Quabendus, S Kaokoveld: one male (KM 5309); one female (KM 5310). Rasputin Farm 137, 19.4 km S, 28.0 km W Outjo, Outjo District: two females (KM 28509-10). Rheinvels Farm, 35 km SSW Keetmanshoop: one male (TM 32574); one female (TM 32617). Sandfontein: eight males ([DM 419], [KM 5281, 5382-84, 5386-87, 5389); two females (KM 5385, 5390). Sanitatas: one female (KM 17632). Sesfontein: one female (KM 17634). Stampriet, E Gobabis: four males (KM 5369, 5371-72, 5376); five females (KM 5368, 5370, 5373, 5377, 5380). Swakalskuppe South African Railways Siding on Keetmanshoop-Luderitz Road: one male (TM 22125). Swartboois Drift: one female (TM 22199). Tjirundo Farm 91, 24.5 km N, 7.8 km W Omaruru, Omaruru District: one female (KM 31857). Uis, 1.0 km S, 36.0 km W, S Brandberg, Karibib, Damaraland: one male (KM 31855); one female (KM 31856). Usakos, near Swakopmund: six males (TM 16250, 16254-55, 16257, 16280-81); one female (TM 12932). Valencia, Rehoboth District: one female (TM 14771). Waterberg, Otjiwarongo District, north-central Namibia: one male (TM 8160). Windhoek: five males (TM 16267-69, 16272-73); four females (TM 16270-71, 16274); one female (TM 22198). Witvlei (= Witvley), 40 mi W Gobabis: one male (KM 5353); one female (TM 22213). **SOUTH AFRICA: CAPE PROVINCE:** Addo National Park, Port Elizabeth: four males (KM 19882, 20017, 20027, 20032); 10 females (KM 19881, 19890, 19903, 20007, 20010, 20019, 20025, 20031, 20402, 20425). Alexander Bay, 14.2 km N, 58.5 km E, Namaqualand District: two males (KM 28476, 28478); one female (KM 25537). Alexandria, 11.5 km S, 2.1 km W, Alexandria District: five males (KM 25532-33, 25535, 25538-39); three females (KM 25531, 25534, 25536). Alexandria, 0.5 km N, 35.9 km W, Alexandria District: one male (KM 25844). Alexandria, 3.8 km S, 44.8 km W, Alexandria District: three males (KM 25908, 25913-14); two females (KM 25911-12). Alexandria, 6.8 km S, 6.0 km W, Alexandria District: two females (KM 25917-18). Alexandria, 6.5 km S, 50.3 km W, Alexandria District: one male (KM 25916). Algeria Forest Station, 28 km SSE Clanwilliam: nine males (TM 28295, 28326, 28391, 35040, 35053, 35162, 35170, 40597, 40611); 11 females (TM 28296, 35041, 35043-44, 35054, 35082, 35138, 35169, 40594-95, 40612). Aliwal North: one male (TM 4871). Ammosal Shooting Range, 6.5 km WNW Postmasburg: six males (MMKM 3956, 3960, 3963-64, 3966, 3971); four females (MMKM 3953, 3969, 3970, 3974). Anysberg Nature Reserve, Ladismith: eight males (MMKM 4664-65, 4673-74, 4676, 4679, 4687, 4791); five females (MMKM 4666-67, 4669, 4671, 4677). Augrabies Falls, Orange River: seven males (KM 18170-72, 18174, 18176, 18178-79); three females (KM 18173, 18175, 18177). Augrabies Waterfall National Park: two males (TM 16946, 27439); five females (TM 16934, 16943, 16945, 27437-38). Baden Farm, 10.2 km N, 0.1 km E Montagu, Montagu District: one male (KM 30924); three females (KM 30914, 30916, 30922). Balderja, Piet Retief: two males (KM 18597, 18609); one female (KM 18602). Barkly East, 7.9 km S, 22.6 km W, Barkly East District: one female (KM 25068). Barkly East, 9.9 km S, 22.0 km W, Barkly East District: two females (KM 25071-72). Beaufort West, Karoo (= Karroo) National Park: six males (TM 29541, 29546-47, 29563-64, 29567); five females (TM 29538-40, 29565-66). Bedford, Bedford District: two males (KM 5215, 5217); three females (KM 5216, 5218-19). Bellsbank Estates Farm, 44 km W Warrenton: nine males (MMKM 4260-62, 4273, 4275-76, 4278, 4283, 4288); 18 females (MMKM 4258-59, 4263-72, 4277, 4280-82, 4286-87). Benbecula, Elliot: four males (NMB 4869, 4874, 4881, 4883); three females (NMB 4867, 4873, 4882). Betty's Bay, 1.5 km S, 8.3 km W Kleinmond, Caledon District: two males (KM 30526-27); two females (KM 30524-25). Beuksfontein Farm, 53.9 km N, 40.5 km E Ceres, Ceres District: three males (KM 29906, 29909-10); two females (KM 29904, 29908).

Biesjespoort, Karoo (= Karroo): four males (KM 11303, 11305, 11307, 11312); two females (KM 11304, 11308). Biljetsfontein, 3.0 km N, 34.2 km W Ladismith, Uitspan, Ladismith District: two males (KM 29545-46); three females (KM 29544, 29547-48). Boesmansberg Farm, 60 km NW Van Wyk's Vlei: three males (MMKM 4290-92). Brandlaagte Farm 130, Lady Grey: two males (NMB 4337, 4348); two females (NMB 4336, 4345). Breekkiere Farm, 37 km NW Van Wyk's Vlei: one male (MMKM 4303, 4306). Brucedell Farm 192, Rhodes: four males (NMB 4229, 4240, 4243-44); one female (NMB 4242). Bustard Island: one female (MMKM 4544). Carnarvon, subdivision of Grootvlei Farm 191, Sterkstroom: nine males (NMB 5511, 5516-17, 5539, 5555-57, 5559, 5564); seven females (NMB 5501, 5503, 5535-36, 5548-49, 5558). Carnarvon Commonage, 1 km NE Carnarvon: four males ([KM 13218-19], [MMKM 3975, 3979]); one female (MMKM 3978). Ceres, 40 km E, Lat B: three males (TM 33879, 33928, 33992); five females (TM 33862, 33910, 34015, 34024, 34027). Cetrusdal (= Citrusdal): two males (KM 5533-34); seven females (KM 5523, 5526, 5529-30, 5532, 6513-14). Cheddar Farm, 5 km E Pomfret: two females (MMKM 4388, 4390). Chestnut Grove, Bedford District: one female (KM 18654). Clifford Farm, 12.3 km S, 14.1 km W Barkly East, Barkly East District: one male (KM 25076). Cnydas Farm, 12 km NW Lutzput: four males (TM 32479, 32519, 32536-37); one female (TM 32538). Cradock: five males (KM 8894, 8899, 8901-03); two females (KM 8897, 8900). Dammetjie, 100 km NNE Upington: one female (MMKM 4572). De Aar, 9.6 km S, 8.5 km W, De Aar District: one male (KM 23059); two females (KM 23057-58). De Aar, 12.0 km S, 10.5 km W, De Aar District: one male (KM 23065); three females (KM 23063, 23066-67). De Aar, 15.0 km S, 13.3 km W, De Aar District: one male (KM 23071). Deelfontein, Richmond, Karoo (= Karroo): one male (KM 11297); three females (KM 11294, 11298, 11301). De Grootefontein Farm 437, 3.9 km S, 0.4 km E Albertinia, Riversdale District: three females (KM 29931, 29933, 29936). De Hoop Nature Reserve, 10.1 km N, 31.5 km E Bredasdorp, Bredasdorp District: two females (KM 30907, 30910). Denorbin Farm 344, Barkly East: one male (NMB 4923). Derde Heuvel Farm 149, 4.8 km S, 5.4 km E Montagu, Montagu District: three males (KM 30930, 30935, 30956); four females (KM 30929, 30931-32, 30937). Dikbosch Farm 29, 69 km ENE Grikwastad: eight males (MMKM 4309, 4312, 4314, 4326-28, 4330, 4761); 11 females (MMKM 4213, 4308, 4310-11, 4316, 4320, 4322, 4331-32, 4336, 4338). Dikgatlong (= Dikgatlhong), Limebanks, Kuruman River, 15 mi W Kuruman: two males ([KM 10931], [TM 22152]); two females ([KM 10932], [TM 22153]). DoornbOom, 6.6 km S, 33.0 km W Ladismith, Ladismith District: one male (KM 29562). Doornkloof Nature Reserve, 45 km NNW Colesberg: one male (MMKM 4694); four females (MMKM 4690-91, 4692, 4696). Doornlaagte Farm, 24 km NNW Panielskuil: two males (MMKM 4041-41); one female (MMKM 4043). Doringbult, 24 km SW Ulco: two females (MMKM 3981, 4735). Douglas, Hopetown (= Hopetuin): one male (TM 22168). Dragepoort, Korannaberg: three males (MMKM 1246, 1258, 1263). Drumbo Farm 80, Barkly East: one female (NMB 4529). Duinwal Farm, 30 km W Vorstershoop: one male (MMKM 4387). Eendekuil: one female (NMB 1308). Eenriet (= Einriet), near Steinkopf, Little Namaqualand: nine males (KM 5418-19, 5422-23, 5425, 5428-29, 20797, 33032); five females (KM 5421, 5432, 20814, 20809, 20906). Ester Farm, 49 km N Vorstershoop: one females (MMKM 4762). Ezelfontein (= Eselfontein), near Leliefontein, Kamiesberg, Little Namaqualand: 13 males (KM 5469, 5474-76, 5478, 5487-90, 5493, 5500, 5511, 20798); 16 females (KM 5471, 5473, 5480-81, 5484, 5486, 5491-92, 5496-97, 5499, 5501, 5505, 5509, 20778, 33036). Franschhoek Farm, 16 km NW Olifantshoek: nine males (MMKM 4143, 4145, 4151, 4154, 4156-59, 4163); six females (MMKM 4146-47, 4152, 4155, 4160-61). Gamkapoort Nature Reserve, Prince Albert: four males (MMKM 4614, 4628, 4630, 4655). Gathlose, 28 km ESE Sishen: six males (MMKM 4344-45, 4357, 4358-60); 10 females (MMKM 4346-48, 4350-55, 4362). Glen Cave Farm, 4.5 km N, 13.6 km E Molteno, Molteno District: one female (KM 25086). Glen Gyle Farm 39, Barkly East: one male (NMB 4471).

Gloria, subdivision of Olyvekloof Farm 184, Jamestown: five males (NMB 5000-01, 5004, 5007, 5014); eight females (NMB 4999, 5003, 5006, 5008, 5010, 5020, 5022-23). Goedgedacht, 21 km ENE Postmasburg: one male (MMKM 4034); one female (MMKM 4027). Goegap Nature Reserve, Springbok: one female (TM 42171). Goodhouse (Orange River), Namaqualand: one male (KM 5237); three females (KM 5236, 5240, 5244). Goodlands Sector A, Quiston Nature Reserve: one male (MMKM 4537); three females (MMKM 4535-36, 4547). Goodstone Farm 62, Indwe: 10 males (NMB 6184, 6190-93, 6197, 6199, 6201, 6204, 6253); 15 females (NMB 6183, 6185-89, 6194-96, 6200, 6203, 6205-06, 6208, 6254). Goodwin's Kloof, Grahamstown, E Cape Province: one male (TM 1412). Goraas Farm FrQ 29, 62 km W Carnavon: four males (TM 27310, 27384-85, 27388); five females (TM 27309, 27314, 27317, 27336, 27347). Gosa Farm, 54 km WSW Hotazel: five males (MMKM 4088, 4090, 4092-94); three females (MMKM 4085, 4089, 4091). Gougo Farm, 39 km NW Van Wyk's Vlei: four males (MMKM 4104, 4108, 4110-11); three females (MMKM 4107, 4109, 4112). Gowies Kloof, Grahamstown: three females (KM 32905, 32911-12). Graaff-Reinet: one male (KM 18559); one female (KM 18562). Grahamstown: eight males ([KM 5209, 5212-13, 32892, 32955-56, 32960], [TM 6691]); three females (KM 5214, 32895, 32957). Groote Drift Farm, 8.4 km S, 10.9 km E Elandsbaai, Piketburg District: three males (KM 29119, 29121, 29132). Grootfontein, Middelburg: three males (TM 12358-59, 12431); one female (TM 12433). Groot Tafelbergsfontein Farm, 9.4 km N, 90.6 km W Beaufort West, Beaufort West District: one male (KM 29538); two females (KM 29541, 29543). Halstone (= Halseton) Farm 36, Barkly East: four males (NMB 4948, 4950, 4954-55); three females (NMB 4951, 4957-58). Hamilton Farm 64, Rhodes: eight males (NMB 5717, 5735, 5756-58, 5760-61, 5764); four females (NMB 5716, 5718, 5734, 5759). Haweqwas State Forest, 8.2 km N, 12.0 km E Wellington: five males (KM 30588-91, 30593); two females (KM 30587, 30592). Haweqwas State Forest, 1.8 km N, 8.7 km E Wellington: three males (KM 30584-86); one female (KM 30579). Heather Glen, Kofi (= Kafi) River, Bathurst: one female (KM 32975). Heimat, subdivision of Embotokwa Commonage, Indwe: two females (NMB 4173, 4176). Hester Malan Wild Flower Reserve: two males (TM 27547, 27567); four females (TM 27566, 27569, 27571, 27574). Het Kruis: four females ([KM 5520-22], [TM 12904]). Hex River (= Heksrivier) Estate, 10 mi (= km) N Cetrusdal (= Citrusdal): two males (KM 5535, 5550); three females (KM 5539, 5542, 5545). Hopefield Estate Farm 552, 25 km NNE Grikwastad: one male (MMKM 4339); two females (MMKM 4340-41). Janu Mayenzar (Stutterheim): one male (KM 19977); eight females (KM 19978, 19981, 19983, 19985-86, 19988-89, 19991). Kalkoenkrans, subdivision of Pisa Farm 107, Dordrecht: five males (NMB 4718, 4724, 4728-29, 4732); six females (NMB 4716, 4720, 4722, 4726-27, 4730). Kalkoenkrantz Farm 189, Sterkstroom: six males (NMB 5432-33, 5435, 5438, 5458, 5461); four females (NMB 5392, 5431, 5434, 5437). Kamiesberg, Witwater Plateau: four males (KM 33050, 33053-55); two females (KM 33051-52). Kangnas Farm, 48 km ENE Springbok: 13 males (TM 28118, 28134-35, 28137-38, 33746-47, 33754, 33771, 33805-07, 33819); five females (TM 28116-17, 28126, 28136, 33744). Kauki-Morokwa Road: one male (TM 22131). Keikamspoort Farm 71, 20 km SE Prieska: 13 males ([MMKM 4184], [TM 27189, 27191, 27193-94, 27202-03, 24205, 27222-23, 27244-46]); seven females (TM 27187-88, 27190, 27192, 27195, 27204, 27224). Keimoes Island, Orange River: 20 males ([TM 27247], [USNM 451913-14, 451921, 451933-34, 451941, 451948, 451950-51, 451983, 451990-91, 452000, 452002, 452019, 452028, 452039, 452041, 452045]); 13 females (USNM 451915, 451924, 451956, 451992, 451994, 452003, 452006, 452016, 452020, 452031a-b, 452035, 452053). Kersbos Farm, 10 km NNE Bitterfontein, Namaqualand: three females (TM 28087-88, 28105). King William's Town: two males (KM 18492-93); one female (KM 18494). King William's Town, 2.0 km N, 7.2 km E: 15 males (KM 5394, 5396, 5399, 5405, 5407, 5410, 6178, 6180, 6182, 18401-02, 18415, 18427-27, 20992); 16 females (KM 5393, 5395, 5398, 5402-04, 5406, 5408, 5412-15, 6185, 18403, 18544, 24409). Klawer (= Klaver), Olifants River, W Cape Province: one male (TM 2230); three females (TM 2228-29, 2231).

Kleinfontein I Farm, 26 km ENE Noupoort: 12 males (TM 34028, 34030, 34037, 34039-40, 34044, 34062-64, 34073-74, 34092); nine females (TM 34036, 34038, 34060-61, 34068, 34087, 34095, 34128-29). Kleinpoort, Grahamstown: five males ([KM 32904], [TM 6695-96, 6699, 6700]); six females (TM 6684, 6692-93, 6697-98, 6701). Kleinpotfontein Farm, 47 km NNE De Aar: one female (MMKM 4457). Kliphuis, 11 mi NE Clanwilliam: five males (KM 5573, 5579-80, 5585, 5594); five females (KM 5564-65, 5586, 5596, 5598). Klipkraal Farm 48, Lady Grey: four males (NMB 4197, 4199-4201); two females (NMB 4196, 4198). Kloppersbosch Farm 338, 0.2 km N, 20.3 km E Worcester, Worcester District: two males (KM 30954-55). Koofmansfontein, Barkly West: one male (KM 9569). Korannasberg Farm, 88 km NNW Olifantshoek: eight males (MMKM 4245-47, 4249-50, 4254, 4256-57); three females (MMKM 4251, 4253, 4255). Koningsrivier Dam Farm, 12.2 km S, 5.2 km W Robertson, Robertson District: one male (KM 26389); one female (KM 26388). Kwartelfontein (Sandfontein) Farm, 3.2 km S, 16.6 km W Touwsrivier, Ceres District: two females (KM 29921-22). Lady Grey: seven males (KM 11251, 11253, 11255, 11257-58, 11269, 11276); 11 females (KM 11250, 11254, 11260, 11262, 11264-67, 11274-75, 13989). Lamberts Bay: one male (TM 2232). Leelykstaat Farm, 31 km NE Marydale: 19 males (MMKM 4165-69, 4185-87, 4196-97, 4200-03, 4205-06, 4210, 4214, 4220); 24 females (MMKM 4164, 4171-74, 4177-80, 4182-83, 4188, 4190-93, 4198-99, 4207-08, 4211, 4213, 4217-18). Lidney Farm, 3.6 km S, 38.0 km W Alexandria, Alexandria District: eight males (KM 25421, 25424, 25426-27, 25430-32, 25530); 11 females (KM 25416-17, 25419-20, 25422-23, 25425, 25428-29, 25529, 25845). L'Ormarin's Farm, Franschhoek Valley, near Paarl: two males (TM 2224, 2226). Louisvale, Upington: three males (TM 22146, 22150, 22176). Mariba, subdivision of Joubertskop Farm 162, Dordrecht: one male (NMB 5122); three females (NMB 5081, 5090, 5108). Marthasdale Farm 190, 23 km NNE Danielskuil: two females (MMKM 4391-92). Marthasrust, 9 km NW Olifantshoek: one female (MMKM 4562). Melkspruit Farm 12, Aliwal North: three males (NMB 4397, 4399, 4402). Mierekraal Farm, 6.9 km S, 5.1 km W Bredasdorp, Bredasdorp District: three males (KM 30518-19, 30523); two females (KM 30521-22). Mierfontein Farm, 2.7 km S, 34.9 km W Ladismith, Uitspan, Ladismith District: two males (KM 29556, 29561); two females (KM 29558-59). Milton Farm 4, Maclear: one male (NMB 5836); one female (NMB 5820). Modderfontein Farm 193, Jamestown: eight males (NMB 5614-16, 5620-22, 5624, 5627); five females (NMB 5618-19, 5625-26, 5628). Molopo Nature Reserve, 10 km W Vorstershoop: two males (MMKM 1633, 4585); eight females (MMKM 1596, 1635, 1639, 1673, 1676, 1683, 4586-87). Molteno, 1.9 km N, 16.5 km E, Molteno District: two females (KM 25090-91). Mountain Zebra National Park, Cradock: one male (TM 17605); three females (TM 17607, 17609, 17611). Mouton's Valley Farm A80, 15.2 km N, 5.7 km W Piketburg, Piketburg District: one male (KM 30222); three females (KM 30218, 30223, 30226). Municipal Farm, Middelburg: one male (KM 11287); three females (KM 11283-84, 11289). Murraysburg, 7.5 km N, 14.1 km W, Murraysburg District: one male (KM 23093). Murraysburg, 23.4 km S, 15.2 km E: two males (KM 23276-77). Murraysburg, 24.3 km S, 16.1 km E, Murraysburg District: two males (KM 23289, 23297); six females (KM 23280, 23283, 23286, 23290-92). Naauwte, 23 km NNW Prieska: six males (MMKM 4045, 4048, 4050, 4058, 4075, 4077); 16 females (MMKM 4044, 4051, 4053, 4055, 4057, 4060-61, 4069, 4071-74, 4078, 4081-82, 4084). Namaqualand: one male (KM 20775). Narap Farm, 28 km SSE Springbok: seven males (TM 27811, 27813, 27837-38, 27843, 27945, 27948); four females (TM 27798-27800, 27946). New Upington (= Upington), South Bank of Orange River: one male (KM 5230); one female (KM 5229). Nieuwe Plaats Farm 567, 4.1 km S, 8.5 km W Darling, Malmelsbury District: one female (KM 30217). Northern Cape Nature Conservation Station, 8 km W Hartswater: four females (MMKM 4745-48). Ookiep: one male (TM 8114). Oorlogskloof Nature Reserve, Nieuwoudtville: 36 males (MMKM 4589-90, 4592-93, 4596-98, 4600-01, 4604-05, 4609-11, 4615-17, 4620-21, 4632-33, 4636, 4639, 4642, 4645-48, 4651, 4653, 4657, 4659-61, 4787-88); nine females (MMKM 4591, 4602, 4606-08, 4634, 4643, 4650, 4662).

Orinway Farm, Albany District: 17 males (KM 14737-38, 14742, 14746, 14748-49, 14751-54, 14758, 14760-61, 14763-64, 14766, 14768); nine females (KM 14739, 14741, 14744-45, 14747, 14750, 14759, 14769, 31349). Ossa Farm 38, Lady Grey: four males (NMB 4429-32); one female (NMB 4433). Pakhuis Pass, Clanwilliam: one male (KM 18180). Petrusville, 11.7 km S, 11.7 km E, Philipstown District: two males (KM 23103, 23108); four females (KM 23100-01, 23106, 23110). Petrusville, 12.3 km S, 10.8 km E, Philipstown District: one male (KM 23107); one female (KM 23105). Pniel Estate Farm, 8 km SW Barkly West: two females (MMKM 4018, 4020). Port Alfred, 0.9 mi N, 9.2 mi W, Bathurst District: six males (KM 21126, 21129, 21133, 21138, 21141, 21146); two females (KM 21134-35). Prieska Commonage, 6 km SSE Prieska: nine males (MMKM 3986, 3995-97, 3999-4000, 4003, 4005-4006); eight females (MMKM 3987-88, 3991-93, 4004, 4008, 4012). Prince Albert, 12.8 km S, 11.4 km W, Prince Albert District: 12 males (KM 30533, 30535, 30537, 30539, 30541-43, 30545-48, 30550); six females (KM 12591, 30531-32, 30534, 30536, 30538). Quaggaskerk, Tarkastad: one female (KM 8997). Ras Zyn Puts Zuid Farm 18, 37.9 km N, 11.5 km W Brandvlei, Calvinia District: two males (KM 28457-58). Rhabdomys Island: one male (MMKM 4546). Richtersveld, 19.2 km N, 48.8 km E Alexander Bay, Namaqualand District: one male (KM 28463). Richtersveld, 15.1 km N, 57.6 km E Alexander Bay, Namaqualand District: four males (KM 28465-67, 28479); two females (KM 28473-74). Riemuasmaak, 47 km NW Kakamas: four males (MMKM 4460-61, 4468-69); 13 females (MMKM 4463-67, 4470-74, 4556-58). Rietfontein: two males (TM 11078, 11082); two females (TM 11080-81). Rietfontein Farm 82, 8.7 km N, 25.8 km W Steynsburg, Steynsburg District: 13 males (KM 25670-71, 25676, 25678, 25681, 25684, 25686-87, 25689-90, 25697-99); 13 females (KM 25672-75, 25677, 25679, 25682-83, 25685, 25691-93, 25695). Riries Farm, 29 km NW Kuruman: seven females (MMKM 4363-65, 4373-75, 4378); eight females (MMKM 4367-72, 4376-77). Risler Farm 30, Maclear: one male (NMB 5851); two females (NMB 5850, 5854). Rodeseput, 44 km NE Brandvlei: four males (MMKM 4114, 4118-19, 4122); four females (MMKM 4115-16, 4120-21). Roodewal Farm 96, Aliwal North: five males (NMB 4301-03, 4305-06); one female (NMB 4307). Rooidam, 10 km N Windsorton: four males (MMKM 4098, 4102-03, 4743); four females (MMKM 4096-97, 4101, 4741). Roseglen, 76 km WNW Griekwastad: one male (MMKM 4520); three females (MMKM 4514, 4517, 4524). Ruford Elanor River Valley, Uitenhage: two males (KM 5207-08). Schuitklip Farm, 42 km NE Pofadder: one male (MMKM 4458). Sevenweeks Pass: one female (TM 9074). Skoorsteenmantel Farm 20, Jamestown: nine males (NMB 4815, 4819-20, 4823, 4830, 4836-37, 4840, 4843); seven females (NMB 4802-04, 4806-07, 4828, 4838). Slang Gat Lad Farm, 2.8 km N, 25.6 km W Ladismith, Ladismith District: four males (KM 29551, 29553-55); one female (KM 29550). Snowhill Farm 206, Dordrecht: one male (NMB 5804); one female (NMB 5811). Sterkstroom Farm, 70 km N Williston: one male (MMKM 4459). Steytlerville, 11.8 km N, 2.5 km E, Steytlerville District: one male (KM 23909); four females (KM 23901-02, 23907, 23911). Steytlerville, 9.6 km N, 5.0 km E, Steytlerville District: three males (KM 23919-20, 23930); one female (KM 23916). Steytlerville, 8.5 km N, 3.0 km E, Steytlerville District: one male (KM 23929). Steytlerville, 1.7 km N, 11.1 km E, Steytlerville District: three males (KM 23934-35, 23937); three females (KM 23940-41, 23955). Strydenburg, 21.9 km N, 5.1 km W, Hopetown (= Hopetuin) District: nine males (KM 23072-77, 23079-80, 23083); six females (KM 23078, 23082, 23084, 23086-88). Strydenburg, 18.7 km N, 7.6 km W, Hopetown (= Hopetuin) District: one male (KM 23089). Sunnyside Farm, 14 km N Copperton: one male (MMKM 4299); one female (MMKM 4298). Swartberg Forest Reserve, 13.9 km S, 7.4 km W Prince Albert, Prince Albert District: three males (KM 30572-74). Swartberg Forest Reserve, 12.6 km S, 0.2 km E Prince Albert, Prince Albert District: one male (KM 30553). Swartberg Forest Reserve, 13.3 km S, 5.7 km W Prince Albert, Prince Albert District: five males (KM 30558, 30562, 30564, 30567, 30570); three females (KM 30566, 30569, 30571).

Sydney on Vaal Farm, 4 km SW Delportshoop: seven males (MMKM 4408, 4410, 4413-15, 4420-21); eight females (MMKM 4412, 4416, 4418-19, 4422, 4424-25, 4767). Takoon Bantu Reserve, 22 mi NW Lykso: one male (TM 22116); two females (TM 22117, TM 22140). Tambookies Vlei, Stockenstrom (= Stockenstroom): eight males (KM 8905, 8907, 8909-12, 8915-16); three females (KM 8906, 8908, 8913). Tanbosleegte, SE Cradock: one female (KM 8896). Tierkop Farm, 17 km SSW Kuruman: eight females (MMKM 4478-81, 4484, 4489, 4491, 4498). Traveller's Rest, 18 mi NE Clanwilliam: one female (KM 5516). Tshidilamolomo: one female (TM 22114). Twee Rivieren, K.G.N.P. (= Kalahari Gemsbok National Park): one male (MMKM 4786); one female (MMKM 4785). Uniondale, 12 km WNW, Kammanassie: four males (TM 29715-16, 29725, 29744); three females (TM 29714, 29735, 29745). Uniondale, 3.8 km N, 3.4 km E, Uniondale District: 12 males (KM 23957, 23959, 23962-64, 23966-69, 23972, 23977, 23979); five females (KM 23956, 23958, 23960-61, 23974). Upington, 6 mi on Prieska Road: one male (TM 22136). Van der Merwesrus, 33 km NW Bray: one female (MMKM 3985). Veldblom Nature Reserve: one male (MMKM 4588); two females (MMKM 4594, 4599). Venture Farm 139, Aliwal North: 22 males (NMB 4579, 5665, 5669, 5671-74, 5676-78, 5680, 5683, 5687, 5692-93, 5695-96, 5698-5701, 5707); 10 females (NMB 5647, 5668, 5670, 5675, 5686, 5688, 5690-91, 5694, 5697). Verwoerd, H. F. Dam Island: two males (MMKM 4533-34); five females (MMKM 4528-32). Victoria West, 13.1 km N, 4.0 km E, Victoria West District: one male (KM 23302). Vinci Farm, 12 km NE Postmasburg: one male (MMKM 4028). Vissersville, 25 km SW Kenhard: one male (TM 32448); two females (TM 32445-46). Vlaktefontein Farm 51, Lady Grey: two males (NMB 6229, 6266); two females (NMB 6267-68). Vogelfontein Farm, 12 km SSW Campbell: one male (MMKM 1557); three females (MMKM 4550, 4552-53). Vredendal, State Land, 10,7 km S, 26.9 km W, Vredendal District: six males (KM 29138, 29140-41, 29143-44, 29147); three females (KM 29131, 29137, 29148). Vrisgewaagd Farm 152, 5.7 km S, 13.5 km W Prince Albert, Prince Albert District: one male (KM 29929); three females (KM 28828, 29925, 29927). Vryburg: two males (TM 5450, 22220); one female (TM 22154). Waaikloof Farm 333, 1.1 km N, 20.4 km E Worcester, Worcester District: three females (KM 30949-51). Waterford Farm, 13 km NNE Hopetown (= Hopetuin): three males (MMKM 4394, 4397, 4405); four females (MMKM 4395-96, 4401, 4404). Witput Farm, 12 km NW Campbell: one male (MMKM 4771); one female (MMKM 4770). Witsand Farm, 63 km SW Postmasburg: eight males (MMKM 4125, 4129, 4131, 4136-39, 4141); three females (MMKM 4123, 4126-27). Witwater Plateau, Kamiesberg: 15 males (KM 5439, 5445, 5449-50, 5452-54, 5456-60, 5462, 5464, 5466); 10 females (KM 5438, 5440, 5442-44, 5446, 5448, 5463, 5465, 5467). Wolseley: 12 males (TM 5910, 5912-14, 5916-19, 5922-24, 5927); eight females (TM 5911, 5915, 5925-26, 5928-30, 12901). Wonderwerk Farm, 44 km SSE Kuruman: one male (MMKM 4513); nine females ([KM 9570-71, 9574-75], [MMKM 4500, 4502-04, 4509]). Woodstock Farm, 10 km SW Kuruman: four males (MMKM 3939, 3941-42, 4725); two females (MMKM 3938, 3948). Zeekoebaard Farm 306, 28 km SE Groblershoop: 11 males (MMKM 4222-23, 4226-29, 4240-44); 10 females (MMKM 4225, 4230-31, 4233-39). Zoetvlei (= Soetvlei), Vryburg: four males (TM 6877-80). **FREE STATE**: Alfa Farm 4, Ladybrand: one male (NMB 4059). Alleman's Drift Farm 37, Philippolis: two males (NMB 3710, 3713); one female (NMB 3716). Allemanskraal, W Pretorius Reserve: two females (TM 13697, 13701). Alma, subdivision 1 of Glen Aspen Farm 1389, Frankfort: one female (NMB 3873). Asem Farm 371, Senekal: one male (NMB 3129); one female (NMB 3130). Bakenfontein, Windburg (= Winburg): one female (NMB 2667). Bellevue Farm 1416, Bethlehem: one male (NMB 2976). Bethulie: one female (TM 7831). Braklaagte, Parys: one male (TM 3825); one female (TM 3826). Bloemfontein: six males (NMB 2215-16, 2225, 2236-37, 2244); three females (NMB 2217, 2219, 2512). Brandfort Municipal Commonage: one male (TM 22172). De Berg Farm 453, Dewetsdorp: one male (NMB 2602). De Poort Farm 378, Ventersburg: two females (NMB 2927-28). Donkerpoort Farm 218, Weppener: one male (NMB 4117); one female (NMB 4116). Driehoek Farm 218, Luckoff (= Luckhoff): four males (NMB 2906-07, 2909, 2913); one female (NMB 2914).

Eendrag, Bethulie: four males (NMB 3733-34, 3752-53). Eureka Farm 674, Senekal: two males (NMB 3275-76). Fish Eagle, Orange Free State (= Free Stae) Peninsula: one male (MMKM 4541); two females (MMKM 4542-43). Golden Gate Highland Park: one male (TM 14979). Hartbeeshoek Farm 115, Zastron: four females (NMB 4075-76, 4078-79). Hertzogville on Hoopstad Road: one male (TM 22167); two females (TM 22164, 22166). Hexrivier Farm 405, Reddersburg: one male (NMB 3605); one female (NMB 3607). Hobhouse: one female (TM 4974). Kleinfontein Farm 202, Bethulie: five males (NMB 1845, 1851, 1853, 1857, 1864). Koeberg Farm 1663, Clarens: one male (NMB 2750); one female (NMB 2758). Koele Farm 97, Thaba Nchu: one female (NMB 2958). Kommetjiesfontein Farm 798, Springfontein: five males (NMB 2889-93); one female (NMB 2895). Koppiesdam Farm 473, Petrusburg: two males (NMB 1765, 1785); four females (NMB 1764, 1784, 1794, 1796). Kraaifontein Farm 109, Rouxville: seven males (NMB 3970-71, 3973, 3978, 3980-81, 3983); five females (NMB 3974-76, 3979, 3982). Larala, Senekal: one male (NMB 2723). Lestoana Stad, Fourisburg (= Fouriesberg): two females (NMB 4138, 4141). Leeukop Farm 105, Dewetsdorp: two males (NMB 3579, 3581). Lemoenboord, Philippolis: one male (NMB 2385). Lockshoek Farm 192, Jagersfontein: one male (NMB 2688); two females (NMB 2686, 2722). Malutizight Farm 565, Ficksburg: one male (NMB 3459); one female (NMB 3466). Middelbron Farm 501, Philippolis: one female (NMB 1487). Mooifontein Farm 368, Reddersburg: one male (NMB 2839). Mooihoek Farm 130, Harrismith: three males (NMB 3112-13, 3115). Mount Brand Farm 278, Bethulie, Springfontein: two males (NMB 3424-25). Northend Farm 75, Ficksburg: one male (NMB 1762); two females (NMB 1763, 1766). Nova Farm 667, Ladybrand: one male (NMB 1790). Prarie Farm 576, Smithfield: four males (NMB 2726, 2639-40, 2642); one female (NMB 2641). Preezfontein Farm: three males (MMKM 4432, 4443, 4445); 15 females (MMKM 4427-29, 4434, 4437, 4440-42, 4447-49, 4451-53, 4455). Roodepoort Farm 105, Edenberg (= Edenburg): one male (NMB 2996). Rosendal Farm 364, Ladybrand: three males (NMB 3225, 3230, 3233). Rotondo Farm 1046, Rouxville: one female (NMB 2771). Sebastopol Farm 51, Zastron: one female (NMB 1949). Spitskop Farm 398, Fauresmith: one male (NMB 3692); two females (NMB 3684, 3688). Strathearn Farm 396, Thaba Nchu: six males (NMB 4004-05, 4007, 4009, 4011, 4013); four females (NMB 4006, 4010, 4012, 4014). Summerslie Farm 350, Harrismith: one male (NMB 3943). Versamelkop Farm 68, Ladybrand: two males (NMB 4028, 4033); four females (NMB 4029-32). Vierkant Farm 798, Brandfort: one male (NMB 2871). Wittekoppies Farm 169, Vredefort: two males (NMB 1597-98), one female (NMB 1600). Zyferfontein, Parys: one male (TM 3824). **KWAZULU-NATAL**: Dundee, 5.3 km on road to Pomeroy: two males (TM 22151, 22162). Graigadam Farm (= Craigadam), Itala Nature Reserve, 9 km NE Louwsburg: six males (TM 28825, 31658, 31660, 31713, 31731, 31737); one female (TM 28820). Ladysmith, 11.5 mi on Van Reenen Main Road: two males (TM 22143, 22187). Langewacht, Babanango: four males (DM 1847-48, 1853, 1857); one unknown sex (DM 1861). Magut Farm, Goedehoop, portion of Broedersrus: one male (TM 22133). Nagle Dam: one female (DM 1871). Pomeroy (= Pameroy), 10.5 mi on road to Greytown: two females (TM 22147, 22170). Ubombo: three males (TM 5623-24, 5628); two females (TM 5627, 22135). Umlalazi Nature Reserve: one male (TM 31788). Weenen Nature Reserve, Weenen District: one female (TM 38101). **TRANSVAAL**: Arnhem (= Arnhemburg), Carolina: one male (TM 1390); one female (TM 1389). Arnhemburg, Carolina: one female (TM 1787). Blijdschap Private Nature Reserve, 5 km N Bandolierskop: three males (TM 24221-23); one female (TM 24220). Blyde Forest Reserve, 10 km N Graskop: two males (TM 24321-22); two females (TM 24323, 24499). Bochum, Wilhanshohe, Magalakwin (= Magalakuin, Magalakwena): one male (TM 3718); two females (TM 3719, 3726). Boekenhoutkloof: 21 males (TM 30430, 30433-34, 30441-42, 30959-60, 30967, 30969, 30971-73, 30975-77, 30979, 30984, 31259, 31262-63, 31267); 19 females (TM 30431, 30435-38, 30458, 30961-62, 30964, 30968, 30970, 30974, 30980-83, 31261, 31265-66). Boskop Dam Nature Reserve, N Potchefstroom: one male (TM 41866). Broederstroom Farm: one female (TM 34277).

Daspoortberg: eight males (TM 4607, 4609-12, 4614, 4617, 4619); two females (TM 4618, 4620). De Hoop Private Nature Reserve: one male (TM 25356); three females (TM 25328, 25341, 25383). Dinokana (= Linokane), 3.1 mi on road to Zeerust: one male (TM 22184). Donkerpoort and Zandspruit Farm 449, 24 km E Thabazimbi: two males (TM 20617, 20642); eight females (TM 20582-83, 20585, 20586a-b, 20609-10, 20616). Dordrecht Farm 578, 20 km S Marken: one male (TM 24664); three females (TM 24665, 24674, 24682). Elandsfontein Farm 74, 6.3 mi De Wilt Post Office on Pretoria W-Brits Road: one male (TM 22121); one female (TM 22098). Gravellote, Tzaneen: one female (TM 4034). Greefswald Farm 37, 73 km W Messina: two males (TM 20351, 20370); nine females (TM 20343, 20348-50, 20369, 20380-82, 20384). Groothoek Farm 99, 25 km ESE Potgietersrus: one male (TM 23350); three females (TM 23356, 23365-66). Grootsuikerboschkop and Elandlaagte Farm, Dullstroom: one female (TM 23807). Guldenskat Farm, 9 km Jan Kempdorp: one male (MMKM 4026). Hans Merensky Provincial Nature Reserve, 30 km NE Letsitele: two males (TM 24539, 24573); three females (TM 24540-41, 24572). Hennops River: two males (TM 3697, 22233). Houghton Estate, Johannesburg: one female (KM 33065). Huwi Private Nature Reserve, 7 mi SE Ellisras: four males (TM 19954, 19985-87); one female (TM 19993). Ingelele (= Ngelele): two males (TM 2034, 2036); two females (TM 2029, 2035). Irene, Pretoria: one male (TM 1231). Jan Amsterdam, Pietersburg: one male (KM 19776); two females (KM 19720, 19758). Johannesburg: five males ([KM 5205], [TM 490, 492, 494, 30376]); five females (TM 482, 488, 491, 493, 498). Joshua Moolman Private Nature Reserve, 9 km WSW Amsterdam: two males (TM 20180, 20234); one female (TM 20179). Khandizwe Plateau, 9 km W Malelane, Kruger National Park: (one male (TM 30029). Kilnerton: one male (TM 3940). Klopperfontein, Kruger National Park: one male (TM 36672). Kosterfontein Farm 460, Koster: one male (TM 4203). Letaba Ranch 8, 40 km N Phalaborwa: two males (TM 25549, 25571); two females (TM 25572-73). Lichtenburg, 4.5 mi N on road to Ottoshoop: one male (TM 22100); one female (TM 22128). Loskop Dam Nature Reserve: three females (TM 19828, 19867, 40924). Madimbo, 10 km E, Limpopo River: two males (TM 24651-52); two females (TM 24613, 24638). Madimbo, Mabilingwe Area, Limpopo River: one female (TM 41165). Magalakwin (= Magalakuin, Magalakwena) Farm 666, Potgietersrus: one male (TM 3722); one female (TM 3724). Magaliesberg, Pretoria: one female (TM 4335). Malmaniesoog, N Zeerust: one male (TM 42048). Messina Nature Reserve: one female (TM 42353). Mmabolela Estates, 14 km NW Maasstroom: one male (TM 19731); one female (TM 19701, 19759). Mokeetsi Farm 376, Duiwelskloof, Zoutpansberg: one male (TM 4035). Mooigenoeg Farm 83, 8 km S Derdepoort: one male (TM 23537); one female (TM 23564). Moorddrift Farm 289, Waterberg, Potgietersrus: one female (TM 1449). Moormeisiesfontein, Rustenburg, Thabazimbi: one female (TM 1713). Nooitgedacht Nature Reserve: one male (TM 42433). Olifants River Gorge, 3.5 mi S, Satara Road junction, Satara, Kruger National Park: one male (TM 22204); one female (TM 22223). Olifantspoort Farm 328, 12 mi S Rustenburg: one female (TM 19628). Palala-Limpopo River junction, Waterberg: one male (TM 2334). Paramie (= Uitkyk) Private Nature Reserve, 12 km SSE Nelspruit: two males (TM 20082, 20090); one female (TM 20083). Platbos Farm, 32 km NW Vaalwater: four females (TM 24741, 24759, 24782-83). Potgietersrus, 72 km NW: one male (TM 16610); one female (TM 16608). Ratsegaai Farm 204, 13 km W Ventersdorp: four males (TM 27705, 27731-32, 27761); four females (TM 27703-04, 27733-34). Renosterpoort Private Nature Reserve, 15 km NE Bronkhorstspruit: three males (TM 23827, 23829, 23846); three females (TM 23826, 23828, 23830). Rhoda Farm 9, 13 km S Phalaborwa: one female (TM 24246). Rietondale, Pretoria: two males (TM 1229-30). Rietspruit, Nylstroom: one female (TM 3882). Rochdale Farm 700 MS, 5 mi E Waterpoort: one male (TM 19774); five females (TM 19767-69, 19783, 19787). Roodeplaat, Pretoria: one male (TM 1540); one female (TM 1541). Rykvoorby Farm, 9 km N Zeerust: four males (TM 20535-38); three females (TM 20526-28).

Scrutton Farm 23 MT, 32 km E Messina: one male (TM 20310); three females (TM 20293, 20304, 20311). Steenkampsberg Provincial Nature Reserve, 13 km NNE Dullstroom: one female (TM 39196). Suikerboschrand Provincial Nature Reserve: four males (TM 25139, 25160, 25164, 25171); six females (TM 25121, 25138, 25162-63, 25170, 25172). Suikerboschrand Nature Reserve: one female (TM 41682). Swartkrans, Sterkfontein, Krugersdorp: three males (TM 10029, 12172, 12176); five females (TM 12174, 22097, 22099, 22104, 22110). Thabazimbi: one male (TM 20587). Theespruit Farm 156, Carolina/Barberton Glens: one male (TM 1391). Uitkomst Farm 499, 35 mi W Pretoria: one female (TM 22124). Urk Farm 10, Blouberg Private Nature Reserve, 13 km W Vivo: one male (TM 24061). Waterkloof, Pretoria: two males (TM 1406, 3823). Witpoort Farm 419, 24 km E Potchefstroom: three males (TM 23488-89, 23501); three females (TM 23490, 23509, 23511). Wonderboom, Pretoria: 12 males (TM 1228, 3950, 17406-07, 17410-15, 17418-19); four females (TM 3951-52, 17408, 17416). Wonderfontein Farm 103, Oberholtzer: one female (TM 480). Zoo Hill, Pretoria: one male (TM 4616). **ZIMBABWE:** Banti: one male (NHMZ 70262); three females (NHMZ 70260-61, 70263). Bulawayo: 30 males (NHMZ 11, 749, 841, 2550, 3001, 53325, 53329, 80184, 80213, 80216, 80661, 81462, 81705, 81716, 81724, 81735, 81738, 81742, 81744, 81746-47, 81750-51, 81755-56, 81758, 82000-01, 82008, 82038); 33 females (NHMZ 776, 7205, 53323, 53945, 54026, 54342-44, 54349, 54377, 80185, 80212, 80997, 81000, 81011, 81029, 81134, 81708, 81710, 81712, 81719, 81725, 81730, 81732, 81736, 81745, 81749, 81995, 81997, 82002, 82004, 82010, 82102). Bumboosie: one male (NHMZ 70240). Calgary, Harare: one male (NHMZ 69826). Chete (Old Camp): one male (NHMZ 57401); one female (NHMZ 57400). Chibero: four males (NHMZ 70254, 70257-59); five females (NHMZ 70251-53, 70255-56). Chikupe (= Chikupo) Cave, Bindura: one male (NHMZ 53157); one female (NHMZ 53156). Chipinga: one female (NHMZ 1644). Corner Chimanimani (= Chimanimani): four males (NHMZ 53491, 70303-04, 70311); one female (NHMZ 70305). Deka: one male (NHMZ 70238); three females (NHMZ 70234, 70237, 70245). Deteema Dam: two males (NHMZ 53222, 53225); three females (NHMZ 53223, 53227, 64743). Doddieburn Ranch: 21 males (NHMZ 80005-06, 80009, 80012, 80017, 80020, 80023, 80025-26, 80028, 80032-33, 80038, 80041-44, 80046, 80048, 80051, 80053); 21 females (NHMZ 80007-08, 80010-11, 80013-16, 80018-19, 80021, 80024, 80030-31, 80034-35, 80037, 80039, 80045, 80047, 80052). Dorowa Mine: three males (NHMZ 80399, 80407, 80415); two females (NHMZ 80401, NHMZ 80408). Essexvale: one female (TM 477). Fort Victoria: one female (NHMZ 70018). Gomo Dam (South): one male (NHMZ 53302); two females (NHMZ 53301, 53303). Harare: one male (NHMZ 53153). Ingeli Farm, Gweru (= Gwelo): one male (NHMZ 1842); one female (NHMZ 1559). Kamaziyo (= Kamazeyo) Camp: two males (NHMZ 18538, 18545). Kariba (southern river), Game Camp: one female (NHMZ 18169). Kyle National Park: one female (NHMZ 70314). Lake McIlwaine National Park: one female (NHMZ 53135). Longani Dam, Lone Star Ranch: one male (NHMZ 54053); one female (NHMZ 54051). Makoholi (= Makaholi) Research Station: one female (NHMZ 53083). Maleme Rest Camp, Matopos (= Motopos): one male (NHMZ 50713). Manzituba: one female (NHMZ 53668). Masera Tribal Trust Land: one female (NHMZ 53315). Matetsi Wildlife Leisure Camp: seven males (NHMZ 55518, 55535, 55537, 55540, 56173-74, 70236); seven females (NHMZ 55519, 55538, 56175-76, 70203, 70246-47). Matopos (= Motopos) (above Maleme): one female (NHMZ 51134). Matopos (= Motopos) National Park: eight males (NHMZ 50652, 53245, 53248-49, 53254, 53259, 53262, 53609); three females (NHMZ 53246, 53253, 53255). Matusiadona Tashinga (= Tashinga Matusiadona): one male (NHMZ 53350); two females (NHMZ 53351, 53630). Mavhuradonha (= Mavuradonha) Wilderness Area: one male (NHMZ 82479); two females (NHMZ 82423, 82430). Mtoko, 40 mi: one female (NHMZ 53152). Muchabezi, Matopos (= Motopos): one male (NHMZ 4841). Mushandike National Park: eight males (NHMZ 53040, 53054, 53059, 53064, 53685, 53700, 53769, 70280); eight females (NHMZ 53041, 53063, 53070-71, 53691, 53767, 53782, 70275). Mutare (= Umtali): one male (NHMZ 53371). Ngezi National Park: three males (NHMZ 70210, 70301-02); one female (NHMZ 70206).

Nyamunyeche (= Nyamyeche) Chikonyora: two males (NHMZ 70220-21). Pombadzi/Lundi Rivers confluence: one male (NHMZ 53435). Ranelia Farm Cashel: three females (NHMZ 53118, 53126, 69934). Rhodes Inyanga National Park: one male (TM 34746). Rusape: two males (NHMZ 425, 465). Sable Park, Kwekwe (= Que-Que): two males (NHMZ 53524, 61989), one female (NHMZ 61991). Sebakwe Dam, Kwekwe (= Que-Que): two males (NHMZ 53340, 70308). Sengwa Wildlife Research Station (= Sengwa Camp): four males ([NHMZ 70284, 70291], [TM 34869, 34877]); two females (NHMZ 70286, 70290). Sentinel Ranch, Limpopo River: five males (NHMZ 29533, 29561, 29564, 29567, 29569); five females (NHMZ 29562-63, 29565, 83877, 83881). Shinda Estates: two females (NHMZ 69882-69883). Siakobo Rest Camp, Gokwe: three males (NHMZ 53128, 53130, 53155); two females (NHMZ 53127, 53129). Sinamatela Hwange (= Wankie) National Park: three males (NHMZ 53207, 53215, 53218); seven females (NHMZ 53209, 53211, 53214, 53219-21, 70312). Tsabalala Sanctuary, Matopos (= Motopos): one female (NHMZ 80666). Tsakabika, Wankie (= Hwange): one male (NHMZ 53285); four females (NHMZ 53284, 53290, 53293, 53295). Tuli Safari Area, Sashi River: one female (NHMZ 83861). Umvukwesi (= Umvukwes): two males (NHMZ 56149, 56924). Umzingwane (= Umzingwani)/Limpopo Rivers junction: three females (NHMZ 9505-06, 9521). Vashu Farm: one male (NHMZ 53192). Zimbabwe National Park: four males (NHMZ 53092, 53097, 53103, 70097); six females (NHMZ 53098, 53105, 53108, 53776, 53788, 70098).

Aethomys nyikae: **MALAWI**: Likabula (= Likhubula) Mission, Mount Mulanje, Mulanje District: one male (KM 12046). Nyika Plateau, Rumphi: one male (MM 1441). Zomba Plateau, Zomba District: three males (KM 12062-63, 12068); three females (KM 12064-65, 12069).

Aethomys silindensis: **ZIMBABWE**: Ngorima Reserve (East), Melsetter District: one male (USNM 427200). Stapleford, Nyamkwarara River, Umtali (= Mutare) District, Manicaland: two males (USNM 427196-97), one female (USNM 427198).

Aethomys stannarius: **CAMEROON**: Eseka, Mbakaou: one male (AMNH 236407). Ndokayo (= Ndoukou), 5 km E: one male (AMNH 241210). Tongo, 10 km W: one female (AMNH 241208). **NIGERIA**: Ugar Jabar: two males (USNM 404414, 404416); three females (USNM 404408, 404419-20).

Aethomys thomasi: **ANGOLA**: Chitau: ten males (AMNH 81951, 81953-54, 85746, 85748, 85922-24, 88224-25); six females (AMNH 81901, 81952, 85930-31, 88236, 88241). Mombola (= Mombolo): three males (TM 5163, 5165-66); two females (TM 5164, 5167).

Dasymys incomtus: **ANGOLA**: Mombola (= Mombolo): one female (TM 5161). **MALAWI**: Ncheu (= Ntcheu): two females (TM 9259-60). **SOUTH AFRICA**: **CAPE PROVINCE**: Diepwalle Forest Station, 14 km NNE Knysna: two females (TM 26274, 26338). **KWAZULU-NATAL**: Itala Provincial Nature Reserve, 10 km NW Louwsburg: one male (TM 31797); two females (TM 31767, 31780). **TRANSVAAL**: Tzaneen Estates: five males (TM 212-13, 215, 217-18); three females (TM 211, 214, 216). **ZAMBIA**: Nsange (Nsangi)-Kabompo Rivers confluence: two males (TM 12677-78). **ZIMBABWE**: Zimbabwe Ruins, 25 km SE Fort Victoria: one male (TM 34596).

Rattus rattus: **ANGOLA**: Mombola (= Mombolo): two females (TM 5229-30). **KENYA**: Nanyuki: two females (TM 9384-85). **MALAWI**: Ncheu (= Ntcheu): two males (TM 9245-46); one female (TM 9244). **SOUTH AFRICA**: **CAPE PROVINCE**: Belville, Cape Town: one male (TM 5107); three females (TM 5105, 5108-09). Wynberg, Alphen: one female (TM 2223). **FREE STATE**: Coalbrook Station: two males (TM 3674, 3676); two females (TM 3675, 3677). **KWAZULU-NATAL**: Karkloof: two males (TM 41936-37); one female (TM 41938). **TRANSVAAL**: Pretoria: 11 males (TM 5141, 5143-45, 5241, 5246, 5340, 5437, 5931, 5934, 5941, 7090); 12 females (TM 5142, 5243-44, 5245, 5247, 5932, 5935-40). **SWAZILAND**: Phophonyane: one male (TM 44881); one female (TM 44882). **TANZANIA**: Amani: three males (TM 16016, 16018, 16021); seven females (TM 16015, 16019-20, 16022-25). **ZAMBIA**: Ndola: one male (TM 2685); one female (TM 2684). **ZIMBABWE**: Gwelo (= Gweru): three males (TM 10165-67); one female (TM 10164).

APPENDIX VI

GAZETTEER

Co-ordinates were obtained from gazetteers of the United States Board on Geographic Names (Geographic Names Division, United States Army Topographic Command), Davis and Misonne (1964), Skead (1973), Smithers (1971), Smithers and Tello (1976), Broadley's (1966) unpublished personal gazetteer based on herpetological material collected in southeastern Africa, and a variety of maps and specimen labels. The former South African Cape Province includes the new Eastern, Northern, North-West and Western Cape provincial boundaries, while the Transvaal includes Gauteng, Mpumalanga, Northern, and North-West Provinces (see Figure 1.1). Different versions of the same locality are indicated in brackets.

ANGOLA: Chinoque (= Chiengue), 20 km E Danile (11° 13'S, 16° 01'E); Chitau (11° 25'S, 17° 09'E); Galanga (12° 04'S, 15° 08'E); Hanha (13° 18'S, 14° 12E'); Lussinja, Bocoio (12° 28'S, 14° 08'E); Mombola (= Mombolo) (11° 59'S, 14° 56'E); Pongo (= Pungo) Andongo (09° 40'S, 15° 35'E). **BOTSWANA**: Aha Hills, 10 mi N (19° 40'S, 21° 00'E); Ahartts, Batawana Reserve (19° 50'S, 23° 20'E); Artesia, 14 mi E (24° 00'S, 26° 00'E); Bosha Bohola (= Bosho Boholu, Bosobogolo) Pan (25° 16'S, 22° 13'E); Bushman's Pits, Nata-Maun Road (20° 12'S, 23° 25'E); Chaugule, Magogopate (= Magogophate, Magogaphate) (21° 00'S, 28° 00'E); Chukutsa Pan (21° 07'S, 25° 20'E); Debeeti (= Debeti) (23° 46'S, 26° 29'E); Dikomo di kai (= Dikgomodikae, Kgomodikae) (24° 45'S, 24° 40'E); Drodsky's Caves (20° 00'S, 21° 00'E); Foley Siding (21° 41'S, 27° 19'E); Francistown (21° 10'S, 27° 30'E); Francistown, 40 mi NW (20° 48'S, 27° 03'E); Gaberones (= Gaberone), 5 mi W (24° 39'S, 25° 54'E); Gensond (= Gesond) Limited (22° 12'S, 28° 54'E); Ghansi (= Ghanzi), 35 mi S (21° 30'S, 21° 50'E); Goha Pan (18° 27'S, 24° 20'E); Kalamari (= Kalahari) (23° 00'S, 22° 00'E); Kgolo (= Kgale) Hill, Barabong (24° 50'S, 25° 55'E); Khuis (26° 40'S, 21° 50'E); Kuki, Makalababedi (20° 20'S, 23° 49'E); Lehutitung (= Lehututu), Kalahari Desert (23° 58'S, 21° 53'E); Lobatse (= Lobatsi) (25° 13'S, 25° 40'E); Mabate (= Mabati, Mabote) (22° 00'S, 28° 00'E); Mabuwa Sefubi (= Mabuasehube, Mabua Sefhubi) Pan (25° 01'S, 22° 09'E); Madinare (21° 55'S, 27° 45'E); Makoba Gate, 7 mi W (21° 00'S, 25° 00'E); Mamono (= Mamuno), 150 mi S (24° 00'S, 20° 00'E); Mangwedi Hill, Serowe (22° 23'S, 26° 43'E); Matjemloeji (21° 23'S, 27° 23'E); Matopo Quarantine (20° 00'S, 24° 00'E); Maun (19° 59'S, 23° 25'E); Moame, 10 mi on Toteng-Maun Road (20° 22'S, 22° 50'E); Moeloutsie Siding (21° 00'S, 27° 00'E); Molopo River, W War Graves (25° 00'S, 22° 00'E); Mosetse, 62 mi on Francistown-Nata Road; Mosetsi (= Mosetse) River (20° 45'S, 26° 39'E); Moshaneng (24° 54'S, 25° 16'E); Moshupa (24° 48'S, 25° 23'E); Nata (20° 12'S, 26° 11'E); Nata River (20° 14'S, 26° 10'E); Nokanen (= Nokaneng), 9.3 km SE (19° 40'S, 22° 12'E); Nthane (21° 00'S, 26° 00'E); Okwa (22° 19'S, 21° 45'E); Ootsi (= Ootse) (25° 02'S, 25° 45'E); Ootsi (= Ootse), NE Ootsi (= Ootse) (25° 02'S, 25° 21'E); Ootsi (= Ootse) Siding, W Ootsi (= Ootse) (25° 05'S, 25° 42'E); Pilane (24° 26'S, 26° 05'E); Ramatlabana (= Ramatlhabama), 10 mi W (25° 38'S, 25° 24'E); Ramoutsa Village (25° 51'S, 25° 47'E); Riverslea, Tuli Block (23° 30'S, 27° 30'E); Samadupi (20° 00'S, 23° 00'E); Selinda Spillway (= Makwegana); Serowe, 40 mi NW (22° 00'S, 26° 00'E); Sevuti (18° 00'S, 24° 00'E); Shakawe (18° 00'S, 21.00'E); Shakawe, 50 mi W, 12 mi S (18° 21'S, 21° 52'E); Shashi Siding, 10 mi N (21° 26'S, 27° 27'E); Tamafupi (= Thamafipa) (19° 00'S, 23° 00'E); Tierputts (= Tierpits), Ghanzi (= Ghansi) (21° 00'S, 21° 00'E); Tsabong (26° 03'S, 22° 26'E); Tsane, 5 mi S (24° 01'S, 21.50'E); Tsanga (20° 00'S, 23° 00'E); Tsanoga (20° 10'S, 23° 48'E); Tsau, 3 mi S (20° 09'S, 22° 26'E); Tsodilo (= Tsodila) Hills (18° 42'S, 21° 45'E); Wolf's Hills, 12 mi S Francistown (21° 20'S, 27° 30'E).

CAMEROON: Eseka, Mbakaou (06° 20'S, 12° 48'E); Ndokayo (= Ndoukou), 5 km E (03° 10'S, 12° 04'E); Tongo, 10 km W (15° 04'N, 10° 19'W). **KENYA**: Konglei, 3 mi S (01° 28'N, 35° 02'E); Machakos (01° 31'S, 37° 16'E); Nanyuki (00° 01'N, 37° 05'E). **LESOTHO**: Kofa, Qacha's Nek (White Hill) (30° 03'S, 28° 29'E); Makhoebeng, Thaba-Tseka (29° 31'S, 28° 35'E); Makhotlong (29° 18'S, 29° 05'E); Malhanapeng, Thaba-Tseka (29° 00'S, 28° 00'E); Marakabei (= Marakabeis), Maseru (29° 32'S, 28° 09'E); Mateanong, Makhotlong (29° 21'S, 29° 13'E); Moqotoane, Thaba-Tseka (Sehonghong) (29° 48'S, 28° 49'E); Mount Morosi (= Moorosi), Quthing (30° 11'S, 27° 52'E); Sekakes (30° 00'S, 28° 00'E); Siles Village, 12.9 mi E Mafeteng (= Mafeleng) (29° 50'S, 27° 15'E); Tsoelike Bridge (30° 01'S, 28° 40'E). **MALAWI**: Likabula (= Likhubula) Mission, Mount Mulanje, Mulanje District (15° 57'S, 35° 24'E); Liwonde National Park Headquarters (15° 03'S, 35° 15'E); Ncheu (= Ntcheu) (14° 49'S, 34° 38'E); Nyika Plateau, Rumphi (10° 00'S, 33° 00'E); Zomba Plateau, Zomba District (15° 20'S, 35° 16'E). **MOZAMBIQUE**: Beira (19° 50'S, 34° 55'E); Banamana (22° 10'S, 33° 54'E); Chicoa, Tete District (15° 37'S, 32° 22'E); Chitenga (= Chitengo), Gorongoza National Park (18° 59'S, 34° 20'E); Dondo (19° 34'S, 34° 44'E); Estatuane (= Changalane) (26° 18'S, 32° 12'E); Inhaminga, 8 mi (18° 25'S, 35° 01'E); Magudi (25° 02'S, 32° 39'E); Mague, Tete District (15° 41'S, 31° 40'E); Malanguene (21° 20'S, 34° 55'E); Maringa, North Bank (21° 22'S, 33° 30'E); Mazambo (24° 35'S, 33° 15'E); Moamba (25° 25'S, 32° 05'E); Muamdzame (= Muandzane), Libondos (26° 00'S, 32° 00'E); Pico Mapenduine (= Meponduine) (25° 00'S, 31° 00'E); Ponta S.L., Banamana (22° 00'S, 33° 00'E); Revue River (21° 00'S, 33° 00'E); Sabi/Lundi Rivers, north of junction (21° 18'S, 32° 24'E); Save River (19° 00'S, 33° 00'E); Tete (16° 10'S, 33° 35'E); Zambesi (= Zambezi), South Bank (15° 43'S, 31° 12'E); Zavera (= Zavora) (24° 31'S, 35° 11'E); Zinave, 1.0 km S (21° 26'S, 33° 52'E); Zinave National Park (21° 00'S, 33° 00'E). **NAMIBIA**: Andara (Okavango), W Caprivi (18° 04'S, 21° 27'E); Aus, 38 mi on road to Hehuring Hansen (26° 40'S, 16° 15'E); Bellerode Farm, Windhoek (22° 30'S, 17° 00'E); Berseba, Great Namaqualand (26° 00'S, 17° 46'E); Bubus Farm 213, 9 mi Grootfontein on road to Otjituno Reserve (19° 38'S, 18° 14'E); Canes Okawa, NW Outjo (19° 30'S, 14° 30'E); Diwai (Okavango), near Bagane Drift, W Caprivi (18° 00'S, 23° 00'E); Ehomba Mountains, N Kaokoveld (17° 34'S, 13° 52'E); Gellap-ost Number 3, 16 km N Keetmanshoop (22° 26'S, 18° 06'E); Gobabis (22° 27'S, 18° 58'E); Kamanjab (19° 34'S, 14° 48'E); Karachas, Outjo (20° 07'S, 16° 09'E); Karakuwisa, Grootfontein District (18° 57'S, 19° 43); Karibib, S Damaraland (21° 58'S, 15° 52'E); Katijhuru, central Kaokoveld (19° 00'S, 13° 00'E); Kobos (23° 34'S, 16° 38'E); Kovares (= Otjokavare), S Kaokoveld (19° 03'S, 14° 22'E); Lupala (= Lupela), Okavango (17° 50'S, 19° 06'E); Marula Tree Camp, 24 mi NW Andoni Ortesian Well on Nemutoni-Ondangua Road (18° 00'S, 16° 00'E); Mohango (= Mahango Omuramba) Drift (Okavango), W Caprivi (18° 08'S, 21° 41'E); Musterland Farm 113, 11.8 km S, 4.0 km W Outjo, Outjo District (20° 13'S, 15° 54'E); Namkaub, Grootfontein District (19° 00'S, 19° 00'E); Nossib, near Tsumeb (19° 25'S, 17° 52'E); Ohopoho (18° 03'S, 13° 50'E); Okowekuatjiuci Farm, 13.0 km S, 3.8 km E Kalkfeld, Otjiwarongo District (21° 00'S, 16° 13'E); Okosongomingo, Otjiwarongo District, Damaraland (20° 38'S, 17° 05'E); Ombarahewa Farm 22, 0.7 km N, 35.2 km W Otjiwarongo, Otjiwarongo District (20° 28'S 16° 19'E); Ombika Gate, Etosha Park, Outjo District (19° 20'S, 15° 56'E); Ombombo, Kaokoveld (18° 42'S, 13° 55'E); Ombu, Erongo (21° 40'S, 15° 44'E); Omuramba Ovambo, 2.8 mi E Tsintsibis (18° 45'S, 17° 00'E); Opelo Sud Farm 39, 14.9 km N, 4.6 km E Omaruru, Omaruru District (21° 17'S, 15° 06'E); Oropembe (= Orupembe) (18° 09'S, 12° 32'E); Oshikanga (= Oshikango), Ovambo-Angola Border (17° 25'S, 15° 54'E); Otavifontein Farm, 3.5 mi E Otavi on road to Grootfontein (19° 40'S, 17° 23'E); Otjibingwe, Karibib (22° 22'S, 16° 08'E); Otjitambi, near Epembe, N Kaokoveld (18° 22'S, 12° 50'E); Otjitambi Farm 25, 20.0 km S, 35.0 km E Outjo (19° 48'S, 15° 11'E); Otjitundua, central Kaokoveld (18° 35'S, 14° 09'E).

Otjongoro Farm 20, 0.8 km N, 57.8 km E Kalkfeld (20° 53'S, 15° 38'E); Oudekaremba Siding, along Elephant River Banks (22° 00'S, 17° 00'E); Pederborne, Huab River, Kaokoveld (20° 55'S, 13° 28'E); Popa Falls, Okavango, W Caprivi (18° 06'S, 21° 37'E); Quabendus, S Kaokoveld (18° 00'S, 13° 00'E); Quickborn, Okahandja (21° 08'S, 17° 07'E); Rasputin Farm 137, 19.4 km S, 28.0 km W Outjo, Outjo District (20° 17'S, 15° 53'E); Rheinvels Farm, 35 km SSW Keetmanshoop (26° 57'S, 17° 56'E); Rua Cana Falls, Cunene (= Kunene) (17° 23'S, 14° 12'E) Sandfontein (22° 59'S, 14° 35'E); Sanitatas (18° 17'S, 12° 40'E); Sesfontein (19° 09'S, 13° 37'E); Sijemba, Okavango, W Caprivi (18° 00'S, 23° 00'E); Stampriet, E Gobabis (22° 29'S, 19° 32'E); Swakalskuppe South African Railways Siding on Keetmanshoop-Luderitz Road (26° 33'S, 18° 09'E); Swartboois Drift (17° 20'S, 13° 50'E); Tjirundo Farm 91, 24.5 km N, 7.8 km W Omaruru, Omaruru District (21° 13'S, 15° 52'E); Tshandi Finnish Mission, Ukualuthi, Ohopoho (17° 45'S, 14° 53'E); Uis, 1.0 km S, 36.0 km W, S Brandberg, Karibib, Damaraland (21° 14'S, 14° 31'E); Usakos, near Swakopmund (21° 59'S, 15° 35'E); Valencia, Rehoboth District (23° 20'S, 17° 03'E); Waterberg, Otjiwarongo District, north-central Namibia (20° 30'S, 17° 14'E); Windhoek (22° 34'S, 17° 06'E); Witvlei (= Witvley), 40 mi W Gobabis (22° 26'S, 18° 30'E). **NIGERIA:** Kabwir, Bauch (= Bauchi) (11° 16'N, 09° 50'E); Ugar Jabar (09° 31'N, 08° 23'E); **SOUTH AFRICA: CAPE PROVINCE:** Addo National Park, Port Elizabeth (33° 32'S, 25° 50'E); Alexander Bay, 14.2 km N, 58.5 km E, Namaqualand District (28° 29'S, 17° 05'E); Alexandria, 11.5 km S, 2.1 km W, Alexandria District (33° 45'S, 26° 23'E); Alexandria, 0.5 km N, 35.9 km W, Alexandria District (33° 39'S, 26° 01'E); Alexandria, 3.8 km S, 44.8 km W, Alexandria District (33° 41'S, 25° 56'E); Alexandria, 6.8 km S, 6.0 km W, Alexandria District (33° 43'S, 25° 51'E); Alexandria, 6.5 km S, 50.3 km W, Alexandria District (33° 43'S, 25° 52'E); Algeria Forest Station, 28 km SSE Clanwilliam (32° 22'S, 19° 03'E); Aliwal North (30° 41'S, 26° 42'E); Ammosal Shooting Range, 6.5 km WNW Postmasburg (28° 19'S, 23° 01'E); Anysberg Nature Reserve, Ladismith (33° 30'S, 20° 41'E); Augrabies Falls, Orange River (28° 35'S, 20° 21'E); Augrabies Waterfall National Park (29° 15'S, 17° 05'E); Baden Farm, 10.2 km N, 0.1 km E Montagu, Montagu District (33° 42'S, 20° 07'E); Balderja, Piet Retief (32° 30'S, 26° 32'E); Barkly East, 7.9 km S, 22.6 km W Barkly East District (31° 02'S, 27° 22'E); Barkly East, 9.9 km S, 22.0 km W, Barkly East District (31° 03'S, 27° 22'E); Beaufort West, Karoo (= Karroo) National Park (32° 20'S, 22° 33'E); Bedford, Bedford District (32° 41'S, 26° 06'E); Belville, Cape Town (33° 54'S, 18° 38'E); Bellsbank Estates Farm, 44 km W Warrenton (28° 06'S, 24° 25'E); Benbecula, Elliot (31° 00'S, 28° 00'E); Betty's Bay, 1.5 km S, 8.3 km W Kleinmond, Caledon District (34° 21'S, 18° 57'E); Beuksfontein Farm, 53.9 km N, 40.5 km E Ceres, Ceres District (32° 53'S, 19° 44'E); Biesjespoort, Karoo (= Karroo) (31° 43'S, 23° 11'E); Biljetsfontein, 3.0 km N, 34.2 km W Ladismith, Uitspan, Ladismith District (33° 28'S, 20° 54'E); Boesmansberg Farm, 60 km NW Van Wyk's Vlei (30° 07'S, 21° 15'E); Brandlaagte Farm 130, Lady Grey (30° 43'S, 27° 11'E); Breekkiere Farm, 37 km NW Van Wyk's Vlei (30° 06'S, 21° 35'E); Brucedell Farm 192, Rhodes (30° 48'S, 27° 58'E); Bustard Island (30° 34'S, 25° 37'E); Carnarvon, subdivision of Grootvlei Farm 191, Sterkstroom (31° 00'S, 26° 00'E); Carnarvon Commonage, 1 km NE Carnarvon (30° 58'S, 22° 08'E); Ceres, 40 km E, Lat B (33° 20'S, 19° 43'E); Cetrusdal (= Citrusdal) (32° 35'S, 19° 01'E); Cheddar Farm, 5 km E Pomfret (25° 50'S, 23° 34E); Chestnut Grove, Bedford District (32° 40'S, 26° 00'E); Clifford Farm, 12.3 km S, 14.1 km W Barkly East, Barkly East District (31° 04'S, 27° 27'E); Cnydas Farm, 12 km NW Lutzput (28° 19'S, 20° 34'E); Cradock (33° 54'S, 25° 34'E); Dammetjie, 100 km NNE Upington (28° 11'S, 22° 02'E); De Aar, 9.6 km S, 8.5 km W, De Aar District (30° 44'S, 23° 55'E); De Aar, 12.0 km S, 10.5 km W, De Aar District (30° 45'S, 23° 54'E); De Aar, 15.0 km S, 13.3 km W, De Aar District (30° 47'S, 23° 52'E); Deelfontein, Richmond, Karoo (= Karroo) (30° 59'S, 23° 48'E).

De Grootefontein Farm 437, 3.9 km S, 0.4 km E Albertinia, Riversdale District (34° 14'S, 21° 35'E); De Hoop Nature Reserve, 10.1 km N, 31.5 km E Bredasdorp, Bredasdorp District (34° 26'S, 20° 23'E); Denorbin Farm 344, Barkly East (31° 09'S, 27° 45'E); Derde Heuvel Farm 149, 4.8 km S, 5.4 km E Montagu, Montagu District (33° 50'S, 20° 11'E); Diepwalle Forest Station, 14 km NNE Knysna (33° 57'S, 23° 10'E); Dikbosch Farm 29, 69 km ENE Griekwastad (28° 40'S, 23° 55'E); Dikgatlong (= Dikgatlhong), Limebanks, Kuruman River 15 mi W Kuruman (27° 06'S, 22° 56'E); Donkerhoek Farm, 24 km WSW Setlagoli (26° 20'S, 25° 53'E); DoornbOom, 6.6 km S, 33.0 km W Ladismith, Ladismith District (33° 40'S, 21° 15'E); Doornkloof Nature Reserve, 45 km NNW Colesberg (30° 20'S, 25° 02'E); Doornlaagte Farm, 24 km NNW Danielskuil (28° 00'S, 23° 27'E); Doringbult, 24 km SW Ulco (28° 29'S, 24° 03'E); Douglas, Hopetown (= Hopetuin) (29° 04'S, 23° 47'E); Dragepoort, Korannaberg (27° 15'S, 22° 30'E); Drumbo Farm 80, Barkly East (30° 00'S, 27° 00'E); Duikerbult, 16 km W Setlagoli (26° 17'S, 24° 58'E); Duinwal Farm, 30 km W Vorstershoop (25° 57'S, 22° 45'E); Elibank Farm, 36 km SW Setlagoli (26° 03'S, 24° 55'E); Eendekuil (32° 42'S, 18° 25'E); Eenriet (= Einriet), near Steinkopf, Little Namaqualand (29° 12'S, 17° 52'E); Ester Farm, 49 km N Vorstershoop (25° 24'S, 22° 57'E); Ezelfontein (= Eselfontein), near Leliefontein, Kamiesberg, Little Namaqualand (30° 27'S, 18° 13'E); Franschhoek Farm, 16 km NW Olifantshoek (27° 52'S, 22° 36'E); Fraserburg, 12.8 km S, 10.5 km E, Fraserburg District (32° 02'S, 21° 37'E); Gamkapoort Nature Reserve, Prince Albert (33° 14'S, 22° 05'E); Gathlose, 28 km ESE Sishen (27° 55'S, 23° 14'E); Glen Cave Farm, 4.5 km N, 13.6 km E Molteno, Molteno District (31° 12'S, 26° 30'E); Glen Gyle Farm 39, Barkly East (30° 45'S, 27° 41'E); Gloria, subdivision of Olyenkloof Farm 184, Jamestown (31° 07'S, 26° 49'E); Goedgedacht, 21 km ENE Postmasburg (28° 13'S, 23° 15'E); Goegap Nature Reserve, Springbok (29° 40'S, 17° 59'E); Goma Farm, Renoster River, 54 mi E Calvinia (31° 28'S, 19° 47'E); Goodhouse (Orange River), Namaqualand (28° 54'S, 18° 13'E); Goodlands Sector A, Quiston Nature Reserve (30° 38'S, 25° 33'E); Goodstone Farm 62, Indwe (31° 30'S, 27° 15'E); Goodwin's Kloof, Grahamstown, E Cape Province (33° 19'S, 26° 30'E); Goraas Farm FrQ; 29, 62 km W Carnavon (31° 10'S, 21° 35'E); Gosa Farm, 54 km WSW Hotazel (27° 18'S, 22° 18'E); Gougo Farm, 39 km NW Van Wyk's Vlei (30° 11'S, 21° 28'E); Gouna Farm, Rhenoster River, 54 mi E Calvinia (31° 30'S, 20° 30'E); Gowies Kloof, Grahamstown (33° 18'S, 26° 32'E); Graaff-Reinet (31° 16'S, 24° 33'E); Grahamstown (33° 19'S, 26° 32'E); Groote Drift Farm, 8.4 km S, 10.9 km E Elandsbaai, Piketburg District (32° 23'S, 18° 28'E); Grootfontein, Middelburg (31° 29'S, 25° 02'E); Grootfontein Farm, 19 km SW Reivilo (27° 39'S, 24° 01'E); Groot Tafelbergsfontein Farm, 9.4 km N, 90.6 km W Beaufort West, Beaufort West District (32° 16'S, 21° 37'E); Halstone (= Halseton) Farm 36, Barkly East (31° 30'S, 26° 45'E); Hamilton Farm 64, Rhodes (30° 48'S, 27° 58'E); Hantam Range (slopes of), 3 mi NE Calvinia (31° 28'S, 19° 48'E); Haweqwas State Forest, 8.2 km N, 12.0 km E Wellington, (33° 34'S, 19° 08'E); Haweqwas State Forest, 1.8 km N, 8.7 km E Wellington (33° 37'S, 19° 06'E); Heather Glen, Kofi (= Kafi) River, Bathurst (33° 31'S, 26° 50'E); Heimat, subdivision of Embotokwa Commonage, Indwe (31° 00'S, 27° 00'E); Hester Malan Wild Flower Reserve (29° 00'S, 18° 00'E); Het Kruis (32° 35'S, 18° 45'E); Hex River (= Heksrivier) Estate, 10 mi N Cetrusdal (= Citrusdal) (32° 26'S, 18° 58'E); Hopefield Estate Farm 552, 25 km NNE Griekwastad (28° 38'S, 23° 18'E); Janu Mayenzar (Stutterheim) (32° 54'S, 27° 25'E); Kalkoenkrans, subdivision of Pisa Farm 107, Dordrecht (30° 52'S, 26° 46'E); Kalkoenkrantz Farm 189, Sterkstroom (31° 00'S, 26° 00'E); Kamiesberg, Witwater Plateau (30° 19'S, 18° 04'E); Kangnas Farm, 48 km ENE Springbok (29° 35'S, 18° 21'E); Kansvat Farm, 22 km NW Vryburg (26° 50'S, 24° 23'E); Kauki-Morokwa Road (26° 00'S, 20° 00'E); Keikamspoort Farm 71, 20 km SE Prieska (29° 50'S, 22° 47'E); Keimoes Island, Orange River (28° 43'S, 20° 50'E); Kersbos Farm, 10 km NNE Bitterfontein, Namaqualand (30° 57'S, 18° 12'E); King William's Town (32° 52'S, 27° 23'E).

King William's Town, 2.0 km N, 7.2 km E (32° 52'S, 27° 28'E); Klawer (= Klaver), Olifants River, W Cape Province (31° 47'S, 18° 37'E); Kleinfontein I Farm, 26 km ENE Noupoort (31° 07'S, 25° 12'E); Kleinpoort, Grahamstown (33° 08'S, 26° 50'E); Kleinpotfontein Farm, 47 km NNE De Aar (30° 13'S, 24° 06'E); Kliphuis, 11 mi NE Clanwilliam (32° 08'S, 18° 57'E); Klipkraal Farm 48, Lady Grey (30° 42'S, 27° 06'E); Kloppersbosch Farm 338, 0.2 km N, 20.3 km E Worcester, Worcester District (33° 39'S, 19° 25'E); Koofmansfontein, Barkly West (28° 05'S, 24° 15'E); Korannaberg Farm, 88 km NNW Olifantshoek (27° 14'S, 22° 27'E); Koningsrivier Dam Farm, 12.2 km S, 5.2 km W Robertson, Robertson District (33° 55'S, 19° 50'E); Kuruman, 3 km W (27° 28'S, 23° 26'E); Kuruman, 11.9 mi on Digatlong Road (27° 27'S, 23° 26'E); Kwartelfontein (Sandfontein) Farm, 3.2 km S, 16.6 km W Touwsrivier, Ceres District (33° 22'S, 19° 51'E); Lady Grey (33° 57'S, 19° 49'E); Laingsburg, 19 km SSW (33° 00'S, 20° 00'E); Lamberts Bay (32° 05'S, 18° 18'E); Leelykstaat Farm, 31 km NE Marydale (29° 11'S, 22° 18'E); Letakun, Kuruman (27° 27'S, 23° 26'E) Lidney Farm, 3.6 km S, 38.0 km W Alexandria, Alexandria District (33° 41'S, 26° 00'E); L'Ormarin's Farm, Franschhoek Valley, near Paarl (33° 53'S, 19° 03'E); Louisvale, Upington (28° 34'S, 21° 12'E); Mariba, subdivision of Joubertskop Farm 162, Dordrecht (30° 50'S, 26° 35'E); Marthasdale Farm 190, 23 km NNE Danielskuil (27° 58'S, 23° 40'E); Marthasrust, 9 km NW Olifantshoek (27° 53'S, 22° 42'E); Matjiesfontein (33° 15'S, 20° 35'E); Melkspruit Farm 12, Aliwal North (30° 44'S, 26° 37'E); Middlepost (= Middelpost, Middelpos), 11 mi (30° 03'S, 26° 01'E); Mierekraal Farm, 6.9 km S, 5.1 km W Bredasdorp, Bredasdorp District (34° 36'S, 19° 59'E); Mierfontein Farm, 2.7 km S, 34.9 km W Ladismith, Uitspan, Ladismith District (33° 31'S, 24° 51'E); Milton Farm 4, Maclear (31° 04'S, 28° 22'E); Modderfontein Farm 193, Jamestown (30° 24'S, 26° 03'E); Molopo Nature Reserve, 10 km W Vorstershoop (25° 47'S, 22° 56'E); Molteno, 1.9 km N, 16.5 km E, Molteno District (31° 23'S, 26° 32'E); Mountain Zebra National Park, Cradock (32° 10'S, 25° 37'E); Mouton's Valley Farm A80, 15.2 km N, 5.7 km W Piketburg, Piketburg District (32° 46'S, 18° 42'E); Municipal Farm, Middelburg (31° 30'S, 25° 00'E); Murraysburg, 7.1km N, 17.0 km W, Murraysburg District (31° 54'S, 23° 35'E); Murraysburg, 7.5 km N, 14.1 km W, Murraysburg District (31° 54'S, 23° 37'E); Murraysburg, 23.4 km S, 15.2 km E (32° 10'S, 23° 55'E); Murraysburg, 24.3 km S, 16.1 km E, Murraysburg District (32° 11'S, 23° 56'E); Naauwte, 23 km NNW Prieska (29° 28'S, 22° 38'E); Namaqualand (30° 00'S, 18° 00'E); Narap Farm, 28 km SSE Springbok (29° 53'S, 17° 45'E); New Upington (= Upington), South Bank of Orange River (28° 26'S, 21° 14'E); Nieuwe Plaats Farm 567, 4.1 km S, 8.5 km W Darling, Malmelsbury District (33° 25'S, 18° 17'E); Northern Cape Nature Conservation Station, 8 km W Hartswater (27° 46'S, 24° 45'E); Ookiep (28° 46'S, 19° 17'E); Oorlogskloof Nature Reserve, Nieuwoudtville (31° 25'S, 19° 10'E); Orinway Farm, Albany District (33° 30'S, 26° 30'E); Ossa Farm 38, Lady Grey (30° 46'S, 27° 24'E); Pakhuis Pass, Clanwilliam (32° 08'S, 19° 00'E); Petrusville, 11.7 km S, 11.7 km E, Philipstown District (30° 11'S, 24° 47'E); Petrusville, 12.3 km S, 10.8 km E, Philipstown District (30° 12'S, 24° 46'E); Pitsane, 12 mi E, 3 mi S on Mafeking Road (25° 45'S, 25° 05'E); Pniel Estate Farm, 8 km SW Barkly West (28° 35'S, 24° 28'E); Port Alfred, 0.9 mi N, 9.2 mi W, Bathurst District (33° 35'S, 26° 44'E); Prieska Commonage, 6 km SSE Prieska (29° 42'S, 22° 46'E); Prince Albert, 12,8 km S, 11.4 km W, Prince Albert District (33° 21'S, 21° 55'E); Quaggaskerk, Tarkastad (32° 01'S, 26° 16'E); Ramatulabama, Mafeking (25° 52'S, 25° 38'E); Ras Zyn Puts Zuid Farm 18, 37.9 km N, 11.5 km W Brandvlei, Calvinia District (30° 08'S, 20° 22'E); Rhabdomys Island (30° 36'S, 25° 32'E); Richtersveld, 19.2 km N, 48.8 km E Alexander Bay, Namaqualand District (28° 27'S, 16° 59'E); Richtersveld, 15.1 km N, 57.6 km E Alexander Bay, Namaqualand District (28° 29'S, 17° 04'E); Riemuasmaak, 47 km NW Kakamas (28° 27'S, 20° 19'E); Rietfontein (26° 44'S, 20° 02'E); Rietfontein Farm 82, 8.7 km N, 25.8 km W Steynsburg, Steynsburg District (31° 13'S, 25° 33'E).

Riries Farm, 29 km NW Kuruman (27° 19'S, 23° 11'E); Risler Farm 30, Maclear (30° 46'S, 28° 17'E); Rodeseput, 44 km NE Brandvlei (30° 11'S, 20° 48'E); Roodewal Farm 96, Aliwal North (30° 24'S, 26° 43'E); Rooidam, 10 km N Windsorton (28° 14'S, 24° 43'E); Roseglen, 76 km WNW Griekwastad (28° 47'S, 23° 29'E); Ruford Elanor River Valley, Uitenhage (33° 46'S, 25° 24'E); Schuitklip Farm, 42 km NE Pofadder (28° 51'S, 19° 42'E); Sevenweeks Pass (26° 35'S, 22° 52'E); Skoorsteenmantel Farm 20, Jamestown (31° 07'S, 26° 48'E); Slang Gat Lad Farm, 2.8 km N, 25.6 km W Ladismith, Ladismith District (33° 28'S, 20° 59'E); Snowhill Farm 206, Dordrecht (31° 22'S, 27° 03'E); Sterkstroom Farm, 70 km N Williston (30° 42'S, 21° 01'E); Steytlerville, 11.8 km N, 2.5 km E, Steytlerville District (33° 13'S, 24° 22'E); Steytlerville, 9.6 km N, 5.0 km E, Steytlerville District (33° 15'S, 24° 24'E); Steytlerville, 8.5 km N, 3.0 km E, Steytlerville District (33° 15'S, 24° 23'E); Steytlerville, 1.7 km N, 11.1 km E, Steytlerville District (33° 19'S, 24° 28'E); Strydenburg, 21.9 km N, 5.1 km W, Hopetown (= Hopetuin) District (29° 45'S, 23° 38'E); Strydenburg, 18.7 km N, 7.6 km W, Hopetown (= Hopetuin) District (29° 46'S, 23° 36'E); Sunnyside Farm, 14 km N Copperton (29° 50'S, 22° 21'E); Sutherland (32° 23'S, 20° 40'E); Sutherland, 12 mi (32° 23'S, 20° 41'E); Swartberg Forest Reserve, 13.9 km S, 7.4 km W Prince Albert, Prince Albert District (33° 21'S, 21° 57'E); Swartberg Forest Reserve, 12.6 km S, 0.2 km E Prince Albert, Prince Albert District (33° 20'S, 22° 02'E); Swartberg Forest Reserve, 13.3 km S, 5.7 km W Prince Albert, Prince Albert District (33° 21'S, 21° 58'E); Sydney on Vaal Farm, 4 km SW Delportshoop (28° 27'S, 24° 17'E); Takoon Bantu Reserve, 22 mi NW Lykso (27° 05'S, 23° 59'E); Tambookies Vlei, Stockenstrom (= Stockenstroom) (32° 30'S, 26° 45'E); Tanbosleegte, SE Cradock (32° 10'S, 25.40'E); Tierkop Farm, 17 km SSW Kuruman (27° 37'S, 23° 23'E); Traveller's Rest, 18 mi NE Clanwilliam (32° 04'S, 19° 05'E); Tshidilamolomo (25° 50'S, 24° 41'E); Twee Rivieren, K.G.N.P. (= Kalahari Gemsbok National Park) (26° 27'S, 20° 34'E); Uniondale, 12 km WNW, Kammanassie (33° 37'S, 22° 54'E); Uniondale, 3.8 km N, 3.4 km E, Uniondale District (33° 37'S, 23° 10'E); Upington, 6 mi on Prieska Road (28° 26'S, 21° 14'E); Van der Merwesrus, 33 km NW Bray (25° 19'S, 23° 25'E); Veldblom Nature Reserve (31° 20'S, 19° 10'E); Venture Farm 139, Aliwal North (30° 50'S, 26° 50'E); Verwoerd, H. F. Dam Island (30° 36'S, 25° 35'E); Victoria West, 1.9 mi N, 1.8 mi E, Victoria West District (31° 22'S, 23° 09'E); Victoria West, 7 mi N, 1.5 mi E, Victoria West District (31° 23'S, 23° 09'E); Victoria West, 13.1 km N, 4.0 km E, Victoria West District (31° 17'S, 23° 09'E); Vinci Farm, 12 km NE Postmasburg (28° 15'S, 23° 09'E); Vissersvillele, 25 km SW Kenhardt (29° 23'S, 20° 54'E); Vlaktefontein Farm 51, Lady Grey (30° 42'S, 26° 59'E); Vogelfontein Farm, 12 km SSW Campbell (28° 54'S, 23° 39'E); Voorspoed, 17.8 km S, 36.6 km W Williston, Calvinia District (31° 30'S, 20° 32'E); Vredendal, State Land, 10,7 km S, 26.9 km W Vredendal District (31° 46'S, 18° 13'E); Vrisgewaagd Farm 152, 5.7 km S, 13.5 km W Prince Albert, Prince Albert District (33° 17'S, 21° 53'E); Vryburg (26° 57'S, 24° 44'E); Waaikloof Farm 333, 1.1 km N, 20.4 km E Worcester, Worcester District (33° 38'S, 19° 40'E); Waterford Farm, 13 km NNE Hopetown (= Hopetuin) (29° 36'S, 24° 05'E); Witput Farm, 12 km NW Campbell (28° 43'S, 23° 39'E); Witsand Farm, 63 km SW Postmasburg (28° 30'S, 22° 29'E); Witwater Plateau, Kamiesberg (30° 28'S, 18° 05'E); Wolseley (32° 25'S, 19° 12'E); Wonderwerk Farm, 44 km SSE Kuruman (27° 52'S, 23° 33'E); Woodstock Farm, 10 km SW Kuruman (27° 34'S, 23° 22'E); Wynberg, Alphen (34° 00'S, 18° 28'E); Zeekoebaard Farm 306, 28 km SE Groblershoop (29° 03'S, 22° 13'E); Zoetvlei (= Soetvlei), Vryburg (27° 05'S, 24° 13'E). **FREE STATE:** Alfa Farm 4, Ladybrand (29° 15'S, 27° 20'E); Alleman's Drift Farm 37, Philippolis (30° 33'S, 25° 23'E); Allemanskraal, W Pretorius Reserve (28° 18'S, 27° 09'E); Alma, subdivision 1 of Glen Aspen Farm 1389, Frankfort (27° 15'S, 28° 35'E); Asem Farm 371, Senekal (28° 20'S, 27° 40'E); Bakenfontein, Windburg (= Winburg) (28° 32'S, 27° 01'E).

Bellevue Farm 1416, Bethlehem (28° 14'S, 28° 18'E); Bethulie (30° 29'S, 25° 58'E); Braklaagte, Parys (26° 57'S, 27° 37'E); Bloemfontein (29° 07'S, 26° 13'E); Brandfort Municipal Commonage (28° 42'S, 26° 28'E); Coalbrook Station (26° 00'S, 27° 00'E); De Berg Farm 453, Dewetsdorp (29° 40'S, 26° 40'E); De Poort Farm 378, Ventersburg (28° 10'S, 27° 10'E); Donkerpoort Farm 218, Weppener (29° 31'S, 27° 03'E); Driehoek Farm 218, Luckoff (= Luckhoff) (29° 45'S, 24° 47'E); Eendrag, Bethulie (30° 25'S, 25° 25'E); Eureka Farm 674, Senekal (27° 00'S, 27° 00'E); Fish Eagle, Orange Free State (= Free State) Peninsula (30° 38'S, 25° 38'E); Golden Gate Highland Park (28° 28'S, 28° 38'E); Hartbeeshoek Farm 115, Zastron (30° 15'S, 27° 10'E); Hertzogville on Hoopstad Road (28° 08'S, 25° 30'E); Hexrivier Farm 405, Reddersburg (29° 35'S, 26° 15'E); Hobhouse (29° 32'S, 27° 09'E); Kleinfontein Farm 202, Bethulie (30° 10'S, 26° 53'E); Koeberg Farm 1663, Clarens (28° 31'S, 28° 25'E); Koele Farm 97, Thaba Nchu (29° 10'S, 26° 55'E); Kommetjiesfontein Farm 798, Springfontein (30° 00'S, 25° 00'E); Koppiesdam Farm 473, Petrusburg (29° 07'S, 25° 25'E); Kraaifontein Farm 109, Rouxville (30° 25'S, 26° 40'E); Larala, Senekal (28° 20'S, 27° 40'E); Lestoana Stad, Fourisburg (= Fouriesberg) (28° 30'S, 28° 10'E); Leeukop Farm 105, Dewetsdorp (29° 40'S, 26° 40'E); Lemoenboord, Philippolis (30° 00'S, 24° 00'E); Lockshoek Farm 192, Jagersfontein (29° 43'S, 25° 34'E); Malutizight Farm 565, Ficksburg (28° 00'S, 28° 00'E); Middelbron Farm 501, Philippolis (30° 15'S, 25° 15'E); Mooifontein Farm 368, Reddersburg (29° 39'S, 26° 10'E); Mooihoek Farm 130, Harrismith (28° 17'S, 29° 08'E); Mount Brand Farm 278, Bethulie, Springfontein (30° 16'S, 25° 42'E); Northend Farm 75, Ficksburg (28° 53'S, 27° 53'E); Nova Farm 667, Ladybrand (29° 12'S, 27° 27'E); Prarie Farm 576, Smithfield (30° 05'S, 26° 30'E); Preezfontein Farm (29° 48'S, 25° 23'E); Roodepoort Farm 105, Edenberg (= Edenburg) (29° 40'S, 25° 50'E); Rosendal Farm 364, Ladybrand (29° 15'S, 27° 20'E); Rotondo Farm 1046, Rouxville (30° 25'S, 26° 50'E); Sebastopol Farm 51, Zastron (30° 18'S, 27° 05'E); Spitskop Farm 398, Fauresmith (29° 39'S, 25° 49'E); Strathearn Farm 396, Thaba Nchu (29° 13'S, 26° 55'E); Summerslie Farm 350, Harrismith (28° 17'S, 29° 08'E); Versamelkop Farm 68, Ladybrand (29° 00'S, 27° 00'E); Vierkant Farm 798, Brandfort (28° 40'S, 26° 20'E); Wittekoppies Farm 169, Vredefort (27° 05'S, 27° 30'E); Zyferfontein, Parys (26° 54'S, 27° 27'E). **KWAZULU-NATAL:** Abercorn Port, Site B1, Usutu River Park (26° 51'S, 32° 42'E); Albert Falls Nature Reserve (29° 26'S, 30° 25'E); Ashburton (29° 40'S, 30° 27'E) Black Umfolozi Bridge, South Bank, Nangoma-Mahlabatini Road, Nangoma District (28° 03'S, 31° 32'E); Bumbeni, N Zululand (27° 48'S, 32° 18'E); Candover, 4.7 mi N on road to N Zululand-Swaziland (27° 25'S, 31° 52'E); Dukuduku Forest, 6 km NNE Mtubatuba (28° 22'S, 32° 24'E); Dundee, 5.3 km on road to Pomeroy (28° 10'S, 30° 14'E); Empangeni (= Epangweni), Hluhluwe (28° 46'S, 31° 54'E); Futululu (28° 25'S, 32° 16'E); Graigadam Farm (= Craigadam), Itala Nature Reserve, 9 km NE Louwsburg (27° 31'S, 31° 21'E); Grenshoek Forest (28° 47'S, 30° 05'E); Gumesi Kraal, Usutu River, Line 2 (27° 00'S, 32° 00'E); Gwaliweni, 15 mi S Nqwavuma (= Ngwavuma) (27° 23'S, 32° 03'E); Hazelmere Dam, Verulam (29° 36'S, 31.01'E); Hluhluwe, 100 yards W South African Railways Bridge, Ingweni River (28° 02'S, 32° 17'E); Hluhluwe Game Reserve (28° 16'S, 31° 44'E); Hluhluwe River, 4 mi E on main road to Mtubatuba (28° 02'S, 32° 22'E); Ingwaruma (= Ingwarum) Bush, Otobokwim (= Otobokim, Otobitini), Zululand (27° 24'S, 32° 07'E); Itala Nature Reserve, Ranger's House, Pongola/Zinave Rivers confluence (26° 52'S, 32° 21'E); Itala Provincial Nature Reserve, 10 km NW Louwsburg (27° 34'S, 30° 13'E); Jameson's Drift, Tugela River, Kranskop-Vryheid River (28° 46'S, 30° 55'E); Karkloof (29° 17'S, 20° 23'E); Klipspruit, Utrecht, N Natal (27° 48'S, 30° 25'E); Krantzkloof Nature Reserve (29° 49'S, 30° 50'E); Ladysmith, 11.5 mi on Van Reenen Main Road (28° 34'S, 29° 46'E); Lake St. Lucia (eastern shores), Hlabisa District, Zululand (28° 20'S, 32° 24'E); Lake St. Lucia, north-east Shores, Ubombo District, Zululand (28° 00'S, 32° 30'E).

Langewacht, Babanango (28° 22'S, 31° 05'E); Magut Farm, Goedehoop, portion of Broedersrus (27° 30'S, 31° 30'E); Manaba, NE Zululand (27° 15'S, 32° 26'E); Mangusi Forest, Site C, E Neck, 2.5 mi on Maputa Store-Mosi Store, NE Zululand (26° 58'S, 32° 44'E); Mapelane (28° 25'S, 32° 25'E); Mfongozi (= Mfongosi), Zululand (28° 42'S, 30° 49'E); Mkusi (= Mkuzi) River, Ubombo (27° 53'S, 32° 29'E); Mkuzi (= Mkusi) Game Reserve, Caravan Park, Zululand (27° 37'S, 32° 13'E); Mnuzie Bridge (27° 00'S, 32° 00'E); Nagle Dam (29° 35'S, 30° 37'E); Ngome Forest Area, Ngome, 70 km NE Vryheid (27° 50'S, 31° 24'E); Ngoye Forest, Zululand (28° 50'S, 31° 42'E); Paradise Valley, Pinetown (29° 50'S, 30° 52'E); Pomeroy (= Pameroy), 10.5 mi on road to Greytown (29° 04'S, 30° 35'E); Pongola River, Ubombo (27° 40'S, 32.05'E); Quixotic Farm, 14 km S Mkuzi on farm road to Transvaal (27° 37'S, 32° 02'E); Ringwood, Inchanga (29° 45'S, 30° 40'E); Sand Dune Forest, W Slope, Lake Sibaya (= Sibayi), Zululand (27° 20'S, 32° 42'E); Shihangwane (= Sihangwane, Sihangwana), Zululand (27° 03'S, 32° 25'E); Spiounkop Nature Reserve (28° 42'S, 29° 31'E); Tete Pan, Lake Simbu, Ubombo, Tongaland (27° 34'S, 32° 03'E); Ubombo (27° 34'S, 32° 03'E); Umfolosi (Umfolozi) Rivers (at junction) (28° 21'S, 31° 59'E); Umfolozi (= Umfolosi) (28° 27'S, 32° 10'E); Umkomaas River, Ixopo-Richmond Road (30° 12'S, 30° 49'E); Umlalazi Nature Reserve (28° 58'S, 31° 43'E); Vryheid Nature Reserve (27° 45'S, 30° 48'E); Weenen Nature Reserve, Weenen District (28° 51'S, 29° 59'E).

TRANSVAAL: Acornhoek (24° 35'S, 31° 05'E); Acre 2KT Farm, near Serala, Haenertzburg (23° 59'S, 30° 03'E); Al-te-ver Farm, 1 km SSE Maasstroom (22° 46'S, 28° 28'E); Arnhem (= Arnhemburg), Carolina (26° 04'S, 30° 06'E); Arnhemburg, Carolina (26° 03'S, 30° 50'E); Barberton (25° 47'S, 31° 03'E); Blijdschap Private Nature Reserve, 5 km N Bandolierskop (23° 15'S, 29° 15'E); Blouberg (23° 08'S, 29° 01'E); Blyde Forest Reserve, 10 km N Graskop (24° 52'S, 30° 51'E); Bochum, Wilhanshohe, Magalakwin (= Magalakuin, Magalakwena) (23° 12'S, 29° 04'E); Boekenhoutkloof (25° 31'S, 28° 30'E); Boskop Dam Nature Reserve, N Potchefstroom (26° 34'S, 27° 07'E); Broederstroom Farm (25° 49'S, 27° 52'E); Buffelsdraai, Brits (25° 07'S, 27° 40'E); Buffelspoort Farm 149 JQ, 3 mi NE Assen (25° 07'S, 27° 37'E); Buzzard Mountain Sanctuary, Louis Trichardt District (23° 00'S, 29° 46'E); Chromedale South African Railways Station, 5 mi N (24° 40'S, 27° 20'E); Cyprus Farm 68, 13 km SW Ofcolaco (24° 12'S, 30° 17'E); Daspoortberg (25° 44'S, 28° 03'E); De Hoop Private Nature Reserve (24° 57'S, 29° 57'E); Derby Post Office, Skeenshoek Malaria Camp (23° 21'S, 29° 25'E); Dinokana (= Linokane), 3.1 mi on road to Zeerust (25° 28'S, 25° 55'E); Dinokana (= Linokane), Zeerust (25° 27'S, 25° 52'E); Donkerpoort and Zandspruit Farm 449, 24 km E Thabazimbi (24° 35'S, 27° 40'E); Dordrecht Farm 578, 20 km S Marken (23° 50'S, 28° 23'E); Elandsfontein Farm 74, 6.3 mi De Wilt Post Office on Pretoria W-Brits Road (25° 38'S, 27° 51'E); Fontana Military Area, near Petronella (25° 30'S, 28° 17'E); Fort Klipsdam Farm, 27 km N Pietersburg (23° 42'S, 29° 33'E); Fountains Valley, Pretoria (25° 57'S, 28° 12'E); Geelhoutkloof Farm 275, Waterberg (24° 15'S, 28° 35'E); Georges Valley Farm 632, Haenertzburg (24° 01'S, 30° 04'E); Gravellote, Tzaneen (23° 57'S, 30° 36'E); Greefswald Farm 37, 73 km W Messina (22° 12'S, 29° 23'E); Grenshoek Forest (23° 47'S, 30° 05'E); Groothoek Farm 99, 25 km ESE Potgietersrus (24° 21'S, 29° 08'E); Groot Marico, Koster (25° 35'S, 26° 25'E); Grootsuikerboschkop and Elandlaagte Farm, Dullstroom (25° 25'S, 30° 06'E); Guldenskat Farm, 9 km Jan Kempdorp (27° 56'S, 24° 57'E); Hans Merensky Provincial Nature Reserve, 30 km NE Letsitele (23° 40'S, 30° 41'E); Hectorspruit (25° 26'S, 31° 41'E); Hennops River (25° 48'S, 27° 59'E); Hennops River on Hartebeesportdam Road, Johannesburg (25° 46'S, 27° 59'E); Hermanus-Doorns Post Office (24° 06'S, 27° 36'E); Houghton Estate, Johannesburg (26° 12'S, 28° 05'E); Huwi Private Nature Reserve, 7 mi SE Ellisras (23° 45'S, 27° 50'E); Ingelele (= Ngelele) (22° 54'S, 30° 13'E); Irene, Pretoria (25° 52'S, 28° 14'E); Jacksonstuin (= Jacksonstown) Post Office (25° 43'S, 27° 46'E).

James' Hut, Limpopo (22° 23'S, 31° 16'E); Jan Amsterdam, Pietersburg (23° 16'S, 29° 27'E); Johannesburg (26° 12'S, 28° 05'E); Joshua Moolman Private Nature Reserve, 9 km WSW Amsterdam (26° 41'S, 30° 36'E); Khandizwe Plateau, 9 km W Malelane, Kruger National Park (25° 28'S, 31° 25'E); Kilnerton (25° 45'S, 28° 18'E); Klopperfontein, Kruger National Park (22° 40'S, 31° 10'E); Komatipoort, Kruger National Park (25° 25'S, 31° 58'E); Koster (25° 52'S, 26° 54'E); Kosterfontein Farm 460, Koster (25° 48'S, 26° 56'E); Krugerkloof Nature Reserve, Lydenburg (25° 06'S, 30° 31'E); Lanjan Nature Reserve, 7 mi N Vivo (22° 50'S, 29° 12'E); Letaba Ranch 8, 40 km N Phalaborwa (23° 43'S, 31° 05'E); Letaba Rest Camp, Kruger National Park (23° 51'S, 31° 55'E); Leydenburg (25° 06'S, 30° 27'E); Leydsdorp (23° 59'S, 30° 31'E); Lichtenburg, 4.5 mi N on road to Ottoshoop (26° 05'S, 26° 07'E); Loskop Dam Nature Reserve (25° 25'S, 29° 20'E); Louis Trichardt (23° 03'S, 29° 54'E); Madimbo, 10 km E, Limpopo River (22° 20'S, 30° 58'E); Madimbo, Mabilingwe Area, Limpopo River (22° 26'S, 31° 04'E); Magalakwin (= Magalakuin, Magalakwena) Farm 666, Potgietersrus (23° 36'S, 28° 36'E); Magaliesberg, Pretoria (25° 41'S, 28° 12'E); Mal Cont Camp, Mogol River, Vaalwater (24° 18'S, 28° 07'E); Malelane Camp (25° 28'S, 31° 31'E); Malensan Singwetsi Game Reserve (23° 06'S, 31° 27'E); Malmaniesoog, N Zeerust (25° 48'S, 26° 03'E); Malta Farm (24° 09'S, 30° 13'E); Mamarango (= Mamaranga), Letaba (23° 52'S, 30° 37'E); Mariepskop (24° 41'S, 30° 54'E); Messina (22° 17'S, 30° 17'E); Messina Nature Reserve (22° 21'S, 30° 03'E); Mmabolela Estates, 14 km NW Maasstroom (22° 41'S, 28° 15'E); Moedwil Post Office, 2.5 mi E on Rustenburg-ZwartrUggens Road (25° 39'S, 27° 01'E); Mokeetsi Farm 376, Duiwelskloof, Zoutpansberg (23° 40'S, 30° 05'E); Molopene River, near Molopene Rest Camp, Kruger National Park (23° 50'S, 31° 12'E); Mooigenoeg Farm 83, 8 km S Derdepoort (24° 43'S, 26° 17'E); Moonlight, Potgietersrus District (23° 14'S, 28° 11'E); Moorddrift Farm 289, Waterberg, Potgietersrus (24° 17'S, 28° 57'E); Moormeisiesfontein, Rustenburg, Thabazimbi (25° 01'S, 27° 37'E); Mosdene Private Nature Reserve, 2 mi SE Naboomspruit (24° 36'S, 28° 46'E); Mutale (= Motale) River (22° 30'S, 30° 50'E); Narina Farm, 8 km W Duiwelskloof (23° 42'S, 30° 16'E); Nelspruit, E Transvaal (25° 28'S, 30° 59'E); Newgate Farm, Soutpansberg (= Zoutpansberg) (22° 58'S, 29° 56'E); Newington, 7 mi NE (24° 45'S, 31° 25'E); Njelele River, Zoutpansberg (= Soutpansberg) (22° 55'S, 30° 18'E); Nooitgedacht Nature Reserve (25° 57'S, 30° 02'E); Nwambia, 1 mi E (22° 41'S, 31° 27'E); Nwambienepan, 26 km SSE Pafuri, Kruger National Park (22° 41'S, 31° 22'E); Nwanetsi River Ford (= Fold), 10.7 mi N Letaba on Shingwedzi (23° 47'S, 31° 29'E); Nylstroom (24° 47'S, 28° 25'E); Olifants River Gorge, 3.5 mi S, Satara Road junction, Satara, Kruger National Park (24° 09'S, 31° 50'E); Olifantspoort Farm 328, 12 mi S Rustenburg (25° 46'S, 27° 16'E); Othawa Farm, 32 km NW Skukuza, Sabie Sands (24° 25'S, 31° 26'E); Palala-Limpopo River junction, Waterberg (23° 05'S, 27° 53'E); Paramie (= Uitkyk) Private Nature Reserve, 12 km SSE Nelspruit (25° 36'S, 31° 07'E); Pery (= Percy) Fyfe Nature Reserve (24° 03'S, 29° 07'E); Pienaar's river (25° 12'S, 28° 23'E); Platbos Farm, 32 km NW Vaalwater (24° 13'S, 27° 52'E); Potgietersrus, 72 km NW (24° 11'S, 29° 00'E); Pretoria (25° 43'S, 28° 11'E); Pretoria Noord (= North) (25° 40'S, 28° 10'E); Ratsegaai Farm 204, 13 km W Ventersdorp (26° 22'S, 26° 32'E); Renosterpoort Private Nature Reserve, 15 km NE Bronkhorstspruit (25° 45'S, 28° 56'E); Rhoda Farm 9, 13 km S Phalaborwa (24° 03'S, 31° 06'E); Rietondale, Pretoria (25° 43'S, 28° 14'E); Rietspruit, Nylstroom (24° 40'S, 28° 27'E); Rochdale Farm 700 MS, 5 mi E Waterpoort (22° 54'S, 29° 42'E); Roodeplaat, Pretoria (25° 37'S, 28° 22'E); Rosslyn, Pretoria (25° 38'S, 28° 06'E); Rustenburg Nature Reserve (25° 46'S, 27° 16'E); Rykvoorby Farm, 9 km N Zeerust (25° 29'S, 26° 04'E); Sand River, near Messina (22° 16'S, 30° 06'E); Schurweberg, Pretoria (25° 48'S, 27° 59'E); Scrutton Farm 23 MT, 32 km E Messina (22° 17'S, 30° 17'E); Sekororo (24° 15'S, 30° 24'E); Shingwedzi/Dzombo Rivers confluence, 13 mi SE Shingwedzi (23° 14'S, 31° 33'E).

Skukuza, Kruger National Park (25° 05'S, 31° 36'E); Skukuza Camp (24° 59'S, 31° 35'E); Soetdoorns Farm 173, 15 mi S Vivo on Kalkfontein Road (23° 23'S, 29° 25'E); Steenkampsberg Provincial Nature Reserve, 13 km NNE Dullstroom (25° 18'S, 30° 07'E); Suikerboschrand Provincial Nature Reserve (26° 32'S, 28° 12'E); Suikerboschrand Nature Reserve (26° 30'S, 28° 13'E); Swartkrans, Sterkfontein, Krugersdorp (26° 01'S, 27° 42'E); Tamboekieskloof, Mogol River (23° 55'S, 27° 44'E); Ten Bosch Estates, 10 km NE Hectorspruit (25° 20'S, 31° 50'E); Thabazimbi (24° 35'S, 27° 40'E); Theespruit Farm 156, Carolina/Barberton Glens (26° 01'S, 30° 51'E); Tshakuhma Malaria Camp (23° 04'S, 30° 18'E); Tzaneen, Letaba (23° 50'S, 30° 10'E) Tzaneen Estates (23° 48'S, 30° 11'E); Uitkomst Farm 499, 35 mi W Pretoria (25° 55'S, 27° 45'E); Urk Farm 10, Blouberg Private Nature Reserve, 13 km W Vivo (23° 02'S, 29° 07'E); Vaalkop Dam Nature Reserve (25° 23'S, 27° 28'E); Vendaland on Levuvhu River (22° 40'S, 30° 53'E); Warmbaths (= Warmbad), 4 mi on Nylstroom Road (24° 50'S, 28° 20'E); Waterkloof, Pretoria (25° 47'S, 28° 15'E); Watervalonder on Nelspruit Road (25° 39'S, 30° 24'E); Welgedaan Farm, 28 km NNE Christiana (27° 41'S, 25° 14'E); Welgevoden Farm, 16 km W Steilloop (23° 32'S, 28° 25'E); Wilgekuil Farm 181, Rustenburg, Brits (25° 14'S, 27° 45'E); Wilhanshohe, Magalakuin (= Magalakwin, Magalakwena) River (23° 13'S, 29° 04'E); Windhoek, Louis Trichardt (22° 50'S, 29° 54'E); Witpoort Farm 419, 24 km E Potchefstroom (26° 40'S, 27° 20'E); Wonderboom, Pretoria (25° 41'S, 28° 12'E); Wonderfontein Farm 103, Oberholtzer (26° 19'S, 27° 28'E); Woodbush Village, Houtbosdorp (23° 49'S, 29° 54'E); Worcester Mine, Barberton (25° 49'S, 31° 01'E); Zandspruit Farm 449, 63 km NNW Rustenburg (24° 35'S, 27° 40'E); Zebediela Citrus Estates, 32 km SE Potgietersrus (24° 17'S, 29° 18'E); Zoo Hill, Pretoria (25° 44'S, 28° 11'E); Zoutpan (= Soutpan), 30 mi N Pretoria (25° 24'S, 28° 06'E); Zoutpansberg (= Soutpansberg) (23° 00'S, 29° 40'E). **SWAZILAND**: Phophonyane (25° 53'S, 31° 17'E); Ranches Limited (26° 02'S, 31° 42'E). **TANZANIA**: Amani, Tanga (05° 06'S, 38° 38'E); Gonja (04° 21'S, 38° 03'E); Iringa (07° 46'S, 35° 42'E); Manyara National Park, N Tanzania (03° 55'S, 35° 50'E); Muheza, Tanga (05° 10'S, 38° 47); Tengeru, Arusha District (03° 23'S, 36° 50'E). **UGANDA**: Rhino Camp, W Nile (02° 58'N, 31° 24'E). **ZAMBIA**: Abercorn Londe National Park (08° 50'S, 31° 22'E); Balovale (= Zambezi) (13° 33'S, 23° 07'E); Chibale (13° 36'S, 30° 08'E); Chikungu Stream (13° 55'S, 32° 00'E); Chilanga (15° 35'S, 28° 18'E); Lavushi Manda Game Reserve, Lukulu River (12° 18'S, 30° 57'E); Msofu (= Musofu) Mission, Mkushi District (13° 22'S, 29° 02'E); Ndola (12° 58'S, 28° 38'E); Ndola, 10 mi SSW (12° 39'S, 27° 38'E); Nsange (=Nsangi)/Kabompo Rivers confluence (12° 30'S, 24° 53'E); Solwezi Boma (12° 11'S, 26° 25'E). **ZIMBABWE**: Ainsby Farm, Richmond (20° 00'S, 28° 00'E); Alsace (= Alsage) Farm, Harare (17° 50'S, 31° 04'E); Atlantica Ecological Research Station, Harare (17° 48'S, 30° 03'E); Banti (19° 20'S, 32° 47'E); Benga (17° 40'S, 27° 40'E); Birchenough Bridge (19° 57'S, 32° 20'E); Borrowdale Brook, Harare (17° 50'S, 31° 02'E); Bulawayo (20° 10'S, 28° 35'E); Bumboosie (18° 33'S, 26° 13'E); Calgary, Harare (17° 55'S, 31° 06'E); Chete (Old Camp) (17° 22'S, 27° 36'E); Chibero (17° 00'S, 31° 00'E); Chikupe (= Chikupo) Cave, Bindura (17° 25'S, 31° 17'E); Chinomwe Clinic, Raffingora (17° 01'S, 30° 25'E); Chipinda Pools (21° 13'S, 31° 53'E); Chipinga (20° 12'S, 32° 37'E); Corner Chimanimani (= Chimanimani) (19° 49'S, 33° 05'E); Deka (18° 05'S, 26° 40'E); Deteema Dam (18° 40'S, 26° 08'E); Doddieburn Ranch (21° 00'S, 29° 00'E); Dorowa Mine (19° 00'S, 31° 00'E); Eirene Marondera (18° 00'S, 31° 00'E); Essexvale (20° 17'S, 28° 56'E); Essexvale (Esigodini) Ranch (20° 00'S, 29° 00'E); Falcon College, Strcom Bed (20° 00'S, 28° 00'E); Fishon, Lundi (21° 00'S, 32° 00'E); Fletchers, Bembesi (19° 00'S, 26° 00'E); Fort Victoria (20° 03'S, 30° 50'E); Gomo Dam (South) (19° 00'S, 26° 00'E); Gwelo (= Gweru) (18° 41'S, 28° 36'E); Harare (17° 50'S, 31° 04'E); Haroni-Lusitu Beacon (20° 02'S, 33° 01'E); Humani (= Humai) Ranch (20° 21'S, 32° 02'E); Ingeli Farm, Gwelo (= Gweru) (19° 25'S, 29° 50'E).

Kabera (18° 00'S, 28° 00'E); Kadoma (= Gatooma) (18° 20'S, 29° 57'E); Kamaziyo (= Kamazeyo) Camp (18° 10'S, 27° 40'E); Kanyemba (15° 00'S, 30° 00'E); Kariba (southern river), Game Camp (16° 32'S, 28° 48'E); Kyle National Park (20° 13'S, 31° 01'E); Lake McIlwaine National Park (17° 55'S, 30° 46'E); Longani Dam, Lone Star Ranch (21° 00'S, 31° 00'E); Lusitu River (20° 03'S, 32° 57'E); Makoholi (= Makaholi) Research Station (19° 00'S, 30° 00'E); Maitengwe Dam, Nata Reserve (20° 02'S, 27° 02'E); Maleme Rest Camp, Matopos (= Motopos) (20° 33'S, 28° 31'E); Malugwe Pan (21° 40'S, 31° 46'E); Manda Farm (18° 00'S, 32° 00'E); Manzituba (17° 00'S, 28° 00'E); Maranke Reserve (18° 00'S, 32° 00'E); Masera Tribal Trust Land (21° 00'S, 29° 00'E); Matetsi Wildlife Leisure Camp (18° 17'S, 25° 56'E); Matika Farm, Mutare (= Umtali) (18° 57'S, 32° 40'E); Matopos (= Motopos) (above Maleme) (20° 45'S, 28° 38'E); Matopos (= Motopos) (eastern) (20° 23'S, 28° 28'E); Matopos (= Motopos) National Park (20° 23'S, 28° 28'E); Matopos (= Motopos) Research Station (20° 23'S, 28° 28'E); Matusiadona Tashinga (= Tashinga Matusiadona) (16° 52'S, 28° 40'E); Mavhuradonha (= Mavuradonha) Wilderness Area (16° 30'S, 31° 20'E); Mazoe, Mashonaland, eastern Zimbabwe (17° 31'S, 30° 58'E); Mount Selinda (20° 27'S, 32° 40'E); Msingwenyani, Matibi District (22° 00'S, 30° 30'E); Mtilikwe (= Mtilekwe) River Triangle (21° 05'S, 31° 20'E); Mtoko, 40 mi (17° 21'S, 32° 12'E); Muchabezi, Matopos (= Motopos) (20° 00'S, 28° 00'E); Muneni River, Mutare (= Umtali) (18° 59'S, 32° 41'E); Mushandike National Park (20° 07'S, 30° 25'E); Mutare (= Umtali) (18° 58'S, 32° 42'E); Ngezi National Park (18° 42'S, 30° 22'E); Ngorima Reserve (East), Melsetter District (20° 00'S, 32° 00'E); Nkai (19° 00'S, 28° 54'E); Nyamucheche Umvukwes (= Umvukwesi) (= Nyamuyeche Farm) (16° 46'S, 30° 57'E); Nyamunyeche (= Nyamuyeche) (16° 00'S, 30° 00'E); Nyamunyeche (= Nyamyeche) Chikonyora (16° 00'S, 30° 00'E); Pombadzi/Lundi Rivers Confluence (21° 23'S, 32° 09'E); Queens, Bulawayo Area (19° 59'S, 28° 30'E); Ranelia Farm Cashel (19° 00'S, 32° 00'E); Rekomitjie River (15° 00'S, 29° 00'E); Rhodes Inyanga National Park (18° 17'S, 32° 46'E); Rhodes Matopos (= Motopos) National Park (20° 33'S, 29° 28'E); Rusape (18° 32'S, 32° 06'E); Rusito Forest (on Rusito River) (20° 02'S, 32° 59'E); Sabi/Lundi Rivers confluence (21° 18'S, 32° 24'E); Sable Park, Kwekwe (= Que-Que) (18° 56'S, 29° 50'E); Saffron Walden, near Harare (17° 00'S, 30° 00'E); Sebakwe Dam, Kwekwe (= Que-Que) (19° 02'S, 30° 16'E); Sengwa Wildlife Research Station (= Sengwa Camp) (18° 10'S, 28° 23'E); Sentinel Ranch, Limpopo River (22° 00'S, 29° 00'E); Shinda Estates (19° 00'S, 32° 00'E); Siakobo Rest Camp, Gokwe (17° 00'S, 28° 00'E); Sinamatela Hwange (= Wankie) National Park (18° 35'S, 26° 18'E); Sinoia (17° 22'S, 30° 12'E); St. Paul's Mission (18° 00'S, 28° 00'E); Stapleford, Nyamkwarara River, Umtali (= Mutare) District, Manicaland (18° 00'S, 32° 00'E); Thornpark, Harare (17° 59'S, 31° 04'E); Tsabalala Sanctuary, Matopos (= Motopos) (20° 00'S, 28° 00'E); Tsakabika, Wankie (= Hwange) (18° 20'S, 26° 30'E); Tuli Safari Area, Sashi River (21° 55'S, 29° 13'E); Umhlanyane, Matopos (= Motopos) (20° 00'S, 28° 00'E); Umvukwesi (= Umvukwes) (17° 00'S, 30° 53'E); Umzingwane/Limpopo Rivers junction (= Umzingwani) (22° 12'S, 29° 55'E); Vashu Farm (20° 00'S, 28° 00'E); Wankie (= Hwange) National Park (18° 00'S, 26° 00'E); Zambezi/Chiwore Rivers junction (15° 00'S, 29° 00'E); Zana Farm, Umvukwesi (= Umvukwes) (16° 00'S, 30° 00'E); Zewa Hill, Inyanga (18° 16'S, 32° 45'E); Zimbabwe Ruins, 25 km SE Fort Victoria (20° 17'S,30° 56'E); Zimbabwe National Park (20° 17'S, 30° 55'E).

APPENDIX VII

DEFINITION OF CHARACTERS USED IN THE PHYLOGENETIC ANALYSIS OF *AETHOMYS* (CHAPTER 9)

Characters were either assigned character-states ranging from 0 to 4, or coded as present or absent. Character-states presumed to be plesiomorphic are denoted by a "P". All other characters are presumed to be unordered transformation series of apomorphic characters.

1) *Skull robustness/ossification.*-- (1) Skull less robust and not well ossified. (2) Moderately robust and moderately ossified. (3) Robust and well ossified (P).

2. *Cranial ridge development.*-- (0) Skull ridges, particularly supraorbital and occipital ridges, slight or weak. (1) Supraorbital ridges with distinct, but no strongly developed ridges. (2) Developed, but only extending downwards to edge of parietal. (3) Pronounced or well developed, and extending posteriorly along outer part of frontals and parietals to corners of interparietal where it meets occipital crest (P). (4) Developed, and widely divergent posteriorly.

3. *Development of the alisphenoid process of the squamosal.*-- (1) Alisphenoid process of the squamosal narrow (P). (2) Wide.

4. *Development of interorbital constriction.*-- (1) Interorbital constriction relatively weak. (2) Moderate. (3) Strong or pronounced.

5. *Zygomatic arch development.*-- (0) Anterior half of zygomatic arch not broadened. (1) Strongly broadened.

6. *Lower anterior zygomatic plate development.*-- (0) Lower anterior corner of zygomatic plate without clearly defined mesenteric knob (P). (1) With well-defined mesenteric knob.

7. *Presence/absence of foramina posterior to anteorbital foramina.*-- (0) Extra pair of foramina posterior to anteorbital foramina absent (P). (1) Present.

8. *Extent of bulla inflation.*-- (1) Bullae strongly inflated (P). (2) Relatively flattened.

9. *Upper molar toothrow development.*-- (1) Molars relatively narrower than palate between them (P). (2) Relatively wider.

10. *Lower molar cusp development.*-- (0) Anterior median cusp (Sm) on M_1 absent. (1) Represented by a small anterior cusplet (Smc). (2) Present.

11. *General molar cusp development.*-- (1) Molars generally weakly cuspidate (P). (2) Well defined and strongly cuspidate.

12. *Number of roots on M^1.*-- (1) M^1 four-rooted (P). (2) Five-rooted.

13. *Extent of cusp development on M^3.*-- (1) t_1 on M^3 conspicuously larger and isolated. (2) Smaller and not isolated.

14. *Central upper molar row cusp development.*-- (1) Central upper molar row cusps not pronounced (P). (2) Enlarged or pronounced.

15. *Development of t_8 on third lamina of upper molars.*-- (1) t_8 on third lamina of upper molars narrow. (2) Broadened (P).

16. *Development of t_9 on third lamina of upper molars.*-- (0) t_9 on third lamina inconspicuous or absent. (1) Small and not projecting outwards (P). (2) Medium, and tending to project outwards.

17. *t_3 development on M^1.*-- (1) t_3 on M^1 small and conspicuously isolated. (2) Relatively larger and not isolated (P).

18. *t_4, t_5 and t_6 development on second lamina of M^2.*-- (0) t_4, t_5 and t_6 on second lamina of M^2 suppressed. (1) Well developed and exaggerated (P).

19. *t_4, t_5 and t_6 development on second lamina of M^3*.-- (0) M^3 with central lamina not bent backwards (P). (1) Bent backwards on each side, overlapping two-cusped last lamina.
20. *Development of t_3 and t_5 on M^2*.-- (0) t_3 on M^2 not associated with t_5 (P). (1) Associated with t_5.
21. *General cusp development on M^3*.-- (0) M^3 with no evidence of six cusps in three laminae, t_1, t_3 and t_7 being absent (P). (1) With clear evidence of six cusps.
22. *Mandibular development*.-- (0) Mandible weakly built. (1) Strongly built (P).

APPENDIX VIII

DATA MATRIX OF CHARACTER-STATE VALUES CODED FOR EACH CURRENTLY RECOGNIZED SPECIES OF *AETHOMYS* AND OUTGROUPS (*) USED FOR PHYLOGENETIC ANALYSIS (CHAPTER 9)

Characters and character-states are numbered as described in Appendix VII. Characters were either assigned character-states ranging from 0 to 4, or coded as present or absent. A "9" denotes unknown character-states.

Taxon	Character number																					
	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.	20	.	.
	1	2	3	4	5	6	7	8	9	.	1	2	3	4	5	6	7	8	9	.	1	2
Aethomys bocagei	3	2	1	2	1	0	0	1	2	0	2	1	1	1	2	0	2	0	0	0	0	1
A. chrysophilus	2	2	1	2	1	0	0	1	2	1	2	1	2	2	2	2	2	0	0	1	0	1
A. ineptus	2	2	2	2	1	0	0	1	2	1	2	1	2	2	2	2	2	0	0	1	0	1
A. granti	1	0	1	1	0	1	0	2	2	2	2	1	2	1	2	2	2	1	1	1	0	0
A. hindei	2	3	1	2	1	0	0	1	2	1	2	1	2	1	2	2	2	0	0	0	0	1
A. kaiseri	3	3	1	2	1	0	1	1	2	1	2	1	1	1	2	1	2	0	0	0	0	1
A. namaquensis	1	0	1	1	0	1	0	2	2	2	2	1	2	1	1	1	2	0	0	0	0	0
A. nyikae	3	4	1	2	1	0	1	1	2	1	2	9	2	1	2	2	2	0	0	0	0	1
A. silindensis	3	3	1	2	1	0	1	1	2	1	2	2	1	1	2	0	1	0	0	0	0	1
A. stannarius	2	1	1	2	1	1	0	1	2	1	2	9	2	1	2	1	2	0	0	0	0	1
A. thomasi	2	2	1	2	1	0	1	1	2	0	2	1	1	2	2	0	2	0	0	0	1	1
**Dasymys incomtus*	3	3	1	3	1	0	0	1	1	1	1	1	1	1	2	1	2	1	0	0	0	1
**Rattus rattus*	3	3	1	2	0	0	0	1	1	0	1	1	2	1	2	1	2	1	0	0	0	1

APPENDIX IX

PUBLICATIONS EMANATING FROM THIS STUDY

ANNALS OF CARNEGIE MUSEUM
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THE SELECTION OF TAXONOMIC CHARACTERS FOR MORPHOMETRIC ANALYSIS: A CASE STUDY BASED ON SOUTHERN AFRICAN *AETHOMYS* (MAMMALIA: RODENTIA: MURIDAE)

CHRISTIAN T. CHIMIMBA[1,2]

NICO J. DIPPENAAR[2]

ABSTRACT

Prior to a systematic revision of southern African rock rats of the genus *Aethomys* Thomas, statistical procedures were used to select morphometric characters for recording and subsequent use in a revision of the group. The procedure advocated could have wider application in morphometric studies. An initial set of 66 cranial characters was reduced to 51 after the data set was subjected to routine assumptions tests. The remaining 51 characters, considered to be statistically problem-free, were reduced to a final set of 11 characters after subjecting them to cluster and ordination procedures to summarize patterns of correlations between characters, develop criteria for the selection of representative measurements within cluster analysis-generated subclusters, and the subsequent removal of redundant variables. The procedure attempts to economize while at the same time adequately represent the phenotype, an approach consistent with the concept of morphological integration. Four additional cranial and four standard external characters are also included in the final data set, but for descriptive and comparative purposes only.

INTRODUCTION

African rock rats of the genus *Aethomys* are endemic to east, west, central, and southern Africa where the genus is represented by ten species (Wilson and Reeder, 1993). Five species, *A. namaquensis, A. silindensis, A. granti, A. nyikae,* and *A. chrysophilus* are currently recognized in southern Africa (Meester et al., 1986; Skinner and Smithers, 1990), but the latter species has been shown to include two forms based on chromosome (Gordon and Rautenbach, 1980; Gordon and Watson, 1986; Visser and Robinson, 1986; Baker et al., 1988), electrophoresis (Gordon and Watson, 1986), and sperm morphology (Gordon and Watson, 1986; Visser and Robinson, 1987; Breed et al., 1988). Schlitter (1978) considered the genus in critical need of revision.

The present paper forms part of a revision of southern African species of *Aethomys,* and in particular examines the selection of quantitative taxonomic characters, a critical but often neglected step in many systematic studies (Strauss and Bookstein, 1982; Rohlf, 1990). In small mammals, no established procedure is available for selecting appropriate character sets. Approaches used to date generally fall into four categories: 1) selection of character sets that have been used in the past, often with the ad hoc addition or deletion of characters after elementary correlation analysis (Power, 1971; Chapman et al., 1992); 2) selection of as many measurements as practicable (Watson and Dippenaar, 1987; Chimimba

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and Kitchener, 1991), reflecting the influence of numerical taxonomy as advocated in Sneath and Sokal (1973); 3) selection based on an assessment of functional units of the cranium (Taylor, 1990; Taylor and Meester, 1993); and 4) selection of landmarks as advocated in the most recent developments in morphometrics (Strauss and Bookstein, 1982; Bookstein et al., 1985; Zelditch et al., 1989; Rohlf and Bookstein, 1990; Rohlf and Marcus, 1993).

Although characters selected on the basis of the first two categories can perform well, it is important to assess character redundancy in morphometric studies (Blackith and Reyment, 1971; Sneath and Sokal, 1973; Thorpe, 1976; James and McCulloch, 1990; Rohlf, 1990). Nevertheless, apart from a few studies (Thomas, 1968; Best, 1978; Taylor, 1990; Taylor and Meester, 1993), it has been rarely considered in practice. The utilization of unevaluated characters could have a profound effect on analyses (Pimentel and Smith, 1986*b*), ranging from distortion of inter-Operational Taxonomic Unit (OTU: Sneath and Sokal, 1973) relationships (Blackith and Reyment, 1971) to an increase in analysis time that often results in analytical problems while processing large data matrices (Chimimba and Kitchener, 1991). Some studies have shown that after the assessment of linear dependence (redundancy) and colinearity, sets of many quantitative characters can be reduced to a few and still contain equivalent information (Mahalanobis et al., 1949; Albrecht and Blackith, 1957).

Various approaches that have been used to screen for reliable characters include either analysis of variance (ANOVA) or correlations between characters (Pimentel and Smith, 1986*b*). The former procedure is restricted to multigroup studies in which character redundancy is sometimes ignored (Pimentel and Smith, 1986*b*). The latter approach summarizes correlations between characters by principal component (PCA), factor (Thomas, 1968; Johnston, 1973; Gould et al., 1974) and cluster analyses (Power, 1971; Taylor, 1990; Taylor and Meester, 1993) with the selection of characters from within highly correlated subsets of characters. Another strategy has been to employ Mahalanobis' (1936) D^2 statistic (Thorpe, 1976), a similarity coefficient that takes into account the degree of information redundancy in each character as summarized by the within-group covariance. However, owing to the instability of correlation coefficients for sample sizes smaller than 20, Van Valen (1974) considered this an oversimplification (Thorpe, 1976).

The approach used in the present study stems from current theory of evolutionary change that emphasizes the unity of the genotype (Mayr, 1963, 1976; Lewontin, 1974; Wright, 1978, 1980) in which organisms are the integrated functional units that evolve (Waddington, 1957; Riedl, 1978; Gould and Lewontin, 1979; Selzer, 1993; Borgia, 1994). Embryological studies have, for instance, demonstrated that the cranium represents a functional character suite that interacts and has a common ontogenetic origin (Noden, 1978, 1983; Gans and Northcutt, 1983; Zelditch et al., 1993). Olson and Miller (1958) hypothesized, and subsequently demonstrated, that the degree of cranial integration can be measured by the intensity of statistical associations in the phenotype. Therefore, developmentally and functionally related traits ought to be relatively highly correlated in the phenotype. On both empirical and theoretical grounds these authors placed developmentally and functionally interdependent morphological characters into "Functional sets" ("F-sets"). Empirically derived sets of characters that were relatively highly correlated were placed into "Phenotypic sets" ("P-sets"). Other studies support the a priori-defined morphologically integrated functional units

of Olson and Miller (1958) (Moss and Young, 1960; Cheverud, 1982; Cheverud et al., 1989; Cane, 1993). Taylor (1990) and Taylor and Meester (1993) extended the morphological integration concept into a character selection protocol.

The present study is aimed at selecting meaningful morphometric characters for use in a revision of southern African *Aethomys*. Accordingly, the procedure of Taylor (1990) and Taylor and Meester (1993), which summarized character correlations in the yellow mongoose (*Cynictis penicillata*, Viverridae) by cluster analysis, is expanded upon to meet three important requirements: 1) "comprehensiveness" (i.e., the consideration of adequate coverage of the phenotype), 2) "economy" (by the removal of redundant characters), and 3) "pattern summary" (of relationships between characters consistent with the morphological integration concept of Olson and Miller, 1958). Southern African *Aethomys* is here used as a case study for this character selection protocol that could find wider application in morphometric studies of other taxa.

Recent developments in landmark-based methods (Mousseau, 1991; Rohlf and Marcus, 1993), especially their extension to three-dimensional space, suggest a modification of the morphological integration concept, involving a more rigorous morphometric assessment of functional units (Van der Klaauw, 1948–1952) based on landmarks (rather than measuring points) and a closer integration with more recent advances in ontogenetic cranial development (Thorogood and Tickle, 1988).

MATERIAL AND METHODS

The present study is based mainly on a single homogeneous sample, representing an island population of *Aethomys namaquensis* (21 males, 13 females) from Keimoes Island, Orange River, Cape Province, but additional samples of *A. granti* (seven males, seven females) from Sutherland, Cape Province, and *A. chrysophilus* (six males, ten females) from Maasstroom, Transvaal, were used to develop criteria for the selection of the final set of measurements. The material examined is listed in Appendix I.

Individuals were assigned to seven toothwear classes (with reference to Morris, 1972; Perrin, 1982; Dippenaar and Rautenbach, 1986), but to reduce the effect of age variation, only adult, toothwear class VI (Chimimba and Dippenaar, 1994) individuals with complete data sets were considered.

An initial set of 66 linear cranial (40 skull, nine mandible, and 17 dental) measurements (Fig. 1a–k) were recorded by one observer (CTC) to the nearest 0.05 mm using a pair of Fowler digital calipers, a Fowler Interface and EASYCAL program developed by S. Reig for direct data input to rBase (Ashton-Tate Software, Inc., USA). While the character set reflects an attempt to distribute measurements across functional units of the skull, this was not always possible because of constraints imposed by the use of calipers and the taxonomic need to include traditional characters which were not selected on the basis of the morphological integration concept. Owing to the unreliability of external characters, only cranial characters were considered.

Univariate and multivariate data screening (Pimentel and Smith, 1986*a*, 1986*b*; Reig, 1989) revealed two male specimens with outlier values not consistent with toothwear class VI. One was exceptionally large (USNM 451966) in most measurements and the other (USNM 452055) had an abnormally small greatest cross-sectional crown width of M_3 (66-WMT). To avoid the introduction of bias in the

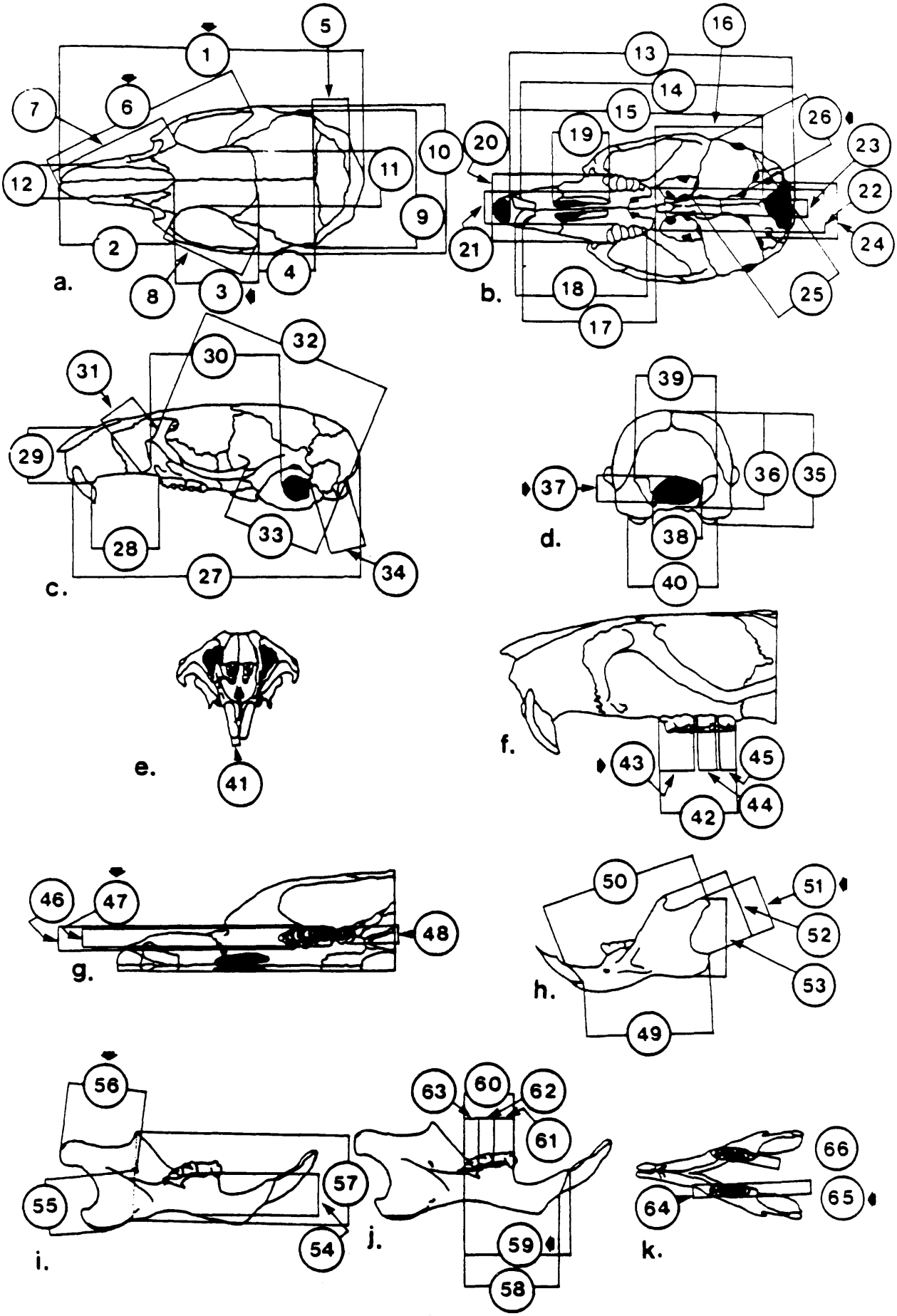

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Fig. 1.—Reference points of cranial measurements. Asterisks indicate measurements used in original descriptions.

a. *1-GLS—Greatest length of skull, from anterior edge of nasals to posterior edge of occipital condyle, along longitudinal axis of skull; 2-GLN—Greatest length of nasals, from longest posterior projection of nasal wings to anteriormost edge of nasal bones; *3-FRO—Greatest length of frontals; *4-PAR—Greatest length of parietals; *5-INT—Interparietal length, from intersection of sagittal suture and posterior end of parietal, perpendicular to posterior end of interparietal; 6-NPP—Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch; 7-NPO—Distance from anterior edge of nasals to posterior edge of postorbital bar; 8-ZAL—Zygomatic arch length, from posteriormost part of anterior part of zygomatic arch to anteriormost part of posterior part of zygomatic arch; *9-BBC—Breadth of braincase—width at dorsal root of squamosals; *10-ZYW—Greatest zygomatic width, between outer margins of zygomatic arches, perpendicular to longitudinal axis of skull; *11-IOB—Least breadth of interorbital constriction—least distance dorsally between orbits; *12-NAS—Nasal width, at anteriormost point where nasals join premaxillae.

b. 13-CBL—Condylobasal length of skull, from posteriormost projection of occipital condyles to anterior edge of premaxillae; *14-PIC—Incisor to condyle length, from posterior surface of I^1 at alveolus to posteriormost projection of occipital condyle; *15-BSL—Basal length of skull, from anteriormost point of lower border of foramen magnum to anterior edge of premaxilla; *16-PPL—Postpalatal length, from anteriormost edge of hard palate to anteriormost point on lower border of foramen magnum; *17-PAL—Palatilar length, from posterior edge of I^1 alveolus to posterior edge of hard palate; 18-TRL—Toothrow length, from anterior alveolus to posterior surface of M^3 alveolus; *19-LPF—Greatest length of longest palatal foramen; *20-MAW—Greatest maxillary width between labial crown edges of M^1; *21-PWM—Hard palate width at M^1 measured on lingual side of teeth at alveolus; 22-PAC—Hard palate width at point of constriction immediately posterior to M^3; 23-VCW—Vidian canal width at foramen lateral to pterygoid processes; 24-FJW—Least distance between foramina jugulare on posterior edge of bullae; *25-BUL—Greatest bulla length at 45° angle to skull axis; *26-BUW—Greatest bulla width at 45° angle to skull axis.

c. *27-ITC—Incisor to condyle length, from anterior surface of I^1 at alveolus to posteriormost projection of the occipital condyle; *28-LOD—Length of diastema, from posterior base of I^1 alveolus to anterior base of M^1 alveolus; 29-HOR—Height of rostrum, perpendicularly from a point directly behind incisors; 30-IOE—Distance from anterior base of zygomatic plate to anterior edge of ear opening; 31-IZD—Infraorbital–zygomatic plate distance, from dorsal edge of infraorbital foramen to anterior base of zygomatic plate; 32-MPO—Foramen magnum–postorbital bar length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of postorbital bar; 33-MPZ—Foramen magnum–zygomatic arch length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of posterior part of zygomatic arch; 34-FME—Foramen magnum–external auditory meatus length, from lateral edge of foramen magnum (at notch in lateral view) to posterodorsal edge of external auditory meatus.

d. *35-GHS—Greatest height of skull perpendicular to horizontal plane through bullae; 36-BCH—Braincase height, from dorsal surface of sagittal crest to midventral surface of basioccipital between anterior bullae; 37-FMH—Foramen magnum height—widest part of foramen in vertical plane; 38-FMW—Foramen magnum width—widest part of foramen magnum in a horizontal plane; 39-CNW—Greatest occipital condyle width perpendicular to skull axis; 40-WAB—Width at bullae on ear openings perpendicular to skull axis.

e. 41-FIB—I^1 breadth—breadth of principal upper incisor at level of median edge of alveolus.

f. 42-UTR—Crown length of maxillary toothrow, from anterior edge of M^1 at alveolus to posterior edge of M^3 at alveolus; 43-LFM—Length of M^1 along cingulum; 44-LSM—Length of M^2 along cingulum; 45-LTM—Length of M^3 along cingulum.

g. 46-WFM—Greatest cross-sectional crown width of M^1; 47-WSM—Greatest cross-sectional crown width of M^2; 48-WTM—Greatest cross-sectional crown width of M^3.

h. *49-GML—Greatest mandible length, in a straight line, from anterior edge of I_1 alveolus to posterior surface of angular process; *50-MDL—Greatest length of mandible (excluding teeth), from posterior surface of condylar process to anteroventral edge of incisor alveolus; 51-AFA—Angular process–mandibular condyle length, in straight line from ventral edge of angular process to middorsal ridge of mandibular condyle; 52-MRH—Mandible–ramus height, from dorsal edge of coronoid process to ventral edge of angular process; 53-MCA—Mandibular condyle–angular process distance, in straight line from dorsal edge of mandibular condyle to ventral edge of angular process.

i. 54-LMH—Least mandible height, perpendicularly from between posterior M_1 alveolus and anterior M_2 alveolus; 55-MFA—Mandibular foramen–angular process length, from anterior edge of

sample, the two specimens were considered as not representative of the population, and excluded from subsequent analyses.

Homoscedasticity was tested for by Hartley's (1950) F_{max}-test (Sokal and Rohlf, 1981) and a one-way analysis of variance (ANOVA) was used to assess sexual dimorphism. Skewness (g_1), kurtosis (g_2), and normality (Chi-square test) also were tested for (Zar, 1974; Sokal and Rohlf, 1981; Pimentel and Smith, 1986*a*, 1986*b*).

Following Cheverud (1982), character associations were investigated by cluster analysis of principal component (PCA) scores generated from standardized, statistically problem-free characters. Results of three Q-mode principal components analyses (sexes pooled and separate) of correlations among all OTUs were similar so that only the pooled sample is considered below. The first 14 components (explaining 99.98% of the sample variance) were retained and Euclidean distances between each pair of characters subjected to Ward's (1963) hierarchical clustering algorithm to generate phenotypic sets (P-sets). This algorithm produces homogeneous clusters by minimizing the squared positional variation of elements in a cluster independently at each step (Cheverud, 1982).

Selection of characters from within the cluster analysis-generated subclusters depended on six ancillary criteria in the following order of priority: (1) relative weightings of characters in R-mode principal component (Thorpe, 1980; Gould, 1984; James and McCulloch, 1990) and correspondence analyses (Benzecri, 1977; Greenacre, 1984, 1986, 1990) of three known species, *A. chrysophilus, A. granti,* and *A. namaquensis*; (2) consideration of coefficients of variation (CV) incorporating Haldane's (1955) correction (Sokal and Rohlf, 1981); (3) measurement error (ME) (Ostle and Mensing, 1975; Pankakoski et al., 1987; Bailey and Byrnes, 1990; Lougheed et al., 1991) expressed as percentage of total variability due to *within*-individual variation (percent measurement error [% ME]), based on three independent sets of repeated measurements recorded by CTC on separate occasions for *A. namaquensis*; (4) relative ease of measurement; (5) measuring points associated with frequently damaged areas of the skull (with reference to analyses that require complete data sets; Kim, 1975; Klecka, 1975); (6) previous use, particularly in original descriptions.

All analyses were undertaken with BIOΣTAT I and II (Pimentel and Smith, 1986*a*, 1986*b*), UNIVAR (Power, 1970), STATGRAPHICS (STSC Inc., USA) and SimCA (Greenacre, 1990).

Morphological cranial terminology follows Thomas (1905), Hill (1935), Hall (1946), Rosevear (1969), Hebel and Stromberg (1976), DeBlase and Martin (1981), and DeGraaff (1981).

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mandibular foramen to posterior edge of angular process; 56-MAF—Mandibular foramen–articular facet length, from ventral edge of mandibular foramen to midposterodorsal edge of articulating facet; *57-CMH—Coronoid mandible height, from dorsal edge of coronoid process to ventral edge of mandible in line with mandibular foramen.

j. 58-MTL—Mandibular toothrow, from anterior edge of I_1 alveolus to posterior edge of M_3 alveolus; 59-IML—Posterior incisor–M_3 length, in a straight line from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus; 60-MTR—Mandibular toothrow length, from anterior edge of M_1 alveolus to posterior edge of M_3 alveolus; 61-LLM—Length of M_1, along cingulum; 62-LMS—Length of M_2, along cingulum; 63-LMT—Length of M_3, along cingulum.

k. 64-WLM—Greatest cross-sectional crown width of M_1; 65-WMS—Greatest cross-sectional crown width of M_2; 66-WMT—Greatest cross-sectional crown width of M_3.

RESULTS

Univariate Screening of Measurements

Hartley's (1950) F_{max}-test for homogeneity of variances between males and females of *A. namaquensis* indicated significant ($P < 0.05$) heteroscedasticity in four measurements, 19-LPF, 20-MAW, 38-FMW, and 50-MDL (see Figs. 1a–k for measurements; univariate statistics are available on request either from the first author or the Transvaal Museum Library).

Descriptive statistics and results of a one-way analysis of variance indicated a generally low level of sexual dimorphism in *A. namaquensis*, with significant differences in only six of the 66 characters: 4-PAR ($P < 0.05$), 21-PWM ($P < 0.05$), 31-IZD ($P < 0.01$), 51-AFA ($P < 0.01$), 53-MCA ($P < 0.01$), and 57-CMH ($P < 0.01$). This finding justified the pooling of sexes in subsequent analyses.

Results of tests for skewness and kurtosis based on the pooled male and female sample of *A. namaquensis* showed three of the 66 characters to be both skewed and kurtotic: 34-FME (both $P < 0.01$), 38-FMW ($P < 0.05$ and $P < 0.001$, respectively), and 50-MDL (both $P < 0.05$). One character, 65-WMS, was skewed only ($P < 0.05$). Three characters were kurtotic only: 49-GML ($P < 0.01$), 55-MFA ($P < 0.05$), and 62-LMS ($P < 0.001$).

Chi-square tests for normality in the pooled male and female sample of *A. namaquensis* showed that 26 of the 66 characters were non-normally distributed: 2-GLN ($P < 0.01$), 4-PAR ($P < 0.05$), 7-NPO ($P < 0.05$), 9-BBC ($P < 0.05$), 11-IOB ($P < 0.05$), 12-NAS ($P < 0.01$), 16-PPL ($P < 0.05$), 17-PAL ($P < 0.01$), 23-VCW ($P < 0.001$), 26-BUW ($P < 0.05$), 28-LOD ($P < 0.01$), 29-HOR ($P < 0.001$), 31-IZD ($P < 0.05$), 34-FME ($P < 0.05$), 38-FMW ($P < 0.001$), 40-WAB ($P < 0.05$), 41-FIB ($P < 0.001$), 47-WSM ($P < 0.05$), 49-GML ($P < 0.001$), 51-AFA ($P < 0.05$), 55-MFA ($P < 0.05$), 56-MAF ($P < 0.05$), 57-CMH ($P < 0.05$), 61-LLM ($P < 0.01$), 62-LMS ($P < 0.001$), 66-WMT ($P < 0.01$). These results may reflect the instability of this class of tests when sample sizes are small, but draw attention to potentially problematic characters.

After the assumptions tests, the following highly conservative criteria were used to either reject or retain a character: (1) a character was rejected if it differed significantly at the 5% level in more than one test; (2) a character was rejected if it was significant in one or more tests at the 1% level of significance; and (3) a character was retained if test statistics for sexual dimorphism, homoscedasticity, and normality did not differ significantly, or were significant in one of the three tests but only at the 5% level of significance. As a consequence, 15 potentially problematic characters were rejected (2-GLN, *12-NAS, *17-PAL, 23-VCW, *28-LOD, 29-HOR, 34-FME, 38-FMW, 41-FIB, *49-GML, *50-MDL, 55-MFA, 61-LLM, 62-LMS, 66-WMT, which included the five traditional characters indicated by asterisks). Although sample sizes were small for this class of tests, reconsideration of the 15 characters indicated that most were problematic with respect to one or more of the following: (1) unclearly defined recording points, which made the placement of caliper tips difficult and therefore subject to error; (2) high variability between individuals; and (3) association with frequently damaged parts of the skull.

Analysis of Character Associations

In the phenogram derived from Ward's (1963) cluster analysis of the 51 remaining characters, three relatively discrete character groupings are apparent (Fig.

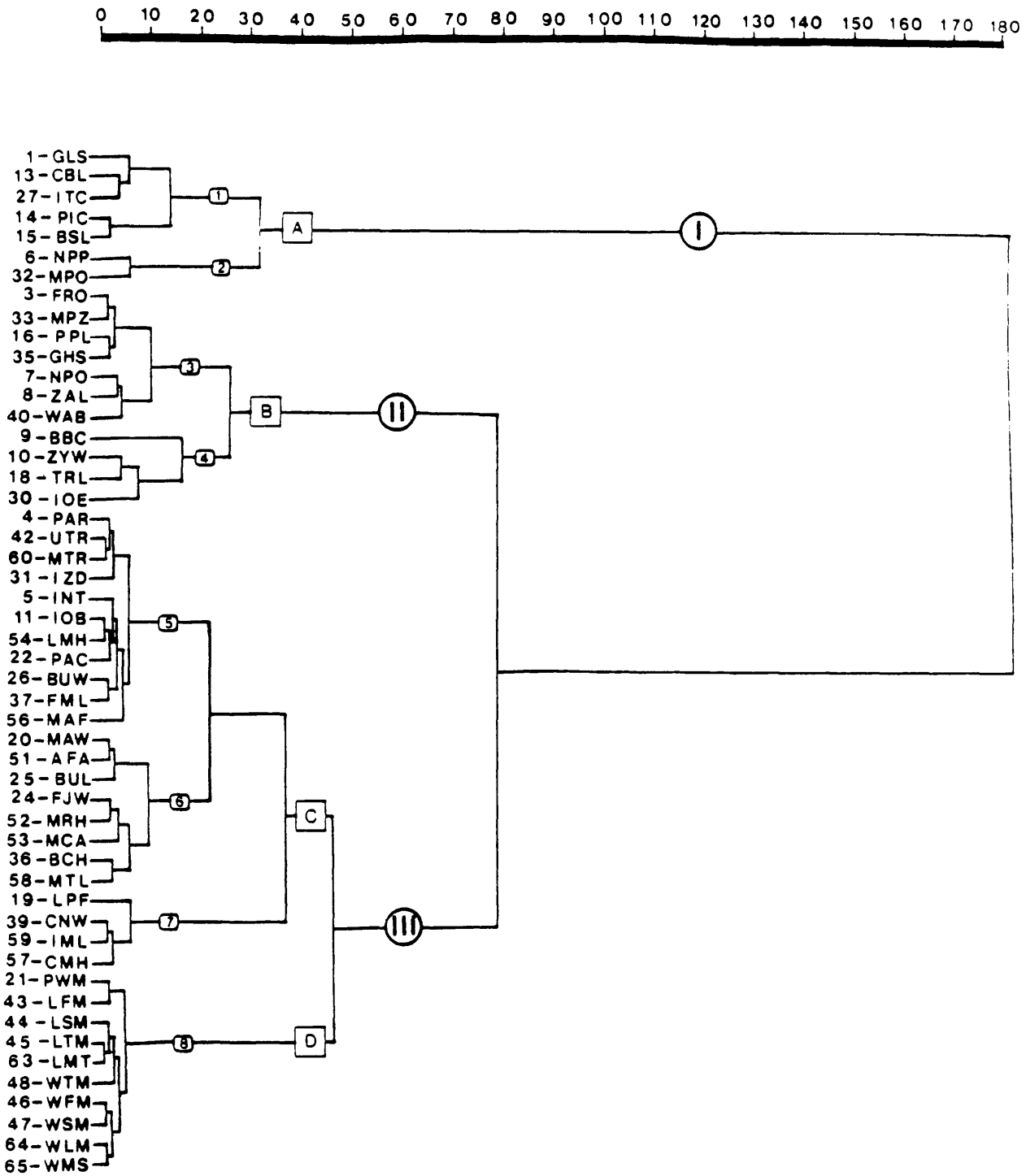

Fig. 2.—Phenogram depicting relationships between cranial measurements in *Aethomys namaquensis*. Clusters formed at the three-, four- and eight-cluster stages are indicated by enclosed letters and numbers. Characters are defined in Fig. 1a–k. The cophenetic correlation coefficient is 0.81.

2). The three major clusters, designated I, II, and III, are summarized in Table 1. Although some characters are apparently not related to the majority of characters within a given subset (indicated by question marks in Table 1), subclusters at both the four- and eight-cluster stages in general form logical subsets. Major cluster I relates mainly to what may be termed a "Mixed" Neurocranial/orofacial functional set (F-set). Characters in this major cluster reflect size-related measurements that span the major functional units of the skull, if not the entire length of the skull. This cluster of characters is further subdivided into a subcluster

comprising "Longitudinal distances" (1) and the other comprising "Oblique distances" (2).

Major cluster II relates mainly to the Neurocranial functional set. Although there are no clear demarcations at the eight-cluster stage in terms of three partially independent submatrices (frontal, parietal, and occipital; Cheverud, 1982) of the Neurocranial functional set, characters in subcluster 3 include measurements of the dorsal side of the cranium and various measurements related to the configuration of the braincase itself, the exception being 8-ZAL which belongs to the orbital submatrix of the Orofacial functional set. Subcluster 4 also includes two measurements related to the configuration of the braincase, as well as upper toothrow length (18-TRL), which belongs to the dental phenotypic set in the Orofacial functional set, and distance from anterior base of zygomatic plate to anterior edge of ear opening (30-IOE) of "Mixed" Orofacial/neurocranial origin.

Major cluster III relates mainly to the Orofacial functional set. Most characters (23 of 33) collectively fit into orbital/oral/masticatory phenotypic set in the Orofacial functional set. In cluster C, subcluster 5 includes measurements of the lateral region of the rostrum, the orbital and postpalatal regions and the toothrows, and one mandibular measurement, while almost all mandibular measurements appear in subclusters 6 and 7. Of interest is that almost all measurements related to the bullae and the foramen magnum also appear in cluster C.

Most prominent at the eight-cluster stage is subcluster 8, which, with the exception of hard palate width at M^1 (21-PWM), are masticatory characters joining up at relatively low distances, suggestive of a tightly integrated dental submatrix.

Selection of Measurements

One of the criteria developed to select measurements from within subclusters relied on ordinations, both principal component (Fig. 3) and correspondence (Fig. 4) analyses, of known taxa (*A. namaquensis, A. chrysophilus,* and *A. granti*). The first two axes from the principal component analysis show *A. granti* to separate from both *A. chrysophilus* and *A. namaquensis* along the second axis, whereas the latter two species are separated from each other along the first axis; there was little or no differentiation between the three taxa along components 3 to 14. Principal component I generally has high and negative loadings on all measurements (Table 1), with generally high percent variances associated with each character's component contribution (in parentheses in Table 1). This suggests that the separation between *A. chrysophilus* and *A. namaquensis* is primarily size-related. The second axis, which is instrumental in separating *A. granti* from both *A. chrysophilus* and *A. namaquensis,* has character loadings and percent variances of different magnitudes (the former with different signs), suggesting shape-related variation. The important characters with relatively high loadings (regardless of sign) on the second axis are: 3-FRO, 4-PAR, 5-INT, 6-NPP, 26-BUW, 31-IZD, 37-FMH, 47-WSM, 53-MCA, 56-MAF, 58-MTL, 59-IML, and 65-WMS.

Two-dimensional symmetric profiles from correspondence analysis (Fig. 4), with individuals from the same taxon enclosed in minimum convex polygons, show clear separation among the three species along both principal axes I (Inertia = 25.27% and $\lambda_1 = 0.0004$) and II (20.59%; $\lambda_2 = 0.0003$). A plot of individual characters, which allows examination of the level of association between rows (in this case, individuals) and columns (characters), is superimposed on the same figure. The scattergram shows that separation of the three taxa can be explained in terms of the corresponding opposition of the following characters in the planes

Table 1.—*Principal component (PCA) (including percent variance contributions, in parentheses) and principal coordinate (CA) (in permills) loadings for the first two axes, coefficients of variation (CV), and percent measurement error (% ME) for each character. Letters and numbers to the left indicate clusters formed at the three-, four- and eight-cluster stages of the cluster analysis. Characters followed by a question mark do not belong in the particular functional (F-set) or phenotypic (P-set) set. Characters in parentheses were important in principal components and correspondence analyses. Underlined characters were selected for descriptive and comparative purposes. Characters preceded by an asterisk were selected for use in subsequent morphometric analyses. Characters are defined in Fig. 1a–k.*

Character/F-set	PCA I	PCA II	CA I	CA II	CV	% ME
I. "MIXED" NEUROCRANIAL/OROFACIAL F-SET						
A. (Interfrontal, -parietal, and -occipital)						
1. "Incisor–condyle distances"						
*1-GLS	−0.957 (91.65)	0.130 (1.69)	11	−3	1.93	0.013
13-CBL	−0.959 (91.93)	0.130 (1.68)	10	−1	2.02	0.014
27-ITC	−0.973 (94.71)	0.049 (0.24)	4	−3	1.05	0.015
14-PIC	−0.974 (94.84)	−0.074 (0.55)	−2	−8	2.02	0.008
15-BSL	−0.968 (93.63)	−0.026 (0.07)	−3	1	2.53	0.014
2. "Oblique distances"						
*(6-NPP)	−0.856 (73.23)	0.294 (8.66)	26	−13	2.18	0.014
32-MPO	−0.857 (97.50)	0.026 (0.07)	−1	5	1.91	0.014
II. NEUROCRANIAL F-SET						
B. (Braincase and dorsal part of skull)						
3. *(3-FRO)	−0.668 (44.60)	0.594 (35.23)	63	50	4.44	0.006
33-MPZ	−0.973 (94.60)	−0.050 (0.25)	−18	22	2.49	0.013
16-PPL	−0.947 (89.61)	0.061 (0.37)	−3	22	3.08	0.012
35-GHS	−0.892 (79.59)	0.239 (5.71)	14	1	2.71	0.010
7-NPO	−0.888 (78.89)	0.154 (2.38)	16	−4	3.32	0.015
8-ZAL ?	−0.941 (88.47)	0.085 (0.73)	9	−9	2.14	0.012
40-WAB	−0.941 (88.64)	0.033 (0.11)	2	1	2.55	0.014
4. 9-BBC	−0.952 (90.60)	−0.010 (0.01)	−3	−1	2.91	0.008
10-ZYW	−0.977 (95.43)	−0.070 (0.49)	−12	8	2.34	0.015
18-TRL ?	−0.971 (94.25)	−0.134 (1.81)	−9	−6	2.11	0.014
30-IOE ?	−0.959 (91.91)	0.177 (3.13)	7	22	1.82	0.014
III. OROFACIAL F-SET						
C. (Oral and orbital cavities, exoccipital bullae)						
5. (4-PAR ?)	−0.797 (63.53)	−0.301 (9.06)	−40	−1	7.34	0.008
42-UTR	−0.905 (81.89)	−0.040 (0.16)	−15	3	3.71	0.013
60-MTR	−0.827 (68.39)	0.061 (0.37)	3	−10	2.43	0.006
(31-IZD)	−0.615 (37.85)	0.500 (24.97)	49	19	6.65	0.014
(5-INT ?)	−0.345 (11.92)	−0.714 (51.00)	−62	−64	9.55	0.007
11-IOB	−0.898 (80.70)	−0.142 (2.02)	−12	0	2.81	0.013
54-LMH	−0.904 (81.74)	0.106 (1.12)	−2	19	5.44	0.009
22-PAC	−0.720 (51.90)	0.105 (1.11)	10	−15	5.55	0.015
*(26-BUW ?)	−0.865 (74.76)	−0.250 (6.25)	−35	8	3.73	0.001
*(37-FMH ?)	−0.436 (19.03)	0.437 (19.07)	36	−30	4.90	0.012
*(56-MAF)	−0.421 (17.73)	−0.662 (43.77)	−48	−55	5.60	0.013
6. 20-MAW	−0.943 (88.21)	−0.047 (0.22)	−1	−12	2.98	0.013
*(51-AFA)	−0.934 (87.22)	−0.147 (2.17)	−63	75	5.52	0.010
25-BUL ?	−0.855 (73.17)	0.003 (0.01)	−7	9	4.64	0.012
24-FJW ?	−0.718 (51.58)	−0.050 (0.25)	4	−23	5.45	0.008
52-MRH	−0.781 (60.93)	0.113 (1.28)	5	14	5.87	0.011
(53-MCA)	−0.850 (72.32)	−0.254 (6.43)	−21	−5	4.36	0.006
36-BCH ?	−0.900 (80.91)	0.035 (0.12)	3	−8	2.93	0.013
(58-MTL)	−0.866 (75.06)	−0.374 (14.00)	−35	−7	3.89	0.008
7. 19-LPF ?	−0.722 (52.10)	0.152 (2.31)	18	−13	5.00	0.013

Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa

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Prior to a systematic revision of African rock rats (genus *Aethomys* Thomas) in southern Africa, the nature and extent of non-geographic variation due to sex and age in two samples each of *A. chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) were examined using both univariate and multivariate statistical procedures. Results of Model I two-way analysis of variance, % sum of squares and a series of multivariate procedures were congruent and showed a lack of sexual dimorphism in all samples examined, but marked variation between seven age categories based on the degree of tooth wear on the maxillary tooth row. When univariate and multivariate results were considered together, pooling of sexes as well as individuals of tooth-wear classes IV, V and VI for subsequent recording and analysis was justified. Very few tooth-wear class VII individuals were available and their exclusion was largely arbitrary. Few measurements showed sex-age interaction. The largest per cent contribution to the total variance was due to *error*. In general, variance partitioning indicated that if comparisons are to be made, caution needs to be exercised on the type of characters, number of factor levels and methodology used.

Voor 'n sistematiese hersiening van Afrika-kliprotte in Suider-Afrika (genus *Aethomys* Thomas) onderneem is, is die aard en omvang van nie-geografiese variasie toeskryfbaar aan geslag en ouderdom by twee monsters elk van *A. chrysophilus* (De Winton, 1897) en *A. namaquensis* (A. Smith, 1834) deur middel van beide eenveranderlike en meerveranderlike statistiese prosedures ondersoek. Resultate van Model I variansie-analise, % som van kwadrate en 'n reeks meerveranderlike prosedures het ooreengestem, en het die gebrek aan geslagsdimorfisme by al die monsters wat ondersoek is uitgewys, asook dat beide grootte- en vormvariasie tussen sewe ouderdomskategorieë voorkom wat op tandslytasie van die maksilêre tandry gegrond is. By die vertolking van beide eenveranderlike en meerveranderlike resultate in 'n breër konteks, was die samevoeging van geslagte sowel as individue van ouderdomsklasse IV, V en VI vir daaropvolgende optekening en analises geregverdig. Baie min individue van ouderdomsklas VII was beskikbaar en hul uitsluiting was arbitrêr. Min karakters het geslag-ouderdom interaksie getoon. Die hoogste persentasie bydrae tot die totale variansie was aan *fout* toe te skryf. Oor die algemeen het variansieverdeling getoon dat indien geldige vergelykings getref wil word, die tipe karakters, aantal faktore en metodologie wat toegepas word, omsigtig benader moet word.

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As part of a systematic revision of African rock rats of the genus *Aethomys* Thomas, the present study examines non-geographic variation in two species, *A. chrysophilus* (De Winton, 1897) (*sensu lato*, see below) and *A. namaquensis* (A. Smith, 1834), from four localities in southern Africa. The assessment of non-geographic variation is of particular importance in morphometric studies of geographic variation, and in the morphometric delineation of taxa (Thorpe 1976; Van der Straeten & Dieterlen 1992). Decisions regarding the components of variation to consider for statistical evaluation are of fundamental importance (Straney 1978). While some authors (e.g. Leamy & Bader 1968; Mayr 1969) consider non-geographic variation to be composed of genetic and non-genetic components, most workers view it as a function of differences in, for example, sex, age, season, cohort, and individuals within populations (Thorpe 1976; Straney 1978; Leamy 1983; Webster & Jones 1985; Dippenaar & Rautenbach 1986; Van der Straeten & Dieterlen 1992).

Non-geographic variation has, in the past, been assessed by a variety of univariate statistics and procedures such as the coefficient of variation (Genoways & Jones 1972), multiple *t*-tests (Straney 1978) and two-way analysis of variance (Robbins 1973), but their application has been criticized (Straney 1978; Leamy 1983). Two novel methods that rely either on the partitioning of variance components (Straney 1978) or the per cent contribution of the sum of squares (% *SSQ*) of each source of variation to the total *SSQ* (Leamy 1983), have been proposed more recently. The former method is computationally involved, but yields results that are generally comparable to the latter, which can be computed directly from a conventional two-way ANOVA table. Willig, Owen & Colbert (1986) expressed reservations about the univariate approach, arguing that significance tests for equality of means for each variable independently present the dilemma of having to consider the number of characters that must exhibit significance before overall significance is declared. They recommend the use of multivariate analysis of variance for evaluating overall group differences since it utilizes rather than ignores correlations among variables.

Some workers have attempted to adjust for sexually dimorphic and age-influenced characters (e.g. Cheverud

1982) by regression analyses of transformed characters (Thorpe 1976; Reist 1985) or by principal component analysis (Leamy & Thorpe 1984; Somers 1986). Such adjustments, however, require adequate samples from throughout the study area (Thorpe 1976; Dippenaar & Rautenbach 1986), a requirement hardly ever met by small mammal data sets. As an alternative to the sampling problem, other workers have attempted to pool geographic samples, but this is a dubious practice (Dippenaar & Rautenbach 1986).

This study evaluates non-geographic variation at the level of sexual dimorphism and age variation using the *SSQ* approach (and for comparison Model I two-way analysis of variance) and a series of multivariate procedures, with the objective of establishing criteria for the selection of specimens to consider for measurement recording and analysis in subsequent studies.

Material and Methods

The present study is based on samples of *A. namaquensis* from Boekenhoutkloof, Transvaal (25°31'S, 28°30'E; 25 males, 23 females), and Farm Narap, 28 km SSE of Springbok, Cape Province (29°53'S, 17°45'E; 15 males, 17 females), and *A. chrysophilus* from Farm Al-te-ver, 1 km SSE of Maasstroom, Transvaal (22°46'S, 28°28'E; 9 males, 13 females), and Olifantspoort Farm 328, 19,2 km S of Rustenburg, Transvaal (25°46'S, 27°16'E; 13 males, 8 females), South Africa. Specimens examined are listed in Appendix 1. The homogeneity of the samples of *A. chrysophilus (sensu lato)*, which is apparently composed of two sibling species (Gordon & Rautenbach 1980; Gordon & Watson 1986; Visser & Robinson 1986; 1987; Breed, Cox, Leigh & Hawkins 1988), was confirmed by preliminary analyses of cytogenetically known specimens.

Examination of the maxillary tooth-row, with reference to Verheyen & Bracke (1966), Morris (1972), Perrin (1982) and Dippenaar & Rautenbach (1986), led to the recognition of seven tooth-wear classes (Figure 1).

A basic set of 11 linear cranial measurements (5 skull, 3 mandible and 3 dental) was recorded by one of us (CTC) to the nearest 0,05 mm using Mitutoyo digital callipers and DataQ (D.L. Schultz) for direct data input into Quattro (Borland International Inc.). In addition, four descriptive characters (breadth of brain-case, least breadth of interorbital constriction, greatest bulla length and greatest height of skull) were taken. The measurements are defined and illustrated in Figure 2.

After data screening, which resulted in the exclusion of one outlier from Boekenhoutkloof (TM 30432), the four samples were independently subjected to Model I two-way analysis of variance (ANOVA). From the ANOVA tables, estimates of % *SSQ* of four sources of variation (sex, age, sex-age interaction and error (= residual)) were computed by the division of the *SSQ* associated with each source of variation by the total *SSQ*. Analysis also included *a posteriori* Student-Newman-Keuls (SNK) tests for maximally non-significant subsets ($P < 0,05$; Sokal & Rohlf 1969; 1981). Haldane's (1955) correction was used in the computation of coefficients of variation (CV).

All univariate analyses were based on the 11 basic and four descriptive characters. The material available was characterized by small sample sizes, particularly of tooth-wear classes I and VII, so that not all (and in some cases not consecutive) tooth-wear classes were represented. This led to univariate analyses based on either *three* (Narap: tooth-wear classes II, III and VI; Olifantspoort: II, III and IV, and Al-te-ver: III, IV and V) or *four* (Boekenhoutkloof: III, IV, V, VI) tooth-wear classes.

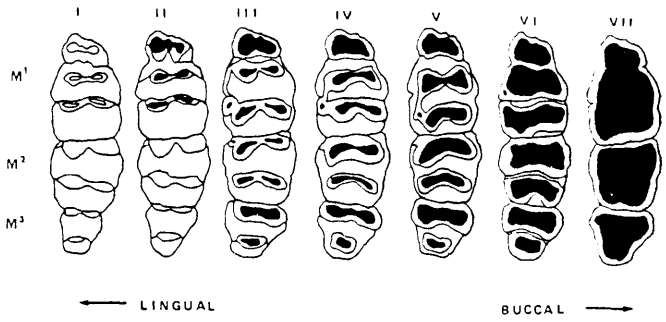

Figure 1 Right maxillary tooth-row of *Aethomys namaquensis* illustrating seven tooth-wear classes. Tooth-wear class I: cheek-teeth not fully erupted, M^3 conspicuously below eruption level of M^1 and M^2 (TM 27832); tooth-wear class II: cheek-teeth fully erupted, M^3 somewhat smaller, cusps conspicuous but with no or very little wear (TM 27842); tooth-wear class III: all cheek-teeth in apposition, minimal cusp wear (TM 31258); tooth-wear class IV: cusp wear obvious, but not extensive (TM 30433); tooth-wear class V: cusp wear extensive, but most cusps still distinguishable (TM 30432); tooth-wear class VI: cusp wear extensive, but traces of cusps not completely lost (TM 30438); tooth-wear class VII: tooth-wear severe, occlusal surfaces worn smooth with no traces of cusps (TM 30428).

Variation due to sex and age was also examined by principal component (PCA) (Thorpe 1980; Gould 1984; James & McCulloch 1990) and cluster analyses (Sneath & Sokal 1973) based on standardized characters. PCA was computed from a correlation matrix while unweighted pair-group arithmetic average cluster analysis (UPGMA) was based on average taxonomic distances (Rohlf 1986; Sneath & Sokal 1973). Unlike univariate analysis, PCA and UPGMA allowed the analysis of a wider range of tooth-wear classes that also included the poorly represented tooth-wear classes I and VII. Canonical variates analyses (CVA) (Pimentel & Smith 1986b) of tooth-wear classes (excluding those with too few observations) were also undertaken. Multivariate analysis of variance (MANOVA) was used to test for significant differences between group centroids. All multivariate analyses were based on the basic set of 11 cranial measurements.

Statistical analyses were undertaken with BIOΣTAT I and II (Pimentel & Smith 1986a; 1986b) and NTSYS-pc (Rohlf 1986).

Univariate assessment

Univariate results for the four samples analysed were broadly congruent for the 11 basic and four descriptive measurements and, therefore, predominantly the results for *A. namaquensis* from Boekenhoutkloof and *A. chrysophilus* from Olifantspoort are presented. The former sample was the largest individual sample and also included the widest range of consecutive tooth-wear classes (III – VI), whereas

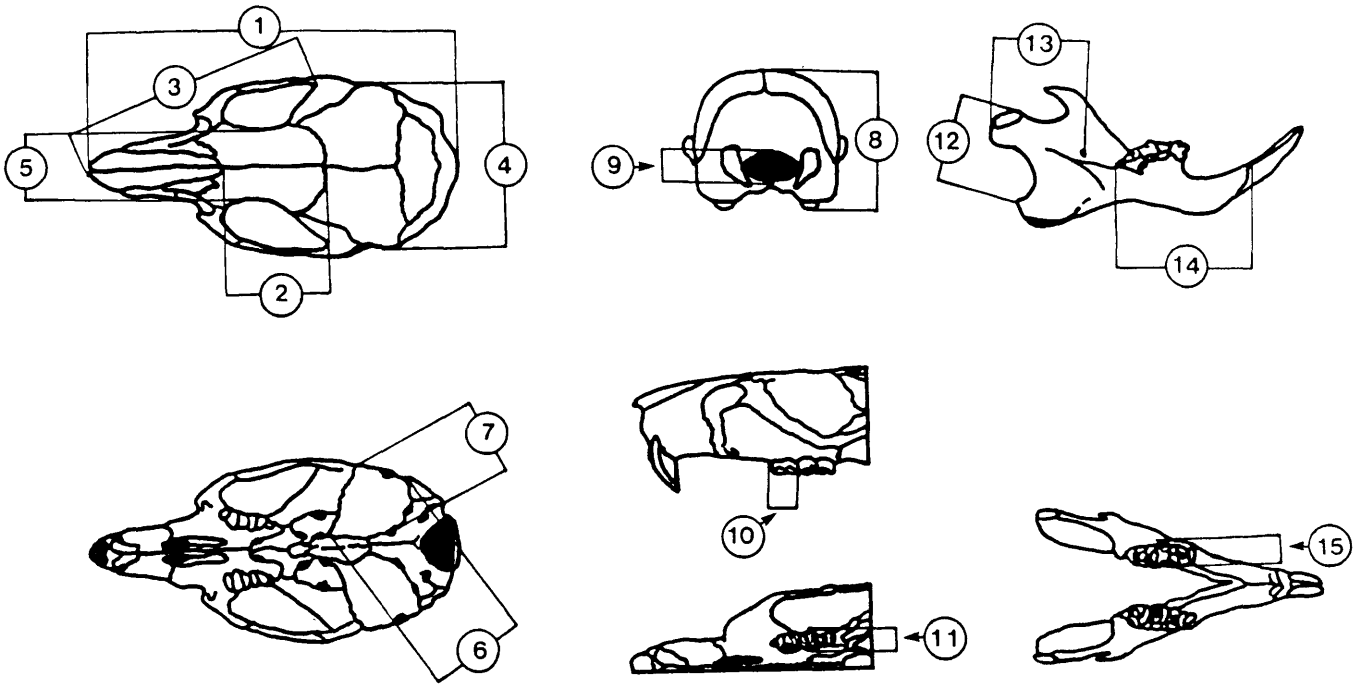

Figure 2 Abbreviations and reference points of skull measurements: 1. GLS: greatest length of skull, from anterior edge of nasals to posterior margins of the skull, along longitudinal axis; 2. FRO: greatest length of frontals; 3. NPP: distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch; 4. BBC: breadth of brain-case – width at dorsal root of squamosals; 5. IOB: least breadth of interorbital constriction – least distance dorsally between orbits; 6. BUL: greatest bulla length at 45° angle to skull axis; 7. BUW: greatest bulla width at 45° angle to skull axis; 8. GHS: greatest height of skull perpendicular to horizontal plane through bullae; 9. FMH: foramen magnum height – widest part of foramen in vertical plane; 10. LFM: length of M^1 along cingulum; 11. WSM: greatest cross-sectional crown width of M^2; 12. AFA: angular process – mandibular condyle length, in straight line from ventral edge of angular process to mid-dorsal ridge of mandibular condyle; 13. MAF: mandibular foramen – mandibular condyle length, from ventral edge of mandibular foramen to mid-posterodorsal edge of mandibular condyle; 14. IML: posterior incisor – M_3 length, in a straight line from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus; 15. WMS: greatest cross-sectional crown width of M_2.

the latter sample included tooth-wear classes II – IV. *F*-values from Model I two-way ANOVA and % *SSQ* for the two samples (Table 1) show that more measurements have significant ($P < 0,01$) *F*-values for age than for sex in both samples. Similarly, age generally gave higher % *SSQ* values (range % *SSQ* = 1,57–45,56 for *A. namaquensis*; 7,41–83,59 for *A. chrysophilus*) than sex (0,00–9,99 for *A. namaquensis*; 0,05–40,00 for *A. chrysophilus*). Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (NPP), angular process – mandibular condyle length (AFA) and mandibular foramen – mandibular condyle length (MAF) showed significant age variation in both samples. The importance of these measurements was also apparent in the *A. namaquensis* sample from Narap and the *A. chrysophilus* sample from Al-te-ver. Generally, these measurements also contributed relatively more to the total variance due to age.

Only one measurement, least breadth of interorbital constriction (IOB) in the Boekenhoutkloof sample, and two measurements, greatest height of skull (GHS) and greatest cross-sectional crown width of M^2 (WSM) in the *A. chrysophilus* sample from Olifantspoort, showed significant sexual dimorphism. These measurements also showed the largest per cent contribution to the total variance due to sex (Table 1).

Only one measurement from each sample (distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (NPP) and greatest cross-sectional crown width of M_2 (WMS)) showed significant interaction between age and sex. The negligible contribution due to sex-age interaction was also shown by the relatively small % *SSQ* means in both samples (mean % *SSQ* = 6,39 in *A. namaquensis;* 10,67 in *A. chrysophilus*). In both samples, the largest per cent contribution to the total variance was due to error (mean % *SSQ* = 79,54; range % *SSQ* = 44,11–92,00 in *A. namaquensis*; 45,45, 14,07–73,65 in *A. chrysophilus*).

Despite the congruence of univariate results among the four samples, % *SSQ* contributions generally showed a much higher degree of congruence between 'three tooth-wear class'-group analyses in samples of *A. chrysophilus* from Olifantspoort (mean % *SSQ* contributions for sex = 7,48; age = 36,40; interaction = 10,67; error = 45,45) and Al-te-ver (sex = 8,75; age = 32,76; interaction = 13,43; error = 45,06), and *A. namaquensis* from Farm Narap (sex = 2,70; age 43,42; interaction = 7,23; error = 46,65) than the 'four tooth-wear class'-group analysis in the *A. namaquensis* sample from Boekenhoutkloof (sex = 1,71; age = 12,36; interaction = 6,39; error = 79,54). In addition, except for the error component, the 'three tooth-wear class'-group analyses showed higher % *SSQ* values than the 'four tooth-wear class'-group analysis.

In the SNK tests, a large number of measurements in all samples showed no significant differences between tooth-wear classes analysed: Boekenhoutkloof (10; classes III –

Table 1 *F*-values and % Sum of Squares (% *SSQ*) of each source of variation from a Model I two-way ANOVA of (a) four tooth-wear classes (III – VI) of male and female *Aethomys namaquensis* from Boekenhoutkloof and (b) three tooth-wear classes (II – IV) of male and female *Aethomys chrysophilus* from Olifantspoort. Statistical significance: * = $P < 0,05$; ** = $P < 0,01$; *** = $P < 0,001$. Measurements are defined in Figure 2

Measure-ment	*F*-value			% *SSQ*			
	Sex(S)	Age(A)	S × A	Sex(S)	Age(A)	S × A	Error
(a) Boekenhoutkloof							
GLS	1,26	0,56	0,31	3,00	4,04	2,23	90,73
FRO	0,96	0,75	0,13	2,31	5,40	0,94	91,35
NPP	0,49	13,08***	2,80*	0,57	45,56	9,76	44,11
BBC	0,00	0,66	1,52	0,00	4,43	10,26	85,31
IOB	6,07*	2,87*	2,71	9,99	14,14	13,41	62,46
BUL	0,52	0,40	1,13	1,21	2,79	7,86	88,14
BUW	0,25	1,07	0,20	0,59	7,59	1,42	90,40
GHS	0,05	1,15	1,02	0,11	7,76	6,86	85,27
FMH	0,90	0,22	0,92	2,10	1,57	6,54	89,79
LFM	0,45	1,59	1,94	0,94	9,74	11,85	77,47
WSM	0,07	0,68	1,84	0,00	4,71	12,04	83,25
AFA	0,03	5,04**	0,80	0,05	27,22	4,33	68,40
MAF	0,15	4,21**	0,34	0,30	24,39	1,96	73,35
IML	2,02	3,50*	0,99	3,78	19,61	5,55	71,06
WMS	0,24	0,88	0,06	0,80	6,40	0,80	92,00
Mean				1,71	12,36	6,39	79,54
(b) Olifantspoort							
GLS	0,52	11,21**	0,43	1,44	62,62	2,41	33,53
FRO	0,14	6,03*	1,24	0,53	45,21	9,32	44,94
NPP	0,95	5,04*	2,88	3,23	36,60	19,52	40,65
BBC	0,21	6,17**	0,49	0,82	48,31	3,86	47,01
IOB	2,22	2,00	0,45	11,57	21,00	4,71	62,72
BUL	1,48	35,66***	0,26	1,73	83,59	0,61	14,07
BUW	0,06	1,40	0,72	0,33	17,18	8,84	73,65
GHS	7,95**	1,37	1,92	29,97	10,33	14,49	45,21
FMH	2,30	1,82	0,05	12,79	20,23	0,57	66,41
LFM	1,00	1,57	2,13	4,68	15,21	21,05	59,06
WSM	11,26**	1,76	0,69	40,00	12,31	4,62	43,07
AFA	0,02	18,35***	2,11	0,05	69,33	7,96	22,66
MAF	0,50	12,96***	0,57	1,25	65,53	2,90	30,32
IML	0,02	3,05	0,71	0,11	31,18	7,32	61,39
WMS	1,38	1,07	8,50**	3,70	7,41	51,85	37,04
Mean				7,48	36,40	10,67	45,45

VI), Narap (6; II, III, VI), Olifantspoort (6; II – IV), and Al-te-ver (8; III – V), the highest numbers being recorded in the first and last samples which included only tooth-wear class III and older individuals. (Representative results for the four samples are presented in Table 2.) Conversely, in the samples that included tooth-wear class II and older individuals (Olifantspoort and Narap), most measurements (9 of 15 in each sample) showed significant variation between tooth-wear classes. In instances in which significance was recorded, either all tooth-wear classes differed significantly in a few measurements (Olifantspoort and Narap three measurements, Al-te-ver four), or were variously grouped into non-significant subsets: in *A. namaquensis* from 1) Boekenhoutkloof (which represented the widest range of consecutive tooth-wear classes) classes V and VI were mostly grouped in non-significant subsets, and sometimes IV and VI, and III and IV; and from 2) Narap, tooth-wear classes II and III were consistently grouped into the same non-significant subset, with both differing significantly from tooth-wear class VI. In *A. chrysophilus* from both Olifantspoort and Al-te-ver, tooth-wear classes III and IV were consistently grouped in the same non-significant subset. The pattern that emerges from the SNK analyses is that the inclusion of tooth-wear class II individuals with tooth-wear class III and older individuals leads to an increase in the number of measurements showing significant age variation, and that analysis of only tooth-wear class III and older specimens also show a large proportion of measurements with significant differences; tooth-wear class III individuals either fall in the same non-significant subset as those of either tooth-wear class II or tooth-wear class IV. The SNK results therefore suggest that individuals of tooth-wear classes II and III should be excluded from the final data set, and that an argument could even be made for the exclusion of tooth-wear class IV individuals.

Descriptive statistics of all samples show a direct relationship between character magnitude and age, as exemplified by samples from Boekenhoutkloof and Olifantspoort (Table 3).

Multivariate assessment

The multivariate assessment focuses on the relatively large samples of *A. namaquensis* from Boekenhoutkloof and Narap, with reference to the samples of *A. chrysophilus* from Olifantspoort and Al-te-ver. The Narap sample is of particular interest in the multivariate analyses since it includes individuals representing all seven tooth-wear classes. Because of insufficient cell sizes for a combined CVA of males, females and tooth-wear classes, the data were first subjected to principal component and cluster analyses.

The first two principal components from analyses of the Boekenhoutkloof and Narap samples are shown in Figure 3. Both scattergrams reflect age rather than sex as the major source of variation in both samples. Tooth-wear class III individuals from Boekenhoutkloof tend to separate from those of tooth-wear classes IV – VII at an oblique angle. There is no clear separation between tooth-wear classes IV – VII along either axis. In the PCA of the Narap sample, there is clear separation between tooth-wear classes IV – VII and tooth-wear classes I – III, especially along the first axis. An examination of the remaining axes (3 – 14) for both samples did not reveal any separation of tooth-wear classes. In both samples, the first principal component generally had high and negative loadings on most measurements (Table 4), with generally high per cent variances associated with each measurement's component contribution (in parentheses in Table 4). The important measurements with relatively high loadings on the first axis (35,4% of the total variance) in the Boekenhoutkloof sample (Table 4a) are: greatest length of skull (GLS), distance from anterior edge of nasals to

Table 2 Multiple range SNK tests of tooth-wear classes in *Aethomys namaquensis* from (a) Boekenhoutkloof (tooth-wear classes III – VI) and (b) Narap (II, III and VI), and *Aethomys chrysophilus* from (c) Olifantspoort (II – IV) and (d) Al-te-ver (III – V). Non-significant subsets ($P < 0,05$) are indicated by vertical lines; NS = no significant differences; AS = all means significantly different; *n* = sample size; *SD* = standard deviation. Measurements are defined in Figure 2

Measurement	Tooth-wear class (*n*)	*SD*	Mean		Measurement	Tooth-wear class (*n*)	*SD*	Mean	
(a) Boekenhoutkloof									
GLS	III(5)	0,66	28,78		NPP	III(5)	0,56	20,34	
	VI(11)	0,80	29,57	NS		V(17)	0,66	21,48	
	IV(17)	0,45	29,87			V(13)	0,65	22,01	
	V(13)	0,68	30,28			VI(11)	0,68	22,27	
AFA	III(5)	0,48	5,58		IML	III(5)	0,29	8,56	
	IV(17)	0,33	6,07			V(13)	0,21	8,81	
	V(13)	0,34	6,13			IV(17)	0,30	8,78	
	VI(11)	0,18	6,23			VI(11)	0,29	9,01	
(b) Narap									
GLS	II(4)	0,93	27,19		BBC	II(4)	0,26	12,39	
	III(11)	0,69	28,36	AS		III(11)	0,30	12,73	
	VI(5)	0,93	31,80			VI(5)	0,35	13,25	
BUW	II(4)	0,10	4,73		WMS	II(4)	0,05	1,67	
	III(11)	0,19	4,89			III(11)	0,04	1,67	NS
	VI(5)	0,16	5,16			VI(5)	0,04	1,69	
(c) Olifantspoort									
FRO	II(4)	0,38	9,71		BUL	II(4)	0,07	6,71	
	III(10)	0,48	10,31			III(10)	0,14	7,24	AS
	IV(4)	0,18	10,84			IV(4)	0,03	7,41	
FMH	II(4)	0,14	4,59		MAF	II(4)	0,17	3,89	
	III(10)	0,16	4,64	NS		III(10)	0,31	4,69	
	IV(4)	0,19	4,80			IV(4)	0,23	4,81	
(d) Al-te-ver									
BBC	III(8)	0,30	14,03		IOB	III(8)	0,14	4,83	
	IV(7)	0,61	14,31			IV(7)	0,32	4,88	NS
	V(5)	0,46	14,89			V(5)	0,22	5,08	
LFM	IV(7)	0,12	2,80		AFA	III(8)	0,24	6,44	
	III(8)	0,11	2,83			IV(7)	0,30	6,87	AS
	V(5)	0,09	2,98			V(5)	0,45	7,51	

anterior edge of posterior part of zygomatic arch (NPP), angular process – mandibular condyle length (AFA), mandibular foramen – mandibular condyle length (MAF) and posterior incisor – M_3 length (IML). In addition to these measurements, greatest length of frontals (FRO), greatest bulla width (BUW) and greatest cross-sectional crown width of M_2 (WMS) are important on the first axis (64,9%) of the Narap sample (Table 4b). Important measurements on the second axis (16,1%) of the Boekenhoutkloof sample are: greatest length of frontals (FRO), greatest cross-sectional crown widths of M^2 (WSM) and M_2 (WMS) (Table 4a). In the Narap sample, foramen magnum height (FMH) was important on the second axis (11,5%) (Table 4b). Collectively, most of these measurements also feature either as significantly different or contribute highly towards the total % *SSQ*s in the univariate statistics. Results for *A. chrysophilus* from Olifantspoort reflected those for the Boekenhoutkloof sample in that there was some overlap between tooth-wear classes III and IV, but in the *A. chrysophilus* sample from Al-te-ver, the overlap was greater. However, both these samples included tooth-wear class II individuals (and in the case of Al-te-ver a single tooth-wear class I individual) and their positions in the PCA graphs closely reflected the pattern observed in the Narap sample. In all PCA graphs there was little, if any, indication of sexual dimorphism.

Because of the relatively low level of variation explained by successive components (e.g. first three axes for *A. namaquensis:* Boekenhoutkloof (62,3%), Narap (86,3%); *A. chrysophilus:* Al-te-ver (84,5%), Olifantspoort (76,4%)), the samples were also examined by cluster analyses. In the Boekenhoutkloof sample, the phenogram showed no discrete

Table 3 Standard statistics of 15 measurements of males and females in (a) five tooth-wear classes of *Aethomys namaquensis* from Boekenhoutkloof and (b) three tooth-wear classes of *Aethomys chrysophilus* from Olifantspoort. $\bar{Y}$ = arithmetic mean; $2SE$ = two standard errors; CV = coefficient of variation; n = sample size. Measurements are defined in Figure 2

(a) Boekenhoutkloof

Sex	Tooth-wear class (n)		Measurement							
			GLS	FRO	NPP	BBC	IOB	BUL	BUW	GHS
Males	III (3)	$\bar{Y}$	28,44	9,35	20,08	12,72	4,36	6,47	4,78	9,60
		$2SE$	0,26	0,16	0,26	0,17	0,04	0,21	0,21	0,22
		CV	1,61	2,90	2,27	2,27	1,53	5,62	7,55	3,91
	IV (8)	$\bar{Y}$	29,40	9,49	21,12	13,19	4,67	6,57	4,87	9,78
		$2SE$	0,31	0,22	0,29	0,16	0,10	0,13	0,09	0,05
		CV	3,02	6,44	3,86	3,40	5,86	5,51	5,30	1,44
	V (7)	$\bar{Y}$	30,40	9,68	22,05	12,92	4,49	6,57	4,85	9,75
		$2SE$	0,24	0,12	0,23	0,12	0,03	0,07	0,10	0,10
		CV	2,26	3,59	2,96	2,71	1,78	3,20	5,75	2,82
	VI (6)	$\bar{Y}$	31,37	9,79	22,54	13,03	4,75	6,80	4,92	9,78
		$2SE$	0,10	0,13	0,10	0,16	0,04	0,08	0,04	0,08
		CV	0,77	3,36	1,05	2,96	2,29	2,78	1,81	1,99
Females	III (2)	$\bar{Y}$	29,28	9,36	20,73	13,32	4,52	6,55	4,68	9,75
		$2SE$	0,49	0,03	0,42	0,08	0,05	0,06	0,01	0,06
		CV	2,37	0,46	2,83	0,80	1,56	1,30	0,30	0,80
	IV (9)	$\bar{Y}$	30,29	9,42	21,80	13,01	4,44	6,62	4,92	9,86
		$2SE$	0,14	0,20	0,08	0,12	0,05	0,08	0,04	0,08
		CV	1,40	6,29	1,06	2,77	3,09	3,64	2,45	2,56
	V (5)	$\bar{Y}$	30,28	9,40	21,94	12,92	4,48	6,51	4,88	9,54
		$2SE$	0,32	0,29	0,32	0,12	0,08	0,15	0,06	0,08
		CV	2,35	6,78	3,21	2,04	4,07	5,04	2,66	1,98
	VI (5)	$\bar{Y}$	30,54	9,60	21,95	13,00	4,53	6,47	4,94	9,68
		$2SE$	0,48	0,33	0,41	0,10	0,07	0,16	0,04	0,18
		CV	3,53	7,67	4,17	1,72	3,49	5,41	1,77	4,22
	VII (2)	$\bar{Y}$	31,17	9,46	22,53	13,01	4,98	6,91	4,90	9,86
		$2SE$	0,30	0,21	0,20	0,50	0,16	0,02	0,13	0,06
		CV	1,34	3,07	1,22	5,44	4,41	0,41	3,75	0,86

Sex	Tooth-wear class (n)		FMH	LFM	WSM	AFA	MAF	IML	WMS
Males	III (3)	$\bar{Y}$	4,56	2,23	1,82	5,44	4,25	8,41	1,68
		$2SE$	0,13	0,16	0,03	0,10	0,06	0,15	0,03
		CV	4,94	12,63	2,77	3,11	2,27	3,14	3,09
	IV (8)	$\bar{Y}$	4,53	2,49	1,76	6,12	4,51	8,72	1,67
		$2SE$	0,08	0,03	0,02	0,09	0,08	0,08	0,02
		CV	4,78	3,53	2,87	4,30	4,82	2,50	3,42
	V (7)	$\bar{Y}$	4,46	2,56	1,80	6,10	4,59	8,81	1,65
		$2SE$	0,06	0,08	0,04	0,11	0,12	0,13	0,01
		CV	3,93	8,78	5,24	5,26	7,16	4,06	2,40
	VI (6)	$\bar{Y}$	4,49	2,53	1,74	6,33	4,71	8,99	1,68
		$2SE$	0,08	0,03	0,02	0,08	0,07	0,12	0,03
		CV	4,55	2,82	3,00	3,05	3,42	3,13	4,82
Females	III (2)	$\bar{Y}$	4,34	2,47	1,80	5,78	4,11	8,79	1,69
		$2SE$	0,03	0,08	0,04	0,60	0,35	0,12	0,04
		CV	0,98	4,58	2,76	14,68	11,89	1,93	2,94
	IV (9)	$\bar{Y}$	4,45	2,48	1,79	6,02	4,61	8,90	1,66
		$2SE$	0,61	0,07	0,02	0,13	0,07	0,06	0,02
		CV	4,12	8,02	3,50	6,53	4,53	2,05	3,16
	V (5)	$\bar{Y}$	4,55	2,38	1,74	6,17	4,54	8,75	1,63
		$2SE$	0,08	0,06	0,02	0,18	0,18	0,08	0,01
		CV	4,08	5,30	3,10	6,67	8,94	2,16	1,76

Table 3 Continued

(a) Boekenhoutkloof

Sex	Tooth-wear class (*n*)		Measurement FMH	LFM	WSM	AFA	MAF	IML	WMS
	VI (5)	$\bar{Y}$	4,38	2,48	1,79	6,17	4,79	9,03	1,67
		2*SE*	0,07	0,02	0,02	0,05	0,19	0,15	0,03
		CV	3,79	2,07	2,55	1,83	8,75	3,72	3,74
	VII (2)	$\bar{Y}$	4,55	2,62	1,83	6,71	5,02	8,99	1,67
		2*SE*	0,16	0,21	0,01	0,25	0,11	0,08	0,09
		CV	4,82	11,34	0,77	5,27	3,10	1,18	7,22

(b) Olifantspoort

			GLS	FRO	NPP	BBC	IOB	BUL	BUW	GHS
Males	II (2)	$\bar{Y}$	31,00	9,72	22,12	13,15	4,70	6,74	5,15	11,22
		2*SE*	0,95	0,13	0,09	0,24	0,07	0,07	0,11	0,11
		CV	4,31	1,88	1,43	2,53	1,96	1,47	2,89	1,32
	III (7)	$\bar{Y}$	33,68	10,42	23,54	13,88	4,90	7,25	5,45	11,33
		2*SE*	0,43	0,15	0,39	0,09	0,09	0,06	0,05	0,12
		CV	3,39	3,68	4,38	1,78	4,64	2,25	2,32	2,74
	IV (2)	$\bar{Y}$	33,87	10,58	23,73	13,99	4,84	7,41	5,38	10,98
		2*SE*	0,46	0,36	0,31	0,44	0,01	0,02	0,01	0,20
		CV	1,92	4,81	1,82	4,40	0,15	0,38	0,13	2,51
Females	II (2)	$\bar{Y}$	30,97	9,67	21,56	13,32	4,55	6,69	5,33	10,64
		2*SE*	0,08	0,45	0,03	0,32	0,07	0,03	0,06	0,29
		CV	0,37	6,51	0,16	3,40	2,02	0,63	1,46	3,79
	III (3)	$\bar{Y}$	33,14	10,06	23,30	13,69	4,71	7,20	5,36	10,86
		2*SE*	0,41	0,40	0,42	0,22	0,15	0,04	0,22	0,15
		CV	2,14	6,84	3,15	2,83	5,45	1,06	7,00	2,31
	IV (2)	$\bar{Y}$	34,36	11,10	24,42	14,06	4,86	7,41	5,40	11,07
		2*SE*	0,92	0,08	0,92	0,10	0,06	0,03	0,15	0,04
		CV	3,77	1,02	5,30	1,01	1,75	0,57	3,93	0,51

			FMH	LFM	WSM	AFA	MAF	IML	WMS
Males	II (2)	$\bar{Y}$	4,74	2,67	1,85	5,55	4,03	9,13	1,80
		2*SE*	0,20	0,02	0,04	0,22	0,05	0,27	0,03
		CV	5,97	0,80	3,06	5,61	1,58	4,18	2,36
	III (7)	$\bar{Y}$	4,60	2,59	1,85	6,60	4,67	9,86	1,68
		2*SE*	0,06	0,03	0,02	0,12	0,13	0,15	0,02
		CV	3,67	3,49	2,68	4,81	7,62	4,10	2,62
	IV (2)	$\bar{Y}$	4,53	2,67	1,91	6,62	4,81	9,82	1,75
		2*SE*	0,10	0,04	0,05	0,22	0,19	0,38	0,01
		CV	2,97	2,12	3,70	4,60	5,59	5,40	0,41
Females	II (2)	$\bar{Y}$	4,86	2,45	1,75	5,82	3,76	9,52	1,65
		2*SE*	0,09	0,03	0,04	0,19	0,08	0,02	0,04
		CV	2,62	1,73	2,84	4,50	3,01	0,22	3,43
	III (3)	$\bar{Y}$	4,72	2,59	1,80	6,37	4,74	9,86	1,72
		2*SE*	0,08	0,08	0,01	0,11	0,12	0,10	0,02
		CV	2,85	5,14	0,85	3,03	4,19	1,71	2,42
	IV (2)	$\bar{Y}$	4,65	2,67	1,81	7,00	4,81	9,64	1,68
		2*SE*	0,12	0,08	0,03	0,06	0,21	0,29	0,01
		CV	3,50	3,98	2,34	1,11	6,17	4,18	0,42

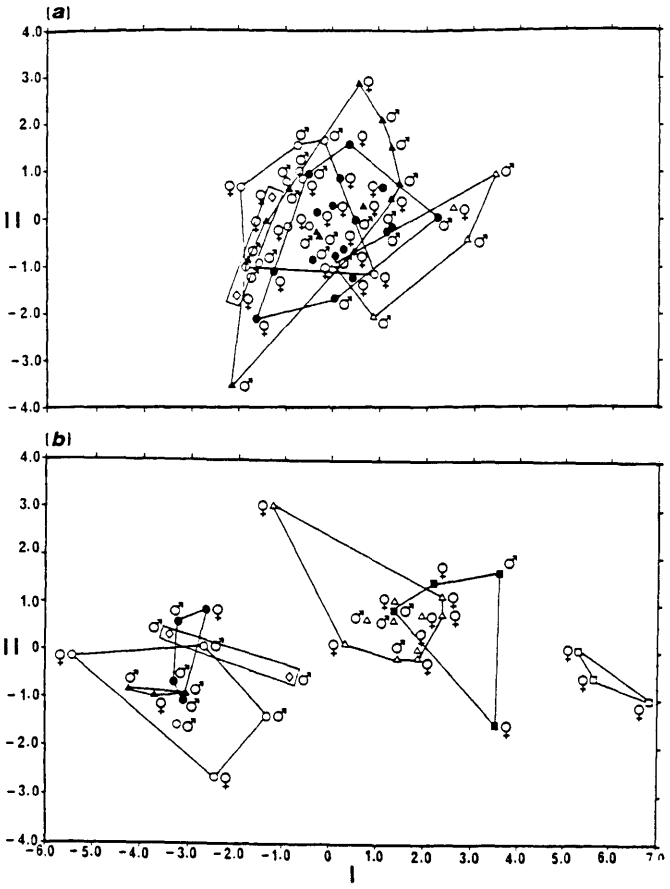

Figure 3 The first two axes from principal component analyses of *Aethomys namaquensis* from (a) Boekenhoutkloof and (b) Narap. The sex and tooth-wear classes [I (□); II (■); III (△); IV (●); V (▲); VI (○); VII (◇)] of all individuals are indicated. Minimum convex polygons enclose individuals of each tooth-wear class.

Table 4 Loadings of measurements on the first two components from principal component analyses of *Aethomys namaquensis* from (a) Boekenhoutkloof and (b) Narap. The per cent variance contribution is given in parentheses. Measurements are defined in Figure 2

(a) Boekenhoutkloof		
	Principal component axes	
Measurement	I	II
GLS	–0,882 (77,75)	0,298 (8,86)
FRO	–0,139 (1,94)	0,563 (31,67)
NPP	–0,890 (79,18)	0,355 (12,63)
BUW	–0,379 (14,35)	–0,269 (7,26)
FMH	0,067 (0,44)	–0,493 (24,31)
LFM	–0,493 (24,26)	–0,288 (8,27)
WSM	0,188 (3,53)	–0,654 (42,72)
AFA	–0,749 (56,04)	–0,011 (0,01)
MAF	–0,814 (66,31)	0,145 (2,11)
IML	–0,768 (59,05)	–0,295 (8,70)
WMS	–0,256 (6,54)	–0,551 (30,38)
% trace:	Axis I = 35,4%;	Axis II = 16,1%
(b) Narap		
GLS	–0,977 (95,42)	–0,058 (0,33)
FRO	–0,772 (59,57)	–0,281 (7,91)
NPP	–0,974 (94,81)	–0,071 (0,51)
BUW	–0,909 (82,65)	0,120 (1,43)
FMH	–0,188 (3,52)	0,781 (60,94)
LFM	–0,618 (38,21)	0,088 (0,78)
WSM	–0,642 (41,27)	0,368 (13,56)
AFA	–0,939 (88,15)	–0,208 (4,31)
MAF	–0,903 (81,61)	–0,206 (4,23)
IML	–0,887 (78,71)	–0,218 (4,77)
WMS	–0,708 (50,15)	0,525 (27,52)
% trace:	Axis I = 64,9%;	Axis II = 11,5%

groupings of either sexes or tooth-wear classes, except for three individuals of tooth-wear class III and one individual each of tooth-wear classes IV and V which seem to form a subcluster in accordance with PCA results (Figure 4a). In the Narap sample, two major clusters were apparent: one comprising all individuals of tooth-wear classes I – III, with a subcluster comprising all individuals of tooth-wear class I (except for one individual of tooth-wear class II), and the other comprising all individuals of tooth-wear classes IV – VII (except for one individual of tooth-wear class III) (Figure 4b). Both samples showed no discrete groupings of sexes. Similar patterns were evident in the *A. chrysophilus* samples from Olifantspoort and Al-te-ver (cophenetic correlation coefficients = 0,69 and 0,83, respectively) in that tooth-wear class I and II individuals formed distinct subclusters, but as in the PCA results, the distinction between tooth-wear classes III and IV – VII were not as marked as in the Narap sample.

MANOVA of males and females, for which specimens of the tooth-wear classes indicated below had to be pooled to increase cell sizes, indicated no significant sexual differences in any of the samples (Boekenhoutkloof, classes IV – VI: $F = 0,63$; $P > 0,05$; Olifantspoort IV – VI: $F = 0,97$; $P > 0,05$; Narap IV – VI: $F = 0,66$; $P > 0,05$; Al-te-ver IV and V: $F = 1,69$; $P > 0,05$). These results, together with the univariate results, led us to pool the sexes for discriminan analyses of tooth-wear classes.

Results of discriminant analyses are exemplified by a 'four tooth-wear class (III – VI) analysis of the relatively large individual sample from Boekenhoutkloof (Figure 5). I produced a 71,0% overall *a posteriori* classification, and in the scattergram of canonical variates I and II, four of five tooth-wear class III individuals tend to plot apart from individuals of tooth-wear classes IV – VI along the firs canonical variate (54,9% variance). Individuals of tooth wear class III are maximally separated from individuals o tooth-wear class V along the second axis (38,9%). Excep for the greatest length of frontals (FRO), greatest bull width (BUW) and greatest cross-sectional crown width o M_2 (WMS), which loaded highly in the PCA's first axis o the Narap sample, all measurements that load highly in th PCA of the Boekenhoutkloof and Narap samples also loa highly in the CVA (Table 5). The posterior incisor – M length (IML), together with greatest cross-sectional crow

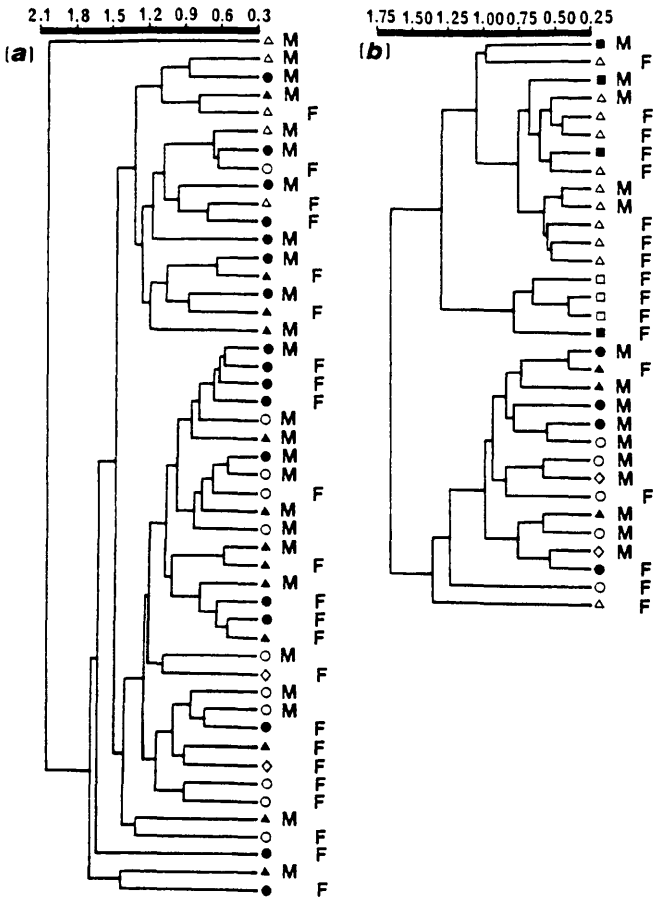

Figure 4 Distance phenograms from UPGMA cluster analyses of *Aethomymys namaquensis* from (a) Boekenhoutkloof and (b) Narap. The sex (M = males; F = females) and tooth-wear classes [I (□); II (■); III (△); IV (●); V (▲); VI (○); VII (◇)] of all individuals are indicated. Cophenetic correlation coefficients = 0,66 and 0,73, respectively.

Table 5 Loadings of measurements on the first two axes from a canonical variates analysis of *Aethomys namaquensis* from Boekenhoutkloof. The per cent variance contribution is given in parentheses. Measurements are defined in Figure 2

	Canonical variates axes	
Measurement	I	II
GLS	0,787 (1,97)	–0,180 (85,13)
FRO	0,211 (59,29)	–0,010 (39,69)
NPP	0,824 (3,47)	0,023 (95,77)
BUW	0,218 (12,48)	–0,208 (1,87)
FMH	–0,048 (9,72)	0,078 (89,16)
LFM	0,281 (13,75)	0,039 (76,91)
WSM	–0,264 (84,81)	–0,069 (14,57)
AFA	0,549 (87,06)	–0,084 (10,39)
MAF	0,497 (2,63)	–0,152 (80,11)
IML	0,409 (1,48)	–0,365 (95,80)
WMS	–0,113 (93,16)	–0,315 (0,23)
% trace:	Axis I = 54,9%;	Axis II = 38,9%

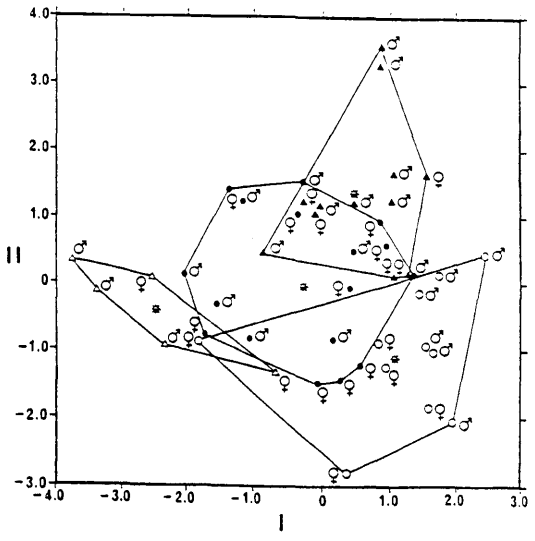

Figure 5 The first two axes from a canonical variates analysis of tooth-wear classes in *Aethomys namaquensis* from Boekenhoutkloof. The tooth-wear classes [III (△); IV (●); V (▲); VI (○)] and sex of all individuals are indicated. Minimum convex polygons enclose individuals of each tooth-wear class. Group centroids are denoted by (✲).

width of M_2 (WMS) are the important measurements on the second canonical variate. MANOVA indicated significant differences between the group centroids of the four tooth-wear classes (F = 1,91; P = 0,01). Except for the Olifantspoort sample that indicated no significant differences between group centroids of the analysed tooth-wear classes (II – IV) (F = 1,76; P = 0,18), the remaining two samples indicated significant differences between group centroids (Narap: F = 2,56; P = 0,01, tooth-wear classes II – IV and VI; Al-te-ver: F = 2.53; P = 0,04, tooth-wear classes III – V).

Discussion and Conclusions

The primary objective of this study was to examine age- and sex-related morphometric variation in *Aethomys* with a view to ascertaining 1) whether the sexes should be treated separately or together, and 2) which subset(s) of tooth-wear classes represent specimens that have reached adult dimensions and therefore are eligible for inclusion in subsequent morphometric studies of the genus.

Both univariate and multivariate results clearly showed a lack of sexual dimorphism in the two species studied. However, with regard to age variation, the univariate SNK tests did not provide unequivocal results as to which tooth-wear classes to consider in subsequent studies. This is resolved when the univariate and multivariate results are interpreted together, showing that there is an increase in dimensions as one progresses from tooth-wear class I to at least IV. The SNK results suggest that individuals of tooth-wear classes II and III should be excluded from the final data set, and that an argument could even be made for the exclusion of tooth-wear class IV individuals. In the principal component analyses both tooth-wear classes I and II, and in two instances, tooth-wear class III as well, plotted well apart from the other tooth-wear classes. In two other instances, there was some

to extensive overlap between tooth-wear class III and some of the higher tooth-wear classes.

With regard to only tooth-wear classes IV – VII, in some of the SNK tests the first tooth-wear class appeared in the same non-significant subset as tooth-wear class III. However, in the principal component analyses, and in the discriminant analysis of the largest sample from Boekenhoutkloof, specimens of tooth-wear classes IV – VII plot close together.

If the tooth-wear classes are visualized as demarcating sections of variable and unknown length on a hypothetical growth curve, then individuals of tooth-wear class III seem to fall at a point on the curve just before it begins to stabilize, and our results provide justification for pooling tooth-wear classes IV – VI for subsequent recording and analyses in the systematic revision of the genus. Tooth-wear class VII individuals are excluded from the final data set because, 1) very few individuals of this tooth-wear class are encountered in collections, 2) extensive tooth-wear often renders measuring points on the teeth uncertain, and 3) there seems to be a higher incidence of age-related deformations in very old rodents in general (N.J. Dippenaar, pers. obs.).

The univariate % *SSQ* analysis of the four samples indicated that most measurements have relatively small sex and age components but a large error component. Similar patterns were observed in six of the seven species examined by Straney (1978). Apart from providing a realistic baseline for the subsequent interpretation of geographic and taxonomic trends and the assessment of relative contributions of population factors, variance partitioning is also useful in determining the relative taxonomic value of characters (Straney 1978; Leamy 1983). If the aim of the study is to compare individuals across populations (as is usually the case) and eliminating or adjusting for extraneous sources of variation due to factors such as age or sex, then characters showing the smallest variances for these factors, but with large error variances, are the most appropriate. Characters utilized in this study were selected on the basis of the morphological integration concept (Olson & Miller 1958; Moss & Young 1960; Moore 1981; Cheverud 1982; Taylor 1990; Taylor & Meester 1993). In the % *SSQ* analyses, their generally large error components place confidence in the systematic usefulness of the selected characters.

Based on the 'four tooth-wear class' analyses, overall % *SSQ* values due to sex and age in the current study are generally lower than those reported both by Leamy (1983), who used a similar approach, and Straney (1978), who used the variance components approach. Leamy (1983) suggested that such differences may be a function of the type of characters used. Unlike this study, these two studies included appendicular characters. It has been demonstrated that appendicular characters exhibit higher growth rates than axial characters (Leamy & Bradley 1982). Although his conclusion was restricted to the age component, Leamy (1983) suggested the existence of a direct proportionality between characters with higher growth rates and larger variance components. The % *SSQ* contributions in this study are comparable to those found in *Cynictis penicillata* (Taylor & Meester 1993), a study restricted to axial characters.

In spite of relatively small sample sizes in the present study, a useful picture emerges from parallel univariate and multivariate analyses. The approach adopted here is useful as a preliminary step to any morphometric study, and the differentiation of some tooth-wear classes cautions against either arbitrary decisions or superficial evaluations of non-geographic variation.

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References

BORLAND INTERNATIONAL INC. 1987. Quattro. Scotts Valley, California.

BREED, W.G., COX, G.A., LEIGH, C.M. & HAWKINS, P. 1988. Sperm head structure of a murid rodent from southern Africa: The red veld rat *Aethomys chrysophilus*. *Gamete Res.* 19: 191–202.

CHEVERUD, J.M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. *Evolution* 36: 499–516.

DIPPENAAR, N.J. & RAUTENBACH, I.L. 1986. Morphometrics and karyology of the Southern African species of the genus *Acomys*. I. Geoffroy Saint-Hilaire, 1838 (Rodentia: Muridae). *Ann. Transv. Mus.* 34: 129–183.

GENOWAYS, H.H. & JONES, Jr., J.K. 1972. Variation and ecology in a local population of the vesper mouse (*Nyctomys sumichrasti*). *Occas. Papers Mus., Texas Tech Univ.* 3: 1–22.

GORDON, D.H. & RAUTENBACH, I.L. 1980. Species complexes in medically important rodents: chromosome studies of *Aethomys, Tatera* and *Saccostomus* (Rodentia: Muridae, Cricetidae). *S. Afr. J. Sci.* 76: 559–561.

GORDON, D.H. & WATSON, C.R.B. 1986. Identification of cryptic species of rodents (*Mastomys, Aethomys, Saccostomus*) in the Kruger National Park. *S. Afr. J. Zool.* 21: 95–99.

GOULD, S.J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: a way of studying non-adaptation. *Syst. Zool.* 33: 217–237.

HALDANE, J.B.S. 1955. The measurement of variation. *Evolution* 9: 484.

JAMES, F.C. & McCULLOCH, C.E. 1990. Multivariate Analysis in Ecology and Systematics: Panacea or Pandora's Box? *Annu. Rev. Ecol. Syst.* 21: 129–166.

MORRIS, P. 1972. A review of mammalian age determination methods. *Mamm. Rev.* 2: 69–104.
MOSS, M.L. & YOUNG, R.W. 1960. Functional approach to craniology. *Amer. J. Phys. Anthr.* 18: 281–292.
OLSON, E.C. & MILLER, R.L. 1958. Morphological Integration. Univ. Chicago Press, Chicago.
PERRIN, M.R. 1982. Prey specificity of the barn owl, *Tyto alba*, in the Great Fish River Valley of the Eastern Cape Province. *S. Afr. J. Wildl. Res.* 12: 14–25.
PIMENTEL, R.A. & SMITH, J.D. 1986a. BIOΣTAT I. A Tutorial Manual. Sigma Soft, Placentia, California.
PIMENTEL, R.A. & SMITH, J.D. 1986b. BIOΣTAT II. A Tutorial Manual. 2nd edn. Sigma Soft, Placentia, California.
REIST, J.D. 1985. An empirical evaluation of several univariate methods that adjust for size variation in morphometric data. *Can. J. Zool.* 63: 1429–1439.
ROBBINS, C.B. 1973. Non-geographic variation in *Taterillus gracilis* (Thomas) (Rodentia: Cricetidae). *J. Mamm.* 54: 222–238.
ROHLF, F.J. 1986. NTSYS-pc. Numerical taxonomy system for the IBM PC microcomputers (and compatibles). Applied Biostatistics Inc., New York.
SCHULTZ, D.L. DataQ. Aitken, South Carolina.
SNEATH, P.H.A. & SOKAL, R.R. 1973. Numerical Taxonomy. W.H. Freeman & Co., San Francisco.
SOKAL, R.R. ROHLF, F.J. 1969. Biometry. 1st edn. W.H. Freeman & Co., San Francisco.
SOKAL, R.R. & ROHLF, F.J. 1981. Biometry. 2nd edn. W.H. Freeman & Co., New York.
SOMERS, K.M. 1986. Multivariate allometry and removal of size with principal components analysis. *Syst. Zool.* 35: 359–368.
STRANEY, D.O. 1978. Variance partitioning and non-geographic variation. *J. Mamm.* 59: 1–11.
TAYLOR, P.J. 1990. Infraspecific systematics of the yellow mongoose. Unpub. Ph.D. thesis, University of Natal, Durban, South Africa.
TAYLOR, P.J. & MEESTER, J. 1993. Morphometric variation in the yellow mongoose, *Cynictis penicillata* (Cuvier, 1829) 91–101.
VISSER, D.S. & ROBINSON, T.J. 1986. Cytosystematics of the South African *Aethomys* (Rodentia: Muridae). *S. Afr. J. Zool.* 21: 264–268.
VISSER, D.S. & ROBINSON, T.J. 1987. Systematic implications of spermatozoan and bacular morphology for the South African *Aethomys*. *Mammalia* 51: 447–454.
WEBSTER, W.D. & JONES, Jr., J.K. 1985. Non-geographic variation, reproduction and demography in the Texas kangaroo rat, *Dipodomys elator* (Rodentia: Heteromyidae). *Texas J. Sci.* 37: 51–61.
WILLIG, M.R., OWEN, R.D. & COLBERT, R.L. 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. *Syst. Zool.* 35: 195–203.

Appendix 1 *Aethomys* specimens examined (all in Transvaal Museum, Pretoria)

Aethomys chrysophilus: Farm Al-te-ver, 1 km SSE Maasstroom, Transvaal, South Africa (22°46'S, 28°28'E): 9 males (TM 26474, 26486, 26541, 26557, 26559, 26562, 26612, 26667, 26684); 13 females (TM 26492, 26510, 26514, 26540, 26561, 26565, 26574–75, 26583, 26585, 26611, 26668–69). Olifantspoort Farm 328, 19,2 km S Rustenburg, Transvaal, South Africa (25°46'S, 27°16'E): 13 males (TM 19614–16, 19618, 19632, 19648–49, 19651, 19656, 19672–75); 8 females (TM 19633–34, 19640–42, 19650, 19670–71).

Aethomys namaquensis: Boekenhoutkloof, Transvaal, South Africa (25°31'S, 28°30'E): 25 males (TM 30430, 30432–34, 30439–42, 30959–60, 30967, 30969, 30971–73, 30975–77, 30979, 30984, 31259, 31262–64, 31267); 23 females (TM 30428, 30431, 30435–38, 30458, 30961–64, 30966, 30968, 30970, 30974, 30980–83, 31258, 31261. 31265–66). Farm Narap, 28 km SSE Springbok, Cape Province, South Africa (29°53'S, 17°45'E): 15 males (TM 27795, 27801, 27811–13, 27836–38, 27841, 27843, 27878, 27906, 27945, 27948, 28006); 17 females (TM 27794, 27798–27800, 27808–09, 27831–34, 27842, 27877, 27907–08, 27946–47, 28007).

Table 1.—*Continued.*

Character F-set	PCA I	PCA II	CA I	CA II	CV	% ME
39-CNW ?	−0.886 (78.43)	−0.190 (3.60)	36	−14	3.82	0.013
*(59-IML)	−0.905 (81.93)	−0.314 (9.86)	−21	−12	3.01	0.011
57-CMH	−0.887 (78.74)	−0.133 (1.78)	−12	−1	3.56	0.006
D. (Dental)						
8. 21-PWM ?	−0.787 (61.91)	−0.099 (0.98)	−16	24	7.98	0.013
*(43-LFM)	−0.896 (75.48)	−0.126 (1.58)	−37	19	6.12	0.013
(44-LSM)	−0.736 (54.13)	−0.048 (0.23)	−62	94	12.99	0.005
(45-LTM)	−0.665 (44.27)	−0.202 (4.08)	−22	−15	7.10	0.007
63-LMT	−0.644 (41.45)	−0.129 (1.67)	−12	−3	6.98	0.005
48-WTM	−0.670 (44.87)	−0.044 (0.19)	−7	−9	6.52	0.013
(46-WFM)	−0.478 (22.90)	0.184 (3.38)	18	−42	5.19	0.014
*(47-WSM)	−0.475 (22.59)	0.339 (11.48)	24	−31	5.78	0.011
64-WLM	−0.704 (49.51)	0.208 (4.34)	12	−22	5.39	0.010
*(65-WMS)	−0.501 (25.11)	0.580 (33.68)	39	−16	4.62	0.012

% Trace: 68.4% (PC Axis I); 6.4% (PC Axis II).
Inertia: 25.3% (λ_1 = 0.0004) (CA Axis I); 20.6% (λ_2 = 0.0003) (CA Axis II).

of separation: 3-FRO, 4-PAR, 5-INT, 6-NPP, 26-BUW, 31-IZD, 37-FMH, 43-LFM, 44-LSM, 45-LTM, 46-WFM, 47-WSM, 51-AFA, 53-MCA, 56-MAF, 58-MTL, 59-IML, and 65-WMS. Characters important in the separation of the three taxa are shown by their relatively high magnitudes in the first and second principal coordinates (Table 1), which for ease of interpretation are presented in permills (thousandths).

The results of the principal component and correspondence analyses correspond closely in that the 13 shape-related characters generated by the second principal component were also generated by the two principal coordinates in correspondence analysis, in which the following characters also featured prominently: 43-LFM, 44-LSM, 45-LTM, 46-WFM, and 51-AFA.

Table 1, in which characters are arranged according to cluster analysis-derived phenotypic sets, summarizes the data used in character selection, including coefficients of variation, percent measurement error values, character loadings on the first and second axes of principal component, and correspondence analyses. Other criteria invoked were relative ease of measurement, potential for non-missing values, previous use, and cranial configuration. Based on the premise that most subclusters represent distinct submatrices of either the Neurocranial or the Orofacial functional unit, one or more characters were selected as representative of the configuration of a particular unit. More than one character was often selected, particularly if the characters were consistently shown to be relevant by both the principal component and correspondence analyses, and these included obviously misplaced characters.

The following is the rationale behind the selection of characters within a subcluster (with subcluster numbering corresponding to the eight-cluster stage in Fig. 2 and Table 1):

Subcluster 1.—The notion that shape is more heritable than size (Humphries et al., 1981) has been criticized by Leamy and Thorpe (1984). Size is certainly important in infraspecific studies. For example, in a principal component analysis of different populations of *C. penicillata,* Taylor (1990) and Taylor and Meester (1993) found that virtually all the significant variation was in the first size-related

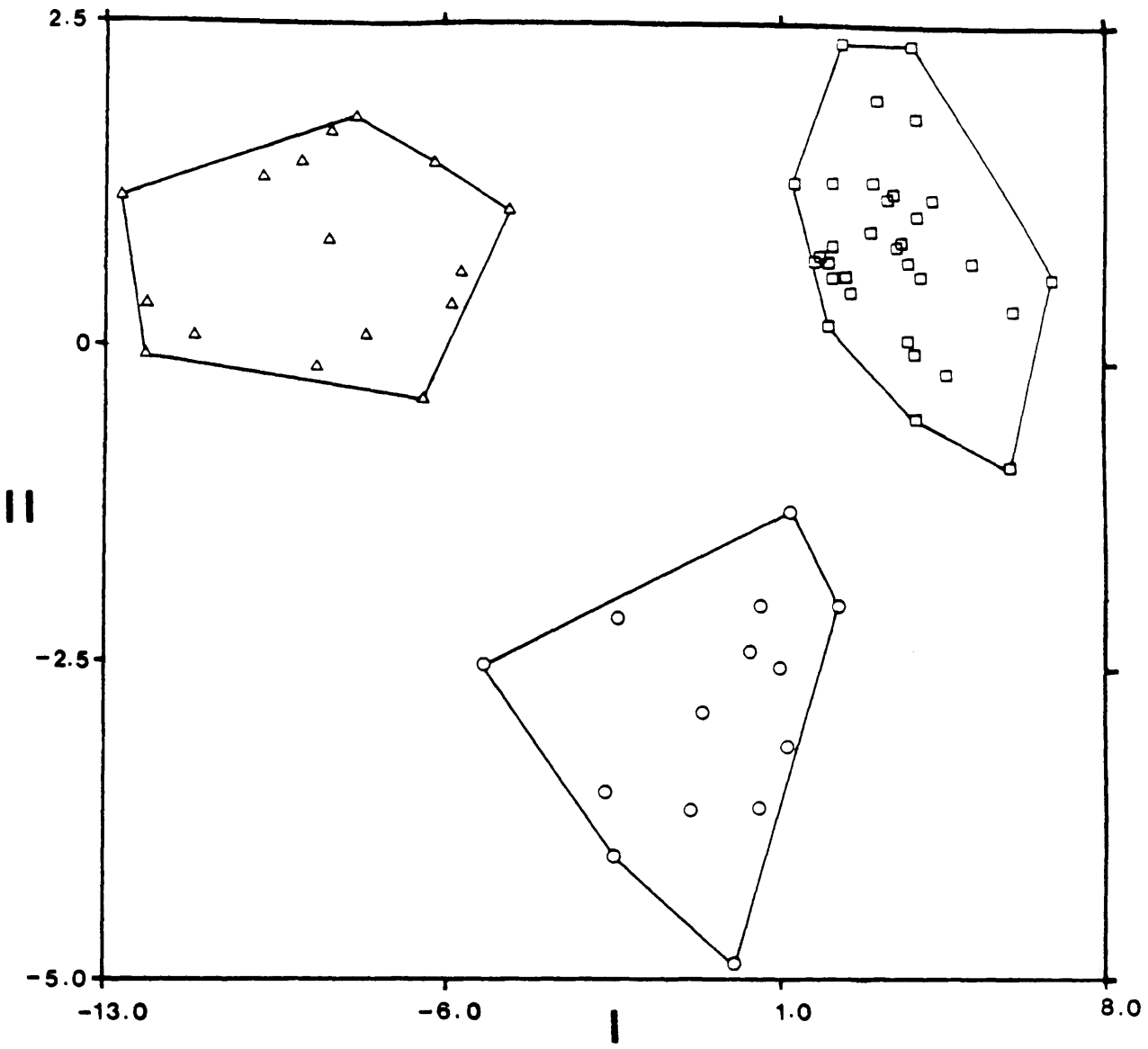

Fig. 3.—First two components from principal components analysis of individuals of *Aethomys chrysophilus*, open triangle; *A. granti*, open circle; and *A. namaquensis*, open square. Polygons include individuals from the same taxon.

axis. Consequently one character from subcluster 1, comprising size-related characters, was selected for inclusion in the basic data suite. High loadings on the first principal component axis (>0.90) indicate that all characters in this major cluster qualify as good predictors of general size. In addition, all the characters have low coefficients of variation and percent measurement error values. However, the greatest length of the skull (1-GLS) was selected because of its relatively high loading on the first principal coordinate in correspondence analysis, relative ease of measurement, and the fact that it features prominently in rodent systematics. This character, in combination with cranial width and depth measurements (see below), also captures descriptive information relating to gross cranial configuration.

Subcluster 2.—Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (6-NPP) was selected because it featured prominently in the first principal coordinate in correspondence analysis. It has relatively low coefficient of variation and percent measurement error values and being an "oblique" measurement, may capture different configurations of the skull.

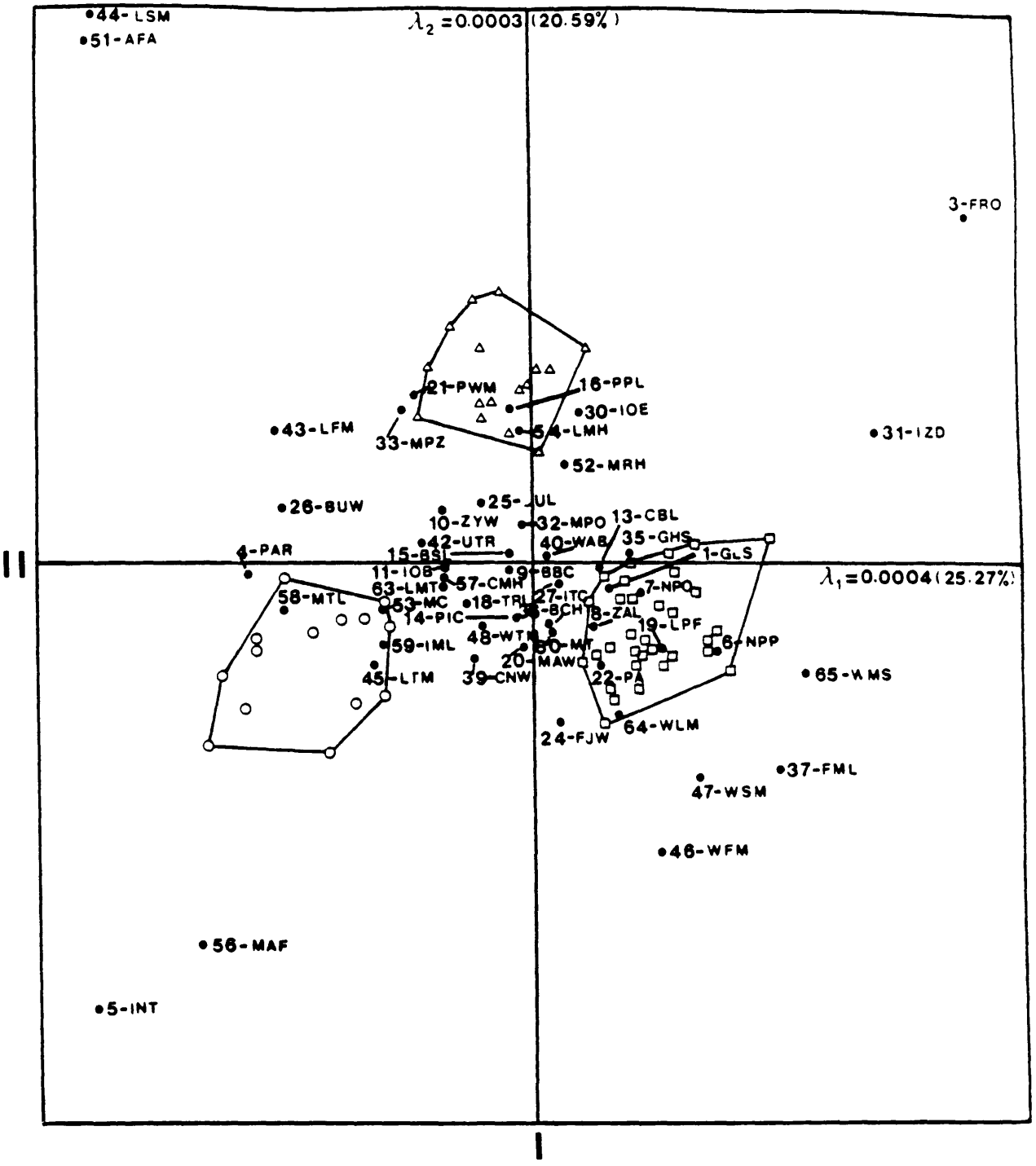

Fig. 4.—Optimal two-dimensional symmetrical map of characters and individuals generated by correspondence analysis of *Aethomys chrysophilus*, open triangle; *A. granti*, open circle; and *A. namaquensis*, open square. Polygons include individuals from the same taxon. Characters are defined in Fig. 1a–k.

Subcluster 3.—Of the seven characters in this subcluster, greatest length of frontals (3-FRO) is the only character selected. In addition to having low coefficient of variation and percent measurement error values, it was consistently singled out by both axes in correspondence analysis as well as the second component of principal component analysis. It also features prominently in original descriptions.

Subcluster 4.—None of the four characters in this subcluster was shown to be of particular relevance, but see discussion on the selection of descriptive characters below.

Subcluster 5.—The following three characters in this subcluster were selected: greatest bulla width (26-BUW), foramen magnum height (37-FMH), and mandibular foramen–articular facet length (56-MAF), all of which were shown to be of importance, either singly or in combination, by both principal coordinates in correspondence analysis and principal component II in principal component analysis. These characters also have low coefficients of variation and percent measurement error values. Collectively, the three characters capture different configurations of the skull, as suggested by the negative and positive loadings, respectively, of foramen magnum height (37-FMH) and mandibular foramen–articular facet length (56-MAF) on the second principal component. Greatest bulla width (26-BUW) features prominently in original descriptions.

Subcluster 6.—Angular process–mandibular condyle length (51-AFA), one of the eight characters in this subcluster, was selected because of its importance in principal coordinate I in correspondence analysis, and low coefficient of variation and percent measurement error values. Mandibular toothrow (58-MTL) is another character shown to be of importance, but see discussion of subcluster 7.

Subcluster 7.—Of the four characters in this subcluster, posterior incisor–M_3 length (59-IML) was selected because of its low coefficient of variation and percent measurement error values and its importance in both correspondence (coordinate I) and principal component (component II) analyses. This character, as well as mandibular toothrow (58-MTL) in subcluster 6, although placed in different subsets, seem to capture the same information, but since the latter measurement is relatively difficult to score, 59-IML was selected.

Subcluster 8.—Three characters in this subcluster were selected: length of M^1 (43-LFM), and greatest cross-sectional crown widths of M^2 (47-WSM) and M_2 (65-WMS) because of their low coefficients of variation and percent measurement error values and their importance (either singly or in combination) in principal coordinates I and II of correspondence analysis, and principal component II of principal component analysis. In combination (an upper jaw tooth length [43-LFM] and width [47-WSM] and lower jaw tooth width [65-WMS]) they may improve the capturing of different tooth configurations.

Three of the 11 selected characters (indicated by asterisks in Table 1 and broad arrows in Fig. 1a–k), 1-GLS, 3-FRO, and 26-BUW, feature prominently in original descriptions.

The underlined characters in Table 1 were selected for descriptive purposes only and include breadth of braincase (9-BBC), greatest height of skull (35-GHS), interorbital constriction (11-IOB), and greatest bulla length (25-BUL). These characters, in combination with greatest length of skull (1-GLS), capture gross cranial configuration. Other descriptive characters incorporated into the data set were the standard external measurements, head and body length, tail length, hind foot length, and ear length, all recorded from specimen labels.

Given the three groupings of characters (11 basic cranial, four descriptive cranial, and four standard descriptive external), their selective use (singly or in combination) will depend on the choice of analyses to be used in the revision. Since multivariate procedures involve the assessment of joint relationships among intercorrelated variables to evaluate overall inter-OTU differences (James and McCulloch, 1990), all subsequent multivariate analyses will be based on the 11 basic cranial characters, and will form the basis of taxonomic conclusions in the revision. The four descriptive cranial characters, in combination with the 11 basic cranial characters, could be used for exploratory multivariate analyses. Univariate analyses, which evaluate the equality of means for each variable independently

and ignore correlations among variables (Willig et al., 1986), could be based on all three groupings of characters, and only used for descriptive and comparative purposes.

DISCUSSION

The approach to character selection adopted in the present paper is an extension of the procedure suggested by Taylor (1990) and Taylor and Meester (1993) who summarized character correlations in *C. penicillata* by means of cluster analysis, and selected representative characters on the basis of low coefficients of variation, previous use, and ease of measurement, and interpreted their results in terms of the morphological integration concept of Olson and Miller (1958). As applied to *Aethomys*, the approach was similar to Taylor (1990) and Taylor and Meester (1993), but expanded upon to include: 1) measuring potentially useful characters from various regions of the cranium and mandible (including characters used previously) in a single homogeneous sample, representing an island population; 2) screening the data set for outliers; 3) subjecting all characters to univariate assumptions tests (normality, equality of variances, and sexual dimorphism); followed by 4) analysis of statistical associations between characters, using principal component and cluster analyses, with reference to a morphometric assessment of functional units of the cranium, an approach consistent with the morphological integration concept of Olson and Miller (1958); and 5) analysis of samples drawn from various taxa in the current classification as an aid in the selection of characters from identified phenotypic sets and their subsets, while considering criteria such as the coefficient of variation, percent measurement error, ease of recording, and previous use.

The procedures followed by Taylor (1990), Taylor and Meester (1993), and the present study are more objective than using untested, previously used characters or simply recording as many characters as possible in the hope of assessing relationships between OTUs. These approaches could have wider application in morphometrics, particularly in organisms in which cranial ontogenetic origins and interactions (Noden, 1978, 1983; Gans and Northcutt, 1983; Zelditch et al., 1993), structural components, evolution, and adaptive functional potential of organismic form can be determined, such as has been demonstrated in some mammalian (Olson and Miller, 1958; Moss and Young, 1960; Moore, 1981; Cheverud, 1982) and avian groups (Noden, 1978, 1983; Cane, 1993).

Analysis of the largest available sample of southern African *Aethomys* from a single locality, representing an island population of *A. namaquensis*, identified two outliers that were considered as not representative of the population and were excluded from the data set to avoid the introduction of bias in the sample. The assumptions tests identified 15 characters as statistically problematic because they were significantly sexually dimorphic, heteroscedastic, and/or non-normally distributed; these results could be related a posteriori to difficulties experienced in their recording, unclearly defined measuring points in some individuals, high variability of characters among individuals, and characters associated with frequently damaged parts of the skull. Interestingly, some of the characters that were found to be problematic have been used extensively in previous studies (Smith, 1834; Roberts, 1951; Ellerman et al., 1953; Meester et al., 1986; Skinner and Smithers, 1990), such as nasal width (12-NAS), palatal length (17-PAL), length of diastema (28-LOD), greatest mandible length (from anterior edge of I_1 alveolus to posterior surface of angular process) (49-GML), and from anteroventral edge of I_1 alveolus to posterior surface of condylar process (50-MDL). The data screen-

ing procedures underscore Pimentel and Smith's (1986*b*) remarks that test statistics are particularly useful in the earliest phases of data analysis in taxonomic studies.

The results of cluster analysis of character associations were encouraging insofar as the major Neurocranial and Orofacial functional units were identified. In this respect, the results are similar to those obtained by Cheverud (1982), Taylor (1990), and Taylor and Meester (1993). Apart from these functional units, some measurements, particularly the length measurements traditionally used by taxonomists (e.g., condylobasal length), did not fit into the above units but formed a major cluster by themselves comprising "Mixed" Neurocranial/orofacial characters. In *C. penicillata*, these "Mixed" measurements were placed in the Neurocranial functional set (Taylor, 1990; Taylor and Meester, 1993) rather than in a separate major cluster as in *Aethomys*.

The primary objective of the study was to evaluate new and previously used characters in order to identify a reduced set of measurements which would summarize most important variations of cranial configuration. Since many of the measurements spanned the major functional units of the cranium, it was not surprising that the classification of measurements was equivocal. However, the analysis did generate highly correlated subsets of measurements, particularly in the case of dental characters. Strong indications of logical subsets were also evident in: 1) the configuration of the braincase and dorsal aspect of the skull; and 2) the orbital/oral/masticatory functional submatrices with which, interestingly, characters related to the bullae and foramen magnum were also associated.

Ancillary to the analysis of character associations, analysis of known taxa was undertaken to develop criteria for the selection of representative characters from within the phenotypic sets generated by cluster-analysis. This step was considered necessary since the analysis of character associations did not produce unequivocal groupings of characters, and because it is also not yet clear how tightly individual functional units are integrated in the phenotype. Final selection of 11 basic measurements to be used for the revision of southern African *Aethomys* was also made with reference to coefficients of variation, measurement error, likelihood of damage, and use by previous authors. The 11 measurements are: greatest length of skull (1-GLS), greatest length of frontals (3-FRO), distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (6-NPP), greatest bulla width (26-BUW), foramen magnum height (37-FMH), length of M^1 (43-LFM), greatest cross-sectional crown width of M^1 (47-WSM), angular process–mandibular condyle length (51-AFA), mandibular foramen–articular facet length (56-MAF), posterior incisor–M_3 (59-IML), and greatest cross-sectional crown width of M_2 (65-WMS). With regard to coefficients of variation, all characters had low values for this statistic except greatest length of parietals (4-PAR), interparietal length (5-INT), hard palate width at M^1 (21-PWM), infraorbital–zygomatic plate distance (31-IZD), length of M^2 (44-LSM) and M^3 (45-LTM), greatest cross-sectional crown width of M^3 (48-WTM), and length of M_3 (63-LMT), while percent measurement error showed this parameter to be negligible in all characters recorded. In contrast, percent measurement error values of over 50% have been recorded in recent studies on birds and mussels (Bailey and Byrnes, 1990).

Principal component and correspondence analyses were used to develop criteria for the selection of representative characters, and both showed a broad concordance between characters shown to be of relevance. Canonical variates analysis (Pimentel, 1979; Campbell and Atchley, 1981; Livezey, 1989, 1990; Livezey and

Storer, 1992) was also considered but in an analysis of the 51-character data set a singular dispersion matrix was encountered, and analysis could not proceed (Pimentel and Smith, 1986*b*). Similar computational difficulties were encountered by Taylor (1990) and Taylor and Meester (1993) in a 48-variable matrix. This may be related to: 1) large numbers of linearly and colinearly constrained variables (Pimentel and Smith, 1986*b*); 2) the presence of ipsative variables (Pimentel, 1979); and 3) the sample size being much smaller relative to number of variables (Williams and Titus, 1988). This finding emphasizes the possibility of encountering analytical problems when using many unscreened variables in morphometric studies (Blackith and Reyment, 1971).

With the recent introduction of sophisticated three-dimensional measuring equipment and recent advances in unit-free, landmark-based morphometric methods (Strauss and Bookstein, 1982; Rohlf and Bookstein, 1990, and references therein; Rohlf and Marcus, 1993), future development of character selection protocols should focus on a clearer demarcation of the functional units of the cranium in relation to the individual cranial elements, and on synergism between landmark selection and the objectives of both species delineation and higher classification. In the present study the emphasis was on the former objective, while a different set of qualitative data will be used for phylogenetic analysis. The emphasis should also shift to a rigorous assessment of traditional characters. This is already apparent in the present study where some of these characters were included simply for descriptive purposes and for comparison with previous studies, particularly with reference to their utility in relating morphometric results to the nomenclature.

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LITERATURE CITED

ALBRECHT, F. O., AND R. E. BLACKITH. 1957. Phase and molting polymorphism in locusts. Evolution, 11:166–177.

BAILEY, R. C., AND J. BYRNES. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Systematic Zoology, 39:124–130.

BAKER, R. J., M. B. QUMSIYEH, AND I. L. RAUTENBACH. 1988. Evidence for eight tandem and five centric fusions in the evolution of the karyotype of *Aethomys namaquensis* A. Smith (Rodentia: Muridae). Genetica, 76:161–169.

BENZECRI, J. P. 1977. Histoire et préhistoire de l'analyse des données. 5-L'analyse des correspondances. Cahiers de l'Analyse des Données, 2:9–40.

BEST, T. L. 1978. Variation in Kangaroo rats (Genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Journal of Mammalogy, 59:160–175.

BLACKITH, R. E., AND R. A. REYMENT. 1971. Multivariate Morphometrics. Academic Press, London, 412 pp.

BOOKSTEIN, F. L., B. C. CHERNOFF, R. L. ELDER, J. M. HUMPHRIES, G. R. SMITH, AND R. E. STRAUSS. 1985. Morphometrics in Evolutionary Biology. Special Publication No. 15, Academy of Natural Sciences of Philadelphia, Philadelphia, 277 pp.

BORGIA, G. 1994. The scandals of San Marco. Quarterly Review of Biology, 69:373–375.

BREED, W. G., G. A. COX, C. M. LEIGH, AND P. HAWKINS. 1988. Sperm head structure of a murid rodent from southern Africa: The red veld rat *Aethomys chrysophilus*. Gamete Research, 19:191–202.

CAMPBELL, N. A., AND W. R. ATCHLEY. 1981. The geometry of canonical variates analysis. Systematic Zoology, 30:268–280.

CANE, W. P. 1993. The ontogeny of postcranial integration in the common tern, *Sterna hirundo*. Evolution, 47:1138–1151.

CHAPMAN, J. A., K. L. KRAMER, N. J. DIPPENAAR, AND T. J. ROBINSON. 1992. Systematics and biogeography of the New England cottontail, *Sylvilagus transitionalis* (Bangs, 1895), with description of a new species from the Appalachian Mountains. Proceedings of the Biological Society of Washington, 105:841–866.

CHEVERUD, J. M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution, 36:499–516.

CHEVERUD, J. M., G. P. WAGNER, AND M. M. DOW. 1989. Methods for the comparative analysis of variation patterns. Systematic Zoology, 38:201–213.

CHIMIMBA, C. T., AND N. J. DIPPENAAR. 1994. Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa. South African Journal of Zoology, 29:107–117.

CHIMIMBA, C. T., AND D. J. KITCHENER. 1991. A systematic revision of Australian Emballonuridae (Mammalia: Chiroptera). Records of the Western Australian Museum, 15:203–265.

DEBLASE, A. F., AND R. E. MARTIN. 1981. A Manual of Mammalogy, with Key to Families of the World. Wm. C. Brown Company Publishers, Dubuque, Iowa, 329 pp.

DEGRAAFF, G. 1981. The Rodents of Southern Africa. Butterworths, Pretoria, 267 pp.

DIPPENAAR, N. J., AND I. L. RAUTENBACH. 1986. Morphometrics and karyology of the southern African species of the genus *Acomys* I. Geoffroy Saint-Hilaire, 1838 (Rodentia: Muridae). Annals of the Transvaal Museum, 34:129–183.

ELLERMAN, J. R., T. C. S. MORRISON-SCOTT, AND R. W. HAYMAN. 1953. Southern African Mammals 1758 to 1951: A Reclassification. British Museum of Natural History, London, 363 pp.

GANS, C., AND R. G. NORTHCUTT. 1983. Neural crest and the origin of vertebrates: A new head. Science, 220:268–273.

GORDON, D. H., AND I. L. RAUTENBACH. 1980. Species complexes in medically important rodents: Chromosome studies of *Aethomys*, *Tatera* and *Saccostomus* (Rodentia: Muridae, Cricetidae). South African Journal of Science, 76:559–561.

GORDON, D. H., AND C. R. B. WATSON. 1986. Identification of cryptic species of rodents (*Mastomys*, *Aethomys*, *Saccostomus*) in the Kruger National Park. South African Journal of Zoology, 21:95–99.

GOULD, S. J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: A way of studying non-adaptation. Systematic Zoology, 33:217–237.

GOULD, S. J., AND R. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptionist program. Proceedings of the Royal Society of London, B205:581–598.

GOULD, S. J., D. F. WOODRUFF, AND J. P. MARTIN. 1974. Genetics and morphometrics of *Cerion* at Pongo Carpet: A new systematic approach to this enigmatic land snail. Systematic Zoology, 23:518–535.

GREENACRE, M. J. 1984. Theory and Applications of Correspondence Analysis. Academic Press, London, 364 pp.

———. 1986. SimCA: A program to perform simple correspondence analysis. American Statistician, 40:230–231.

———. 1990. SimCA, User's Manual. Department of Statistics, University of South Africa (UNISA), Pretoria, 44 pp.

HALDANE, J. B. S. 1955. The measurement of variation. Evolution 9:484.

HALL, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley and Los Angeles, 710 pp.

HARTLEY, H. O. 1950. The maximum *F*-ratio as a short cut test for heterogeneity of variances. Biometrika, 37:308–312.

HEBEL, R., AND M. W. STROMBERG. 1976. Anatomy of the Laboratory Rat. Williams and Wilkens, Baltimore, 173 pp.

HILL, J. E. 1935. Cranial foramina in rodents. Journal of Mammalogy, 16:121–129.

HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, AND S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology, 30:291–308.

JAMES, F. C., AND C. E. MCCULLOCH. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's box? Annual Review of Ecology and Systematics, 21:129–166.

JOHNSTON, R. E. 1973. Evolution in the house sparrow. IV. Replicate studies in phenetic covariation. Systematic Zoology, 22:219–226.

KIM, J. O. 1975. Factor analysis. Pp. 468–514, *in* Statistical Package for the Social Sciences (N. H. Nie, C. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds.), McGraw-Hill Book Company, New York, 675 pp.

KLECKA, W. R. 1975. Discriminant analysis. Pp. 434–467, *in* Statistical Package for the Social Sciences (N. H. Nie, C. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds.), McGraw-Hill Book Company, New York, 675 pp.

LEAMY, L., AND R. S. THORPE. 1984. Morphometric studies in inbred and hybrid house mice. Heterosis, homeostasis and heritability of size and shape. Biological Journal of the Linnean Society, 22:233–241.

LEWONTIN, R. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York, 346 pp.

LIVEZEY, B. C. 1989. Morphometric patterns in recent and fossil penguins (Aves, Spheniscifomes). Journal of Zoology, London, 219:269–307.

———. 1990. Evolutionary morphology of flightlessness in the Auckland Islands teal. Condor, 92: 639–673.

LIVEZEY, B. C., AND R. W. STORER. 1992. Morphometric comparison of skeletons on the western grebe complex *Aechmophorus* of the United States and Canada. Condor, 94:668–679.

LOUGHEED, S. C., T. W. ARNOLD, AND R. C. BAILEY. 1991. Measurement error of external and skeletal variables in birds and its effect on principal components. Auk, 108:432–436.

MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. Proceedings of the National Institute of Science (India), 2:49–55.

MAHALANOBIS, P. C., D. M. MAJUMDAR, AND C. R. RAO. 1949. Anthropometric survey of the United Provinces, 1941; a statistical study. Sankhya, 3:35–40.

MAYR, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts, 797 pp.

———. 1976. Evolution and the Diversity of Life. Harvard University Press, Cambridge, Massachusetts, 719 pp.

MEESTER, J. A. J., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. Transvaal Museum Monograph, 5:1–359.

MOORE, W. J. 1981. The Mammalian Skull. Cambridge University Press, Cambridge, England, 369 pp.

MORRIS, P. 1972. A review of mammalian age determination methods. Mammal Review, 2:69–104.

MOSS, M. L., AND R. W. YOUNG. 1960. Functional approach to craniology. American Journal of Physical Anthropology, 18:281–292.

MOUSSEAU, T. A. 1991. Landmarks in morphometrics, or the shape and size of morphometrics to come. Evolution, 45:1979–1980.

NODEN, D. 1978. The control of avian cephalic neural crest cytodifferentiation. I. Skeletal and connective tissues. Developmental Biology, 67:296–312.

———. 1983. The embryonic origin of avian cephalic and cervical muscles and associated connective tissues. American Journal of Anatomy, 168:257–276.

OLSON, E. C., AND R. L. MILLER. 1958. Morphological Integration. University of Chicago Press, Chicago, 317 pp.

OSTLE, B., AND R. W. MENSING. 1975. Statistics in Research. Third Edition. Iowa State University Press, Ames, 596 pp.

PANKAKOSKI, E., R. A. VAISANEN, AND K. NURMI. 1987. Variability of muskrat skulls: Measurement error, environmental modification and size allometry. Systematic Zoology, 36:35–51.

PERRIN, M. R. 1982. Prey specificity of the barn owl, *Tyto alba*, in the Great Fish River Valley of the eastern Cape Province. South African Journal of Wildlife Research, 12:14–25.

PIMENTEL, R. A. 1979. Morphometrics: The Multivariate Analysis of Biological Data. Kendall/Hunt Publishing Company, Dubuque, Iowa, 276 pp.

PIMENTEL, R. A., AND J. D. SMITH. 1986*a*. BIOΣTAT I. A Tutorial Manual. Sigma Soft, Placentia, California, 392 pp.
———. 1986*b*. BIOΣTAT II. A Tutorial Manual. Second Edition. Sigma Soft, Placentia, California, 212 pp.
POWER, D. M. 1970. Geographic variation of red-winged blackbirds in central North America. University of Kansas. Publications of the Museum of Natural History, 19:1–83.
———. 1971. Statistical analysis of character correlations in Brewer's blackbirds. Systematic Zoology 20:186–203.
REIG, S. 1989. Errors and misjudgment of outliers in morphometric studies. Abstract of Papers and Posters, Fifth International Theriological Congress, Rome.
RIEDL, R. 1978. Order in Living Organisms. John Wiley and Sons, New York, 313 pp.
ROBERTS, A. 1951. The Mammals of South Africa. Trustees of "The Mammals of South Africa" Book Fund, Johannesburg, 700 pp.
ROHLF, F. J. 1990. Morphometrics. Annual Review of Ecology and Systematics, 21:299–316.
ROHLF, F. J., AND F. L. BOOKSTEIN, EDS. 1990. Proceedings of the Michigan Morphometrics Workshop. Special Publication No. 2, University of Michigan Museum of Zoology, Ann Arbor, 380 pp.
ROHLF, F. J., AND L. F. MARCUS. 1993. A revolution in morphometrics. Trends in Ecology and Evolution, 8:129–132.
ROSEVEAR, D. R. 1969. The Rodents of West Africa. British Museum of Natural History, London, 604 pp.
SCHLITTER, D. A. 1978. Problems and priorities of research on the taxonomy and ecology of African small mammals. Pp. 211–214, *in* Ecology and Taxonomy of African Small Mammals (D. A. Schlitter, ed.), Bulletin of Carnegie Museum of Natural History, 6, 214 pp.
SELZER, J., ED. 1993. Understanding Scientific Prose: Rhetoric of the Human Sciences. University of Wisconsin Press, Madison, 388 pp.
SKINNER, J. D., AND R. H. N. SMITHERS. 1990. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria, 771 pp.
SMITH, A. 1834. African zoology: Mammalia. South African Quarterly Journal, 2:160.
SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco, 573 pp.
SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Second Edition. W. H. Freeman and Company, New York, 859 pp.
STRAUSS, R. E., AND F. L. BOOKSTEIN. 1982. The truss: Body form reconstructions in morphometrics. Systematic Zoology, 31:113–135.
TAYLOR, P. J. 1990. Infraspecific systematics of the yellow mongoose. Unpublished Ph.D. thesis, University of Natal, Durban, 345 pp.
TAYLOR, P. J., AND J. MEESTER. 1993. Morphometric variation in the yellow mongoose, *Cynictis penicillata* (Cuvier, 1829) (Carnivora: Viverridae) in southern Africa. Durban Museum Novitates, 18:37–71.
THOMAS, O. 1905. Suggestions for the nomenclature of the cranial length measurements and of the cheek-teeth of mammals. Proceedings of the Biological Society of Washington, 18:191–196.
THOMAS, P. A. 1968. Variation and covariation in characters of the rabbit tick, *Haemaphysalis leporipalustris*. Kansas University Science Bulletin, 47:829–862.
THOROGOOD, P., AND C. TICKLE, EDS. 1988. Cranial Development: Papers Presented at a Meeting of the British Society for Developmental Biology, University of Bath, 1987. The Company of Biologists Ltd, Cambridge, 257 pp.
THORPE, R. S. 1976. Biometric analysis of geographic variation and racial affinities. Biological Review, 51:407–457.
———. 1980. A comparative study of ordination techniques in numerical taxonomy in relation to racial variation in the ringed snake *Natrix natrix* (L.). Biological Journal of the Linnean Society, 13:7–40.
VAN DER KLAAUW, C. J. 1948–1952. Size and position of the functional components of the skull. Archives Neerlandaises de Zoologie, 9:1–559.
VAN VALEN, L. 1974. Multivariate structural statistics in natural history. Journal of Theoretical Biology, 45:235–257. *Erratum* (1974), 48:501.
VISSER, D. S., AND T. J. ROBINSON. 1986. Cytosystematics of the South African *Aethomys* (Rodentia: Muridae). South African Journal of Zoology, 21:264–268.
———. 1987. Systematic implications of spermatozoan and bacular morphology for the South African *Aethomys*. Mammalia, 51:447–454.
WADDINGTON, C. 1957. The Strategy of the Genes. Allen and Unwin, London, 262 pp.

WARD, J. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistics Association, 58:236–243.

WATSON, J. P., AND N. J. DIPPENAAR. 1987. The species limits of *Galerella sanguinea* (Ruppell, 1836), *G. pulverulenta* (Wagner, 1839) and *G. nigrata* (Thomas, 1928) in southern Africa (Carnivora: Viverridae). Navorsinge van die Nasionale Museum Bloemfontein, 5:356–413.

WILLIAMS, B. K., AND K. TITUS. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. Ecology, 69:1275–1285.

WILLIG, M. R., R. D. OWEN, AND R. L. COLBERT. 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. Systematic Zoology, 35:195–203.

WILSON, D. E., AND D. M. REEDER, EDS. 1993. Mammal Species of the World: A Taxonomic and Geographic Reference. Second Edition. Smithsonian Institution Press, in Association with the American Society of Mammalogists, London and Washington, 1206 pp.

WRIGHT, S. 1978. Evolution and the Genetics of Populations. Volume 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago, 580 pp.

———. 1980. Genic and organismic selection. Evolution, 34:825–843.

ZAR, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 620 pp.

ZELDITCH, M. L., R. W. DEBRY, AND D. O. STRANEY. 1989. Triangulation-measurement schemes in the multivariate analysis of size and shape. Journal of Mammalogy, 70:571–579.

ZELDITCH, M. L., F. L. BOOKSTEIN, AND B. L. LUNDRIGAN. 1993. The ontogenetic complexity of developmental constraints. Journal of Evolutionary Biology, 6:621–642.

APPENDIX I

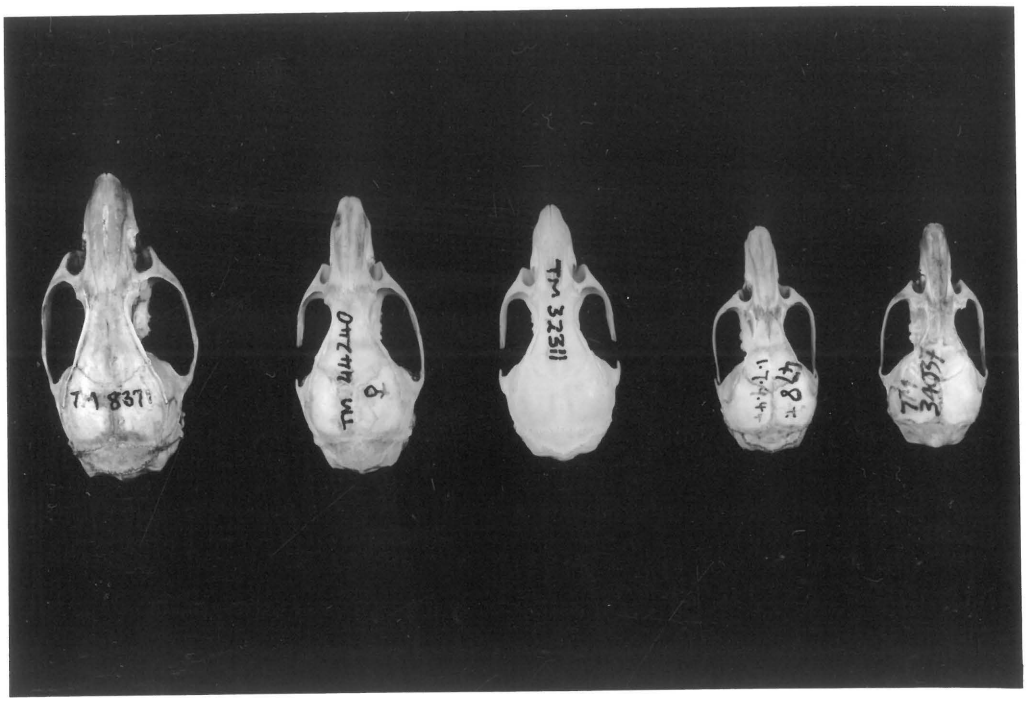
Aethomys specimens examined. TM = Transvaal Museum, Pretoria; USNM = National Museum of Natural History, Smithsonian Institution, Washington D.C.

Aethomys chrysophilus.—Farm Al-te-ver, 1 km SSE Maasstroom, Transvaal, South Africa (22° 46′ S; 28° 28′ E): six males (TM 26474, 26541, 26557, 26559, 26612, 26684); ten females (TM 26510, 26514, 26540, 26561, 26574, 26575, 26583, 26611, 26668–69).

Aethomys granti.—Sutherland, Cape Province, South Africa (32° 23′ S; 20° 40′ E): seven males (TM 38526–28, 38530, 38532, 38536, 38538); seven females (TM 38529, 38533–34, 38537, 38541–43).

Aethomys namaquensis.—Keimoes Island, Orange River, Cape Province, South Africa (28° 43′ S; 20° 50′ E): 21 males (USNM 451913–14, 451921, 451933–34, 451941, 451948, 451950–51, 451966, 451983, 451990–91, 452000, 452002, 452019, 452028, 452039, 452041, 452045, 452055); 13 females (USNM 451915, 451924, 451956, 451992, 451994, 452003, 452006, 452016, 452020, 452031a–b, 452035, 452053).

a.



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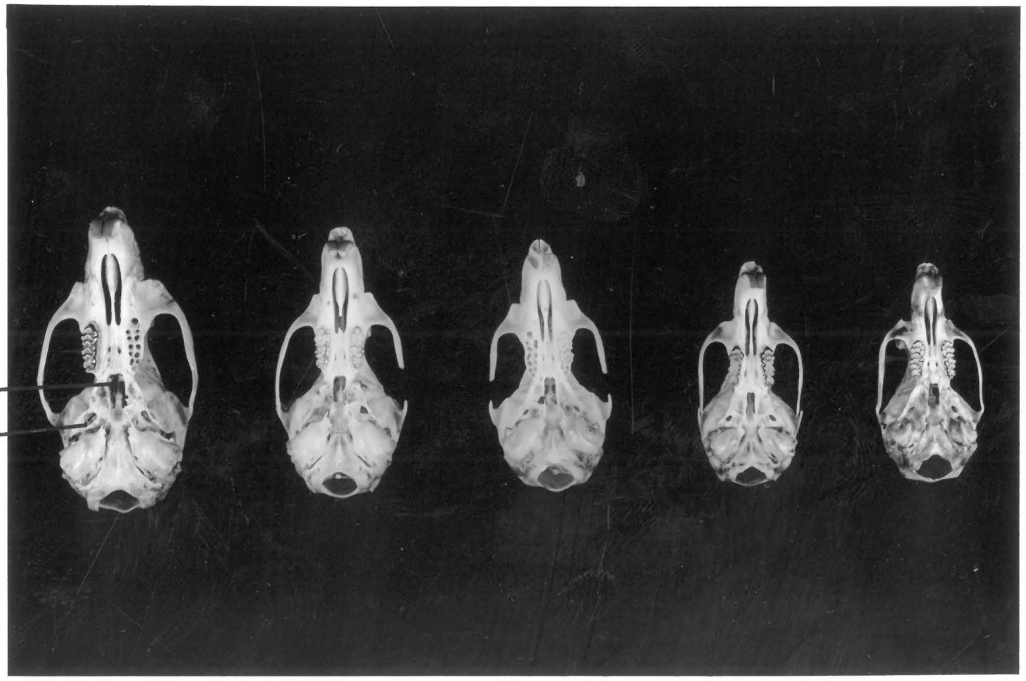
b.



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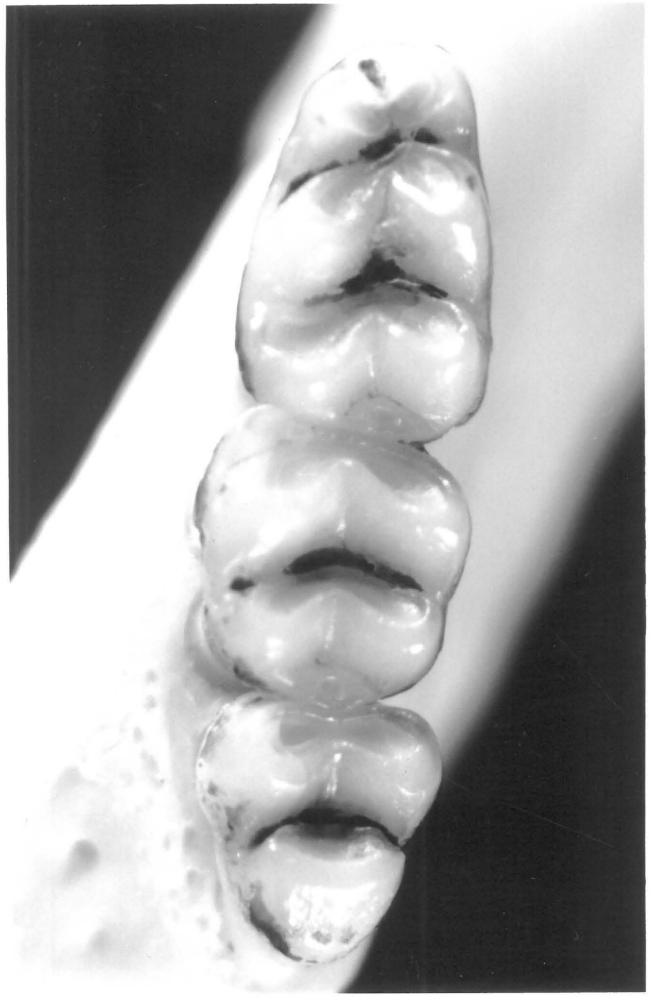

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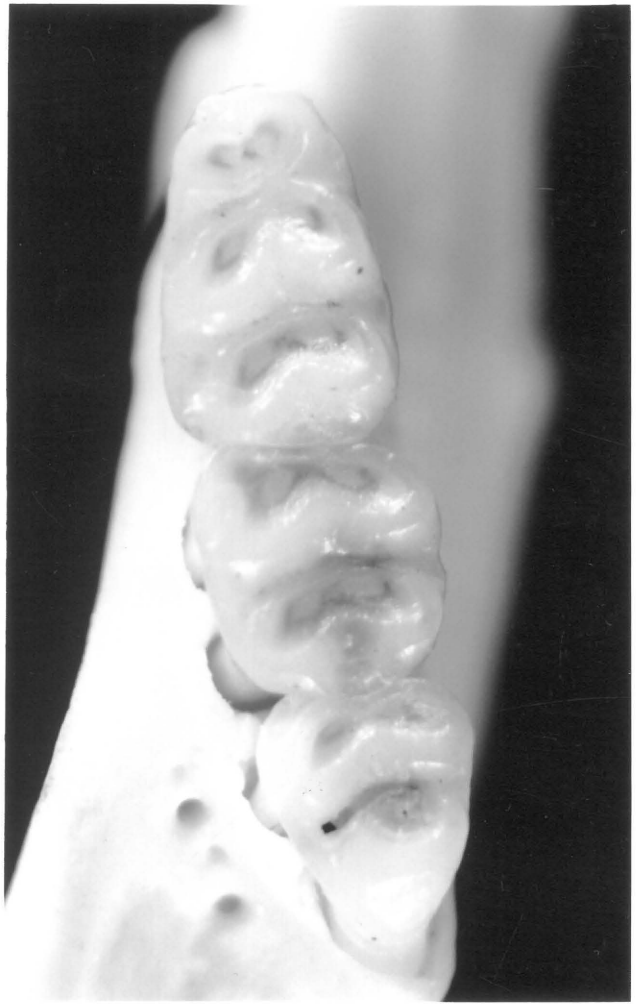

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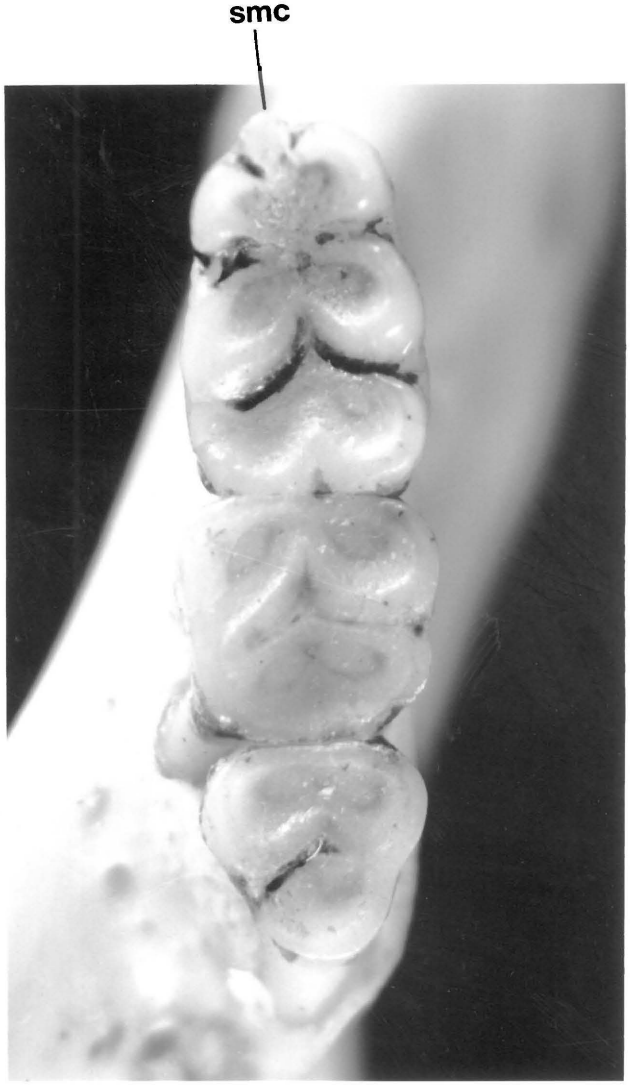

nam

d.